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Relationships among depth distributions, habitat specialisation and demography in coral reef fish communities

Thesis submitted by

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Statement on the Contribution of Others

This thesis includes collaborative work with my supervisors Prof. Geoff Jones and Dr. Nick Graham as well as Dr. Naomi Gardiner. As part of these collaborations I was responsible for project design, data collection, analysis and interpretation of my data. My co-authors provided intellectual guidance, fieldwork support, equipment, technical and statistical advice, editorial assistance and financial support.

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This research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council (NHMRC) Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Qld Animal Care and Protection Act, 2001. The proposed research study received animal ethics approval from the JCU Animal Ethics Committee (approval numbers: A1741 and A2017).

General abstract

Patterns in the distribution and abundance of organisms in nature vary along environmental gradients, such as altitude and depth. These patterns can be determined by the degree of habitat specialisation and environmental constraints of demographic rates. On coral reefs, despite many studies identifying depth as a major source of variation in coral reef fish, few studies have solely focused on the determinants of depth distributions and their relationships with the degree of habitat specialisation and key demographic parameters. Understanding these relationships is becoming critically important in assessing long-term responses to declining coral cover in shallow water and the potential for deep reefs to offer a refuge. The aim of this thesis was to investigate patterns in distribution, habitat use and specialisation with depth in coral reef fishes and to consider how these patterns might affect the depth refuge hypothesis.

Coral reef structure varies with both depth and reef profile, from vertical walls to flat shelf habitats. The differing roles of depth and reef profile in reef fish distribution patterns have received little attention. This was addressed in Chapter 2 by surveying the reef fish community and benthic habitat in quadrats on 3 profiles at 2 depths. Depth and profile showed strong correlations with both the reef fish community and the benthic habitat present. Wall habitats were most distinct from other profiles in terms of community structure, whereas differences between communities on slopes and shelves were driven by depth differences. Depth and profile had similar effects on the benthic habitat structure. A significant correlation between changes in the fish community and changes in the benthic habitat was best explained by differences in the abundance of sand, branching coral, encrusting coral, massive coral and rubble. Depth and profile had a significant interaction suggesting both are clearly important factors affecting reef fish communities. Benthic habitat however appears to only partially explain these patterns.

The ecology of reef fish communities is likely to change along depth gradients. Trends in diversity, community structure and coral reliance have seldom been described. Deeper reef environments could potentially provide refuge for reef fish from shallow water disturbances. In Chapter 3, fish communities were surveyed along a depth gradient (0-20m) down to the bottom of the reef. Communities had species with shallow water distributions as well as species with much broader depth distributions. Diversity showed linear decline with increasing depth. Depth ranges of species were largest for species with mean depths of occurrence around the midpoint of the gradient and species at the extremes of the gradient showed restricted depth ranges. Niche breadth decreased with depth, suggesting deeper species were more specialised. Unexpectedly, there was a higher association with branching corals in the deepest depth strata showing a great reliance on coral in the patchy reef edge habitat. Clearly, there are dramatic changes in the ecology of reef fishes and their habitat over a depth gradient of 0-20m, and a variety of physical and biological processes are likely to be important. Although deep reef coral-specialists may occupy a refuge from shallow water disturbances, the narrow distributions of species at the bottom of the reef and high reliance on corals are unlikely to contribute to long-term resilience in relation to widespread reef degradation.

Patterns in distribution and abundance along depth gradients may be dependent on changes to habitat structure or other environmental factors. In Chapter 4, the separate effects of depth and habitat changes were isolated experimentally by quantifying the community of reef fish that developed on patch reefs involving 4 habitat types, over 3 different depths and at 2 different sites. Depth was strongly correlated with the communities present. Site was also strongly correlated with fish communities. Habitat had a significant correlation with the fish communities present, although this was weaker than depth or site. Depth had an effect on the proportions of different feeding guilds of fish within communities, with herbivores and planktivores more prevalent on shallow patch reefs. Diversity and species richness were highest on shallow patch reefs at site 1 and on the deep and mid patch reefs at site 2. Communities on Mid depth patch reefs at site 1 and deep patch reefs at site 2 showed the highest evenness. This study further demonstrates the important effects depth can have on reef fish communities independently of habitat changes, which may also suggest, in terms of community structure, that habitat changes alone, may not explain depth distribution. The complex nature of depth gradients means there are many other physical and biological factors that could be driving these patterns and further study would be needed to assess the importance of these factors.

Coral reef fishes may be able to move into deeper water in response to declining coral cover on shallow reefs. If so, species should be able to shift distributions downward, while maintaining abundance on disturbed reefs. In addition, there should be no adverse costs to being in deeper water in terms of increased mortality, slower growth and reduced condition. Chapter 5 tested these predictions using two different approaches. First, surveys were carried out to compare distribution and abundance of species on reefs with high and low coral cover in shallow water. Secondly, an experiment in which individuals of three damselfish species were transplanted to three different depths was carried out to test the effects of being within and below normal depth ranges on demographic rates and condition. Some species exploited new space and showed higher abundances on the lower coral cover reefs. Only one species (*Chromis ternatensis*) showed a change in its distribution from being abundant in shallow water to having a deeper distribution. The transplant experiment showed no consistent depth-related patterns in mortality. Overall body condition decreased with depth and growth was higher on deepest reefs. This study suggests a limited capacity to move into deeper water following shallow water disturbances for most species. The underlying mechanisms for higher growth in deep water are unknown, but the results suggest that environmental pressures that cause changes in depth distributions will likely have unexpected demographic consequences.

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Chapter 1. General Introduction

The spatial structure of natural communities is characterised by predictable patterns in distribution, abundance and diversity along strong environmental gradients (Hawkins 1999; La Peyre et al. 2001; Mark et al. 2001). Well known examples of such gradients include changes in diversity with latitude (Hawkins 1999; Connolly et al. 2003; Ricklefs 2004), zonation of vegetation with altitude on mountains (Kappelle et al. 1995; Ricklefs 2004) and the declining significance of macrophytic plants with depth in lakes and oceans. Major changes to the physical environment and types of habitat-forming organisms along these gradients can explain the limits of distributions and abrupt changes in the structure of assemblages. One of the major goals in ecology is to try and explain these spatial gradients in the distributions of organisms and community change along such gradients (Krebs 2006). This requires a quantitative description of the ecological patterns along environmental gradients and experiments designed to test how individuals respond to different factors at the centre and edges of their distribution.

The factors controlling species distributions and community structure along a single gradient may be complex. A species distribution and optimum position along a gradient can be a response to a number of physical and biological parameters. For example, on mountains the distributions of different species of vegetation vary in response to changes in the altitude, slope and substrate type (Kappelle et al. 1995; Xu et al. 2011). Upper and lower distribution limits can be controlled by different factors including environmental harshness at one extreme and biological interaction between species at the other (Connell 1961). Community metrics such as patterns in diversity may not always exhibit a linear change along the gradient, but can instead show a ‘mid-domain’ effect with diversity being highest at the mid-point of the gradient where most species distributions overlap (Bellwood et al. 2005; Connolly 2005; Nogues-Bravo et al. 2008). Measures of specialisation such as niche breadth can also show change along environmental gradients with populations of species at the limits of their range usually having narrower niche breadths (Clavel et al. 2011; Silc et al. 2014). A full description of the key ecological patterns that vary along gradients is necessary to generate hypotheses about the critical factors involved and to understand how environmental changes may determine the future of species.

Spatial gradients in species distributions and diversity are pronounced in tropical coral reef ecosystems. Patterns on reefs can occur across a variety of scales from large scale changes with latitude and longitude (Bellwood et al. 2005), medium scales such as cross-shelf patterns and distance from shore (Russ 1984; Adjeroud 1997) and smaller scales such as exposure and across reef zones (McGehee 1994; Green 1996; Lecchini et al. 2003; Arias-Gonzalez et al. 2006). Depth is one of the strongest gradients, with dramatic changes to the physical environment and habitat structure over a small spatial scale of meters to tens of meters. Coral reef fish assemblages can exhibit distinct changes along depth gradients (Nunez-Lara and Arias-Gonzalez 1998; Brokovich et al. 2008; Gonzalez-Sansen et al. 2009). Not only can the abundance of individual species change with depth, but also familial composition of the community. For example, in the Red Sea, shallow waters tend to be dominated by damselfishes and gobies, whereas wrasses and groupers become more dominant deeper (Brokovich et al. 2008). Differences in abundance can be observed between species of the same family and even the same genus, with examples published for pomacentrids (Bay et al. 2001), pomacanthids (Eagle et al 2001), balistids (Bean et al. 2002) and serranids (Donaldson 2002). In all these examples, species have been found to have different depth distributions with some species or genera showing a preference for particular depths. It has been suggested that some changes in the community of fish are associated with the decline in coral cover with depth (Brokovich et al. 2008). However, by and large, systematic changes to species abundance, depth ranges and niche breadth along depth gradients have seldom been investigated.

Another important physical reef feature that is both common and could potentially have effects of fish distribution is reef profile. Reef profile can be defined as the slope of the reef habitat and can vary over 90°, from horizontal shelf habitats through sloped reef habitats at increasing elevations, to vertical walls and overhangs. This feature commonly changes with depth on reefs with shallow habitats often forming reef flats and deeper habitats forming steep slopes and drop offs. However, on some reefs, profile can change horizontally at the same depth, such as in “spur and groove” habitats or in relation to systematic changes in slope from fore-reef to back-reef habitats (McGehee 1994). Anecdotally, it is recognised that some species have distributions restricted to wall habitats or reef flats but the effects of this factor in relation to depth have received little attention. Surveys of fish communities across different reef zones such as the slope, crest and flat (e.g. Green 1996; Lecchini and Tsuchiya 2008; Medeiros et al. 2010) do not enable the effects of depth and reef profile to be separated from one another, and both factors often co-vary. Changes in reef profile can have important effects on the type and abundance of the substrate present, and therefore is likely to have an effect on coral cover with greater coral development on horizontal surfaces than on vertical walls, where more encrusting sessile organisms dominate. Vertical walls also have a proportionally smaller area exposed to wave surge than more gentle slopes, resulting in changes in the amount of and type of sediment deposits (McGehee 1994). The degree to which depth and reef profile have separate and interacting effects on reef fish distributions is unknown, and the role of changing habitat in relation to reef profile has not been investigated.

Changes in habitat availability and habitat use with depth may well result in different levels of specialisation at different depths. It is thought that shallow water species tend to be more specialised in their depth range (e.g. Bean et al. 2002), with smaller depth ranges in shallow water associated with more substantial changes in physical conditions. It has also been hypothesized that shallow water species will be more specialized on substratum types (Bean et al. 2002). If deeper species tend to be generalists, then their reliance on coral may also decrease with depth, as coral cover and diversity declines toward the limit of the photic zone. However, as few studies have focused on these patterns, generalizations about trends in ecological specialisation with depth have not emerged. Srinivasan (2003) found that survival and growth both decreased in species with more specialised depth distributions, when individuals were transplanted outside of their preferred depths. This suggests there are physical costs of living outside of their preferred depth ranges. Changes in specialisation with depth and the possible effects of these on fish growth and survival may have important implications for the sensitivity of species and communities to impacts and changes in reefs.

Many studies have shown an important link between the structure of reef fish communities and changes in coral cover, complexity and diversity (Friedlander and Parrish 1998; Gratwicke and Speight 2005; Garpe et al. 2006; Graham et al. 2006; Wilson et al. 2006; Bonin et al. 2011; Graham and Nash 2013). It is therefore important to understand how habitat structure changes with depth and how fish reliance on particular habitats also changes. Many fishes have a close association with corals, in particular branching corals, either for food, shelter or living space (Coker et al. 2014). Hence, any gradient that can affect coral cover may have marked effects on fish distribution (Bell and Galzin 1984; Garpe and Öhman 2003). Coral cover has been implicated as an important determinant of depth distributions, with many coral-associated species restricted to shallow water (Chabanet et al. 1997; Srinivasan 2003; Brokovich et al. 2008). However, it has been demonstrated by experimentally manipulating habitat availability at different depths that it may only make a partial contribution to explaining depth distribution patterns (Srinivasan 2003). Depth gradients are complex and associated with changes in many different co-varying physical factors including light attenuation, temperature and water motion (Fulton and Bellwood 2005; Fulton et al. 2005; Brokovich et al. 2008; Irisson et al. 2010). Biological factors may also play a role in depth patterns. Larvae approaching reefs have been shown to have distributions in the water column structured by depth as well as showing habitat choices (Leis 1986; Leis 1991; Gutierrez 1998; Irisson et al. 2010). Competition between species can also play a role in their distribution and the depths at which they prefer to live (Bay et al. 2001; Bean et al. 2002). To better understand depth patterns in reef fish communities it is important to try and understand the relative importance of these physical and biological factors in driving depth distribution. Few studies have attempted to separate the effects of changes in habitat from depth on fish communities as a whole, which would strengthen our understanding of depth gradient patterns and identify potential avenues for future study.

The physiological state and condition of reef fish can be different between individuals in a population across a depth gradient. Hoey et al. (2007) showed that, for the damselfish *Chrysiptera rollandi,* growth dynamics were influenced by depth and in female fish relative gonad weight and overall body condition was higher at shallow depths. It was also reported that physiological costs can occur if fish with restricted depth ranges settle outside of their preferred depth range (Srinivasan 2003). Lower physiological conditions in reef fish can affect overall fitness and reproductive output, and even decrease survivorship of fishes, therefore lead to declines in population size (Pratchett et al. 2001; Hoey and McCormick 2004; Pratchett et al. 2004). There is also a well-supported trend of increased size with depth in populations of depth generalist and mobile species of reef fish (Sale 1969; Choat and Ayling 1987; McCormick 1989; Hoey et al. 2007). There are several different measures used to assess condition in fish but one such measure that has been increasingly used is analysing liver cells (hepatocytes) and hepatocyte vacuolation (Green and McCormick 1999; Pratchett et al. 2004; Hoey et al. 2007). Fish store excess glycogen and lipids within the cytoplasm of hepatocytes, and glycogen storage can be important in assessing condition in fish because it is a result of excess glucose in the diet and may represent changes in amount or quality of food as well as activity levels (Storch and Juario 1983; Ostazewska et al. 2005; Hoey et al. 2007). Pratchett et al. (2004) showed that hepatocyte vacuolation was directly proportional to liver lipid content and therefore a useful measure of physiological condition. Few studies have looked at these sub-lethal effects on condition in relation to depth and comparing such effects on species with restricted depth ranges to those with wider depth ranges may provide important information on a potential driver of depth distribution patterns.

An understanding of the “depth” ecology of reef fishes has become critical, given the increasing array of anthropogenic disturbances such as sedimentation, bleaching and human disturbance (Bridge et al. 2013). Many of these impacts affect shallow reefs more heavily than deeper reefs (Bongaerts et al. 2010; Kahng et al. 2010; Bridge et al. 2013). Exploration of deeper reefs has shown that many species present on deeper reefs are also present on shallow reefs (Bejarano et al. 2014; Linfield et al. 2014). These factors combined have led to the idea that depth could potentially provide reef fish with a refuge from impacts in shallow reef environments, as individuals living deeper can act as a source of juveniles or because individuals can move deeper to lessen or escape impacts (Kahng et al. 2010). This has been shown to occur for some species and depth may well need to be considered in marine reserve design (Goetze et al. 2011; Kahng et al. 2010; Bridge et al. 2013). If shallow species are more specialised and have more specific habitat use (i.e. coral dependency) then it is possible that they may have an increased extinction risk in relation to impacts on coral reefs compared to deeper species. Species with wider depth distributions would potentially be less at risk considering that part of the population would not be impacted by a given disturbance in shallower depths (Graham et al. 2011). However, general predictions about species responses to shallow water anthropogenic disturbance must be founded on basic descriptions of natural changes in ecological traits along depth gradients.

The key to evaluating the depth refuge hypothesis is a basic understanding of the patterns of distribution into deeper water and their underlying causes. To that end, *the overall aim for the thesis was to investigate patterns in distribution, habitat use and specialisation in coral reef fishes along depth gradients and to experimentally investigate the effects of depth and habitat structure on the recruitment, growth, mortality and condition of selected reef fish species.* The thesis takes both an observational and experimental approach to understand both patterns and processes in depth distributions, with different specific issues addressed in the four data chapters.

Firstly, in **Chapter 2** I investigated changes in reef fish communities with both depth and reef profile in order to separate the effects of these two factors. Here the specific hypotheses being tested were 1) that both depth and reef profile have significant effects on the reef fish community and benthic habitat present, and 2) that changes in the reef fish community relates to the changes in the benthic habitat.

Next, in **Chapter 3** I investigated how distribution, diversity and specialisation changed over a depth gradient from 0-20m and considered the implications of these patterns for the depth refuge hypothesis. I expected that 1) most reef fish show limited distributions over the depth gradient, 2) diversity declines overall with increasing depth, 3) species composition changes with depth, with the greatest changes over shallow depths, 4) shallow species have smaller depth ranges compared with deeper species, 5) shallow species show more specialised habitat use than deeper species and finally 6) habitat use changes with depth, with the use of coral as a preferred habitat declining with increasing depth.

In **Chapter 4**, I set out to separate the effects of depth and habitat changes on the development of coral reef fish communities. In this chapter I tested the hypotheses that 1) communities of fish differ on patch reefs at different depths despite habitat availability being kept the same and that these patterns are consistent between sites, 2) communities of reef fish differ on patch reefs of different habitat types, 3) different feeding guilds of fish have different contributions to fish communities at different depths and 4) coral associated species show preferences for shallow patch reefs whereas non-coral associated species would show preferences for deeper patch reefs.

Finally, I investigated what some of the sub-lethal effects of depth may be on fish by experimentally evaluating the effect of depth on the survival, growth and overall body condition of shallow distributed and depth generalist species of fish forced to live outside of their preferred depth ranges. In addition, I examined whether coral-associated fishes on natural reefs shifted downwards in response to shallow water disturbance (**Chapter 5**). In this chapter specific hypotheses were; 1) shallow species show a decrease in the survival, growth and body condition with increasing depth, 2) species with wide depth ranges show no real differences in their survival, growth and body condition with depth and 3) fish do not extend their depth ranges deeper, to use depth as a refuge, in response to shallow disturbances.

Chapter 2. Depth and reef profile: effects on the distribution and abundance of coral reef fishes

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2.1 Summary

The physical and biological structure of coral reef habitats vary in relation to depth and the profile of the reef, from vertical walls to gentle slopes. The differing roles of depth and reef profile on fish distribution and abundance, and the role of habitat structure in explaining these patterns, have received little attention. Here these effects were distinguished by surveying reef fish species and benthic habitat in quadrats on 3 aspects (shelf, slope and wall) at each of 2 depths (5m and 15m) in Kimbe Bay, Papua New Guinea. Both depth and reef profile accounted for considerable variation in reef fish communities. Wall habitats were the most different from the other two profiles in terms of community structure. Depth had a greater influence on fish communities on slope and shelf habitats, with shallow slopes and shelf habitats similar to one another, and deep slopes and shelf habitats also similar. Some rare species, such as *Chromis delta* and *Pictichromis paccagnellae*, were restricted to walls. The relative effects of depth and reef profile on benthic habitat structure were similar to the fish communities, with the sponge and encrusting coral-dominated wall habitats being the most dissimilar to the other aspects, with clear depth patterns also. There was a significant correlation between the fish communities present and the habitat availability at the depths and on the reef profiles studied. The correlation was best explained by sand, branching coral, encrusting coral, massive coral and rubble. Depth and reef profile had a significant interaction which suggests that, clearly, both depth and profile are important factors affecting reef fish communities. Although, benthic habitat appears to only partially explain these patterns.

2.2 Introduction

Some of the most striking patterns in the structure and diversity of animal communities occur along environmental gradients, such as altitude, latitude and depth (Hawkins 1999; La Peyre et al. 2001; Mark et al. 2001). One of the major goals in ecology is to try and explain spatial patterns in the distribution of organisms along such environmental gradients (Krebs 2006) and many different factors are usually implicated. Coral reef fish assemblages are known to vary on a range of environmental gradients, including typical reef zones (Green 1996; Lecchini et al. 2003; Arias-Gonzalez et al. 2006), exposure (McGehee 1994; Green 1996) and depth (Nunez-Lara and Arias-Gonzalez 1998; Brokovich et al. 2006; Brokovich et al. 2008; Gonzalez-Sanson et al. 2009). Spatial patterns of distribution can result from species responding to a number of co-varying or intersecting gradients. For example, the commonly distinguished reef zones, including lagoons and back reef habitats, reef flats, reef crests and reef slopes are defined in relation to several factors including depth, exposure and reef profile – or a change in slope of the reef habitat. Reef profile can vary over 90^{o}, from horizontal or shelf habitats, through sloped reefs at increasing elevations, to vertical walls. In many places, reef profile systematically changes with depth, with shallow areas forming reef flats, and deeper areas often forming steep slopes and drop-offs. However, reef profile can also change along the same depth contour of a reef, in relation to alternating “spur and groove” habitats or systematic changes in slope from fore-reef to back-reef habitats (McGehee 1994).

While the role of depth has received some attention (Srinivasan 2003; Brokovich et al. 2008), the influence of reef profile on reef fish assemblages has not been quantified. Brokovich et al. (2006) have shown that habitat characteristics, such as vertical relief (which could be considered as a proxy for profile), can be used in distinguishing between both different habitats and between fish assemblages. Anecdotally, it is recognised that particular species of fish may have a preference for either reef flats or steep drop-offs, but the importance of reef profile relative to depth gradients has not been investigated. Quantitative surveys of fish stratified according to typical reef zones such as reef slope, reef crest and reef flat (e.g., Green 1996; Lecchini and Tsuchiya 2008; Medeiros et al. 2010) do not enable the effects of depth and reef profile to be distinguished. However, alternative approaches such as stratified sampling in relation to both of depth and reef profile can help assess the relative contributions of these factors in explaining variation in reef fish communities.

One of the key factors affecting the distribution and abundance of coral reef fishes is the structure of the underlying habitat (Friedlander and Parrish 1998; Gratwicke and Speight 2005; Brokovich et al. 2006; Garpe et al. 2006; Graham et al. 2006; Wilson et al. 2006; Bonin et al. 2011). Given that many fishes are closely associated with branching corals, any physical gradient that affects coral cover is likely to have pronounced effects on fish distributions (Bell and Galzin 1984; Garpe and Öhman 2003). Coral cover has been implicated as an important determinant of depth distributions, with many coral-associated species restricted to shallow water (Chabanet et al. 1997; Srinivasan 2003; Brokovich et al. 2008). However, experimental manipulation of habitat availability at different depths has shown that habitat may only make a partial contribution to explaining depth distributions (Srinivasan 2003). A range of other factors may be responsible for depth patterns including physical regimes such as light attenuation (Brokovich et al. 2008; Irisson et al. 2010), water movement (Fulton and Bellwood 2005; Fulton et al. 2005), larval supply (Leis 1986, 1991; Gutierrez 1998; Hendriks et al. 2001) and competition (Bay et al. 2001; Bean et al. 2002). Coral cover is also likely to vary with reef aspect, with greater coral development on horizontal surfaces than vertical walls, where other encrusting sessile invertebrates often dominate. Vertical walls have a proportionally smaller area exposed to wave surge than more gentle slopes, causing changes in the amount of and type of sediment deposits (McGehee 1994). The degree to which benthic habitat structure explains fish distributions in relation to both depth and reef profile has not been investigated. Coral community structure may also be an important factor in influencing fish community structure as many fish species have preference for particular coral species (Bell and Galzin 1984; Jones et al. 2004; Pratchett and Berumen 2008; Pratchett et al. 2012; Brooker et al. 2013)

The aim of this study was to examine the independent effects of reef profile and depth on the diversity and structure of assemblages of small reef fishes in Kimbe Bay, Papua New Guinea. In addition, we set out to compare benthic habitat structure on reefs of different profiles at different depths to assess its potential role in explaining fish distributions. While some patterns in the depth distribution of fishes have been described in this region (e.g., Srinivasan 2003; Bonin et al. 2009), the effects of reef aspect have not been investigated. Few studies have tried to look at both depth and reef profile simultaneously, which may give greater understanding of what could be driving patterns of distribution in reef fish communities. This approach could also give insight into the separate effects of these two important, complex and often co-varying factors.

2.3 Methods

2.3.1 Study Sites

All data was collected between 10th March and 5th April 2010 in Kimbe Bay, on the Bismarck Sea coast of the island of New Britain, Papua New Guinea ($5^{o}26'15.66''S$, $150^{o}05'06.75''E$) (Figure 2-1). The study focussed on small fringing reefs within 1km of the coast, near the Mahonia Na Dari Marine Conservation and Research Centre. The reefs in Kimbe Bay are known for striking horizontal variation in reef profile, which varies greatly, with most reefs having examples of walls, slopes and shelves under conditions of similar exposure. Most reefs drop off to over 40m depth in this area, with substantial changes in fish distributions over this depth range (Jones et al. 2004). Sampling to record distributions in relation to depth and reef profile was spread across 18 different reefs.

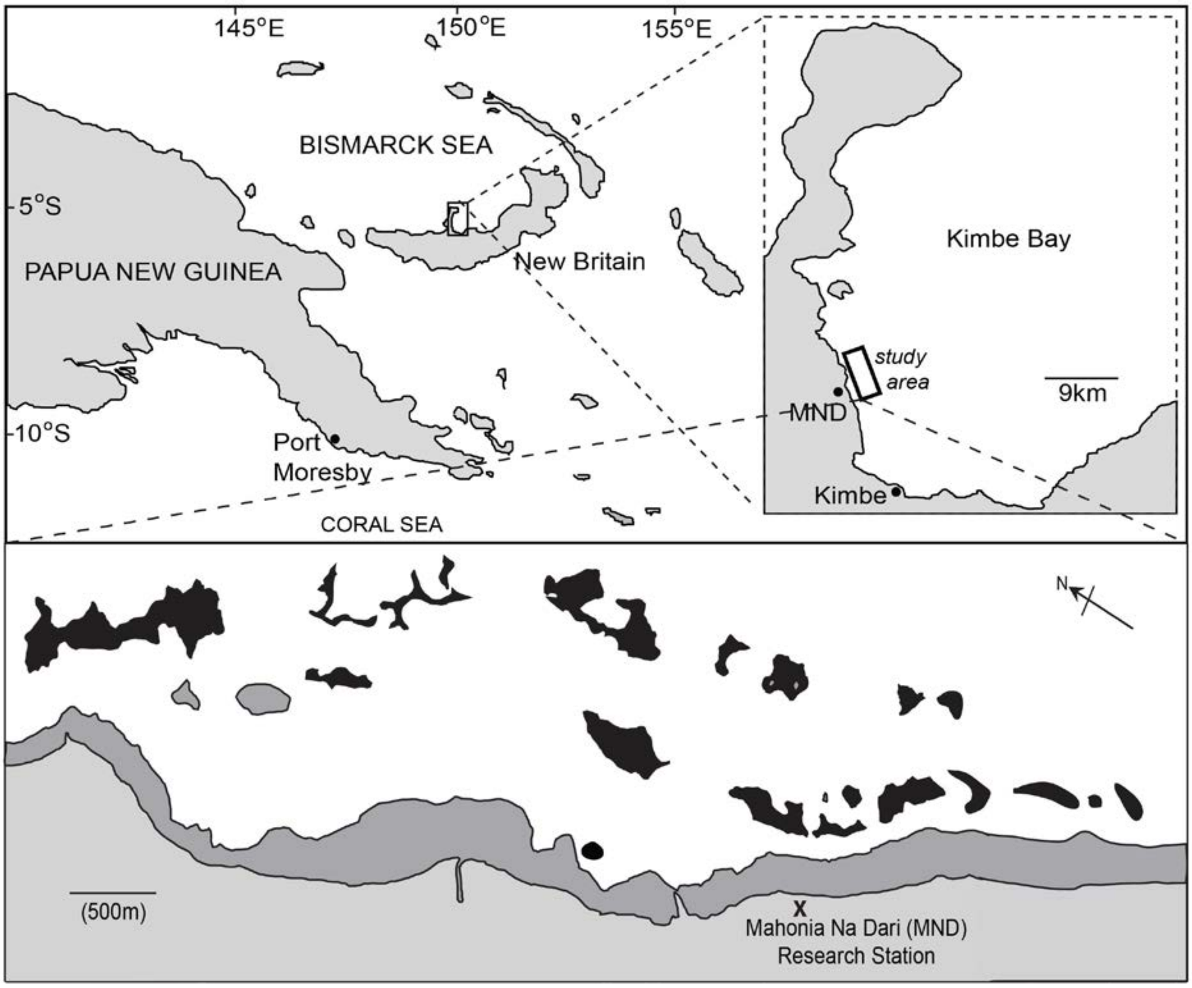

Figure 2-1 Map showing the location of Kimbe Bay in Papua New Guinea as well as the reefs studied. Reefs that were surveyed in the study are coloured black. Replicates were taken from both shore and ocean facing sides of the study reefs.

2.3.2 Sampling design and survey technique

Assemblages of site attached fish and benthic communities were sampled on three different types of profiles (vertical walls, angled slopes and horizontal shelves) at each of two different depths (5 and 15m). An orthogonal sampling design was established to describe fish communities on different aspects at different depths, and explore the interaction between these factors. Reef profile was defined as the 'slope of the reef', with profiles being called angled slopes if they had an angle between that of a vertical wall and a horizontal shelf. For each profile and depth a minimum of 15 replicates were sampled, with replicates haphazardly taken from a number of different reefs. The reefs surveyed in this study show little difference between each other in terms of habitat, and also have examples of all profiles studied and were, therefore, treated as one reef system. Replicates for each profile at each depth came from several reefs in the system, meaning replicates for both depth and profile were surveyed across different reefs. Each replicate consisted of a 4x4m quadrat, temporarily marked out by a rope with each 4m marked by orange tape and a weight. A minimum distance of 10m was left between quadrats to reduce movement of mobile species between replicates. The quadrats were left for about 5-10 minutes before surveying, to allow more mobile fish (e.g. mobile herbivorous and carnivorous species) to return and site-attached fish (e.g. coral and rubble associated fish) to come out of hiding. In each quadrat a fish count was then carried out with all non-cryptic fish >5cm identified and counted over a 5 minute period. After the fish count a 3m tape measure was laid diagonally across the quadrat from the top corner and the benthic cover at every 10cm along the tape was recorded. This was done using the categories of sand, rubble, branching coral, plate coral, massive coral, encrusting coral, sponge or other.

2.3.3 Data Analysis

Benthic habitat was analysed graphically by plotting the mean percentage cover for each habitat category at each depth and profile. To look at the patterns in the benthic habitat with both depth and profile we carried out an nMDS (Primer-E V.6) using a Bray Curtis resemblance matrix. Data was log(x+1) transformed to make sure habitat data fitted general statistical assumptions of normality and linearity. To make sure patterns in habitat between depths and profiles were clear and not masked by the large numbers of replicates we averaged the habitat data by reef for each depth and profile combination. The fact that several reefs (between 6 and 10) were sampled within each combination of depth and profile meant that the nMDS plots would still retain enough replication within them. The groupings seen in the nMDS were then tested for statistical significance by using PERMANOVA (Anderson 2001; Primer-E V.6). Fish abundance data was analysed using univariate and multivariate methods. General ecological community measures were calculated including the species diversity (Shannon-Weiner Index), richness (number of species) and evenness (Evar Evenness Index). Species that were representative of different depths and profiles as well as species which contributed to the greatest differences between depth and profiles were analysed using the SIMPER analysis (Primer-E

V.6). Fish abundance data was square-root transformed to down weight the effect of highly abundant species. We then analysed the patterns in fish abundance with depth and profile using a non-metric nMDS (Primer-E V.6)) and a Bray Curtis resemblance matrix. Another PERMANOVA (Primer-E V.6) was used to test the significance of the nMDS grouping. Fish data was also grouped into feeding guild categories and analysed in order to investigate if there is variation in guilds based on depth and profile. Feeding guilds for each species were determined by using information on feeding and diet according to the online resource, FishBase (www.fishbase.org). The feeding guilds used in this study were omnivores, algal farmers (territorial herbivores), herbivores, carnivores, corallivores, detritivores and cleaners. This was analysed by using the average abundance for each feeding guild in an nMDS (Primer-E V.6) using a Bray Curtis resemblance matrix and then testing the groups using a PERMANOVA (Primer-E V.6) RELATE and BEST analyses were used to test the relationship between the benthic habitat and fish abundance (Clarke 1993; Primer-E V.6). We also examined the effects of depth and profile on individual species using 2-way ANOVAs (Statistica, StatSoft) to show effects of depth and profile on the abundance of the ten most abundant species. We then carried out post-hoc Tukeys HSD tests (Statistica, StatSoft) to determine the driver of statistically significant results.

2.4 Results

2.4.1 Effects of depth and aspect on benthic habitat

The benthic habitat composition changed with both depth and reef profile (Figure 2-2). The main changes in habitat categories with depth were an increase in sponge, encrusting coral, plating coral and other cover percentage at 15m compared to 5m. At 5m there was a higher percentage cover of sand, branching coral and to a lesser extent massive coral compared to 15m. Sand and rubble had a higher percentage cover on shelf and slope profiles and was not common on wall profiles, especially on deep walls. Instead sponge and encrusting corals had the highest percentage cover on wall profiles. Branching corals and massive corals did show decrease in percentage cover between the shelf and the wall profiles although the decrease was small. We observed patterns of change in habitat with depth and profile when looking at an nMDS plot (Figure 2-3a). The data separates out by both depth and aspect. The loading vectors for the plot show that both wall habitats are more represented by encrusting coral, sponge and turf, whereas, slopes and shelfs are more represented by massive coral, branching coral and rubble. Plating coral is more representative of deeper habitats and massive coral and sand of shallow habitats. Both the shallow and deep wall profiles were more closely grouped compared to the shelf and slope profiles, which were more variable. This may suggest that habitat composition on walls is more distinct from shelves or slopes. There was a significant effect of both depth (PERMANOVA, Pseudo-F = 4.512, p = 0.001) and profile (PERMANOVA, Pseudo-F = 4.932, p = 0.001).

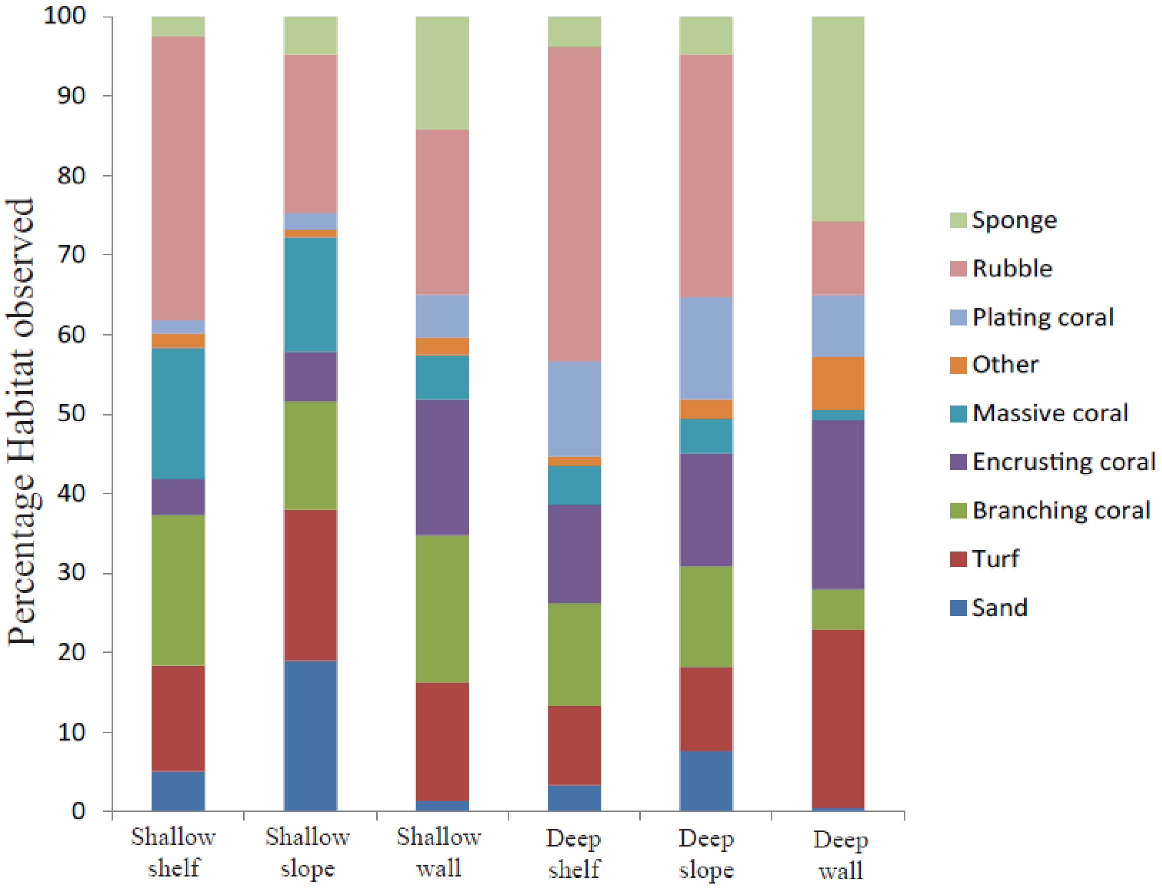

Figure 2-2 Mean percentage cover of the 9 benthic habitat categories observed on all three surveyed reef profiles at both shallow (5m) and deep (15m) waters.

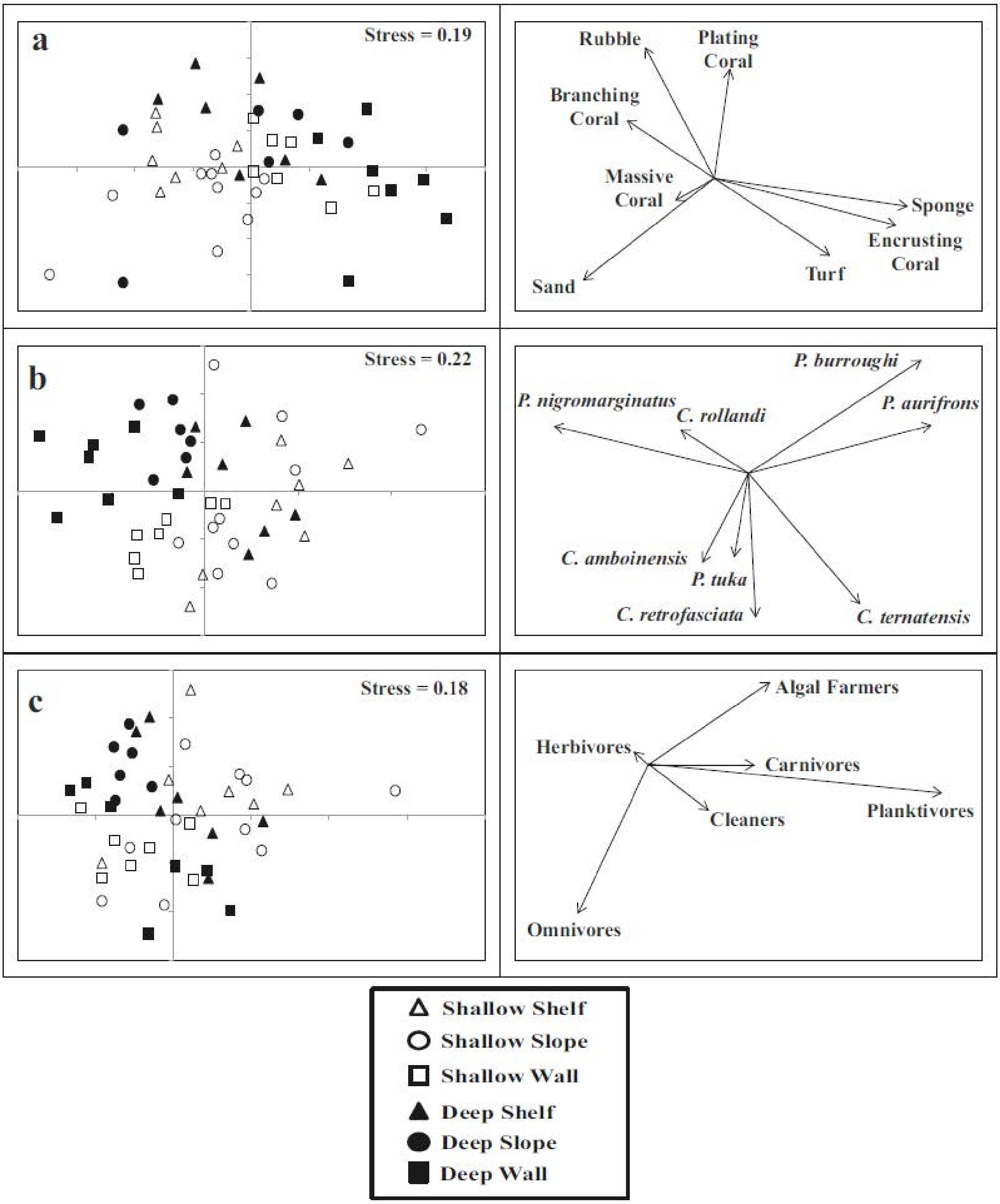

Figure 2-3 nMDS plots showing the similarities of reef profiles (shelf, slope, wall) and different depths (5m and 15m) averaged per reef surveyed for a) percentage cover of the 9 benthic habitat categories, b) fish abundance and c) abundance of 7 common feeding guilds in coral reef fish.

2.4.2 Effects of depth and aspect on fish communities

Both depth and profile had an effect on the fish communities present. A total of 112 species from 20 families of reef fish were observed during this study (Appendix A 2-1). Diversity was higher at 5m compared to 15m in all profiles (Table 2-1). At 5m the highest diversity was found on the shelf and the lowest on the wall, however at 15m the opposite was true. Evenness did not change by much between depths and profiles.

Table 2-1 Results of general ecological indexes including diversity (Shannon Wiener diversity index), species richness (number of species) and the species evenness (Evar evenness index) for each depth and profile surveyed

Depth/Aspect	Diversity	Species richness	Evenness
Shallow shelf	3.082	69	0.258
Deep shelf	2.652	49	0.273
Shallow slope	3.077	78	0.202
Deep slope	2.752	51	0.293
Shallow wall	3.064	55	0.225
Deep wall	2.809	51	0.243

In terms of species composition the communities changed with both depth and aspect (see Table A6-1). On shelf aspects the most abundant fish were *Pomacentrus aurifrons* (mean abundance = 15.9 ± 5.7 S.E.) on the shallow shelf and *Chrysiptera parasema* (mean abundance = 7.7 ± 2.2 S.E.) on the deep shelf. *Pomacentrus aurifrons* was also the most abundant species observed on the shallow slope (mean abundance = 21.1 ± 6.5 S.E.) but *Pseudanthias tuka* was also quite abundant (mean abundance = 8.1 ± 3.5 S.E.). The deep slope however was not dominated by any single species. For the wall aspects the most abundant species on both the shallow and deep wall were *P. nigromarginatus* (mean abundance = 7.1 ± 0.8 S.E. and 10.8 ±1.3 S.E., respectively) and *Pseudanthias tuka* (mean abundance = 5.0 ± 2.8 S.E. and 10.8 ± 2.6 S.E., respectively). *C. rollandi* was also abundant on the deep wall (mean abundance = 6.9 ± 0.8 S.E.). *Chrysiptera talboti* (4.5 ± 0.7 S.E.) and *Neoglyphidodon nigrorus* (mean abundance = 3.0 ± 0.4 S.E.) was observed in its highest abundances on the shallow wall. The deep wall aspect had species that were not observed on any other aspect, which were *Chromis delta* and *Pictichromis paccagnellae* (Appendix A 2-1).

SIMPER analysis shows the most representative species for the different depth and profile surveys were similar but the species driving differences between profile and depth showed the differences in the communities (Table 2-2).The most representative species in terms of percentage contribution to the community included *Halichoeres melanurus*, *C. rollandi* and *P. nigromarginatus*. There were some different species that were some of the most representative species such as *Pomacentrus aurifrons* and on the shallow shelf, *Chrysiptera talboti* on the shallow wall, *Ctenochaetus tominiensis* on the deep shelf and *Pseudanthias tuka* on the deep wall. The main dissimilarity between the shelf aspect and both the slope and wall aspects was the presence of *P. aurifrons*, *C. parasema*, *P. burroughi* and *Chromis ternatensis* in higher abundances on the shelf and *P. nigromarginatus* and *P. tuka* more abundant on the slope and wall. The differences between the slope and wall came from species being more abundant on the wall aspect such as *P. tuka*, *C. retrofasciata*, *Chromis amboinensis*, *P. nigromarginatus* and *C. talboti.* When comparing communities at 5m to those at 15m the main differences were driven by higher abundances of *C. retrofasciata* and *P. aurifrons* at 5m and higher abundances of *C. parasema* at 15m.

Table 2-2 Results of a SIMPER analysis on the fish abundance data showing the top 4 representative species for each depth and profile and their percentage contribution to the community

Depth/Aspect	Representative Species	Mean Abundance ± Standard Error	% Contribution To Community
Shallow Shelf	*Halichoeres melanurus*	4.913 ± 0.397	10.50
	Chrysiptera rollandi	5.435 ± 0.871	9.34
	Chromis ternatensis	7.435 ± 2.417	8.74
	Pomacentrus aurifrons	15.913 ± 5.581	8.31
Shallow Slope	*Halichoeres melanurus*	5.323 ± 0.487	12.9
	Chrysiptera rollandi	6.968 ± 1.224	10.25
	Pomacentrus nigromarginatus	6.000 ±1.004	9.66
	Chromis retrofasciata	4.774 ± 1.046	8.08
Shallow Wall	*Pomacentrus nigromarginatus*	7.091 ± 0.800	13.60
	Chromis retrofasciata	5.136 ± 1.035	11.12

	Chrysiptera rollandi	6.000 ± 1.170	10.42
	Chrysiptera talboti	4.455 ± 0.647	10.22
Deep Shelf	*Chrysiptera parasema*	19.800 ± 4.423	21.01
	Pomacentrus nigromarginatus	5.733 ± 1.465	12.68
	Chromis retrofasciata	6.600 ± 1.753	9.02
	Ctenocheatus tominiensis	2.467 ± 0.413	8.07
Deep Slope	*Chrysiptera rollandi*	6.889 ± 1.143	17.54
	Pomacentrus nigromarginatus	6.389 ± 1.473	16.93
	Chrysiptera parasema	5.889 ± 1.490	16.72
	Halichoeres melanurus	2.222 ± 0.358	9.23
Deep Wall	*Pomacentrus nigromarginatus*	10.833 ± 1.294	22.61
	Chrysiptera rollandi	6.889 ± 0.7796	17.97
	Chromis amboinensis	3.000 ± 0.808	7.05
	Pseudanthias tuka	8.056 ± 2.515	6.32

Concentrating on the community of fish present we can see that the communities on the nMDS (Figure 2-3b) still separated out by both depth and profile. Both the shallow and deep wall appear closer on the plot suggesting they are more similar to each other than to the other aspects, whereas looking at the shelf it appears that depth is important with the shelf habitats appearing similar by depth. The slope habitat seems more variable, although the deep slope was also quite close to both wall aspects. The loading vectors for the plot follow what the SIMPER analysis suggested for species driving the patterns seen. *Pomacentrus nigromarginatus* and *C. amboinensis* were representative of the deep and shallow wall as well as the deep slope to some extent. For the shelf and slope profiles the important species were *P. burroughi*, *P. aurifrons*, *C. ternatensis* and *C. retrofasciata* Testing the differences in the communities showed a significant interaction between both depth and profile (PERMANOVA, Pseudo-F = 1.889, p = 0.004), suggesting both depth and profile have an important effect on the fish community present. The nMDS plot for the abundances of different feeding guilds on different depths and profiles again showed some separation by profile and to a lesser extent depth (Figure 2-3c). The communities were much more mixed, suggesting more variability compared to the previous nMDS plots. The positions of both wall profiles seem to be driven by omnivores whereas the shelf and slope profiles were mainly driven by planktivores, carnivores and algal farmers (territorial herbivores). These patterns were statistically significant for both depth (PERMANOVA, Pseudo-F = 2.763, p = 0.038) and profile (PERMANOVA, Pseudo-F = 3.665, p = 0.003)

A RELATE analysis showed that there was a significant correlation between the habitat data and that of the fish abundance (RELATE, R = 0.508, p = 0.001). There was a significant correlation between habitat and fish data when using a BEST analysis, which found that using Sand, branching coral, massive coral, encrusting coral and rubble had the strongest correlation to the fish abundance (BEST, R = 0.509, p = 0.001).

2.4.3 Effects of depth and aspect on common species

The 10 most abundant species showed a variety of responses to depth and profile (Figure 2-4). Some species showed a significant relationship with profile which included *P. nigromarginatus*, *C. amboinensis* and *C. rollandi* (Table 2-3). Both *P. nigromarginatus* and *C. amboinensis* had significantly higher abundances on the wall profile compared with on the shelf and slope profiles (Figure 2-4). *Pomacentrus nigromarginatus* was most abundant on the deep wall whereas *C. amboinensis* was most abundant on the shallow wall, which was confirmed by post hoc tests. Although *C. rollandi* also showed a significant relationship with profile, post hoc tests revealed there were no true differences in abundance between profile and depth. *Halichoeres melanurus* had a significant relationship with depth rather than with profile (Table 2-3). Here there were significantly higher abundances at 5m compared to 15m (Figure 2-4). Several species showed patterns with both depth and profile separately. This included *C. ternatensis*, *P. burroughi* and *P. aurifrons* (Table 2-3). These species were found in significantly higher abundances at 5m compared with 15m. In terms of profile, both *C. ternatensis* and *P. burroughi* had their highest abundances on the shelf profile and *P. aurifrons* on the shelf and slope profiles (Figure 2-4). Finally some species had a significant interaction between depth and profile. These species were *C. retrofasciata*, *C. parasema* and *P. tuka*. *Chromis retrofasciata* was more abundant at 5m than at 15m on the slope and the wall profile but this switched to being more abundant at 15m on the shelf profile (Figure 2-4). The opposite trend was observed for *P. tuka,* with higher abundances at 5m on the shelf and slope than at 15m but then a significantly higher abundance at 15m on the wall profile. *Chrysiptera parasema* was significantly more abundant on the shelf profile and only showed a significant relationship between depths on this profile (Figure 2-4).

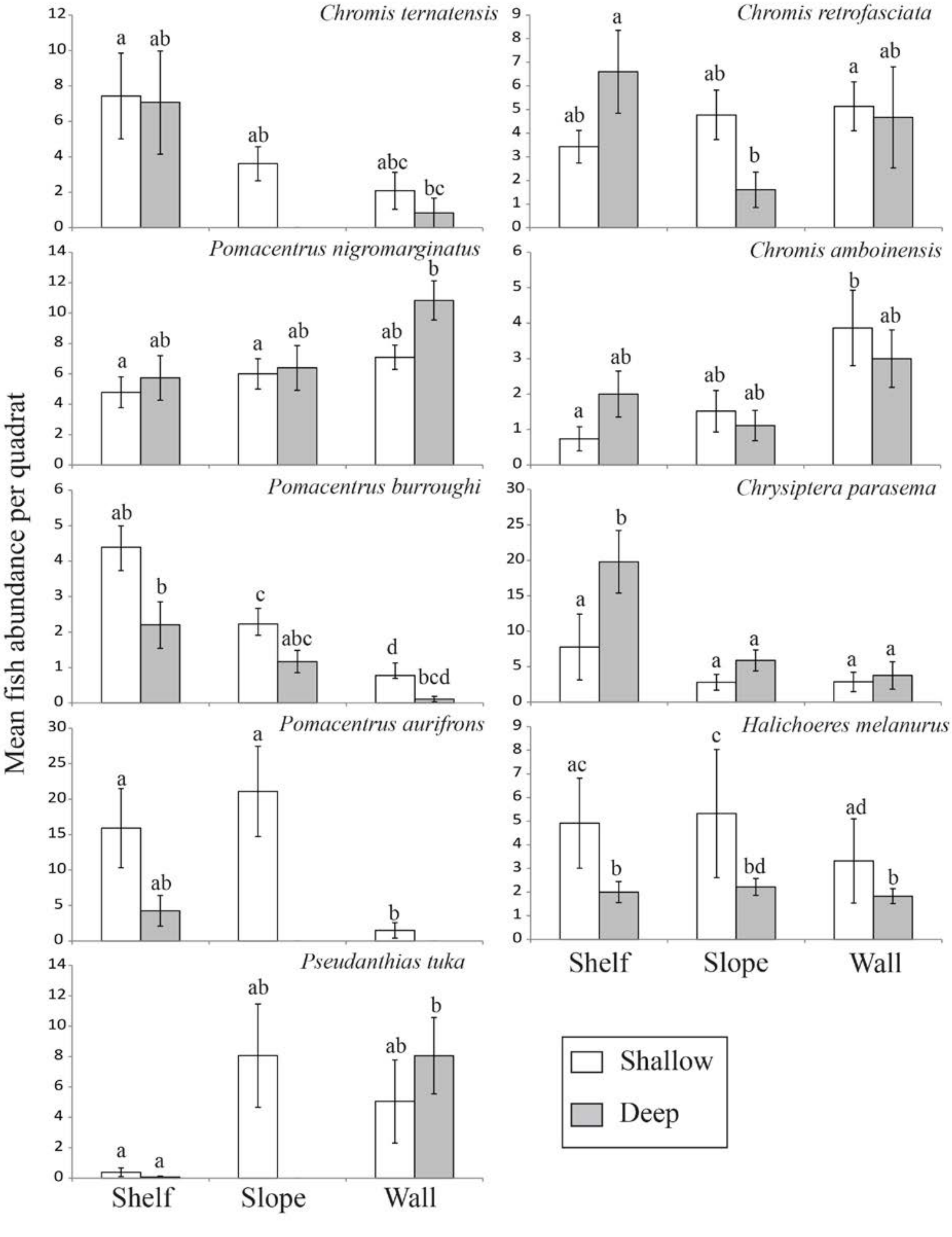

Figure 2-4 Mean fish abundance per quadrat at all depths and reef profiles for 9 of the ten most abundant species observed during the study. Error bars indicate standard error and letters above bars indicate the results of post- hoc Tukeys HSD tests carried out. *C. rollandi* was not included as after the post-hoc Tukeys HSD test there was no true differences found.

Table 2-3 ANOVA table showing the results of 2-way ANOVAs carried out on the 10 most abundant fish species in the study.

Chromis ternatensis	DF	SS	MS	F	P
Depth	1	13.301	13.301	5.831	0.017
Profile	2	33.742	16.871	7.397	0.001
Depth x Profile	2	6.013	3.007	1.318	0.271
Error	121	275.994	2.281		
Chromis retrofasciata	DF	SS	MS	F	P
Depth	1	3.127	3.127	1.685	0.197
Profile	2	10.441	5.220	2.814	0.064
Depth x Profile	2	13.304	6.652	3.585	0.031
Error	121	224.505	1.855		
Pomacentrus nigromarginatus	DF	SS	MS	F	P
Depth	1	4.818	4.818	3.453	0.066
Profile	2	19.021	9.511	6.817	0.002
Depth x Profile	2	1.573	0.787	0.564	0.570
Error	121	168.812	1.395		
Chrysiptera rollandi	DF	SS	MS	F	P
Depth	1	0.033	0.033	0.024	0.878
Profile	2	9.084	4.542	3.270	0.041
Depth x Profile	2	4.005	2.003	1.442	0.241
Error	121	168.058	1.389		
Chromis amboinensis	DF	SS	MS	F	P
Depth	1	0.406	0.406	0.358	0.551
Profile	2	14.726	7.363	6.491	0.002
Depth x Profile	2	2.820	1.410	1.243	0.292
Error	121	137.260	1.134		
Pomacentrus burroughi	DF	SS	MS	F	P
Depth	1	5.636	5.636	7.582	0.007
Profile	2	30.486	15.243	20.504	0.000

Depth x Profile	2	0.919	0.460	0.618	0.541
Error	121	89.954	0.743		
Chrysiptera parasema	DF	SS	MS	F	P
Depth	1	39.575	39.575	12.840	0.000
Profile	2	65.394	32.697	10.609	0.000
Depth x Profile	2	23.981	11.991	3.890	0.023
Error	121	372.937	3.082		
Pomacentrus aurifrons	DF	SS	MS	F	P
Depth	1	76.671	76.671	13.231	0.000
Profile	2	53.115	26.558	4.583	0.012
Depth x Profile	2	29.244	14.622	2.523	0.084
Error	121	701.146	5.795		
Halichoeres melanurus	DF	SS	MS	F	P
Depth	1	19.426	19.426	55.898	0.000
Profile	2	1.969	0.984	2.833	0.063
Depth x Profile	2	1.186	0.593	1.707	0.186
Error	121	42.051	0.348		
Pseudanthias tuka	DF	SS	MS	F	P
Depth	1	1.090	1.090	0.355	0.553
Profile	2	35.797	17.899	5.824	0.004
Depth x Profile	2	25.071	12.535	4.079	0.019
Error	121	371.848	3.073		

2.5 Discussion

While changes in fish community structure with depth are well-recognised (Srinivasan 2003; Brokovich et al. 2006; Brokovich et al. 2008), the role of reef profile has not previously been quantified. This study suggests that both depth and reef profile have separate and interacting effects on the structure of non-cryptic coral reef fish assemblages in Kimbe Bay, Papua New Guinea. Trends in overall community structure could be attributed to both depth and profile, and individual species could be identified that were most abundant at particular depths or on particular profiles. Communities showed differences in diversity and species richness at different depths and profiles. Diversity and species richness were highest at 5m on the shallow shelf. However, at 15m the wall was the most diverse and species rich. In addition, some species were very clearly specialized in relation to reef profile, particularly species confined to vertical walls, such as *C. delta* and *P. paccagnellae*. *C. delta* inhabits cave entrances and overhangs, which are unique features of wall profiles. *P. paccagnellae* inhabited areas between corals where encrusting organisms and sponges were present. The magnitude of the differences between depths depended upon the profile, with greater partitioning among depths on shelfs and slopes, compared with wall areas. Patterns in fish communities appeared to correspond to changes in the benthic habitat structure in relation to depth and profile. The patterns seen in the fish communities and the benthic habitats showed a correlation suggesting that changes in the benthic habitat composition could be important in explaining these patterns. However, the correlation was not very strong and habitat structure also varied in relation to depth and profile. Hence, benthic habitat is likely to be only one of several factors affecting the spatial distribution of fishes with depth and along the edge of the reef.

Few studies have focused on effects of profile as a distinct factor from depth (McGehee 1994; Brokovich et al. 2006), even though the two factors may not be independent. At our study location, fish communities on the wall habitats were most different from those on slopes and shelfs. Although the most characteristic species were similar between the different depths and profiles studied, there were particular species that represented the most dissimilarity between depths and profiles. The biggest differences between 5m and 15m were driven by differences in abundances of *C. parasema*, *C. retrofasciata* and *P. aurifrons*. Some previous studies from the area support, to some extent, this result for *C. parasema* by showing that this species can be more generalist in its depth use (Srinivasan 2003). Recruits of this species are often abundant deeper than other similar species (Srinivasan 2003; Bonin et al. 2009). The biggest differences between reef profiles occurred between shelf and wall habitats. Species distinguishing shelfs were generally coral-associated damselfish species such as *C. parasema*, *P. aufirons* and *C. ternatensis*. The wall community was distinguished by planktonic species such as *P. tuka* and less coral associated species such as *C. rollandi*, *C. talboti* and *P. nigromarginatus*. As expected, there were substantial differences among depths in the structure of fish communities. However, the magnitude of the effects of depths was dependent upon the reef profile. The damselfish *P. aurifons* was common on shallow shelves and slopes, while *C. parasema* was most the most common on the deep shelf and slope. Fish densities were similar between depths on the wall habitats, with *P. nigromarginatus* and *P. tuka* the most common species at both 5m and at 15m. Depth-distribution patterns have been found for many groups of fishes, as well as between different species of the same genus. For example, within the reef fish families Pomacentridae (Bay et al. 2001), Pomacanthidae (Eagle et al. 2001), Balistidae (Bean et al. 2002) and within the genus *Cephalopholis* (Donaldson 2002), species differ in the particular depths and depth zones at which they are most abundant. Anecdotal evidence suggests shallow water species extend further into deeper water on gentle slopes, compared with steep drop-off habitats. Hence, studies may find very different depth distributions, depending on the aspect of the reef that is surveyed. For example, Brokovich et al. (2008) found some species to have depth ranges that were extended by up to 40m compared with the previously reported depth limits for those species.

Benthic habitat is potentially one of the most important factors affecting fish distributions along gradients of profile and depth (McGehee 1994; Nunez-Lara and Arias-Gonzalez 1998; Srinivasan 2003; Brokovich et al. 2006; Brokovich et al. 2008). In our study, both of these factors explained variation in the types of habitat and benthic species dominating the substratum. Shelves and slopes had more branching coral and massive coral compared to walls, which had more encrusting coral and plating coral. The magnitude of the effect of depth varied with profile, but there was also a trend for more branching and massive corals in shallower water. This pattern could at least partially explain some of the patterns observed for individual fish species, with those preferring branching corals being more common on shelf areas and at shallower depths. For example, small coral-associated species such as *C. ternatensis* and *P. aurifrons* were most abundant on the shelf profile. Numerous studies have quantified habitat preferences in reef fishes and the availability of preferred habitats is often critical in explaining spatial patterns in their distribution (Green 1996; Gutierrez 1998; Bay et al.

2001; Bean et al. 2002; Brokovich et al. 2006; Brokovich et al. 2008; Bonin et al. 2009). Many of these patterns may translate into depth distributions. For example, herbivorous damselfishes (Pomacentridae) often dominate shallow reef zones, whereas labrids often dominate in deeper more exposed zones (Russ 1984; Meeken et al. 1995; Friedlander and Parrish 1998; Brokovich et al. 2008; Medeiros et al. 2010). Brokovich et al. (2010) found that grazing pressure on algae decreases dramatically with depth as well as herbivore density and biomass, which also decreased with depth. In our study, there was a miss match in the magnitude of the effects of depth and profile on fish and benthic habitats, with depth potentially being more important for fish communities and habitat on slopes and shelfs compared to on walls. In this study, the fact that there was only a weak correlation between habitat available and fish communities at different depths and reef profiles suggests that factors other than habitat structure may affect fish distributions.

There have been several studies that suggest that depth, in particular, co-varies with many different physical factors, for example light levels, that may have significant effects on reef fish (McGehee 1994; Sirinivasan 2003; Brokovich et al. 2008; Gonzalez-Sanson et al. 2009). Srinivasan (2003) for example, showed that provision of identical benthic habitats at different depths could only partially extend depth distributions for the coral-dwelling *C. parasema* and *Dascyllus melanurus*, suggesting other factors were involved. In our study, *C. parasema* showed significant relationships with both depth and profile and had a significant interaction between both factors, *C. parasema*, occurred everywhere but was most abundant on shelf aspects and at deeper depths. The highest abundances were observed on the shallow and deep shelf. Perhaps this is because there was more branching coral, *C. parasema's* preferred habitat, on the shelf. *C. parasema* can be considered a generalist species when it comes to depth, and so may be more abundant at depth because there may be fewer species that can settle and survive well at greater depths (Srinivasan 2003). It may also be due to competition with other ecologically similar species, such as *D. melanurus*, driving them deeper (Bonin et al. 2009).

With many factors changing and being inter-related with depth and reef profile, and the fact we could not find a strong correlation between the fish abundance data and the habitat availability data, it is possible that some factors not considered in this study may help to explain some of the patterns observed in this study, such as competition, exposure, predation and food availability. Several studies have indicated that competition can influence depth-related patterns of distribution of reef fishes, including tube blennies (Clarke 1989), triggerfish (Bean et al. 2002) and *Cephalopholis* (Shpigel and Fishleson 1989). Exposure is another factor that could influence the observed patterns. Exposure affects water motion, with more exposed sites having a greater flow velocity of water and a greater rate of change in flow direction (Fulton and Bellwood 2005). The interaction of water motion and swimming ability of different fish can directly influence the fish community, with pectoral swimming fish increasing in prevalence with increases in flow and caudal swimming fish decreasing (Fulton and Bellwood 2005; Fulton et al. 2005). The wall may be more exposed than the shelf, and this may cause the patterns seen and the dominance of species like *P. tuka*. The shelf may be less exposed, and lots of smaller more territorial fish therefore dominate. Changes in exposure (water flow) with depth can also effect coral morphology as well as coral metabolism and calcification (Mass et al. 2007; Mass and Genin 2008; Einbender et al. 2009). This could, therefore, have a knock on effect on the distribution of fish, in particular those species that are coral dependent. However, with no measure of water motion taken during the study, and the fact that Kimbe Bay is relatively sheltered, it is very difficult to say if there was a difference in exposure and water motion between reef profiles and whether this would have had an effect in this reef system. Differences in food availability and predation success may also influence fish community composition. Different guilds of reef fish show distribution patterns with food availability. Herbivorous and territorial species have higher abundances on shallow reef flat and crest habitats, whereas planktivorous and omnivorous fish are found in higher abundances on deeper crest and slope habitats (Friedlander and Parrish 1998; Brokovich et al. 2008; Medeiros et al. 2010). Our study supports this idea with a significant effect of both depth and profile on the abundance of different feeding guilds in the community, although, the effect of reef profile was more pronounced than that of depth. Planktivorous, carnivorous and algal farming (territorial herbivores) fish were important for shelf and slope habitats and omnivores were important for both shallow and deep wall habitats.

In conclusion, this study has documented previously undescribed effects of reef profile on fish communities, as well as the potentially complex interactions between profile and depth. Wall profiles appeared to be the most distinct habitats compared with shelf and slope profiles in terms of both fish community present and benthic habitat composition. The correlation between the fish community and benthic habitat composition suggests that changes in habitat are important in structuring communities on different depths and profiles. However, the fact that the correlation was weak and the complex nature of depth and profile gradients means that benthic habitat changes can only partially explain these patterns. Further study is needed to clarify the true physical differences between reef profiles and depths, and the other processes involved. Despite the unique nature of the reefs in the study area this study provides important information on changes in fish communities with depth and reef profile which can provide further understanding for reef systems in general. Overall, the study highlights the complexity in the spatial distributions on coral reefs, both along the reef edge and down the reef slope and the need to consider the full range of physical and biological processes that may be important.

Chapter 3. Depth gradients in diversity, distribution and habitat specialisation in coral reef fishes: implications for the depth refuge hypothesis

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3.1 Summary

Studies assessing the structure of coral reef fish assemblages have focused on shallow reefs and the importance of coral cover. However, the ecology of reef fish communities varies with depth, although trends in diversity, community structure and reliance on corals have seldom been described. Deeper reef habitats may provide refuge from shallow water disturbances, depending on the depth distributions of species and patterns of habitat specialisation with depth. We examined fish communities down to the bottoms of reefs at 20 m. Communities comprised species with shallow water distributions and others with broader depth ranges, which were more abundant at greater depths. Diversity declined linearly with depth. Species that were common around the mid-point of the depth gradient had the greatest depth ranges, whereas depth ranges were more restricted at the shallow and deep extremes. Niche breadth decreased with increasing mean depth of occurrence, suggesting that deeper species were more specialised. Unexpectedly, there was a higher association with branching corals in the deepest stratum, suggesting a greater reliance on coral habitat at the patchy reef edge. Clearly, there are dramatic changes in the ecology of reef fishes and their habitat between 0 and 20 m, and a variety of physical and biological factors are likely to be important. Although coral-associated species found deeper may occupy a refuge from shallow water disturbances, the narrow distributions of species at deeper depths and the high reliance on corals are unlikely to contribute to long-term resilience in relation to widespread reef degradation.

3.2 Introduction

One of the major goals of ecology is to try to explain patterns in distribution, diversity, species composition and niche breadth along environmental gradients (Krebs 2006). Species typically exhibit limited distributions and changes in abundance along environmental gradients such as altitude, latitude and depth (Hawkins 1999; La Peyre et al. 2001; Mark et al. 2001). The optimum position along these gradients may be a response to a number of intersecting physical gradients. For example, on mountains, species distributions may vary in response to altitude, slope and substrate type (Kappelle et al. 1995; Xu et al. 2011). Upper and lower limits of species distribution may be controlled by different factors, with environmental harshness often important at one extreme and biological interaction among species at the other (Connell 1961). Community-level metrics such as diversity also show distinct patterns along environmental gradients. For example, a decrease in diversity and species richness with increasing altitude has been found in communities of plants and insects such as butterflies (Kappelle et al. 1995; Leingartner et al. 2014). Diversity may not always be highest at one extreme of the environmental gradient, but may peak at a mid-point along the gradient where conditions are favourable for a larger number of species (Nogues-Bravo et al. 2008). Measures of specialisation such as niche breadth can also vary along environmental gradients, with populations of species at the limits of their range usually having narrower niche breadths (Clavel et al. 2011; Silc et al. 2014). A full description of the key ecological patterns that vary along gradients is necessary to generate hypotheses about the critical factors involved and to understand how environmental changes may affect species.

Most studies on the distribution, abundance, diversity and community structure of coral reef fishes have focused on horizontal gradients such as exposure (McGehee 1994; Green 1996), reef zone (Green 1996; Lecchini et al. 2003; Arias-González et al. 2006) and spatial patterns in habitat structure (Friedlander & Parrish 1998; Gratwicke & Speight 2005; Garpe et al. 2006; Graham et al. 2006; Wilson et al. 2006; Bonin et al. 2011). These studies often highlight patterns of diversity and specialisation associated with branching coral cover and topographic complexity (Chabanet et al. 1997; Brokovich et al. 2008; Graham & Nash 2013). However, the strongest physical and biological gradients on coral reefs are likely to be associated with depth gradients, where substantial trends in the physical and biotic environment can occur over a few metres (Brokovich et al. 2008; González-Sanson et al. 2009). Some changes in communities of fish have been found with increasing depth and the associated decline in coral cover (Brokovich et al. 2008). Not only can the abundance of individual species change with depth, but also the familial composition of the community. For example, in the Red Sea, shallow waters tend to be dominated by damselfishes and gobies, whereas wrasses and groupers become more dominant at greater depths (Brokovich et al. 2008). Differences in abundance can be observed between species of the same family and even the same genus, with examples known from pomacentrids (Bay et al. 2001), pomacanthids (Eagle et al. 2001), balistids (Bean et al. 2002), serranids (Donaldson 2002) and acanthurids and scarids (Hernandez-Landa et al. 2015). In all of these examples, species have been found to have different depth distributions, with some species or genera showing a preference for particular depths. Despite studies often showing changes in fish communities between different reef profiles or zones (e.g. reef flats, crests and slopes) that would include an aspect of depth (Green 1996; Lecchini et al. 2003; Arias-González et al. 2006), these typical reef zones or profiles are defined in relation to several factors, including depth, exposure and reef profile (Jankowski et al. 2015). Therefore, in general, systematic changes to species abundance, depth ranges and niche breadth, specifically along depth gradients, have seldom been investigated.

Given that one of the key factors affecting the distribution and abundance of coral reef fishes is structure of the underlying habitat, it is important to understand how habitat structure changes with depth and how fish reliance on particular habitats also changes. Coral cover has been implicated as an important determinant of depth distributions, with many coral-associated species restricted to shallow water (Chabanet et al. 1997; Srinivasan 2003; Brokovich et al. 2006). However, experimental manipulation of habitat availability at different depths has shown that habitat may only make a partial contribution to explaining depth distributions (Srinivasan 2003). Depth gradients are associated with numerous, co-varying physical changes, including light attenuation, declining wave-induced disturbance, temperature and so on (Fulton & Bellwood 2005; Fulton et al. 2005; Brokovich et al.

2008; Irisson et al. 2010). Larval supply has also been shown to be influenced by depth, with the distribution of fish larvae in the water column being structured by depth (Leis 1986; Leis 1991; Irrison et al. 2010). This structuring coupled with larval habitat choice can play a role in the distributions of reef fish (Gutierrez 1998). Biological interactions such as competition may also affect fish distribution and the depths at which fish prefer to live (Bay et al. 2001; Bean et al. 2002). Changes in habitat availability and habitat use with depth may well result in different levels of specialisation at different depths. It is thought that shallow water species tend to be more specialised in their depth range (e.g. Bean et al. 2002), with smaller depth ranges in shallow water associated with more substantial changes in physical conditions. It has also been hypothesised that shallow water species will be more specialised on substratum types (Bean et al. 2002). Many coral reef fish are associated with live corals and have been found to be restricted to shallow habitats (Bell & Galzin 1984; Chabanet et al. 1997; Srinivasan 2003; Coker et al. 2014). Deeper habitat can be more heterogeneous and therefore deeper species may be more generalistic (Bean et al. 2002; Brokovich et al. 2008). The ability to exploit a wider range of habitats can potentially allow a fish to live at a wider range of depths. If deeper species tend to be generalists, then reliance on coral may decrease with increasing depth as coral cover and diversity also decline. However, as few studies have focused on these patterns, generalisations about trends in ecological specialisation with depth have not emerged.

Coral reefs are subject to both natural and an increasing array of anthropogenic disturbances. Many of these impacts more heavily affect shallow reefs (Bongaerts et al. 2010; Kahng et al. 2010; Bridge et al. 2013). Reduced effects from disturbances such as tropical cyclones, thermal bleaching, fishing, pollution and run-off have been recorded from depths >10 m, although these reduced effects are more commonly seen at depths >25 m (Bak et al. 2005; Slattery et al. 2011; Bridge et al. 2013). This may afford some species a depth refuge, whereby species with wider depth distributions can survive impacts in shallow waters because individuals living at greater depths can act as a source of juveniles or because individuals can move to greater depths to lessen or escape impacts (Kahng et al. 2010). This has been demonstrated for several species, and depth may well need to be considered in marine reserve design (Kahng et al. 2010; Goetze et al. 2011; Bridge et al. 2013). If shallow species are more specialised and have more specific habitat preference (i.e. coral dependency) then it is possible that they may have an increased extinction risk compared to deeper species. Species that are more generalist in their depth distribution and therefore have extended depth ranges would potentially be less at risk considering that part of the population would not be impacted by a given disturbance in shallower depths (Graham et al. 2011). However, general predictions about species responses to shallow water anthropogenic disturbance must be founded on basic descriptions of natural changes in ecological traits along depth gradients.

The aim of this study was to quantify trends in depth ranges, diversity, species composition, habitat use and specialisation in coral reef fishes along a depth gradient down to the bottom of mid-shelf reefs at around 20 m on the Great Barrier Reef, Australia. Both fish and coral communities were sampled along depth profiles to test the following specific hypotheses for reef fishes. (1) Most damselfishes and wrasses have limited distributions over a 20 m depth range. (2) Taxonomic diversity and taxonomic distinctness declines with depth. (3) Species composition changes with depth, with the greatest changes occurring over shallow depth strata where the greatest changes to the physical environment occur. (4) Shallow species have smaller depth ranges than deeper species. (5) Shallow species are more specialised in their habitat use than deeper species, with a decline in the reliance on coral as a preferred habitat with increasing depth. The identification of common and interacting responses to these factors is a necessary step towards evaluating whether deeper reef habitat may be a refuge to impacts on coral reefs. If so, such findings will have important implications for the future management of coral reef ecosystems.

3.3 Methods

3.3.1 Study site and species

This study was carried out on 5 mid-shelf reefs of the central Great Barrier Reef (GBR) (Wheeler, Davies, John Brewer, Trunk and Rib), with 6 replicate sites sampled once on each reef (Figure 3-1). The reefs were surveyed over 2 trips; 3 reefs were surveyed October 2010 (Wheeler, Davies and John Brewer) and the other 2 in January 2011 (Trunk and Rib). These mid-shelf platform reefs exhibit reef flats exposed at low tide, with reef slopes ending in sand at approximately 20 m (Graham et al. 2014). The fact that these reefs ended at 20 m allowed us to survey fish over the entire depth range of these particular reefs. For this study I focused on habitat use and specialisation in species of the pomacentridae (damselfishes) and labridae (wrasses), 2 species-rich families that show a range in the degree of specialisation. I chose to focus on these 2 families of reef fish because of impracticalities of trying to record the habitat use for every fish in the community due to the time limits of diving to deeper depths.

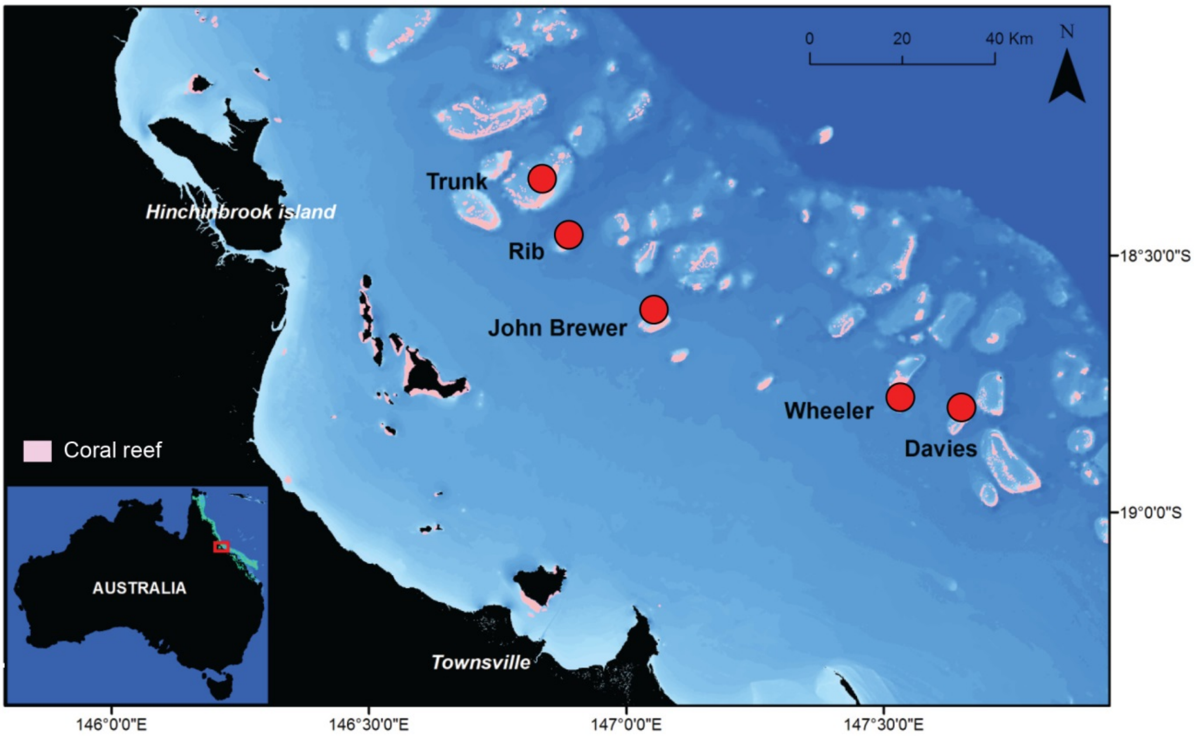


Figure 3-1 Map showing the 5 mid-shelf GBR reefs surveyed during this study and the surrounding region

3.3.2 Fish and benthic surveys

The distribution, abundance and habitat use of pomacentrids and labrids was surveyed at different depths by carrying out a controlled and steady swim from a starting depth of 20 m at the bottom of the reef's profile up to the reef flat, typically ~1 m depth at each of the 6 sites on each reef. Individual damselfishes and wrasses seen ahead within a 2 m belt were recorded. For each individual fish observed, the species, depth at which it was observed, and habitat type immediately below the fish was recorded. Fish seen in schools were counted, but only 5 individuals from each school observed were included to avoid a potential bias from very abundant species, whilst not losing any information from rarer species.

Available benthic habitat was surveyed using photo-quadrats. The reef profile was divided into 4 arbitrary depth strata (0–5, 5–10, 10–15 and 15–20 m). For each depth stratum, 20 to 30 photographs of the substratum were taken, with the camera 50 cm above the bottom, to keep the area photographed consistent and to keep the pictures clear enough to identify what was present. The first photograph for each depth stratum was taken haphazardly and then all other photographs for that depth stratum were taken at least 5 fin kicks away from the previous one. For each photograph the substratum at 5 random points was recorded. This was done using 9 benthic categories similar to those used by Wilson et al. (2008) (branching coral, plating coral, encrusting coral, massive coral, soft coral, algae/dead coral, sand/rubble, consolidated coral pavement and 'other').

3.3.3 Ecological metrics and data analyses

When assessing the distribution patterns with depth we had to take into account unbalanced sampling caused by limitations in the amount of time that could be spent at depth. Due to safety limitations, more time was spent overall at shallow depths when carrying out surveys, which all lasted approximately 40 min. Distribution was, therefore, assessed by looking at the frequency of occurrence of species at the different depth strata studied. This was done by plotting presence/absence of the 6 most common species in each family across all sites and depths studied. We tested the data statistically using a chi-squared test of homogeneity.

Changes in fish diversity with depth were analysed using the measures of taxonomic diversity (Δ) and taxonomic distinctness (Δ^*). These measures of diversity consider relationships between species through taxonomic trees. Taxonomic diversity looks at the average path length between every pair of individuals in a sample, or, in other words, the expected path length between any 2 randomly chosen individuals from the sample. This measure can be considered as being related to standard diversity indices and is a generalisation of the Simpson diversity index incorporating an element of taxonomic relatedness (Clarke & Warwick 1998). The taxonomic distinctness index was modified to remove some of the dependence on the species abundance distribution and therefore is more of a pure function of taxonomic relatedness. It is the expected path length between any 2 randomly chosen individuals from a sample, conditional on the samples being from different species (Warwick & Clarke 1995; Clarke & Warwick 1998). These taxonomic diversity metrics can take into account unbalanced sampling (Clarke & Warwick 1998). As stated earlier, limited bottom time, meant that sampling was unbalanced, with more time spent at shallower depths, making these diversity measures appropriate. Diversity indices were calculated for 2 m depth-strata, based on the depth observations made for all individuals, in order to give a more continuous axis for plotting trends in diversity.

To assess changes in species composition with respect to depth and reefs, I used a non-metric multidimensional scaling (nMDS) (Primer-E V.6) based on a Bray-Curtis resemblance matrix. Data were square root transformed to down-weight the effect of highly abundant species. Differences in depths and reefs were tested using a 2-way ANOSIM (Primer-E V.6). Changes in the depth distribution of species were analysed by calculating the total depth range for each species, which is the size of a species' depth range, and plotting this against the mean depth at which a species was observed. Due to the non-linear relationship in the data, we modelled it using a non-linear model with a polynomial fit using the program R (V.3.1.0) (R Core Team 2014). Normality of residuals and homogeneity of variance were assessed using plots of residuals against fitted values and Q-Q plots, and the data fitted the assumptions.

Specialisation was assessed by calculating niche breadth for each species. Niche breadth is a proportional similarity index, as used by Wilson et al. (2008), which takes into account the proportion of resources used by a population and the proportion of resources available to a population. Niche breadth or the proportional similarity index (PS) was calculated using the following formula:

$$PS = 1 - 0.5\ \Sigma\ (p_i - q_i) = \Sigma\ \min(p_i, q_i)$$

Where p_i is the proportion of resource items in state *i* used in a population and q_i is the proportion of *i* items in the resource base available to the population (Feinsinger et al. 1981).

The data used to calculate this were the habitat use data for each species as well as the habitat data. The index ranges between 0 and 1, where lower values indicate a smaller niche breadth and therefore greater specialisation. We then assessed how niche breadth changed with depth by plotting it against the mean depth of occurrence for each species. This was also done using a non-linear model with a polynomial fit due to the non-linear pattern in the data using the program R (V.3.1.0) (R Core Team 2014). The data met the assumptions of normality of residuals and homogeneity of variance according to plots of residuals against fitted values and Q-Q normal plots.

Habitat use was assessed for the communities of pomacentrids and labrids by combining the observations across all species and splitting them into the same 4 depth categories used when collecting data on habitat availability (0–5, 5–10, 10–15 and 15–20 m). The percentage of fish observed and the percentage of habitat available for each habitat category were plotted. To further assess habitat selection, resource selection functions ($\hat{w}_i$) were calculated following the formula:

$$\hat{w}_i = u_{i+} / (\mathrm{p}_i u_{++})$$

Where where u_{i+} is the number of fish using habitat type i, p_i is the proportion of that habitat type available and u_{++} is the total number of fish using all habitat types (Manly et al. 1993). Confidence intervals (95%) were calculated using the standard errors from the selectivity functions following methods outlined by Manly et al. (1993). These confidence intervals were then used to assess whether fish were using a particular habitat significantly more often than expected based upon its availability. This was considered to be the case when both the selectivity index and associated confidence intervals were >1 (Manly et al. 1993).

3.4 Results

3.4.1 Distribution and abundance

The 6 most common species within each family showed the range in the depth distributions observed, with similar patterns for both pomacentrids and labrids (Figure 3-2a, b). There were species that showed a clear preference for shallow depths, with the damselfishes *Stegastes apicalis* and

Pomacentrus bankanensis and the wrasses *Thalassoma hardwicke*, *T. jansenii* and *T. ambycephalus* all most common in the shallow depths (0–5 and 5–10 m) (Figure 3-2a, b). For the damselfishes, *S. apicalis* and *P. bankanensis* were only observed at 0–5 and 5–10 m. In contrast, *P. moluccensis* and *P. brachialis* occurred at all depths but were observed to be more common at deeper depths (Figure 3-2a). Among the labrids, both *T. hardwicke* and *T. amblycephalus* were only observed at 0–5 and 5–10 m, while *T. lunare* and *Halichoeres melanurus* both occurred throughout the depth gradient but were most common at 10–15 m and least abundant at 0–5 m. All these species showed a significant effect of depth on their distribution (Table 3-1). Three species showed no significant effect of depth on their distributions, these were the damselfishes *Acanthochromis polyacanthus* and *Amblyglyphidodon curacao* and the wrasse *Labroides dimidiatus*. Both *A. polyacanthus* and *A. curacao* were observed at all the depths surveyed, with *A. polyacanthus* being more common at shallow depths and *A. curacao* observed more at deeper depths (Figure 3-2a).

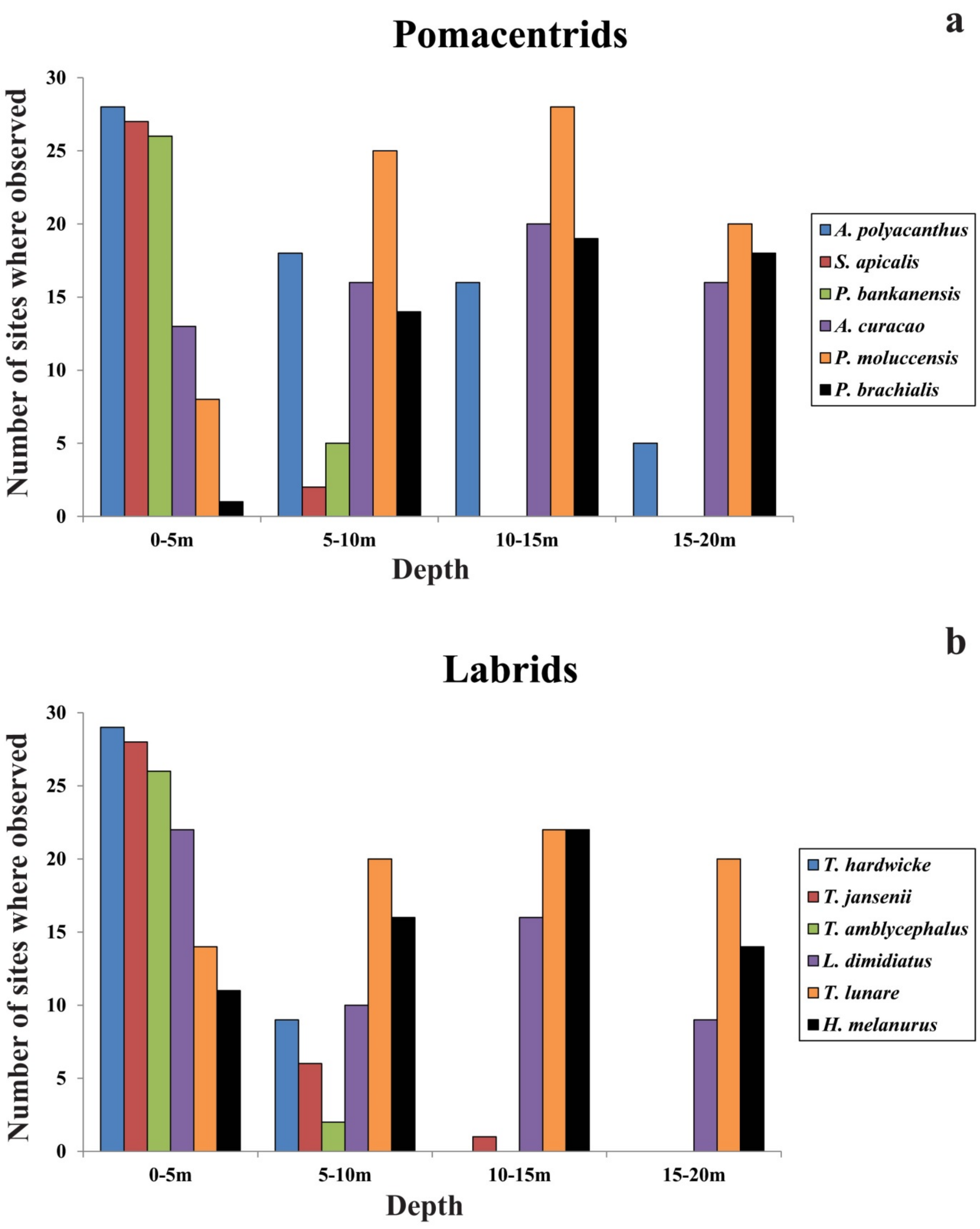


Figure 3-2 Presence/absence data for the most abundant Pomacentrid and Labrid species observed in the study. The graphs show the number of sites in the study that each species was observed at across different depth strata along the gradient surveyed (0-20m) at each site.

Table 3-1 Results of Chi^2 tests of homogeneity on the depth distribution of the 6 most abundant species of pomacentrids and labrids observed during the surveys found in **Figure 3-2**

Pomacentrids	**df**	**Chi^2**	**p**
Acanthochromis polyacanthus	3	5.037	0.169
Stegastes apicalis	3	49.366	0.000
Pomacentrus bankanensis	3	39.566	0.000
Amblyglyphidodon curacao	3	6.887	0.076
Pomacentrus moluccensis	3	19.797	0.000
Pomacentrus brachialis	3	28.609	0.000

Labrids	**df**	**Chi^2**	**p**
Thalassoma hardwicke	3	22.611	0.000
Thalassoma jansenii	3	21.163	0.000
Thalassoma amblycephalus	3	27.831	0.000
Labroides dimidiatus	3	2.352	0.503
Thalassoma lunare	3	22.063	0.000
Halichoeres melanurus	3	19.438	0.000

3.4.2 Species diversity and composition

3.4.2.1 Taxonomic diversity and distinctness

There was a linear decline in taxonomic diversity with depth ($y = -0.6596x + 57.575$, $R^2 = 0.770$), indicating a decline in the taxonomic variety of species between 0 and 20 m (Figure 3-3a). There was also a linear decline in taxonomic distinctness over the observed depth range ($y = -0.435x + 61.672$, $R^2 = 0.585$) (Figure 3-3b). This indicates that in shallow water there is a greater variety of species that are more taxonomically distinct from one another. The fact that both taxonomic diversity and distinctness show similar trends suggests that the distribution of abundance observed is a consistent pattern across the depth gradient.

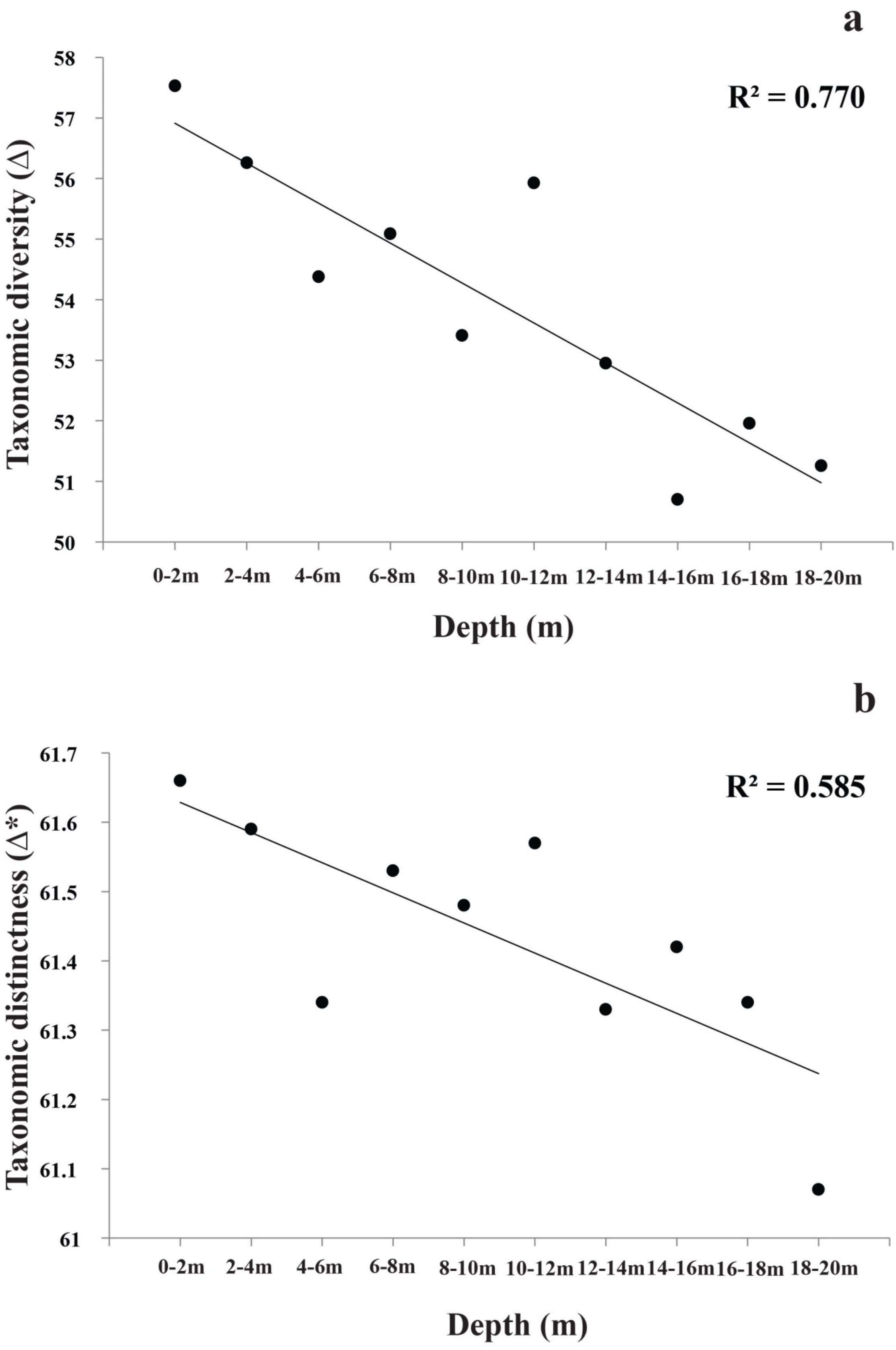


Figure 3-3 Diversity data showing a) the taxonomic diversity (Δ) and b) the taxonomic distinctness (Δ*) plotted against depth. Points represent the diversity measure for each 2m depth strata along the depth gradient surveyed (0-20m).

3.4.2.2 Community composition

Fish community composition showed distinct patterns associated with both depth and reef locations (Figure 3-4). There was a split in the data between communities at 0–5 m and communities at the other depths surveyed. There was also a more gradual change between communities at 5–10 m through to communities at 15–20 m. These patterns with depth were highly significant (ANOSIM: *F* = 0.749, p = 0.003). Multivariate dispersion between the communities in Figure 3-4 increases with depth, showing that the species observed at deeper depths were more spatially different (Table 3-2). The differences among the 5 reefs were not as clear. Wheeler Reef was the most distinct in terms of fish species present compared to the other reefs studied. The communities of fishes at Davies and Rib Reefs were quite similar to each other as were communities at John Brewer and Trunk Reefs. Statistically these trends were marginally significant, suggesting the reef effect was not as strong as that of depth (ANOSIM: *F* = 0.242, p = 0.053).

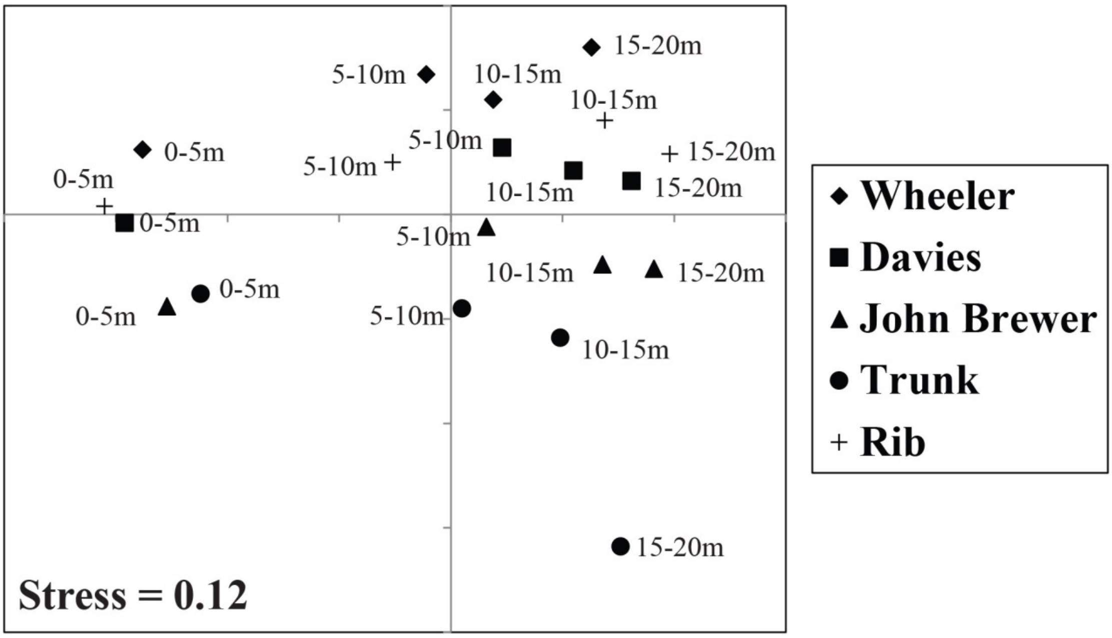


Figure 3-4 nMDS plot showing the similarities of fish communities observed at different depths for the 5 reefs surveyed during the study. Fish abundance data was categorised into 4 different depth strata (0-5m, 5-10m, 10-15m, 15-20m) for each reef. An ANOSIM analysis was carried out on the data to test the significance of the groupings in the nMDS plot with depth (ANOSIM, F = 0.749, p = 0.003) and reef (ANOSIM, F = 0.242, p = 0.053) both showing significant results.

Table 3-2 Multivariate dispersion of communities at each depth stratum surveyed

Depth	Dispersion (MVDISP)
0-5m	0.332
5-10m	1.005
10-15m	1.195
15-20m	1.468

3.4.3 Depth range and niche breadth

There was an unexpected polynomial relationship between the total depth range of a species and the mean depth at which it occurred ($y = –0.2033x^2 + 3.7397x + 1.5537$, $R^2 = 0.5145$; ANOVA: $F = 34.975$, $p < 0.001$ df = 66) (Figure 3-5a, Table 3-3). The species that exhibited the greatest depth ranges were those whose depth ranges were centred on intermediate depths of 6–12 m. There were no species with narrow depth distributions at these intermediate depths. Species that primarily live at shallow depths had smaller, more restricted total depth ranges, as did those primarily found at 16–20 m at the deepest edge of the reef.

Contrary to expectations, niche breadth (specialisation) showed a negative trend in relation to mean depth of occurrence ($y = –0.0026x^2 + 0.0213x + 0.6111$, $R^2 = 0.3509$; ANOVA: $F = 15.138$, $p < 0.001$ df = 56) (Figure 3-5b). Deeper species observed in this study exhibited a narrower, more specialised niche breadth than shallow species. Species with the shallowest mean depth and the greatest niche breadth were mobile planktivorous and benthic invertebrate feeding species, such as *Abudefduf whitleyi* and *Anampses geographicus*. Species with the deepest mean depth and smallest niche breadth included site-attached coral or sand/rubble species such as *Dascyllus reticulatus* and *Chrysiptera rollandi* associated with the edge of the reef. Very mobile omnivorous and carnivorous species, such as *Thalassoma lunare*, had niche breadths that were intermediate. However, overall there was a great deal of variation in niche breadths, particularly among species at shallow and intermediate depths.

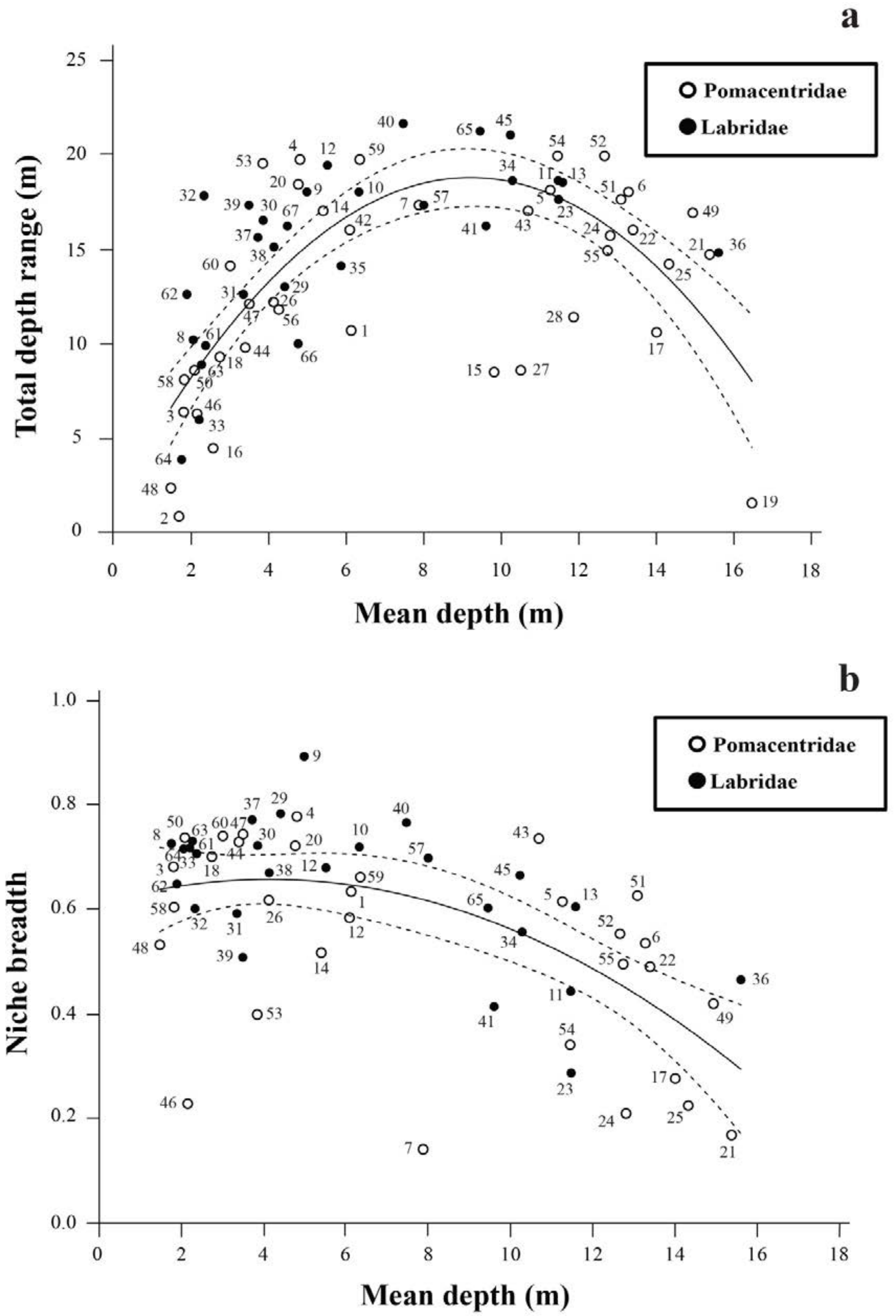


Figure 3-5 Plots showing a) the total depth range and b) the niche breadth against the mean depth of occurrence for each species observed in the study. Total depth range is defined as the size of a species depth range in metres. Niche breath is a measure of specialisation which gives a number between 0 and 1 for each species, where 0 is highly specialised and 1 is highly generalised.

Table 3-3 Species list containing all species of pomacentrids and labrids observed during the study and their feeding guilds. The number for each species corresponds to the data points in **Figure 3-5**

Number	Species	Family	Feeding guild
1	*Abudefduf sexfasciatus*	Pomacentridae	Omnivore
2	*Abudefduf vaigiensis*	Pomacentridae	Omnivore
3	*Abudefduf whitleyi*	Pomacentridae	Omnivore
4	*Acanthochromis polyacanthus*	Pomacentridae	Planktivore
5	*Amblyglyphidodon curacao*	Pomacentridae	Omnivore
6	*Amblyglyphidodon leucogaster*	Pomacentridae	Omnivore
7	*Amphiprion akindynos*	Pomacentridae	Planktivore
8	*Anampses geographicus*	Labridae	Benthic invertivore
9	*Anampses neoguinaicus*	Labridae	Benthic invertivore
10	*Bodianus axilaris*	Labridae	Benthic invertivore
11	*Cheilinus fasciatus*	Labridae	Benthic invertivore
12	*Cheilinus trilobatus*	Labridae	Benthic invertivore
13	*Choerodon fasciatus*	Labridae	Invertivore
14	*Chromis atripectoralis*	Pomacentridae	Planktivore
15	*Chromis lepidolepis*	Pomacentridae	Planktivore
16	*Chromis margaritifer*	Pomacentridae	Planktivore
17	*Chromis ternatensis*	Pomacentridae	Planktivore
18	*Chrysiptera brownriggi*	Pomacentridae	Omnivore
19	*Chrysiptera flavipinnis*	Pomacentridae	Omnivore
20	*Chrysiptera glauca*	Pomacentridae	Herbivore
21	*Chrysiptera rollandi*	Pomacentridae	Planktivore
22	*Chrysiptera talboti*	Pomacentridae	Planktivore
23	*Coris batuensis*	Labridae	Benthic invertivore
24	*Dascyllus melanurus*	Pomacentridae	Planktivore
25	*Dascyllus reticulatus*	Pomacentridae	Planktivore
26	*Dischistodus melanotus*	Pomacentridae	Territorial herbivore
27	*Dischistodus perspicillatus*	Pomacentridae	Territorial herbivore
28	*Dischistodus prospotaenia*	Pomacentridae	Territorial herbivore
29	*Epibulus insidiator*	Labridae	Invertivore
30	*Gomphosus varius*	Labridae	Benthic invertivore
31	*Halichoeres hortulanus*	Labridae	Invertivore
32	*Halichoeres margaritaceus*	Labridae	Benthic invertivore
33	*Halichoeres marginatus*	Labridae	Invertivore
34	*Halichoeres melanurus*	Labridae	Invertivore
35	*Halichoeres nigrescens*	Labridae	Benthic invertivore
36	*Halichoeres prosopeion*	Labridae	Benthic invertivore
37	*Hemigymnus fasciatus*	Labridae	Invertivore
38	*Hemigymnus melapterus*	Labridae	Invertivore
39	*Labrichthys unilineatus*	Labridae	Coralivore
40	*Labroides dimidiatus*	Labridae	Invertivore
41	*Labropsis australis*	Labridae	Coralivore
42	*Neoglyphidodon melas*	Pomacentridae	Omnivore
43	*Neoglyphidodon nigroris*	Pomacentridae	Omnivore

44	*Neopomacentrus azysron*	Pomacentridae	Planktivore
45	*Oxycheilinus diagramma*	Labridae	Invertivore
46	*Plectroglyphidodon dickii*	Pomacentridae	Omnivore
47	*Plectroglyphidodon lacrymatrus*	Pomacentridae	Territorial herbivore
48	*Plectroglyphidodon leucozonus*	Pomacentridae	Territorial herbivore
49	*Pomacentrus amboinensis*	Pomacentridae	Omnivore
50	*Pomacentrus bankanensis*	Pomacentridae	Omnivore
51	*Pomacentrus brachialis*	Pomacentridae	Omnivore
52	*Pomacentrus chrysurus*	Pomacentridae	Herbivore
53	*Pomacentrus coelestis*	Pomacentridae	Planktivore
54	*Pomacentrus mollucensis*	Pomacentridae	Planktivore
55	*Pomacentrus nagasakiensis*	Pomacentridae	Planktivore
56	*Pomacentrus philippinus*	Pomacentridae	Planktivore
57	*Pseudocheilinus hexataenia*	Labridae	Invertivore
58	*Stegastes apicalis*	Pomacentridae	Territorial herbivore
59	*Stegastes fasciolatus*	Pomacentridae	Territorial herbivore
60	*Stegastes nigricans*	Pomacentridae	Territorial herbivore
61	*Stethojulis bandanensis*	Labridae	Benthic invertivore
62	*Thalassoma amblycephalum*	Labridae	Planktivore
63	*Thalassoma hardwicke*	Labridae	Invertivore
64	*Thalassoma jansenii*	Labridae	Invertivore
65	*Thalassoma lunare*	Labridae	Benthic invertivore
66	*Thalassoma lutescens*	Labridae	Benthic invertivore
67	*Thalassoma quinquevittatum*	Labridae	Benthic invertivore

3.4.4 Reliance on coral

The hypothesis that dependence on coral would decline with increasing depth was not supported by this study (Figure 3-6a). In fact the data show the opposite pattern, with deeper fish species having a stronger association with branching coral compared with shallow ones. The main differences in habitat use between shallow and deep fish were that a higher percentage of shallow fish used plating coral, algae/dead coral, consolidated pavement and massive coral, whereas a higher percentage of deep fish used branching coral, soft coral and sand/rubble (Figure 3-6a). Manly selectivity indices showed that shallow species tended to select for plating coral, sand/rubble and soft coral, whereas deep species selected for branching coral and sand/rubble (Figure 3-6a).

Habitat use in fish broadly matched the habitat availability for most habitat categories in the study, with considerable differences in habitat availability among depths (Figure 3-6b). The shallow habitat had a higher percentage cover of branching coral, plating coral, massive coral and algae/dead coral.

Deeper habitat was characterised by having a higher percentage cover of soft coral, sand/rubble and other habitat categories. However, overall branching coral was used more than expected on the basis of availability. Branching corals have greater surface areas compared to other growth forms of coral, and this could have an effect on these results.

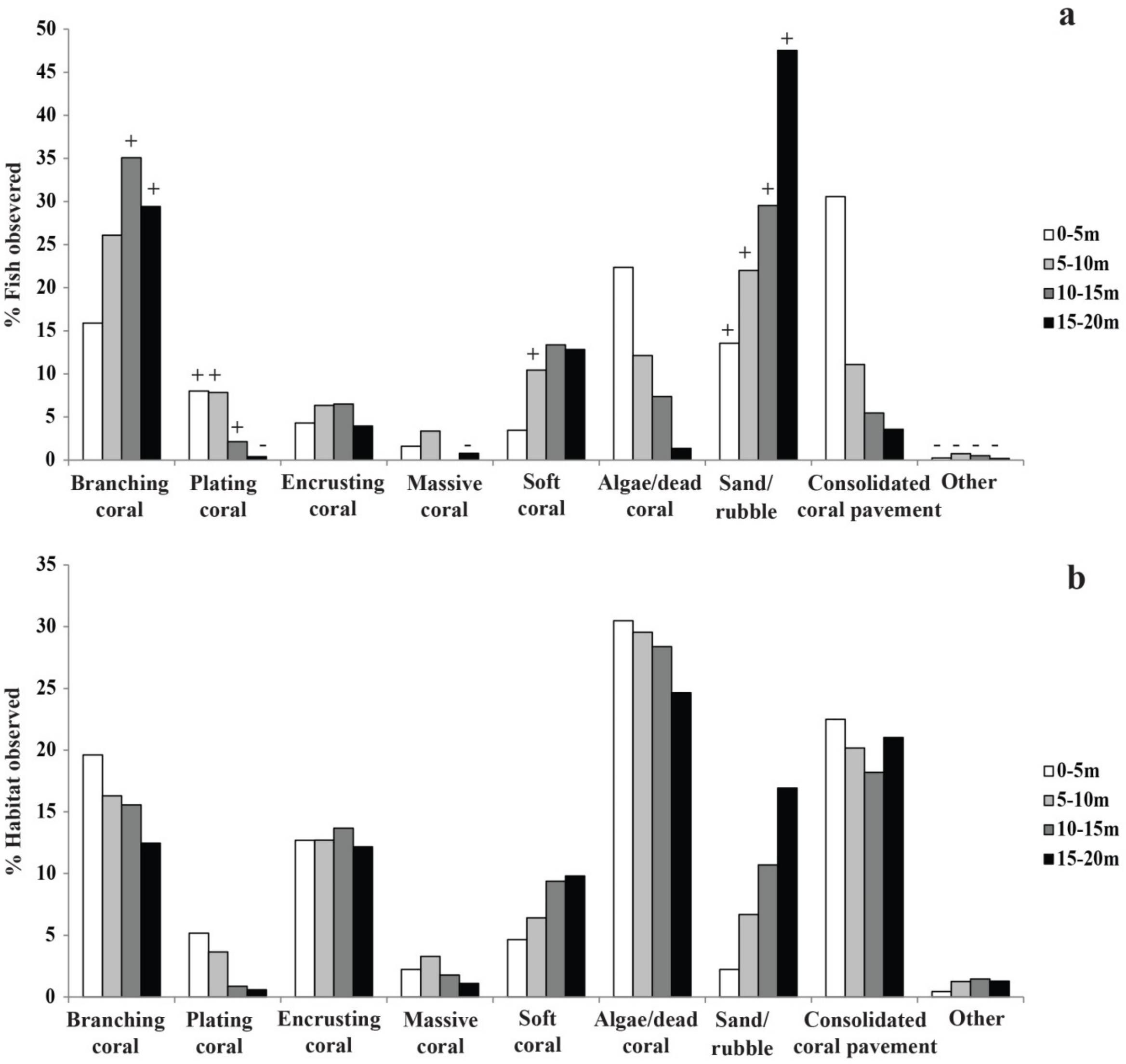


Figure 3-6 Graphs showing a) the percentage of fish observed using each of 9 habitat categories b) the percentage of habitat for each of 9 habitat categories observed at shallow and deep depths along the gradient surveyed in the study. Data was categorised into 4 depth strata (0-5m, 5-10m, 10-15m, 15-20m). A resource function was calculated for the fish data to show which habitats were overused (+) and which were underused (-).

3.5 Discussion

This study confirmed that reef fishes on the Great Barrier Reef exhibit strong patterns in distribution and community structure over depth gradients from 0 to 20 m. Some of these patterns conformed with predictions arising from previous studies (Green 1996; Eagle et al. 2001; Bean et al. 2002; Lecchini et al. 2003; Arias-González et al. 2006), while others were unexpected. There was a large number of pomacentrid and labrid species primarily associated with shallow habitats, as well as numerous species with broader depth distributions and greater abundance in deeper habitats. Species diversity and taxonomic distinctness declined with depth. Other patterns were more complex than expected. The depth ranges of species increased with depth in shallow habitats (as expected), but ranges declined again in deeper habitats, with deeper species also tending to be specialists associated with the bottom edge of the reef at approximately 20 m. Contrary to predictions, deeper habitat species tended to have narrower niches in terms of microhabitat use and were more reliant on branching corals than shallower species.

3.5.1 Distribution and abundance

There were clear patterns in the distribution and abundance with depth for both pomacentrids and labrids, with representative species from each family exhibiting similar patterns. Several species that were very common at shallow depths did not occur at greater depths (e.g. the pomacentrids *Stegastes apicalis* and *Pomacentrus bankanensis* and the labrids *Thalassoma hardwicke* and *Thalassoma amblycephalus*). There were also species that had broader depth distributions and were more common at greater depths (e.g. *Pomacentrus brachialis* and *Thalassoma lunare*). These results confirm previous observations that most reef fishes exhibit changes in abundance over relatively narrow depth ranges, and species-specific depth preferences (Bay et al. 2001; Bean et al. 2002; Donaldson 2002; Hernandez-Landa et al. 2015). The community level analyses showed the greatest difference in species composition, in the nMDS plot, occurred between the shallowest depth stratum (0–5 m) and the deeper reef areas. However, a continuous change in community structure occurred along the depth gradient to 20 m, and these depth patterns were consistent among reefs. It confirms previous findings that depth can be one of the major factors explaining variation in fish distributions and community structure (Green 1996; Lecchini et al. 2003; Brokovich et al. 2008).

3.5.2 Taxonomic diversity and distinctness

Taxonomic diversity and distinctness decreased linearly with depth along the depth gradient, contrasting with previous studies, such as that by Brokovich et al. (2008), in which species diversity and richness increased with depth to the mid-point of the depth gradient before declining rapidly with increasing depth. Unlike the Brokovich et al. (2008) study, our study was limited to 20 m and used different measures of diversity, but encompassed the entire depth range available to reef fishes on the mid-shelf reefs surveyed. The presence of dominant habitat-dependent damselfish, such as *Dascyllus reticulatus*, on the deeper parts of the gradient may also reduce the abundance of other species, thereby reducing diversity. Ben-Tzvi et al. (2009) found that adults of a similar species of damselfish (*Dascyllus aruanus*) were very aggressive to settlers of both conspecifics and heterospecifics to their coral habitats and that this could influence the settlement preferences of juveniles.

3.5.3 Depth ranges and niche breadth

There were a number of unexpected patterns in terms of depth range and niche breadth along the depth gradient. The idea that shallow species are more specialised in terms of their depth and habitat use than deeper species (Bean et al. 2002) was only partially supported. Firstly, we found depth specialists in both shallow habitats and in habitats along the deepest parts of the depth gradient. Species with the broadest depth ranges were those recorded at intermediate depths. Secondly, specialisation in terms of substratum use increased with depth, whilst diversity decreased, in contrast to the results found in previous studies (Friedlander & Parrish 1998; Bean et al. 2002; Brokovich et al. 2008). The dominance of particular species in the community at the deepest parts of the depth gradient may be causing the nonlinear relationship seen between depth and total depth range. A number of the species dominant at the bottom of the gradient are primarily associated with small patch reefs on sand (e.g. *D. reticulatus*) or sandy habitats immediately adjacent to reefs (e.g. *Chrysiptera rollandi*).

This gradient, with potential boundaries and a pattern showing the highest depth ranges at the mid-point of the gradient, could be the result of a 'mid-domain effect'. The concept of a mid-domain effect is that a random distribution of geographic ranges produces a peak in species richness midway between the boundaries of a biogeographic domain (Connolly et al. 2003). Despite these patterns usually being described on much larger scales and the fact that many reefs extend much deeper than 20 m, it is still possible to consider a mid-domain effect in our study because the reefs surveyed did not extend deeper than 20 m, meaning we surveyed the entire depth range available to the fish communities on these reefs. To examine if there truly is a mid-domain effect with depth, further study on more continuous reefs, in terms of habitat, to much deeper depths would be required.

Niche breadth unexpectedly declined with mean depth of occurrence, suggesting that for the fish surveyed in this study, specialisation increased with depth, while diversity declined. This pattern was associated with mobile, less habitat-dependent species being common at shallow depths, such as *Abudefduf whitleyi* and *Anampses geographicus*, whilst more habitat-dependent and less mobile species, such as *D. reticulatus* and *C. rollandi,* were common at greater depths. Predation pressure can increase with depth due to increased abundances of piscivores, which may lead to a closer association between small fishes and substrata that provide significant shelter at the deepest parts of the depth gradient (Shulman 1985; Jordan et al. 2012).

3.5.4 Reliance on coral

Reliance on branching corals did not show the expected decline with increasing depth. When looking at coral use for all species combined in the habitat use analysis, there was a much higher percentage of deeper fish using branching coral compared with shallower fish, despite only a small difference in the availability of branching coral between deeper and shallower habitats. At shallower depths, habitats such as algae/dead coral, consolidated coral pavement, sand/rubble and branching and plating corals were the most common habitats used by fish. In contrast the habitat usage at greater depths was dominated by fewer habitats, which were branching coral and sand/rubble. It is thought that habitat specialists can have an advantage over generalists within a subset of resources, but are more likely to be affected by habitat availability, and that generalists are favoured in more heterogeneous and disturbed environments, whilst specialists occur in more stable environments (Wilson et al. 2008; Clavel et al. 2011). At the deepest parts of the depth gradient there were patches of unconnected branching corals; hence, coral-associated species were common and had depth ranges restricted to their patchy habitat.

Brokovich et al. (2008) suggested that a decrease in branching coral, seen with increases in depth, could help explain the change in dominance between families of reef fish that were more dependent on coral as shelter, such as damselfish at shallower depths compared to those which were generally less dependent on corals for shelter such as species of labrids. Our study found that branching coral habitat was still common at the deepest parts of the reef, allowing more habitat-specialised damselfishes (e.g. *D. reticulatus*) to dominate at depth. It should be noted that Brokovich et al. (2008) surveyed a much broader depth gradient (0–65 m) than we did in our study. Specialists may be able to use their preferred habitat more efficiently than generalists, meaning they could out-compete generalists in that habitat, leading to a dominance of specialists and a potentially less diverse community (Emlen & Oring 1977; Futuyma & Moreno 1988). Alternatively, specialisation can increase diversity by allowing ecologically similar species to coexist in the same environments through the partitioning of resources (Hutchinson 1959; Pereira et al. 2015).

Habitat use was similar to habitat availability, with higher complexity corals (branching and plating) being particularly important for reef fish (Graham & Nash 2013; Coker et al. 2014). The underlying reef habitat and its characteristics are key factors in the distribution and abundance patterns of coral reef fishes (Graham & Nash 2013). However, it has been shown that if habitat is controlled experimentally then depth patterns can still occur independent of habitat, suggesting that other physical factors that co-vary with depth may play a role in depth distribution patterns (Srinivasan 2003). Numerous physical and biological factors change with depth, including light attenuation (Brokovich et al. 2008; Irisson et al. 2010), water movement (Fulton & Bellwood 2005; Fulton et al. 2005), larval supply (Leis 1986; Leis 1991; Gutierrez 1998; Hendriks et al. 2001) and competition (Bay et al. 2001; Bean et al. 2002). In the same study, growth and survival were reduced when species with a particular depth preferences were forced to live outside of their preferred depth range, showing that a cost to fitness is potentially involved (Srinivasan 2003).

3.5.5 Depth: is it a refuge?

For the reefs surveyed, deeper species were more specialised and they may well be just as vulnerable to coral loss as shallower species. This could also suggest that on these shallow reefs depth may not provide much of a refuge, although, this would depend on the extent to which deeper habitat is impacted by a particular disturbance. This is similar to other studies, which have found depth refuges on some reefs and not on others. For example, van Oppen et al. (2011) found evidence of vertical migration in populations of corals at a reef in north western Australia, but not on a reef in north eastern Australia. The fact that the reefs studied in this survey only reached depths of around 20 m is probably a limitation to a depth refuge. There is some evidence that impacts to corals from disturbances such as tropical cyclones and thermal bleaching can be reduced at depths >10 m, but the full depth of the reefs surveyed (20 m) may not be deep enough for the deeper reef habitat to act as a refuge (Woodley et al. 1981; Hoeksema 1991; Bak et al. 2005; Slattery et al. 2011; Bridge et al. 2013). Most of the literature discussing depth refuge involves mesophotic reefs which occur at depths between 30 and 60 m (Bak et al. 2005; Slattery et al. 2011; Bridge et al. 2013). Depth refuge has been shown to occur for coral reef fishes in relation to fishing and marine reserves (Tyler et al. 2009; Goetze et al. 2011). However, there are few studies that have looked into the possibility of depth providing a refuge for coral reef fishes in relation to other impacts. Graham et al. (2011) suggest that depth could be an important factor in the extinction risk of fish species, as those species that have extended depth ranges could in fact be less impacted by disturbances to shallower reef habitats.

This study has revealed a number of trends in the structure of reef fish communities along a depth gradient from 0 to 20 m. These patterns include declining taxonomic diversity with depth, small depth ranges for both shallow and deeper water species, and increasing habitat specialisation and reliance on branching corals in deeper reef habitats. These patterns are likely explained by a range of factors, given the sharp gradients in the physical and biological environment between 0 and 20 m and also the presence of specialised species at deeper reef habitats. However, deeper reef habitats may be a refuge for coral-associated species, as long as these deeper corals have some resilience from bleaching or other depth-restricted disturbances. Our results highlight the need for further study into the causes of depth patterns and the long-term stability and resilience of coral-associated reef fish populations on deeper reef habitats.

Chapter 4. Separating the effects of depth and habitat availability on coral reef fish communities

4.1 Summary

Depth is one of the most important environmental gradients in the marine environment and coral reef fish show distributions limited along depth gradients. However, the precise factors that determine depth distributions are often unknown. Habitat structure co-varies with numerous other depth-related changes to the physical and biological environment. Some studies have suggested that the effects of depth on reef fish can be both dependent on, and independent from, changes in habitat. This study aimed to assess the separate effects of habitat dependent and independent factors by using experimental patch reefs of 4 different habitat types (*Acropora elsyi* reefs, *Seriatopora histrix* reefs, dead coral reefs and rubble reefs) at 3 different depths (3-5m, 8-10m, 18-20m) and at 2 different sites. The reef fish community that developed on the patch reefs over 12 months was surveyed and analysed. Depth had a strong significant effect on the reef fish communities present, with shallow and deep patch reef communities being different and mid patch reefs being a mix of the two. There was also a strong effect of site and a significant interaction between depth and site with mid patch reefs at site 1 being more similar to deep patch reefs, whereas at site 2 mid patch reefs were more similar to shallow patch reefs. Unexpectedly, habitat had a weaker (but still significant) effect on the reef fish communities. The proportions of different feeding guilds of fish in the communities were also affected by depth with herbivores and planktivores being more prevalent on shallow patch reef communities. Diversity and species richness were highest on shallow patch reefs at site 1 and on the deep and mid patch reefs at site 2. Mid patch reef communities showed the highest evenness at site 1 whereas deep patch reef communities had the highest evenness at site 2. This study further demonstrates the important effect that depth can have on reef fish communities independently of habitat changes, which may also suggest, in terms of community structure, that habitat changes are not as important as once thought. The complex nature of depth gradients means there are many other

physical and biological factors that could be driving these patterns and further study is needed to assess the importance of these factors.

4.2 Introduction

In nature organisms are rarely distributed evenly or at random, but instead often form striking distribution patterns. Distributions of organisms are frequently limited along environmental gradients such as altitude, latitude and depth (Connell 1961; Hawkins 1999; La Peyre et al. 2001; Mark et al. 2001). For example, it is well known that plants, as well as other organisms, show strong patterns of distribution and zonation with altitude (Kappelle et al. 1995; Xu et al. 2011; Silc et al. 2014). Describing and trying to understand such patterns is a fundamental goal of ecology (Krebs 2006). These patterns can, however, be quite difficult to understand as the optimum position for an organism along a gradient may be a response to a number of intersecting physical gradients. For instance, on mountains, species distributions may vary in response to changes in altitude, slope and substrate type (Kappelle et al. 1995; Xu et al. 2011). It can therefore be important to try and separate some of these gradients in order to understand how they affect species distributions along with their relative importance on structuring such distributions. Gradients also control distributions of organisms in the marine environment, including depth (Nunez-Lara and Arias-Gonzalez 1998; Brokovich et al. 2008; Gonzalez-Sanson et al. 2009), exposure (McGehee 1994; Green 1996) and distance from shore (Russ 1984). Lots of physical conditions change along these gradients, including light, water motion, slope aspect and temperature (Fulton and Bellwood 2005; Fulton et al. 2005; Huebert et al. 2010; Irisson et al. 2010; Malcolm et al. 2011). Depth is one of the most important gradients in the marine environment, as substantial trends in the physical and biotic environment can occur over distances of just a few meters (Brokovich et al. 2008; Gonzalez-Sanson et al. 2009).

Studies of communities of reef organisms, in particular reef fish communities, often identify depth as being one of the most important factors explaining variation in their studied communities (Lecchini et al. 2003; Brokovich et al. 2006; Brokovich et al. 2008; Gonzalez-Sanson et al. 2009; Fitzpatrick et al. 2012). Diversity of reef fish communities has been found to change with depth, with studies finding that diversity increases with depth to a mid-point along a gradient (around 30-40m) (Brokovich et al, 2008; Garcia-Sais 2010). The species present in a community, as well as the composition of different species on reefs, changes with depth also (Srinivasan 2003; Nunez-Lara et al. 1998; Brokovich et al. 2008; Gonzalez-Sanson et al. 2009). Species of fish often show different preferences for different depths with some species being shallow or deep specialists and some being depth generalists (Bay et al. 2001; Eagle et al. 2001; Bean et al. 2002; Donalson 2002; Srinivasan 2003). The abundance and importance of different reef fish families in the community changes with depth, with families such as pomacentrids and gobies dominant in shallow environments and labrids and serranids being more dominant in deeper environments (Brokovich et al. 2008). The distribution of different feeding groups of reef fish has also been found to change with depth. For example, herbivorous and omnivorous fish are more abundant in shallow environments whereas mobile invertebrate feeders and detritivorous fish are often more abundant at deeper depths (Brokovich et al. 2008; Nemeth and Appledoorm 2009; Pinheiro et al. 2013). Despite these patterns, most studies on the distribution, abundance, diversity and structure of coral reef fish communities have focused on spatial patterns in habitat structure, typically within one depth stratum (Friedlander and Parish 1998; Gratwicke and Speight 2005; Garpe et al. 2005; Graham et al. 2006; Wilson et al. 2006; Bonin et al. 2011).

Habitat and complexity are considered to be very important factors structuring reef fish communities (Pratchett et al. 2008; Graham and Nash 2013). The reef habitat often becomes less complex and has less live coral cover with increasing depth (Brokovich et al. 2008). Live corals are an important biological substrate for many reef associated organisms, providing critical food and shelter (Coker et al. 2014). Coral cover as well as species composition and growth forms all change with depth, with more structurally complex corals, such as branching corals, found shallower and less structurally complex corals, such as encrusting and plating species, found deeper or in sheltered environments (Wellington 1982; Brokovich et al. 2008). A fish’s association with a particular species or growth form of coral could therefore have an impact on its distribution. Fish biomass, abundance and diversity have been shown to increase with increasing coral cover and complexity (Graham and Nash 2013). It is thought that more habitat specialists are found in shallow environments and more habitat generalists are found in deeper environments (Bean et al. 2002). Despite the importance of habitat changes on fish distribution, a study by Srinivasan (2003) found that even with habitat kept constant some species of damselfish still showed depth preferences in their recruitment and showed reduced growth and survival outside of preferred depths. This suggests depth patterns may not be driven by habitat changes and preferences alone.

This aim of this study was to experimentally separate the effects of habitat dependent and independent factors on the depth distributions and community structure of coral reef fishes in Kimbe Bay, Papua New Guinea. The communities of reef fish that recruited and developed on experimental patch reefs made of identical habitat types placed at different depths were surveyed and analysed to test the hypotheses that: 1) Different communities of fish are present at different depths despite habitat availability being the same, and these patterns are consistent between sites 2) There are differences in composition between communities on patch reefs of different habitat types. 3) There are differences in the contributions of different feeding guilds to fish communities at different depths 4) Coral associated species show a preference for shallow patch reefs whereas non-coral habitat associated fishes have a greater preference for deeper patch reefs. Identifying these patterns and their relative importance can strengthen our understanding of depth gradient patterns and identify future avenues of study needed in this field. Understanding patterns of fish distribution is important in ecology and can have implications for the management and future conservation of reef fish communities.

4.3 Methods

4.3.1 Study site

This study was carried out from April 2012 until June 2013 in Kimbe Bay, on the Bismarck Sea coast of the Island of New Britain, Papua New Guinea (5^{o}26’15.66’’S, 150^{o}05’06.75’’E). The two sites used in the study were located around Schumann Island (5^{o}29’33.46’’S, 150^{o}09’35.82’’E), a small unpopulated coastal island surrounded by fringing reefs, and Garua Island, a much larger unpopulated coastal island that was formerly the site of a coconut plantation (Figure 4-1). Most reefs drop off to over 40m in this area, with substantial changes in fish distributions over this depth range (Jones et al.

2004; Jankowski et al. 2015). Sites were surveyed every three months from August 2012 until June 2013.

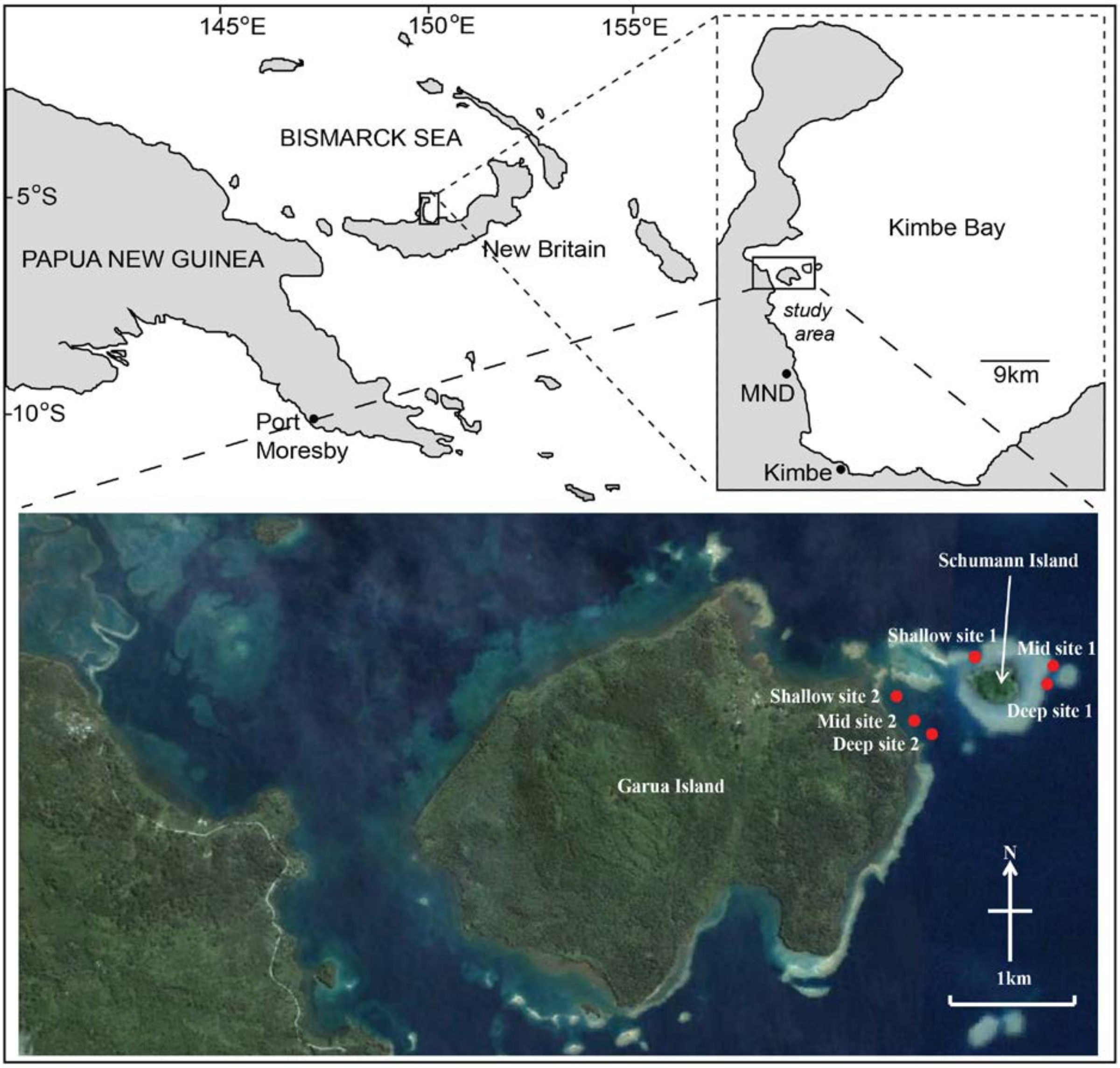


Figure 4-1 Map of Kimbe Bay, Papua New Guinea, showing sites at Schumann and Garua Islands at which patch reefs were built at 3 depths; Shallow (3-5m), Mid (8-10m) and Deep (18-20m).

4.3.2 Sampling design

Experimental patch reefs were built at three depths (3-5m, 8-10m, 18-20m), and two sites (one at Schumann Island and the other at Garua Island). They were constructed on two gently sloping sand areas adjacent to the island, with the same aspect and prevailing winds. To avoid colonisation from nearby reef habitat, patch reefs were built at least 10m away from any existing reef habitat and each patch reef was 5m away from any other neighbouring patch reef. Patch reefs had a base diameter of 1m and consisted of a rubble base with a chosen habitat type on top. Rubble was sourced from nearby reef flats and cleared of fish before being used in the study. We used four different habitat types in this study; *Acropora elsyi,*, *Seriatopora histrix,*, dead coral which still had structure to it, and bare rubble. These species of corals were chosen because they are common in the local area and occurred throughout the range of depths used in the study. In order to maintain the coral habitats for the duration of the experiment, coral habitat was assessed and colonies that had died or been covered with fouling communities were replaced with fresh live coral from nearby reefs. At site 1 there were 20 patch reefs at each depth, giving five replicates for each habitat type. At site 2 there were 16 patch reefs at each depth, giving four replicates of each habitat type (fewer because the sand area was smaller). There were no fish present on the patch reefs at the start of the survey and the community of fish present was surveyed every three months for 12 months. Each patch reef was surveyed until all fish present had been counted, which took around five minutes on average. All non-cryptic fish associating with the patch reefs were identified to species level and counted. Fish surveys were carried out by the same observer to keep surveys consistent and reduce observer error.

4.3.3 Data analysis

The temporal aspect to the study was eliminated from analyses due to the fact that patterns in communities were consistent throughout all months surveyed and the effect of time was not significant in a PERMANOVA test carried out on the survey data (Anderson 2001; Primer v.6). Therefore all analyses were carried out on abundance data which was the average abundance of species across all 12 months of the study. To assess changes in reef fish community among depths, sites and habitat treatments, we plotted the community data using nMDS (Primer-E v.6). Data were square root transformed to down weight highly abundant species, and we used a Bray-Curtis similarity matrix. To test the patterns in the nMDS statistically, we carried out a PERMANOVA (Anderson 2001; Primer-E v.6). We analysed the communities of fish using a SIMPER (Primer-E v.6) analysis to see which species in particular were the most representative and which species were driving the main differences. The most representative coral-associated and non-coral associated species from each depth were analysed individually to look at abundance patterns with depth and habitat. This was done using 2-way ANOVAs with a Tukey's HSD post-hoc test (Statistica v.7, StatSoft). Species data were square root transformed in order to meet assumptions of normality of residuals and homogeneity of variance. The relative contribution of different feeding guilds of fish in the communities present was analysed using the results from the SIMPER test carried out on the fish abundance data. The percentage of different feeding guilds of reef fish was plotted for species that contributed cumulatively to 80 percent of shallow and deep communities on each habitat type. Finally, we examined how the species richness, diversity and evenness changed among the patch reefs across all sites and depths. This was done by calculating the number of species to represent the richness present, the Shannon-Wiener Index for diversity and evenness (Hammer et al. 2001; PAST v.3).

4.4 Results

4.4.1 Community structure

There were substantial changes in the structure of the fish communities with depth that were independent of habitat structure (Figure 4-2). There was also a clear separation between communities at site 1 and those at site 2 (Table 4-1). There was also a strong significant pattern in the communities with depth at both sites (Table 4-1). At site 1, the shallow communities were most distinct from the mid and deep communities. However, there was still a separation in the communities between mid and deep depths. At site 2 there was a similar trend, but at this site the deep communities were the most distinct from the other depths. The deep reefs were characterised by *Cephalopholis boenak* and *Cirrhilabrus punctatus* (Figure 4-2). Mid-depth communities at site 1 were characterised by *Pomacentrus amboinensis* and *Halichoeres melanurus,* whereas shallow communities at site 1 were characterised by *Halichoeres chloropterus* (Figure 4-2). At site 2, both mid and shallow communities were characterised by *Lutjanus gibbus* and *Pomacentrus simsiang*. Overall, habitat had a weaker significant effect on the fish communities (Table 4-1, Figure 4-2). The PERMANOVA identified some significant interactions between all three factors in the study, with the most influential appearing to be an interaction between site and depth (Table 4-1).

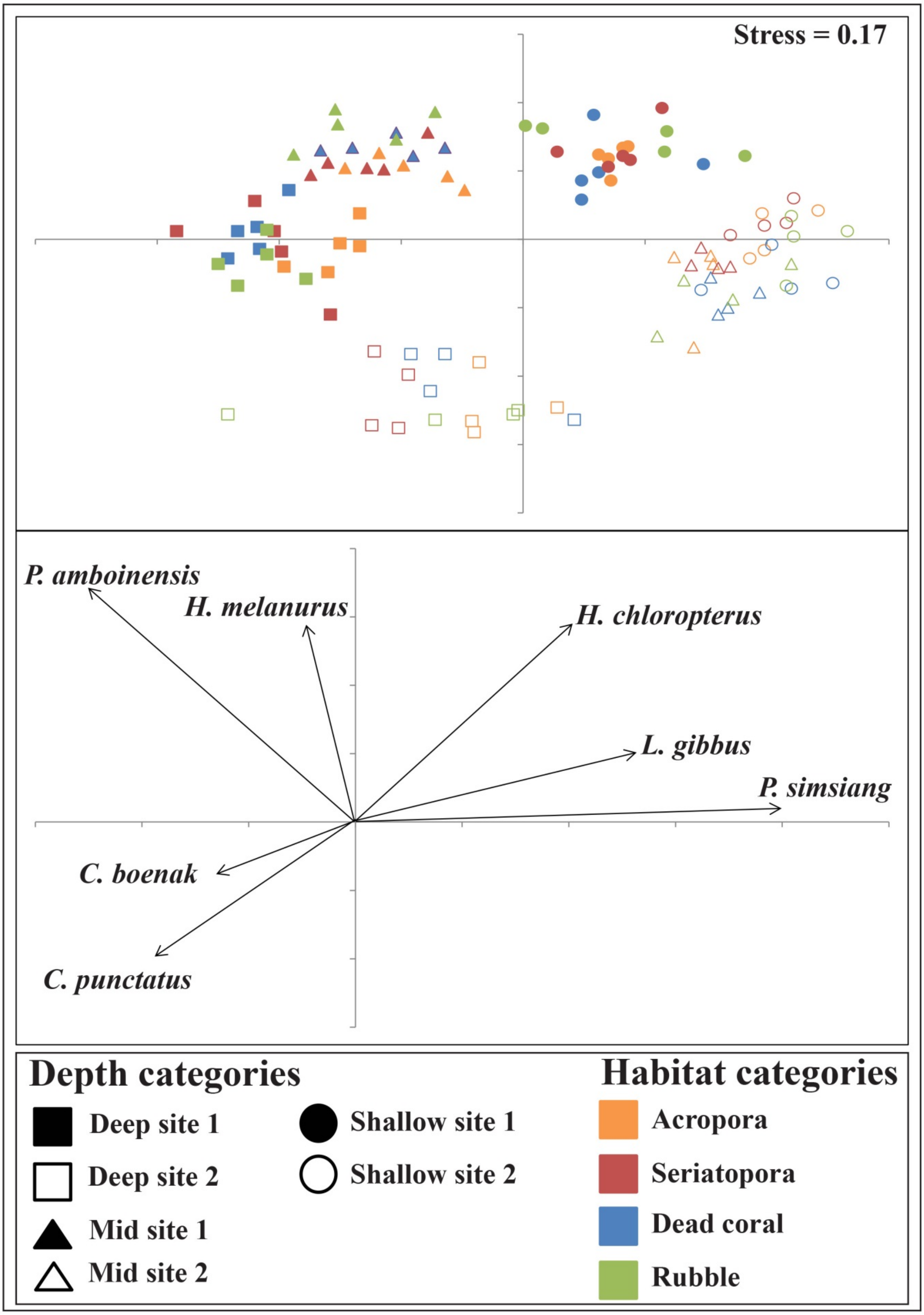


Figure 4-2 nMDS plot showing the similarities between the average fish communities observed on patch reefs over 12 months. Different sites are represented by open and closed symbols, depths by different symbols and habitat by colour.

Table 4-1 Results of PERMANOVA analysis on the average fish communities present on patch reefs over the 12 months of the study.

Source	df	SS	MS	Pseudo-F	P(perm)
Site	1	1.51E+05	1.51E+05	50.862	0.001
Depth	2	1.74E+05	87242	29.294	0.001
Habitat	3	29731	9910.4	3.3277	0.001
Site x Depth	2	73980	36990	12.42	0.001
Site x Habitat	3	14434	4811.3	1.6156	0.006
Depth x Habitat	6	25826	4304.3	1.4453	0.003
Site x Depth x Habitat	6	25695	4282.5	1.438	0.005
Res	408	1.22E+06	2978.1		
Total	431	1.71E+06			

The contribution of different feeding groups to the fish community showed subtle differences with both depth and habitat (Figure 4-3). Across habitat types overall, there was little difference in the contributions of different feeding guilds. *Acropora* and *Seriatopora* patch reef communities had more planktivores compared to dead coral and rubble patch reef communities. Contributions of omnivores and carnivores were very similar throughout. When comparing communities between deep and shallow depths, omnivores and carnivores contributed in similar proportions, however, deep patch reef communities had fewer herbivores and planktivores than shallow communities.

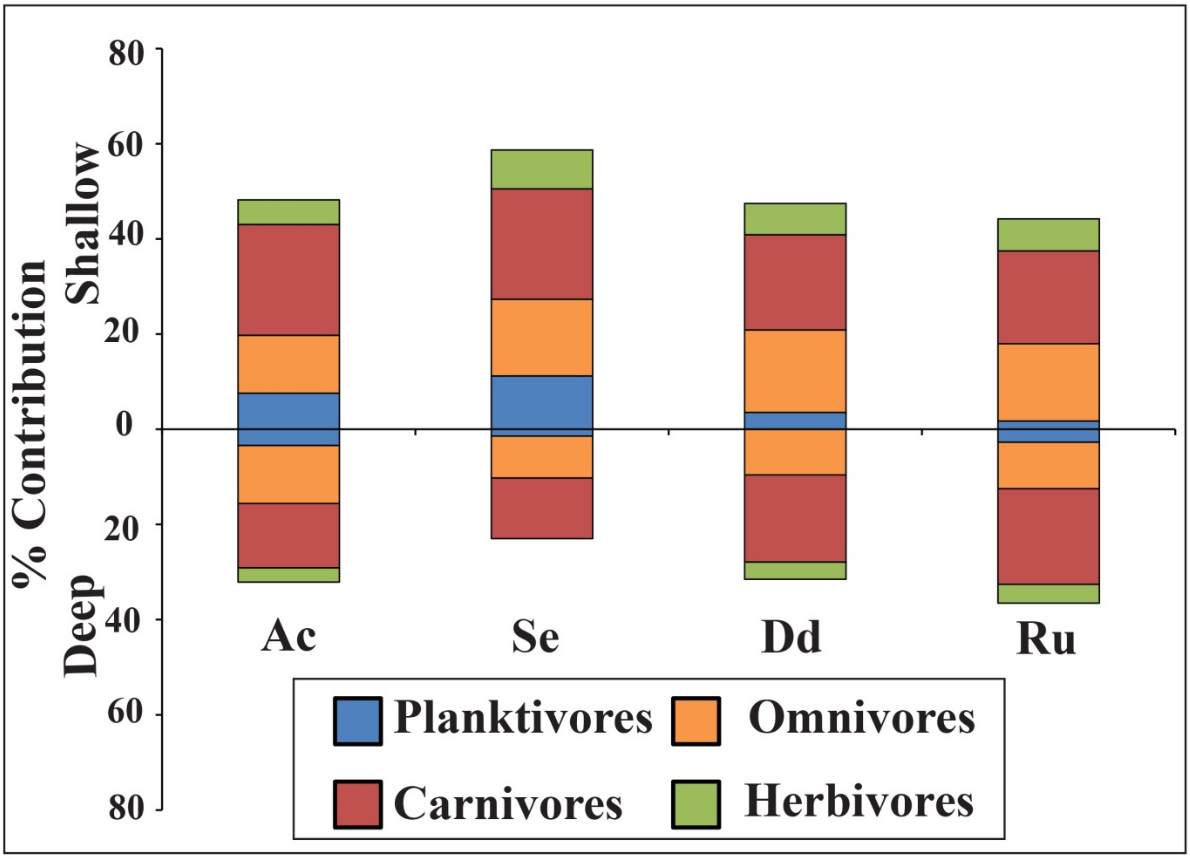


Figure 4-3 Percentage contribution of different feeding guilds of fish to shallow and deep patch reef communities. The contribution was calculated from the results of a SIMPER analysis using the species in the communities that made up 80% cumulatively. The different bars represent the different habitat types (Ac = *Acropora elsyi*, Se = *Seriatopora histrix*, Dd = Dead coral, Ru = Rubble) and the different feeding guilds are represented by colour.

Patterns of diversity and evenness varied with depth, although the specific trends varied between the two sites (Table 4-2). At site one, the most species rich and diverse communities were on shallow patch reefs and the most even communities were on mid patch reefs. Site two, on the other hand, showed some different patterns, where mid patch reefs had the most diverse communities and deep patch reefs had the most species rich and even communities. There was a strong interaction between site and depth (Table 4-1).

Table 4-2 Diversity, species richness and evenness for fish communities on patch reefs at each site and depth in the study.

Index	Shallow site 1	Mid site 1	Deep site 1
Number of species	89	65	65
Diversity	3.477	3.217	2.989
Evenness	0.3635	0.3839	0.3058
Index	**Shallow site 2**	**Mid site 2**	**Deep site 2**
Number of species	66	72	58
Diversity	3.25	3.118	3.272
Evenness	0.3909	0.3138	0.4545

4.4.2 Depth and habitat patterns for individual species

Individual species showed a variety of patterns with both depth and habitat. The most abundant non-coral associated species in the study displayed two different overall patterns (Figure 4-4). Six species showed a significant pattern with depth. *Acanthurus grammoptilus* was significantly more abundant at deep patch reefs compared to mid and shallow patch reefs (Figure 4-4, Table 4-3). Other species were more abundant deeper, including *P. amboinensis* and *C. boenak*, which were both significantly more abundant on the mid and deep patch reefs (Figure 4-4, Table 4-3). *Halichoeres richmondi* was significantly most abundant on the mid patch reefs (Figure 4-4, Table 4-3). Two species showed significantly higher abundances at shallow and mid patch reefs. These were *P. simsiang* and *L. gibbus* (Figure 4-4, Table 4-3). Finally, three species showed significant patterns with both depth and habitat. *C. punctatus* was significantly more abundant on deep patch reefs and also on *Acropora* patch reefs (Figure 4-4, Table 4-3). *H. melanurus* had significantly higher abundances at mid and shallow patch reefs and on *Acropora* and *Seriatopora* patch reefs (Figure 4-4, Table 4-3). Finally, *H. chloropterus* had significantly higher abundances on shallow patch reefs and also on *Acropora* and *Seriatopora* patch reefs (Figure 4-4, Table 4-3). No non-coral associated species were observed to occur solely on shallow patch reefs.

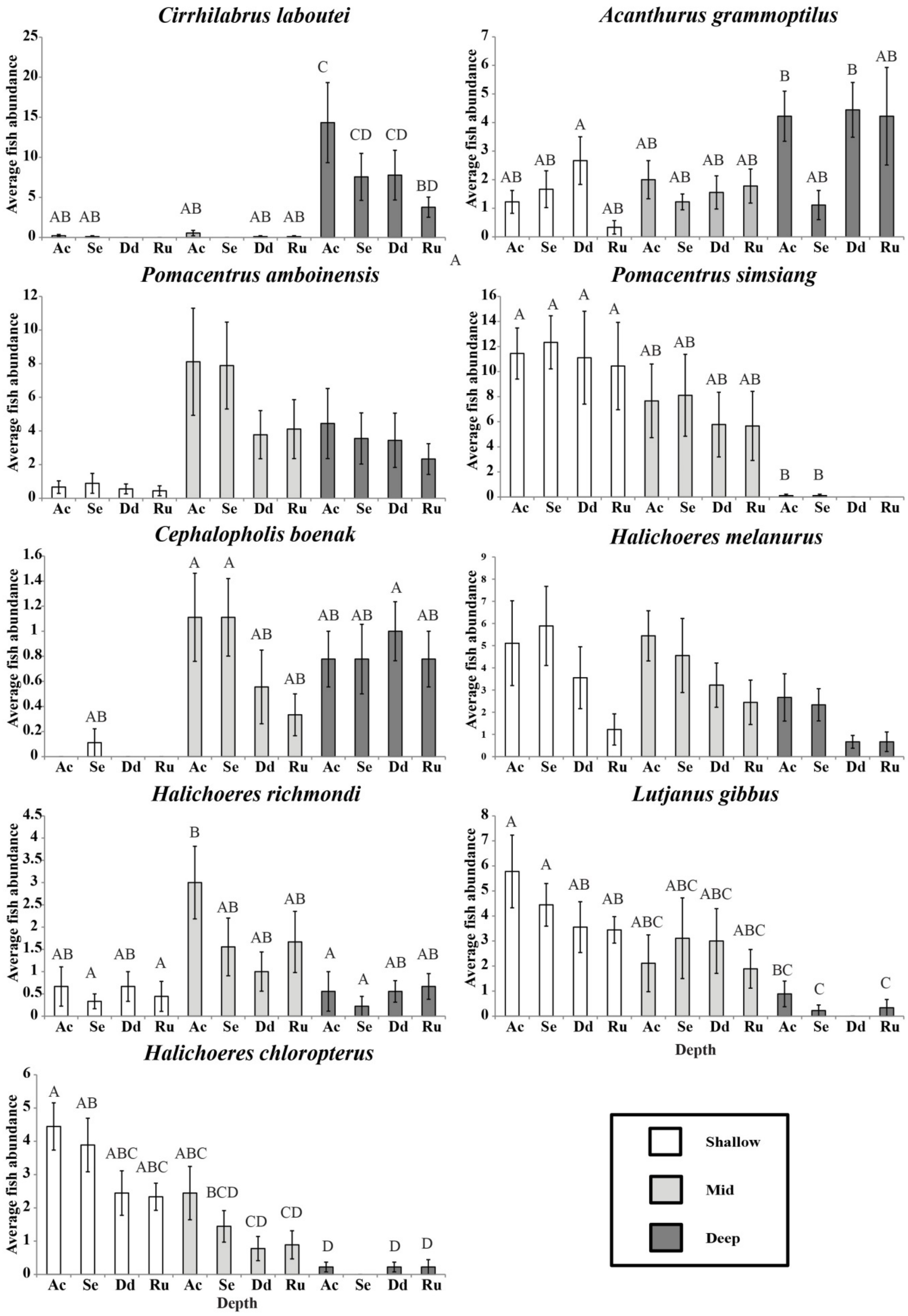


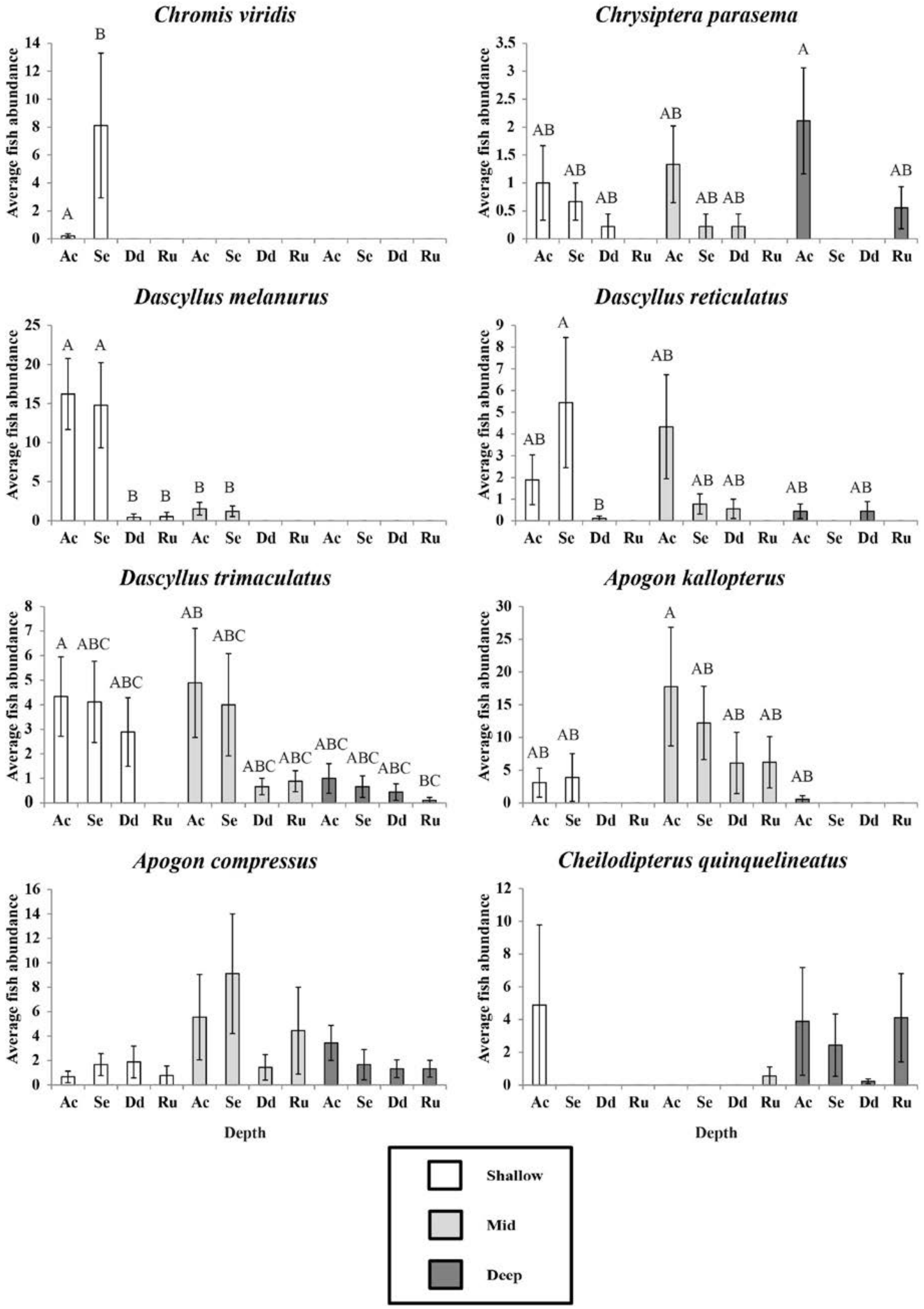
Figure 4-4 Average observed abundance of the most common non-coral associated species observed on patch reefs. Error bars indicate standard error and letters show the results of post-hoc Tukey's HSD tests carried out on 2-way ANOVA tests (**Table 4-3**). Plots without letters indicate that post-hoc tests found no real differences.

Table 4-3 Results of 2-way ANOVA tests carried out on abundance data for the most common non-coral associated species observed on our patch reefs (Figure 4-4). Significant results are highlighted in bold text.

	df	SS	MS	F	P
Cirrhilabrus punctatus					
Depth	**2**	**122.670**	**61.335**	**65.319**	**0.000**
Habitat	**3**	**8.488**	**2.829**	**3.013**	**0.034**
Depth x Habitat	6	7.092	1.182	1.259	0.284
Error	96	90.145	0.939		
Acanthurus gammoptilus					
Depth	**2**	**9.016**	**4.508**	**5.705**	**0.005**
Habitat	3	5.454	1.818	2.301	0.082
Depth x Habitat	6	9.202	1.534	1.941	0.082
Error	96	75.851	0.790		
Pomacentrus amboinensis					
Depth	**2**	**36.877**	**18.438**	**10.550**	**0.000**
Habitat	3	3.664	1.221	0.699	0.555
Depth x Habitat	6	2.676	0.446	0.255	0.956
Error	96	167.785	1.748		
Pomacentrus simsiang					
Depth	**2**	**111.188**	**55.594**	**40.571**	**0.000**
Habitat	3	1.402	0.467	0.341	0.796
Depth x Habitat	6	0.518	0.086	0.063	0.999
Error	96	131.547	1.370		
Cephalopholis boenak					
Depth	**2**	**10.298**	**5.149**	**20.884**	**0.000**
Habitat	3	0.603	0.201	0.816	0.488
Depth x Habitat	6	1.715	0.286	1.159	0.335
Error	96	23.668	0.247		
Halichoeres melanurus					
Depth	**2**	**12.841**	**6.421**	**5.001**	**0.009**
Habitat	**3**	**17.751**	**5.917**	**4.609**	**0.005**
Depth x Habitat	6	2.126	0.354	0.276	0.947
Error	96	123.253	1.284		
Halichoeres richmondi					
Depth	**2**	**9.950**	**4.975**	**9.950**	**0.000**
Habitat	3	1.208	0.403	0.805	0.494
Depth x Habitat	6	3.301	0.550	1.100	0.368
Error	96	47.998	0.500		
Lutjanus gibbus					
Depth	**2**	**54.169**	**27.084**	**32.599**	**0.000**
Habitat	3	1.197	0.399	0.480	0.697
Depth x Habitat	6	1.830	0.305	0.367	0.898
Error	96	79.760	0.831		
Halichoeres chloropterus					
Depth	**2**	**42.428**	**21.214**	**56.314**	**0.000**
Habitat	**3**	**3.851**	**1.284**	**3.408**	**0.021**

Depth x Habitat	6	2.298	0.383	1.017	0.419
Error	96	36.164	0.377		

The most abundant coral-associated fish species also showed a variety of patterns with depth and habitat (Figure 4-5). Two species showed a significant relationship with habitat. These were *Chrysiptera arnarzae* (formerly reported as *Chrysiptera parasema*) and *Dascyllus reticulatus*. *C. arnarzae* was significantly more abundant on *Acropora* patch reefs and *D. reticulatus* on *Seriatopora* patch reefs (Figure 4-5, Table 4-4). Two coral-dependent species showed significant depth-related patterns, *Apogon kallopterus* was more abundant on mid patch reefs and *Cheilodipterus quinquelineatus* was most abundant on the deep patch reefs (Figure 4-5, Table 4-4). *Dascyllus trimaculatus* showed significant patterns with both depth and habitat, being more abundant on shallow and mid patch reefs as well as on *Acropora* and *Seriatopora* patch reefs (Figure 4-5, Table 4-4). There were significant interactions between depth and habitat for *Chromis viridis* and *Dascyllus melanurus*. *C. viridis* was only present on *Acropora* and *Seriatopora* patch reefs at 5m, and was most abundant on the *Seriatopora* patch reefs at that depth (Figure 4-5, Table 4-4). *D. melanurus* was only present at shallow and mid depths, although on shallow patch reefs it was present on all patch reef habitats whereas at the mid depth it was only present on *Acropora* and *Seriatopora* patch reefs (Figure 4-5, Table 4-4). It was most abundant on *Acropora* and *Seriatopora* patch reefs at 5m. *Apogon compressus* showed no significant patterns with either depth or habitat (Figure 4-5, Table 4-4).


Chromis viridis

Chrysiptera parasema

Dascyllus melanurus

Dascyllus reticulatus

Dascyllus trimaculatus

Apogon kallopterus

Apogon compressus

Cheilodipterus quinquelineatus

Figure 4-5 Average observed abundance of the most common coral associated species observed on patch reefs. Error bars indicate standard error and letters show the results of post-hoc Tukey's HSD tests carried out on 2-way ANOVA tests (**Table 4-4**). Plots without letters indicate that post-hoc tests found no real differences.

Table 4-4 Results of 2-way ANOVA tests on abundance data of the most common coral associated species observed on our patch reefs (**Figure 4-5**). Significant results are highlighted in bold text.

	df	SS	MS	F	P
Chromis viridis					
Depth	**2**	**4.691**	**2.346**	**4.246**	**0.017**
Habitat	**3**	**4.975**	**1.658**	**3.002**	**0.034**
Depth x Habitat	**6**	**9.950**	**1.658**	**3.002**	**0.010**
Error	96	53.038	0.552		
Chrysiptera arnarzae					
Depth	2	0.076	0.038	0.098	0.907
Habitat	**3**	**7.341**	**2.447**	**6.325**	**0.001**
Depth x Habitat	6	2.877	0.479	1.239	0.293
Error	96	37.141	0.387		
Dascyllus melanurus					
Depth	**2**	**69.439**	**34.720**	**39.421**	**0.000**
Habitat	**3**	**47.626**	**15.875**	**18.025**	**0.000**
Depth x Habitat	**6**	**52.103**	**8.684**	**9.860**	**0.000**
Error	96	84.552	0.881		
Dascyllus reticulatus					
Depth	2	4.802	2.401	2.870	0.062
Habitat	**3**	**11.085**	**3.695**	**4.417**	**0.006**
Depth x Habitat	6	10.717	1.786	2.135	0.056
Error	96	80.304	0.837		
Dascyllus trimaculatus					
Depth	**2**	**12.879**	**6.440**	**6.208**	**0.003**
Habitat	**3**	**19.459**	**6.486**	**6.253**	**0.001**
Depth x Habitat	6	7.755	1.292	1.246	0.290
Error	96	99.584	1.037		
Apogon kallopterus					
Depth	**2**	**65.458**	**32.729**	**10.343**	**0.000**
Habitat	3	11.222	3.741	1.182	0.321
Depth x Habitat	6	3.797	0.633	0.200	0.976
Error	96	303.772	3.164		
Apogon compressus					
Depth	2	6.644	3.322	1.554	0.217
Habitat	3	3.827	1.276	0.597	0.619
Depth x Habitat	6	8.217	1.370	0.641	0.697
Error	96	205.185	2.137		
Cheiloipterus quinquelineatus					
Depth	**2**	**9.779**	**4.889**	**4.084**	**0.020**
Habitat	3	3.909	1.303	1.088	0.358
Depth x Habitat	6	4.399	0.733	0.612	0.720
Error	96	114.937	1.197		

4.5 Discussion

The results of this study further support the conclusion that there are habitat independent and habitat dependent effects of depth on fish communities on coral reefs. In this case, habitat independent and site effects accounted for most of the variation, both in species composition and feeding guild structure. There was a strong interaction between depth and site, with similar community structures developing on the different habitat types. Closer inspection of the individual species patterns showed that while abundances of most species varied with depth on the same habitat types, coral-associated species clearly differed in abundance across the live coral and dead substrata used in the experiment. There was a variety in the distribution patterns of common species with some species showing strong depth patterns, some habitat patterns and some an interaction between depth and habitat. Overall, this suggests a multi-factorial explanation of depth-related changes in fish assemblages and the need to focus on environmental factors other than benthic habitat structure.

The strong patterns in community structure with depth further supports the idea that depth is an important factor in distribution of reef fish, with effects sometimes independent of habitat structure (Srinivasan 2003). Other studies have also shown the importance of depth. For example, Brokovich et al. (2008) found that patterns in the fish community along a gradient from 0-60m were driven by changes in depth and branching coral cover. Our study highlights, to some extent, the different influences of depth and habitat. Depth appears to have much more of an effect compared to habitat in our study which may suggest that there is an effect of depth that is separate from changes in habitat. It also suggests that, in terms of reef fish community structure, habitat changes may not be as important as once thought. Due to the complex nature of depth gradients, however, it is difficult to say exactly what may be driving these depth patterns. Many physical and biological factors can be associated with depth gradients as substantial changes in the physical and biotic environment can occur over distances of a few metres (Brokovich et al. 2008; Gonzalez-Sanson et al. 2009). Deeper habitats will have lower levels of light, water motion, temperature and increased pressure. It is not well known what the effects of living outside preferred depths might have on a fish species and would need to be investigated further as this may have a part to play in settlement choices.

Biological factors may also have played a part in the results of this study. Competition between species has been shown to influence distribution and settlement of reef fish. This is particularly true for damselfish, which make up a significant part of the communities on the patch reefs (Bay et al. 2001; Ben-Tzvi et al. 2009). Bean et al. (2001) showed that for species of triggerfish the more competitively dominant species were more abundant at certain depths. Once particular species have established themselves, this may also affect the community structure as it has been shown that some juveniles will be attracted to conspecific species (Coppock et al. 2013). Predation is another process that can influence communities of fish (Wellington 1992; Carr and Hixon 1995). This could be one factor in our study as the abundance of predatory fish, such as *Cephalopholis boenak*, was higher on the mid and deeper patch reefs compared with the shallow patch reefs. It is possible that a combination of many of these factors may be driving the depth patterns seen in this study, which further advocates for depth being a complex factor that needs further study.

Habitat still had a significant effect on the fish communities, although unexpectedly, this was not as substantial as the effect of depth or site. The significant result further supports previous studies that show that changes in habitat and complexity can affect fish communities (Friedlander and Parrish 1998; Gratwicke and Speight 2005; Garpe et al. 2006; Wilson et al. 2006; Bonin et al. 2011; Graham and Nash 2013; Graham et al. 2015). Habitat had an effect on the distribution of six of the eight most common coral associated species. Many coral-associated species are quite specialised in their habitat use and so it is logical that their distribution would be heavily influenced by the abundance of their preferred habitat. For example, the damselfish *Chrysiptera arnarzae* (formerly reported as *Chrysiptera parasema*) had significantly higher abundances on *Acropora elsyi* patch reefs. This species has been shown to have a specialised habitat preference in Kimbe Bay (Bonin et al. 2011), but showed some significant depth effects as well, with most being more abundant on the shallow patch reefs. This supports previous studies, in that there are often more coral related species and habitat specialists at shallow depths compared to deeper depths (Chabanet et al. 1997; Srinivasan 2003; Brokovich et al 2008). Coral species need particular habitat conditions for growth and survival and often show strong zonation patterns in relation to many physical variables including light, substrate and water motion (Done 1982; Russ 1984; McGehee 1994; Acosta et al. 2015; Muir et al. 2015). For example, dramatic gradients in water motion occur across reefs with depth and flow mediated processes can have an important influence on population level performance of reef coral species (Madin et al. 2006; Madin et al. 2012).

Depth-related factors appeared to be much more important than habitat for the most abundant non-coral associated species. Six out of the nine most abundant species, showed a significant relationship with depth alone and two more with both depth and habitat. This is probably a result of non-coral-associated species often being more generalist in their habitat use and more mobile. The depth distributions of the most common non-coral-associated species were mixed, with some being more abundant shallow, others deep and some being more generalist in terms of their depth preferences. In the presence of preferred habitat and if conditions are stable, specialists will normally outcompete generalists (Emlen and Oring 1977; Futuyma and Moreno 1988; Pratchett et al. 2013), which may be a factor in why more of the coral associated species had higher abundances on shallow patch reefs and more of the non-coral associated species had higher abundances on deeper patch reefs. In general, deeper reef habitats are often more heterogeneous and variable and hence are more suitable for more generalist species (Bean et al. 2002; Brokovich et al. 2008). The fact that the presence of live coral habitat was kept the same throughout the depths of the study yet coral specialists were still more abundant shallow might suggest the importance of other physical factors and post settlement processes in driving their distribution (Srinivisan 2003).

The contribution of different feeding guilds of fish towards the community structure showed changes between shallow and deep patch reefs, and little difference among habitat types. Again, this further supports the idea that there is an effect of depth-related factors that are independent from changes in habitat structure. Shallow patch reefs had more herbivores and planktivores than deep patch reefs. Herbivores are often more abundant at shallower depths and the process of herbivory decreases with depth (Nemeth and Appledoom 2009; Brokovich et al. 2010; Kopp et al. 2012; Bejarano et al. 2014). Shallow water habitats, such as reef crests, can host the greatest algal productivity (Russ 2003; Fox and Bellwood 2007; Brokovich et al. 2010). Plankton is often structured in the water column by depth, which may influence specie's preferred depth (Leis 1986; Gutierrez 1998; Hendriks et al. 2001; Heubert et al. 2010; Irisson et al. 2010). Deeper water might be less desirable for planktivores due to lower light levels, as less light could make plankton harder to see (Irisson et al. 2010). Water motion also varies at different depths and can in turn affect the fish community present in terms of their ability to swim in strong currents (Fulton and Bellwood 2005; Fulton et al. 2005).

As well as the effects of depth and habitat on the reef fish communities present there was also a strong site effect. There were a few differences in the physical environmental conditions that could have driven the effect of site on reef fish communities. Site 1 was a classic exposed fore reef environment with a mostly sandy bottom and clearer water, whereas site 2 was a sheltered back reef environment where the water was less clear and the bottom was siltier and muddier. These differences in the sites are most likely driven by the presence of a coconut plantation on Garua Island close to site 2. Run off from the plantation could have had an effect on the community of fish present. Sediment and run off from agriculture has been shown to directly affect reef fish by reducing foraging ability, growth and condition, as well as affecting them indirectly by reducing abundance and diversity through habitat loss (Wenger et al. 2012; Wenger at al. 2013). Despite these differences between sites there were still strong and consistent depth patterns in reef fish communities at both sites, highlighting the important effects that depth can have on community structure.

Overall, this study shows that depth can have a significant impact on reef fish communities independently from habitat. Further study is needed to tease out the different effects of the many physical and biological environmental factors that can co-vary with depth. I also found that small-scale physical differences between sites played an important part in shaping the communities that developed on patch reefs and that this site effect showed a significant interaction with depth. This suggests that biophysical environmental changes could be an important part of the patterns seen along depth gradients. Habitat did influence the communities present, but it may not be as important in terms of depth patterns as once thought. This is important in understanding reef fish ecology and in particular the growing interest in depth and deep coral reefs as a refuge. Many impacts facing reefs today are concentrated on shallow water environments, highlighting the need to understand relationships of reef fish with depth (Bongaerts et al. 2010; Kahng et al. 2010; Bridge et al. 2013). Future studies into the direct effects of these physical environmental changes on reef fish communities, as well as the costs of living outside of preferred depths ranges, can help to further knowledge into the concept of depth as a refuge.

Chapter 5. Influence of disturbance and depth on the depth-distributions, demography and condition of coral reef fishes

5.1 Summary

It has been hypothesized that coral reef fishes may be able to move into deeper water in response to declining coral cover on shallow reefs. If so, species should be able to shift distributions downward, while maintaining abundance on disturbed reefs. In addition, there should be no adverse costs to being in deeper water in terms of increased mortality, slower growth and reduced condition. Here I tested these predictions using two different approaches. First, I compared distribution and abundance of a range of species on reefs with high and low coral cover in shallow water. Second, I conducted an experiment in which individuals of three focal damselfish species were transplanted to three different depths to test the effects of being within and below normal depth ranges on demographic rates and condition. The test species included two species that naturally have shallow distributions, one a coral associated species and one a non-coral associated species, and a third species that has a wide depth distribution. In general, most species showed no changes in their depth distributions on disturbed reefs, but were less abundant on reefs with lower coral cover on the reef crest. Some species were able to exploit new space and were more abundant on the lower coral cover reefs. Only one species (*Chromis ternatensis*) showed a change in its distribution from being abundant in shallow water to having a distribution of increasing abundance with depth. The transplant experiment showed no consistent depth-related patterns in mortality, however, overall body condition decreased with depth and growth was higher on the deepest patch reefs. This study suggests the majority of species may have a limited capacity to move into deeper water following shallow water disturbances and those that can, may suffer from the reduced effects of condition. The underlying mechanisms for faster growth in deep water are unknown, but the results suggest that environmental pressures that cause changes in depth distributions are likely to have unexpected demographic consequences.

5.2 Introduction

Coral reefs are subject to natural disturbance and an increasing array of anthropogenic disturbances. Many of these impacts more heavily affect shallow water environments (Bongaerts et al. 2010; Kahng et al. 2010; Bridge et al. 2013), and reefs in deeper water have been shown to recover from disturbance more readily (Graham et al. 2015). This may afford some species a depth refuge, whereby species with wider depth distributions can survive impacts in shallow waters because individuals living deeper can act as a source of juveniles or because deeper individuals may face less of an impact or escape impact altogether (Kahng et al. 2010). The potential for depth to be a refuge for corals follows from the reduced effects of disturbances such as cyclones, thermal bleaching, pollution and run off at depths greater than 10m, although these reduced impacts are normally seen more commonly at depths greater than 25m (Bak et al. 2005; Slattery et al. 2011; Bridge et al. 2013). With many coral reef fish showing close associations with corals, there is potential for depth to act as a refuge for reef-associated fishes (Coker et al. 2014). However, this is likely to depend on the species, with many species showing narrow distributions in shallow water, while others have wider depth ranges (Bean et al. 2002; Brokovich et al. 2008; Jankowski et al. 2015). If depth is to provide a refuge for shallow water species, they must firstly be able to move into deeper water, and secondly, show no adverse negative effects as a consequence. At present, our understanding of these critical factors is limited.

Differential impacts of disturbance on shallow water coral reefs have been well-documented (Woodley 1981; Hoeksema 1991; Bak et al. 2005; Slattery et al. 2011; Bridge et al. 2013). However, the effects of coral decline on depth distributions and abundance have seldom been documented. While we know coral loss has a major impact on the abundance and diversity of fishes occupying the disturbed depth strata (Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006; Wilson et al. 2008b; Coker et al. 2014), it is unknown whether fish move into deeper water, and if so, whether abundances are maintained or reduced. Clearly, natural changes in coral cover with depth can play an important role in limiting depth distributions (Bell and Galzin 1984; Chabanet et al 1997; Garpe and Ohman 2003; Srinivasan 2003). For example, Brokovich et al. (2008) found increasing depth and decreasing cover of branching coral affected changes in the communities of reef fish in the Red Sea. However, experiments have shown that even if preferred coral habitat is available in deeper water, fish cannot necessarily extend their depth distributions to occupy it because species still showed clear depth preferences in their recruitment and both growth and survival were decreased outside of these preferred depths (Srinivasan 2003). Therefore it may be important to transplant species to depths at the extremes as well as outside of their natural depth distribution in order to see what effects fish face if they extend their depth use. To date, no study has examined or compared changes in depth distributions of reef fishes on shallow disturbed and undisturbed reefs, or followed changes in fish distribution and abundance following such disturbances.

The depth refuge hypothesis is founded on the premise that even if fish can move into deeper water there will be minimal lethal or sub-lethal consequences. Depth-related changes in recruitment, mortality and growth have been documented (Shulman 1985; Srinivasan 2003; Jordan et al. 2012). Transplant experiments also show that species can suffer severe increases in mortality and declining growth when transplanted beyond their normal depth range (Srinivasan 2003). These constraints appear to be strongest for shallow water species. Natural patterns in body condition along depth gradients were examined by Hoey et al. (2007), who found that as depth increased, growth rates decreased and there was a decrease in condition and gonad weight in female fish. However, the sub-lethal costs of moving or being transplanted into deeper water have not been investigated. It would be predicted that shallow water specialists may suffer in terms of increased mortality, reduced growth and declining condition in deeper water, while depth generalists should be able to maintain condition over a wide depth range.

The aims of this study were to further investigate potential costs to fish of living outside of preferred depth ranges by measuring how survival, growth and general body condition varied with depth in species with shallow depth preferences as well as in species with more widespread depth distributions. Specific hypotheses tested in the study were 1) that shallow preference species show decreases in survival, growth and body condition with increasing depth, 2) species with more wide spread depth ranges show little difference in survival, growth and body condition with depth, 3) shallow preference species do not shift their depth ranges deeper on reefs with lower coral cover at shallow depths. By investigating these effects of depth and how it may relate to species potential to use depth as a refuge from impacts, we aimed to identify which species may be at risk from the ever increasing impacts on reefs as well as how reef fish communities may change in the future.

5.3 Methods

5.3.1 Study site and species

Data was collected between the 17th of March and the 16th of May 2014 in Kimbe Bay, on the Bismarck Sea coastline of the Island of New Britain, Papua New Guinea (5°26'15.66''S, 150°05'06.75''E) . Surveys were carried out on 10 small fringing reefs within 1km of the coast near Mahonia Na Dari Marine Conservation and Research Centre (Figure 2-1). The transplant experiment was implemented using the same patch reefs from Chapter 4 (once cleared of fish) located around the small uninhabited coastal island of Schumann Island (Site 1, Figure 4-1) (5°29'33.46''S, 150°09'35.82''E).

5.3.2 Distribution and abundance on disturbed reefs

In order to see if shallow fish can potentially extend their depth range deeper from their preferred depths we surveyed fish communities on reefs with higher and lower coral cover on the crest. Communities were surveyed at four depths (2m, 5m, 8m, 12m) on 10 different reefs with five reefs having higher coral cover on the reef crest and five having lower coral cover on the reef crest. Surveys were carried out by underwater visual census using 50x2m belt transects at each depth. All fish observed along transects were counted and identified to species level and the same observer carried out fish surveys on each transect to keep fish identification consistent and reduce observer error.

The survey data was first analysed at a community level by plotting an nMDS plot using a Bray Curtis similarity matrix. The patterns on the nMDS plot were tested statistically with a 2-way ANOSIM. A SIMPER analysis was then carried out to see which species were the most common for communities at 2m on the reefs with a higher coral cover on the crest, which are assumed to have been less impacted. We analysed these species patterns of depth distribution by plotting their average abundances at the different depths and testing these patterns using 2-way ANOVAs with post-hoc Tukey's HSD tests.

5.3.3 Transplant experiment

Patch reefs with a base diameter of 1m were built at three different depths (3-5m, 8-10m, 18-20m) on the sand flats adjacent to Schumann Island. There were 10 patch reefs at each depth and all patch reefs had coral habitat made from *Acropora elseyi*. This species was chosen because it is abundant in the local area and occurs throughout the depths used in the experiment. Patch reefs were built a minimum of 10m away from any local reefs and other patch reefs. Juveniles of three species of damselfish were collected from local reefs between the depths of 2-8m using clove oil and hand nets. These three species were *Dascyllus melanurus* (a coral-associated species with a shallow depth range), *Dascyllus reticulatus* (a coral-associated species with a wide depth range) and *Pomacentrus simsiang* (a non-coral associated species with a shallow depth range). Once collected all individuals were tagged using elastomer tags and measured. A total of 10 individuals of each species were placed on each patch reef. Fish were left on the patch reefs for a period of 6-7 weeks, during which the patch reefs were visited every 3 days and new settlers and predators were removed. The remaining juveniles were then recollected and re-measured to record growth and weighed using scales (± 0.001g). They were then euthanized using a high dose of clove oil and the liver from each was dissected and preserved in 4% phosphate buffered formaldehyde so they could be used to assess overall body condition.

The condition of fish used in the experiment was assessed using liver tissues from each individual. Hepatocyte density as well as hepatocyte vacuole density was measured giving an indication of glycogen and lipid stores in the liver. Fish store lipids and glycogen within cytoplasm of hepatocytes (Storch and Juario 1983; Ostazewska et al. 2005). Studies have demonstrated the size and density of hepatocytes respond to variations in energy demands and diet and that vacuolation was directly proportional to liver lipid content in a tropical butterflyfish (Storch and Juario 1983; Pratchett et al. 2004; Ostazewska et al. 2005).Therefore, a fish with low hepatocyte density and high vacuolation would indicate higher lipid and glycogen storage and hence better body condition. Liver tissues were processed for histology using standard histological techniques. The whole liver was embedded in paraffin wax, thin sectioned in the sagittal plane at 5µm and stained using Mayer's Haematoxylin and Eosin stains. All slides were analysed using a high-power microscope with x400 magnification and photos were taken of each thin section. These photos were then analysed using the program ImageJ (V 1.84) (Rasband 2014). To measure the number of hepatocytes a grid was placed over the image and hepatocytes counted in three random 40 x 40 µm quadrats. With three quadrats sampled per thin section an average of nine counts per individual was calculated. Vacuole density was measured using a Wiebel 42-point system in which vacuoles at intersecting points were counted and density was given as a percentage of the 42 points used. This was done for each thin section giving an average density calculated from three estimates of vacuole density per individual. As well as assessing condition using liver tissues, I also calculated a Fulton's condition index (K = wet weight/standard length3) for each species at each of the different depths to see if fish were heavier or lighter than expected for their length.

Survival in the study species were analysed by calculating the percentage of fish that survived the entire experiment and were collected at the end. It was assumed that those individuals that were not re-captured had died. Differences were then tested using a Chi-squared test of homogeneity. Growth was calculated as the average change in standard length between the start and end of the experiment. The measures of body condition (hepatocytes, vacuoles and Fulton's condition index), growth (standard length) and weight were then tested statistically using one-way ANOVAs and statistical differences were tested further using Tukey's HSD post-hoc tests. Assumptions of homogeneity and normality were assessed using residual analysis.

5.4 Results

5.4.1 Distribution on disturbed and undisturbed reefs

Reef fish communities showed significant differences between reefs with higher or lower coral cover on the reef crest (ANOSIM, R = 0.440, p = 0.001), as well as significant differences between depths (ANOSIM, R = 0.557, p = 0.001) (Figure 5-1). The most common species surveyed on higher coral cover reefs at 2m, according to a SIMPER analysis, were *P. moluccensis, T. lunare, C. ternatensis, P.*

adelus and *P. aurifrons*. These species showed a variety of responses to the reef crest having lower coral cover, in term of their depth distributions (Figure 5-2). Some species, such as *P. moluccensis* and *T. lunare*, showed that their distributions did not change on reefs with lower coral cover at the reef crest, but instead showed a decline in abundance with depth. The patterns with depth and coral cover at the crest were significant for both *P. moluccensis* (2-way ANOVA, F = 17.051, df = 3, p = < 0.001and 2-way ANOVA, F = 6.907, df = 1, p = 0.014) and *T. lunare* (2-way ANOVA, F = 5.644, df = 3, p = 0.005 and 2-way ANOVA, F = 10.072, df = 1, p = 0.005).

The only species that appeared to shift into deeper water was the damselfish *C. ternatensis*. On reefs with higher coral cover on the crest it was most abundant at 2m and had a variable depth distribution, but, on reefs with lower coral cover on the crest it showed a distribution where abundance increased with depth and was lowest at 2m. However, its overall abundance was lower on reefs with lower coral cover on the crest. This interaction between depth and coral cover on the crest was statistically significant (2-way ANOVA, F = 3.367, df = 3 p = 0.031). Some species were more abundant on reefs with lower coral cover on the crest such as *P. aurifrons* and *P. adelus*. *P. aurifrons* was significantly more abundant on reefs with lower coral cover on the crest than on reefs with higher coral cover on the crest (2-way ANOVA, F = 12.948, df = 1, p = 0.001). Although *P. adelus* showed a similar increase in abundance on reefs with lower coral cover on the crest, it only showed a significant pattern with depth where abundances were higher at shallow depths (2-way ANOVA, F = 44.055, df = 3, p = < 0.001).

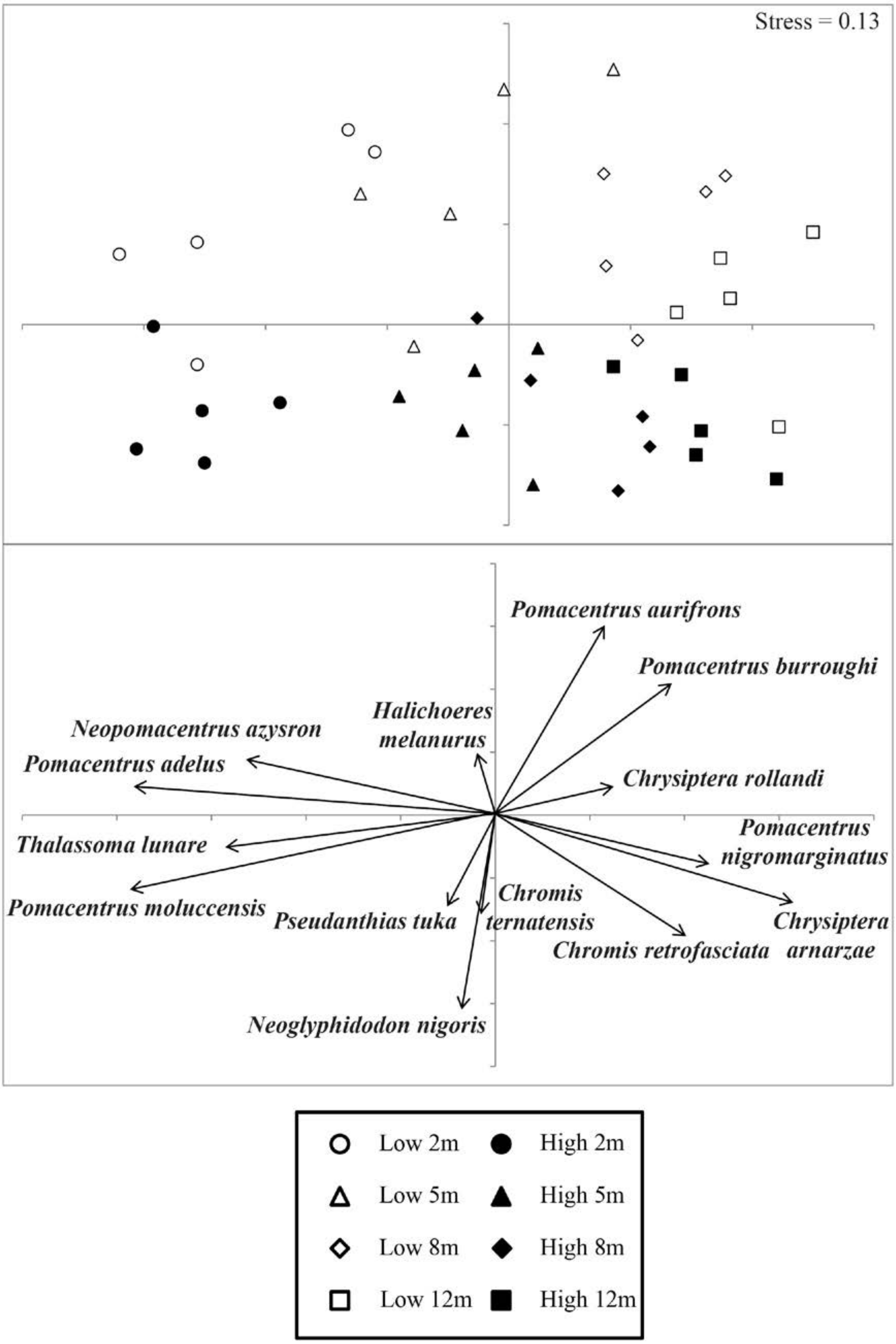


Figure 5-1 nMDS plot showing the differences between communities of fish on reefs with higher and lower coral cover on the reef crest at 4 different depths (2m, 5m, 8m, and 12m). Loading vectors show which of the most abundant species observed during surveys were representative of which reefs and depths

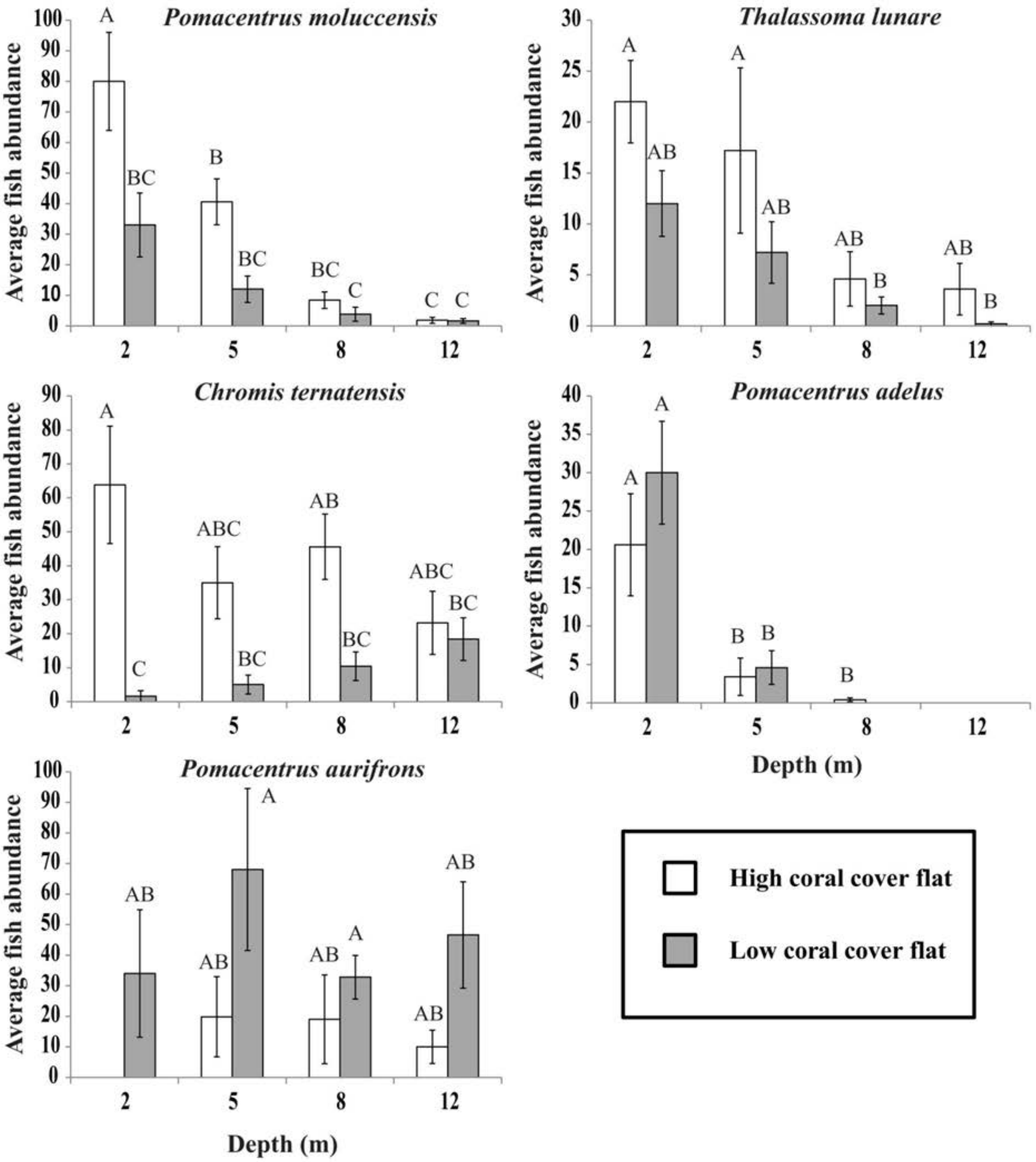


Figure 5-2 Individual abundance patterns with depth for the most representative species, according to a SIMPER analysis, at 2m on reefs surveyed. The error bars refer to standard error and letters show the results of post-hoc Tukey's HSD tests carried out on 2-way ANOVA tests

5.4.2 Transplant experiment

5.4.2.1 Survival

There were no consistent effects of depth on the survival of the three focal species (Figure 5-3). *D. melanurus* had a higher percent survival on deep patch reefs despite being a species with a shallow depth preference (Chi-squared, $X^2 = 2.134$, df = 2, p = 0.344). The other coral associated species, *D. reticulatus*, which has a much wider depth range also showed an unusual trend in that it had a lower percentage survival on deep reefs (Chi-squared, $X^2 = 1.631$, df= 2, p = 0.442). The non-coral associated species, *P. simsiang*, showed no differences between percentage survival at different depths (Chi-squared, $X^2 = 0.253$, df = 2, p = 0.881). Overall, the two shallow speices (*D. melaurus* and *P. simsiang*) had lower percentage survival than the widely distributed species (*D. reticulatus*).

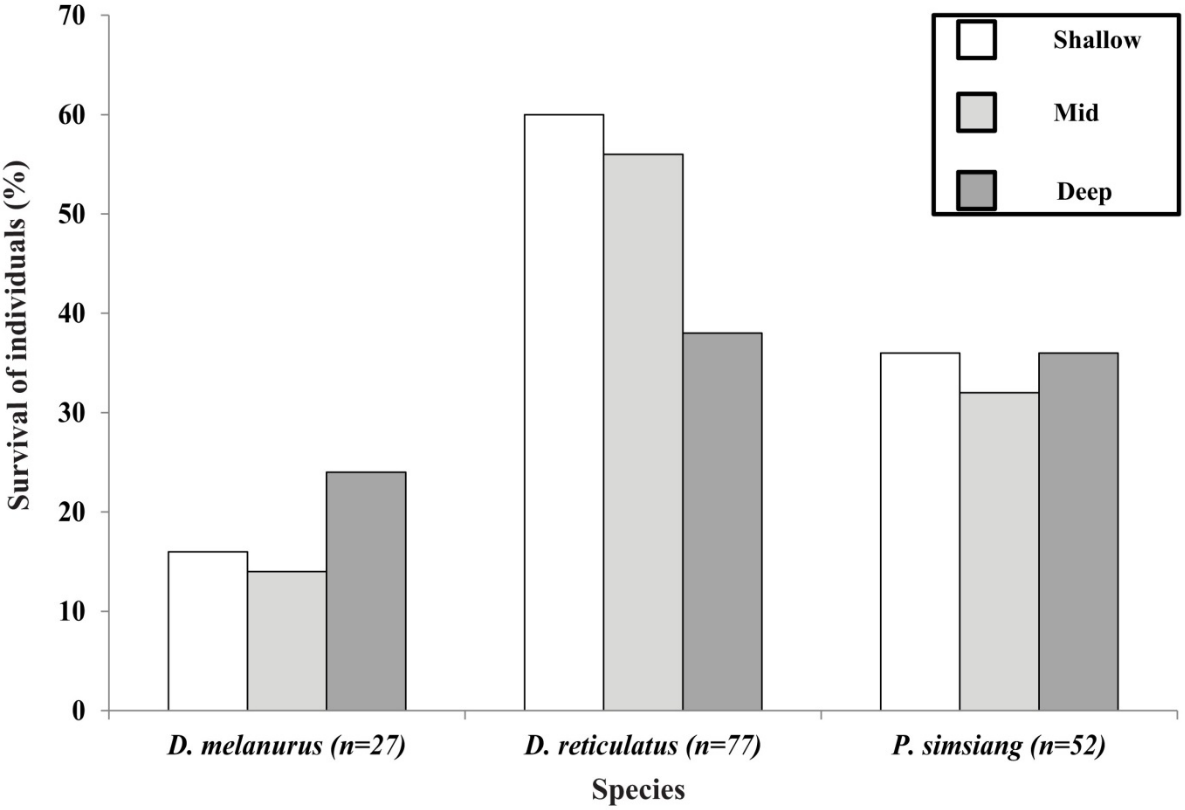


Figure 5-3 Survival of fish for the three species used in this experiment (*D. melanurus*, *D. reticulatus* and *P. simsiang*). n refers to the total number of individuals that survived for each species across all depths out of the 150 individuals that were put out on patch reefs.

5.4.2.2 Body condition

In all three species, there was increased hepatocyte density and lower vacuolation with increasing depth (Figure 5-4). In both shallow species, *D. melanurus* and *P. simsiang*, individuals on deep patch reefs had significantly higher hepatocyte densities (ANOVA, F = 6.259, df = 2, p = 0.008 and ANOVA, F = 4.905, df = 2, p = 0.012). Post-hoc tests showed these patterns were driven by the difference between individuals on shallow and deep patch reefs. Whilst *D. reticulatus* also had significantly higher hepatocyte densities in individuals on deep patch reefs (ANOVA, F = 7.029 , df = 2, p = 0.001), this pattern was driven by the difference between individuals on shallow patch reefs compared to those on mid and deep patch reefs. The trends in vacuole density were, logically, the opposite of those seen in the hepatocyte densities. The density of vacuoles in liver tissues of all three species showed a significant decrease with increased depth (*D. melanurus*: ANOVA, F = 28.264, df = 2, p = <0.001, *D. reticulatus*: ANOVA, F = 6.896, df = 2, p = 0.002, and *P. simsiang*: ANOVA, F = 27.875, df = 2, p = <0.001). In the two coral associated species, *D. melanurus* and *D. reticulatus*, these trends were driven by differences between individuals on shallow patch reefs compared to those on both mid and deep patch reefs, whereas, for the non-coral associated *P. simsiang* the main differences driving this trend were between individuals at all three depths. There was also a difference in the vacuole densities between shallow species (*D. melanurus* and *P. simsiang*) and the depth generalist species (*D. reticulatus*). In the shallow species, vacuole densities in individuals on deep patch reefs were less than half that of densities in individuals on shallow patch reefs for the shallow species. For the depth generalist species the differences were less pronounced but still significant. Trends in both hepatocyte density and liver vacuolation show that body condition in all three species was reduced significantly with depth, even for a depth generalist species. There were no significant differences with depth when looking at Fulton's condition index for any of the species studied suggesting the ratio between weight and length was not affected by depth (*D. melanurus*: ANOVA, F = 2.0193, df = 2, p = 0.158, *D. reticulatus*: ANOVA, F = 3.430, df = 2, p = 0.377, *P. simsiang*: ANOVA, F = 0.003, df = 2, p = 0.910).

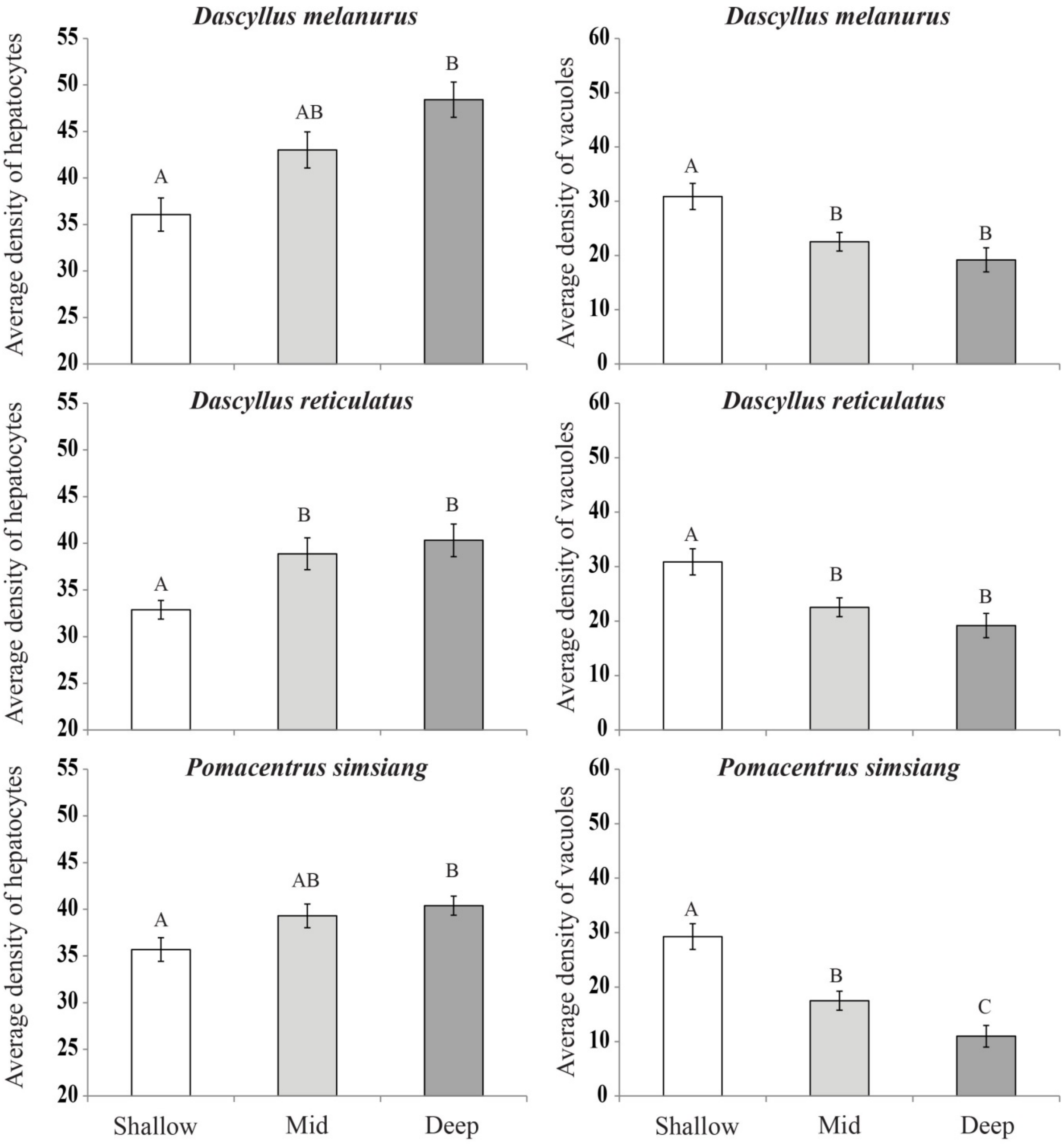


Figure 5-4 Average densities of hepatocytes and vacuoles in liver tissues for each species in the experiment relating to body condition. Error bars represent standard error and letters show the results of post-hoc Tukey's HSD tests carried out on the results of ANOVA tests.

5.4.2.3 Growth and weight

Growth in both coral associated species showed an unusual trend, with the change in standard length being significantly higher in individuals on deep patch reefs suggesting increased growth (Figure 5-5). Individuals of *D. melanurus* showed a dramatic increase in growth with standard length being more than double on deep patch reefs compared with mid and shallow patch reefs (ANOVA, F = 4.218, df = 2, p = 0.029). *D. reticulatus* also showed significantly increased growth in standard length on deep patch reefs, however the differences were not as pronounced and were driven by the difference between those on shallow patch reefs compared to those on mid and deep patch reefs (ANOVA, F = 6.930, df = 2, p = 0.002). For *P. simsiang* (the non-coral associated species) there were no significant differences in growth with depth (ANOVA, F = 0.077, df = 2, p = 0.926). Weight did not show any significant differences with depth in any of the species used in the experiment (*D. melanurus*: ANOVA, F = 2.269, df = 2, p = 0.129, *D. reticulatus*: ANOVA, F = 0.292, df = 2, p = 0.104) and *P. simsiang*: ANOVA, F = 0.012, df = 2, p = 0.989).

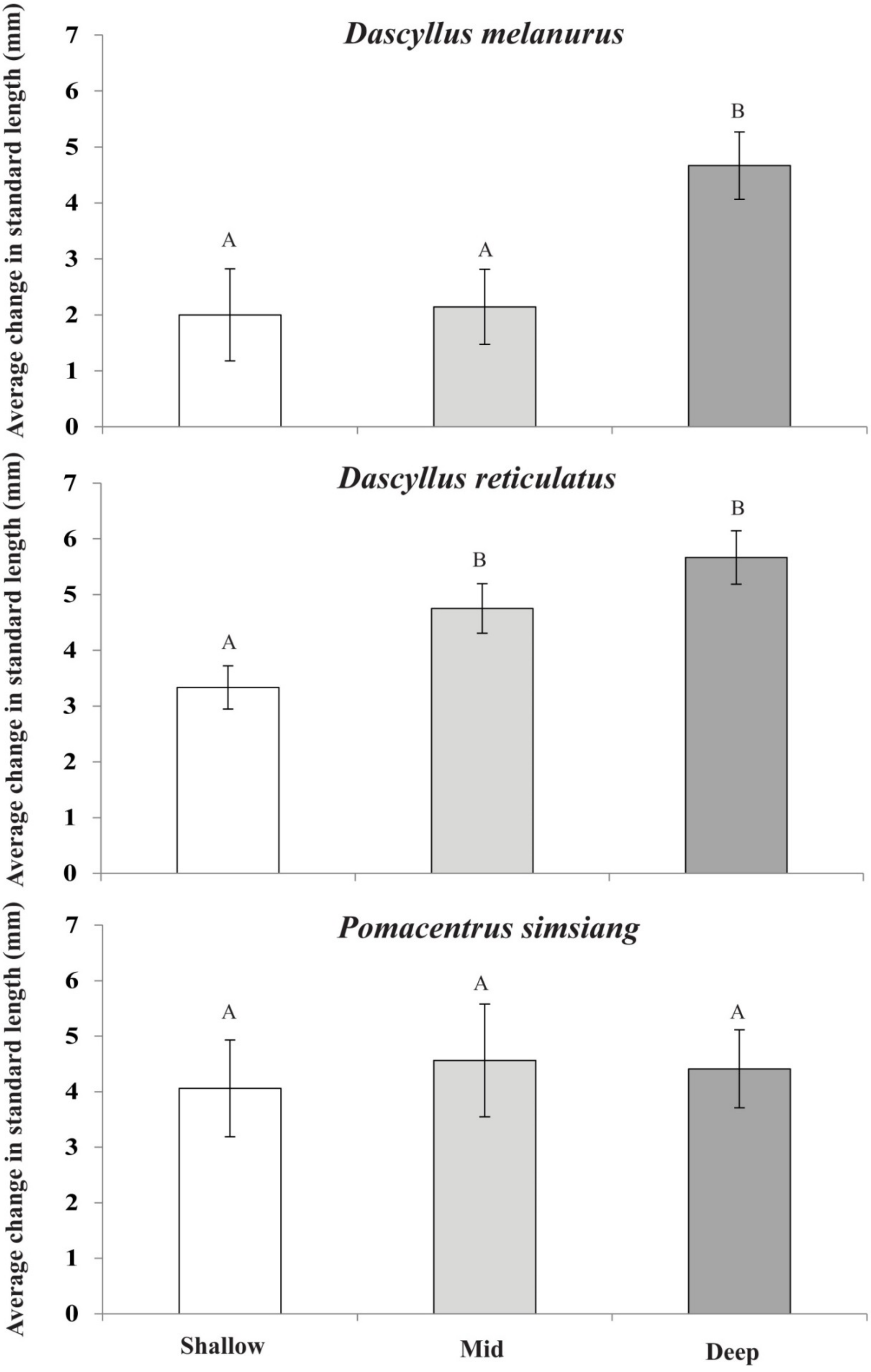


Figure 5-5 Average change in standard length of fish between the beginning and end of the experiment showing changes in growth for each species studied. Error bars represent standard error and letters show the results of post-hoc Tukey's HDS tests carried out on the results of ANOVA tests.

5.5 Discussion

The hypothesis that deeper reefs may provide a refuge for shallow water coral reef fishes following disturbance to shallow habitat was not strongly supported by this study. In general, most species showed no changes in their depth distributions on disturbed reefs, but showed lower abundance on reefs with lower coral cover on the reef crest. The one species that did shift its distribution into deeper water appeared to decline in abundance. The transplant experiment showed no consistent depth-related patterns in mortality, suggesting fish may be able to survive just as well in deeper water. However, body condition decreased with depth, suggesting fish undergoing such a shift would suffer in terms of reduced performance. The higher growth, in length, in deeper water is an unexpected anomaly, but suggests that life history strategies will be altered for species forced into deeper water. Overall, this study suggests the majority of species may have a limited capacity to move into deeper water following shallow water disturbances, and those that can may suffer from the reduced effects of condition.

The surveys of disturbed and undisturbed reefs did not suggest a widespread response of reef fish to shift into deeper water. Hence most species declined in abundance on disturbed reefs, consistent with other studies showing dramatic losses of fish following coral declines (Wilson et al. 2006; Wilson et al. 2008b; Coker et al. 2014). There was only one example of a fish species (*C. ternatensis*) changing its depth distribution on reefs that have been impacted at the crest. This is a coral-associated species with a wide depth range. However, despite its apparent shift into deeper water, it declined in abundance on impacted reefs. Species such as this would present interesting opportunities to further study the complex relationships between depth, fish physiology and performance. Overall, the survey results do not suggest that a shift to deeper water is an option for coral associated species restricted to shallow water.

The decline in fish condition with increasing depth is a further impediment to shifting into deeper water. A decline in vacuolation combined with increases in hepatocyte density in liver tissues of fish with depth suggests that for both species with shallow distributions as well as those with a much wider depth distribution, individuals at shallower depths are in better condition. This is consistent with previous work, such as by Hoey et al. (2007), which demonstrated in female *Chrysiptera rollandi* there was a similar decline in condition with depth. *Chrysiptera rollandi* is a non-coral associated species with a wide depth distribution, whereas in this study the species we used with a wide depth distribution (*D. reticulatus*) was a coral-associated species, demonstrating that these patterns in condition with depth may be consistent across species with different habitat preferences. Measures of liver cell vacuolation are increasingly used to assess condition in fish because it can be directly linked to glycogen stores in fish (Green and McCormick 1999; Pratchett et al. 2001; Pratchett et al. 2004). Glycogen storage can be important in assessing condition in fish because it is a result of excess glucose in the diet and may represent changes in amount or quality of food as well as activity levels (Storch and Juario 1983; Ostazewska et al. 2005; Hoey et al. 2007). This can have an effect on a range of processes such as growth or reproduction as well as a fish's ability to perform bursting movements in prey avoidance or conversely prey capture (Pratchett et al. 2004; Hoey et al. 2007). Increases in depth may represent a reduction in the availability and nutritional quality of particular food. These differences can therefore have very important effects on where a fish may settle and ultimately its depth distribution. Condition has been shown to affect predation risk too, with predation selecting for fish that had lower condition, lower total lipids, showed slower growth and higher standardised weight (Hoey and McCormick 2004), however in our study there was no significant difference in survival with depth.

The increased growth in length of both *D. melanurus* and *D. reticulatus* on the deepest patch reefs was unexpected and in contrast with previous studies. Srinivasan (2003) found that species with specialised depth ranges, such as *D. melanurus*, showed reduced growth in length outside of their preferred depths. A decrease in initial growth with increasing depth has also been demonstrated for a species with a wide depth range, *C. rollandi*, although this is a non-coral associated species (Hoey et al. 2007). The increased growth in standard length of coral associated species links quite well with the condition results as it appears fish may be investing in growth on deep patch reefs as little of the energy consumed is being stored as glycogen in the liver. For coral associated species who may have to compete for space on favoured coral habitat it may be advantageous to grow fast in order to gain a possible size advantage and also reduce predation risk. It may also be possible that, with condition being lower due to poorer food availability and quality, they are attempting to quickly reach a size that may make it less dangerous to move in search of better conditions. Increased growth in length with depth is consistent with the well supported trend that fish often increase in size with depth (Sale 1969; Choat and Ayling 1987' McCormick 1989; Hoey et al. 2007). Many studies have shown that, especially for more generalist mobile species, higher frequencies of larger individuals occur deeper. This was suggested to be possible for small site-attached species too (Hoey et al. 2007) and our results further support the idea that some species can show increases in growth with depth. Whatever the reason for increased growth, the result suggests unexpected life history consequences for fishes that can make the shift into deeper water.

The only result that suggested a possible resilience to shifting into deeper water was the lack of any effect of depth on survival. However, this result is not consistent with other findings. Srinivasan (2003) found decreased survival in depth specialist species outside of their preferred depths. It is possible that competition may have had some influence on the survival results for the coral associated species. Due to limitation in space and therefore the number of patch reefs built, all species were placed on the same patch reefs, which may have caused competition between *D. melanurus* and *D. reticulatus*. However, because patch reefs were completely clear of fish from the start of the experiment and all new settlers were removed every 3 days, the density of fish remained low throughout and so probably only had a small impact. The decline in the abundance of *C. ternatensis* on disturbed reefs where it shifted into deeper water suggests mortality may be higher in deep water for some species.

Further work needs to be done to fully evaluate the depth refuge hypothesis, but there is mounting evidence that widespread shifts of shallow water coral specialists will not occur. A depth refuge has been shown to occur in some species in relation to impacts such as fishing and coral bleaching (Bak et al. 2005; Goetze et al. 2011; Linfield et al. 2014). However, the results of this study suggest that while it can be possible for a few species, it may not be for others. It highlights that potential depth refuge effects are more likely to be driven by populations having wider depth distributions rather than species choosing to move deeper because body condition seems to be reduced with increasing depth. Depth refuge effects at deeper depths also depend heavily on whether deeper environments can remain more stable and less impacted than shallow environments. For example, Neal et al. (2014) described an exception to the idea that deeper environments can be more stable. They found, due to changes in water column stratification, deeper water suffered greater stress during coral bleaching events compared with shallow water.

In conclusion, this study has provided very limited support for the depth- refuge hypothesis for shallow water, coral-associated reef fishes. Overall condition, in terms of storage of glycogen in liver tissues, decreased with depth for both shallow and more widespread species. This may have been because growth in length was increased at depth in coral-associated species in order to gain size advantages against other species and in response to increased predation risk. The fact that overall survival did not change with depth suggests that it is possible for fish to survive outside of their preferred depth range. However, the surveys of disturbed reefs showed that the majority of shallow species still showed similar depth distribution patterns on reefs where the shallow environment have suffered loss in coral cover and therefore showed declines in abundance. Only more habitat generalist species showed increases on the shallow environment on these impacted reefs. These results add to the complexity of processes known to impact on depth distributions, as well as the nature of depth patterns and highlight the importance of previously unknown sub-lethal effects. However, there should be caution against the assumption that deep reefs will be the salvation of reef fish communities in a future where shallow water coral has declined.

Chapter 6. General Discussion

Depth is a major cause of variation in reef fish communities and has an important effect on the distribution and abundance of species on coral reefs (Lecchini et al. 2003; Brokovich et al. 2006; Brokovich et al. 2008; Gonzalez-Sanson et al. 2009; Fitzpatrick et al. 2012). Studying the effects of depth on reef fish communities is therefore vital in trying to understand spatial distribution patterns in reef fish communities, a fundamental part of reef fish ecology (Krebs 2006). It has also become an important focus of understanding how reef fishes will respond to the continued degradation of shallow water reef systems. This thesis adds to relatively few studies to specifically look at depth patterns and so this study attempted to investigate and clarify some of the patterns suggested in this field.

A number of significant findings can be highlighted. The thesis has confirmed the importance of depth in relation to abundance, distribution, diversity and community structure in coral reef fish. Changes in habitat can have an important effect on reef fish communities (Pratchett et al. 2008; Graham and Nash 2013) and changes in habitat with depth can be important in driving depth patterns. However, in attempting to separate habitat changes from depth patterns it has been shown that habitat changes may only partially explain depth patterns in fish and that a range of different physical and biological factors acting together are influential. Assessing specialisation with depth shows that there are specialists in deeper environments too, indicating that deeper species are potentially just as sensitive to impacts on reefs as shallow species. It has also shown that physiological effects of depth on condition and growth are likely to be a major impediment to shifting into deeper water following loss of coral in shallow water. This means that despite the potential for depth to provide a refuge for fish, it is only likely in species with wide depth ranges.

6.1 Effects of depth on reef fish communities

The results throughout this study support the idea that depth gradients have important and significant effects on reef fish communities. There are substantial changes in the abundance, diversity and community structure and depth is likely an important factor in driving the distribution of reef fish supporting some findings from previous studies (Nunez-Lara and Arias-Gonzalez 1998; Brokovich et al. 2008; Gonzalez-Sanson et al. 2009). Brokovich et al. (2008) saw significant changes to fish communities in the Red Sea with increasing depth and Srinivasan (2003) showed the potential importance of factors associated with depth in explaining settlement, growth and survival. Changes in the abundance of different feeding guilds within the communities also fit well with previous studies (Brokovich et al. 2008; Nemeth and Appledoorm 2009; Pinheiro et al. 2013). Herbivores and planktivores are most abundant at shallow depths and decrease in abundance with increasing depth. Depth is a complex gradient making it hard to separate the effects of the many different biophysical factors that can co-vary with it, for example light attenuation, exposure and water motion, competition, food availability and predation (Bay et al. 2001; Bean et al. 2002; Fulton & Bellwood 2005; Fulton et al. 2005; Brokovich et al. 2008; Irisson et al. 2010). These physical factors may play a very important role in structuring fish communities and could help to explain some of the patterns seen.

6.2 Effects of reef profile on fish communities

This study showed previously undescribed effects of reef profile on both the coral reef fish community and the benthic habitat (Chapter 2). I found separate and interacting effects of both depth and reef profile with trends in community structure and diversity as well as the benthic habitat that could be attributed to both factors. Communities showed differences in the diversity at different depths and reef profiles and there were particular species that showed higher abundances at different depth and reef profiles too. Certain species showed specialisation to particular reef profiles, for example *Chromis Delta,* which was found associated with unique features, such as cave entrances and over hangs, on wall profiles. Few studies have focussed on the effects of reef profile on fish communities distinct from depth (McGehee 1994; Brokovich et al. 2006). The main differences in the fish communities seemed to be driven by the differences between wall habitats and shelf habitats. Shelf communities were dominated by coral associated species whereas wall habitats were dominated by planktivores and other non-coral associated species. The correlation between changes in the fish community and changes in the benthic habitat suggest that habitat can explain some of these patterns. Shelf and slope habitats had more branching and massive coral and therefore more structure to them, which is the preferred habitat for many coral associated species (Coker et al. 2014). Wall habitats, on the other hand, were dominated more by encrusting coral and other encrusting organisms, such as sponges, and therefore were more suitable habitat for planktivores and omnivores. However the weakness of the correlation between fish communities and the benthic habitatsuggests that other factors could be having an effect on fish distributions. These could include such factors as competition between species, in particular coral associated species, exposure and water motion and possible differences in food availability (Clarke 1989; Shpigel and Fishelson 1989; Friedlander and Parish 1998; Bean et al. 2002; Fulton and Bellwood 2005; Fulton at al. 2005; Brokovich et al. 2008; Medeiros et al. 2010). Reef profile also had an effect on the magnitude of differences between depths. Anecdotal evidence suggests that some species may extend their depth ranges deeper on gentle slopes compared with vertical drop-offs. This could mean that studies could find very different depth patterns depending on the profiles of the reefs surveyed. For example Brokovich et al. (2008) found some species to have much larger depth ranges than previously recorded (by as much as 40m in some cases).

6.3 Effects of depth on diversity

Diversity changed with depth throughout the study with an overall negative trend, meaning diversity declined with increasing depth (Chapter 2, 3, 4). This contrasts with results from previous studies, such as Brokovich et al. (2008), which found that diversity was highest around the mid-point of a gradient from 0-60m. The depth gradient surveyed in my study however was only to 20m, making a direct comparison difficult although even comparing just 0-20m in both studies shows contrasting results in terms of species richness and diversity. The higher species richness and diversity at deeper depths in Brokovich et al. (2008) was attributed to higher heterogeneity in habitat at depth and decreases in branching coral. The contrasting results I found may be due to the fact that there was quite high environmental heterogeneity in shallow environments at reefs surveyed in Kimbe Bay and the Great Barrier Reef in Chapters 2 and 3. There was no decline in branching coral for flatter, less complex corals on the reefs surveyed in Chapter 3 either, meaning coral associated species could dominate deeper. Some species of coral-associated pomacentrids, such as *Dascyllus aruanus*, can be very aggressive towards settlers of conspecific and heterospecific species to their coral habitats and can therefore have an influence on the settlement preferences of juveniles (Ben-Tzvi et al. 2009). It is also possible that shallow water environments at sites in my study may be more productive and therefore able to support a greater number of habitat specialists.

6.4 Effects of depth on specialisation

Specialisation, in terms of both depth and habitat use, had an unexpected pattern with depth in that deeper fish were found to be just as specialised in their depth distribution and were in fact more specialised in their habitat use than shallower species (Chapter 3). Other studies have suggested that there are more specialist species in shallower environments when looking at depth distributions as well as in habitat use (e.g. Bean et al. 2002). Depth ranges of species were restricted at both extremes of the depth gradient sampled with those species found to live around the mid depths having the largest depth ranges (Chapter 3). The entire depth range of the reefs sampled in the study were surveyed because these reefs did not extend any greater than 20 m. Reef edge habitat at 20m could therefore act as a natural barrier to species using deeper depths just as the surface does for shallow species. This result suggests a "mid-domain effect" on reef fish depth distributions. This effect has been discussed in the literature in terms of large scale patterns in biodiversity and species richness. It is the idea that a random distribution of geographic ranges produces a peak in species richness mid-way between the boundaries of a biogeographic domain (Connolly et al. 2003). This would be the first time it has been demonstrated to occur on a much smaller "reef" scale. Further study would however be needed to truly confirm this by comparing the patterns in depth ranges of species on a reef which had more continuous reef to much deeper depths.

Another unexpected result was the increase in niche breadth, a measure of habitat specialisation, with depth (Chapter 3). This again contrasted with previous studies and was probably linked to the fact that habitat use of corals and sand/rubble did not decline with depth. The deepest parts of the reef were patchy in nature, with patches of branching coral surrounded by sand and rubble. This could have led to more specialised species dominating these reef edge habitats as specialists are thought to normally outcompete generalists as long as environmental conditions are more stable, whereas, generalists are thought to be favoured in more heterogeneous and disturbed environments (Emlen & Oring 1977; Futuyma & Moreno 1988; Claver et al. 2011). This is because it is thought that specialists use their preferred habitats more efficiently, allowing them to out compete generalists, leading to a dominance of specialists and a potentially less diverse community (Emlen & Oring 1977; Futuyma & Moreno 1988). Deeper reef habitats are thought to be more stable with lower exposure and have more stable temperatures than shallow reef habitats (Bak et al. 2005; Slattery et al. 2011; Bridge et al. 2013). This may also help explain the lower diversity observed at deeper depth too. It is also possible that predation pressure could be higher at these reef edge habitats, creating a closer association between smaller fishes and the substrata that can provide them shelter.

6.5 Effects of changes in habitat with depth

The effectsof changes in habitat and complexity on reef fish communities have been well documented in previous studies (Friedlander and Parish 1998; Gratwicke and Speight 2005; Garpe et al. 2005; Graham et al. 2006; Wilson et al. 2006; Pratchett et al. 2008; Bonin et al. 2011; Graham and Nash 2013). This effect can be seen throughout my study in relation to depth (Chapter 2, 3, 4). This was most evident when looking at depth patterns in species with habitat preferences, such as coral-associated species. Many studies have identified habitat preferences in reef fish and shown that changes in the availability of preferred habitats can be critical in explaining their spatial patterns in distribution (Green 1996; Gutierrez 1998; Bay et al. 2001; Bean et al. 2002; Brokovich et al. 2006; Brokovich et al. 2008; Bonin et al. 2009). In general coral-associated species were more abundant at shallow depths (Chapter 2, 4). This pattern would be logical because with such close associations with coral, any physical gradient that can affect coral cover can therefore have pronounced effects on fish distributions (Bell and Galzin 1984; Garpe and Öhman 2003). Numerous other studies have shown coral-associated species are restricted to shallow depths (Chabanet et al. 1997; Srinivasan 2003; Brokovich et al. 2008). Herbivorous species of fish have also been shown to have strong depth patterns. Herbivores are often more abundant at shallow depths and it has been shown that herbivore biomass and density decreases with depth, resulting in a decrease in grazing pressure and the process of herbivory with increasing depth (Nemeth and Appledoorn 2009; Brokovich et al. 2010; Kopp et al.

2012; Bejarano et al. 2014). For example, herbivorous pomacentrids often dominate shallow reef zones whilst labrids tend to dominate deeper zones (Russ 1984; Meeken et al. 1995; Friedlander and Parrish 1998; Brokovich et al. 2008; Medeiros et al. 2010). This is thought to be related to changes in habitat because shallow habitat, such as reef crest habitats, can host the greatest algal productivity (Russ 2003; Fox and Bellwood 2007; Brokovich et al. 2010). This was demonstrated in Chapter 4 with herbivores contributing more to communities on shallow patch reefs compared with deep patch reefs.

Despite showing significant effects on depth distributions, changes in habitat are unlikely to be the only factor driving distribution. Srinivasan (2003) demonstrated that depth patterns in fish were still established independently from changes in habitat. This was further supported by strong differences between communities at different depths as well as clear depth patterns observed for individual species in Chapter 4, with habitat availability being kept constant. There was only a weak correlation between changes in the fish community and changes in the benthic habitat (Chapter 2), which also suggests that other factors may be involved along with habitat changes. Depth is a complex gradient that can be difficult to study specifically because of the many biophysical factors that interact and vary with it (Leis 1986; Leis 1991; Gutierrez 1998; Bay et al. 2001; Hendriks et al. 2001; Bean et al. 2002; Fulton and Bellwood 2005; Fulton et al. 2005; Brokovich et al. 2008; Irisson et al. 2001). Exposure is one such factor as it can affect the water motion faced by a habitat which can have an influence on the fish community present (Fulton and Bellwood 2005). There is an interaction between the swimming ability of species and the water flow, as pectoral swimming fish become more prevalent in areas with higher flow and caudal swimming fish in areas with lower flow (Fulton and Bellwood 2005; Fulton et al. 2005). Changes in water flow with depth can affect coral morphology, metabolism and calcification, which could in turn affect the distribution of coral associated species (Mass et al. 2007; Mass and Genin 2008; Einbinder et al. 2009). Competition between conspecifics and heterospecifics is another factor that has been shown to influence distribution and settlement in reef fish, especially in species of pomacentrids which made up significant proportions of the communities surveyed in my study (Bay et al. 2001; Ben-Tzvi et al. 2009). Once established, fish can affect settlement and recruitment of juveniles, as it has been shown that larvae are attracted to conspecifics (Coppock et al. 2013). Food availability could potentially change with depth and have impact on a reef fish's depth distribution. For example, plankton species composition and abundance show patterns of distribution with depth in the water column and could therefore have an influence on where planktivores choose to live. Different guilds of reef fish show different patterns with depth. Herbivorous and territorial species are often more abundant in shallow reef flat and crest habitats, whereas planktivores and omnivores tend to be more abundant on deeper crest and slope habitats (Friedlander and Parrish 1998; Brokovich et al. 2008; Medeiros et al. 2010). Predation can influence reef fish communities and can potentially change with depth (Wellington 1992; Carr and Hixon 1995). Predatory reef fish species, such as *C. boenak*, were more abundant on deeper patch reefs (Chapter 4) and this could have had an effect on the species recruiting to those patch reefs. It is likely that combinations of many of these different factors interact along depth gradients and drive patterns in fish depth distribution.

6.6 Physiological effects of depth on reef fishes

Physiological effects on fish with increasing depth could potentially have an important effect on where a fish settles and chooses to live. Few studies have looked at these potential effects and so this study has given some important insight into how these physiological effects influence depth distribution. Survival and growth has been shown to decrease with depth in those species that have a shallow depth preference (Srinivasan 2003). Depth can also have an effect on the overall physiological condition of a fish, causing a decrease in condition and initial growth with increasing depth (Hoey et al. 2007). In Chapter 5 there was a decrease in condition, with fish from increasing depths having lower glycogen storage. Glycogen storage in fish can be related to a range of processes including growth, reproduction and the ability to perform burst movements, which are used in predator avoidance or prey capture (Pratchett et al. 2004; Hoey et al. 2007). Lower condition has been linked to increased predation pressure and so lower condition could mean increased predation pressure with depth. However, unexpectedly, there were no significant differences in survival at different depths. The most unusual result was the increased growth in length seen in two species of coral associated species. This growth, combined with low vacuolation in liver tissues, suggests fish are attempting to grow rapidly at depth. This may be to gain a size advantage in competition for limited coral habitat at depth or to cope with predation pressure. In larger more mobile species of fish it is well documented that size often increases with depth (Sale 1969; Choat and Ayling 1987; McCormick 1989; Hoey et al. 2007). This trend may be true for smaller more site-attached species with the increased growth of individuals deeper. Hoey et al. (2007) also demonstrated larger sizes of individuals with depth in a small non-coral associated damselfish.

6.7 Implications and predictions

This study has implications for the hypothesis of depth providing a refuge for reef fish and shows that this idea can be a complex one that is not entirely supported by the data. There is some potential for depth to provide a refuge, as species with shallow depth preferences were able to survive initially at similar rates to those in their normal ranges (Chapter 5) and there were specialised species found in deeper environments (Chapter 3). With these deeper species being potentially just as sensitive to impacts as shallow species, the potential of depth to be a refuge would rely heavily on how stable and resistant to impacts deeper environments truly are. Some studies have shown that deeper coral reef habitats can be affected by changes in thermal conditions and disturbances in the upper water column that affect light penetration (Slattery et al. 2007; Neal et al. 2014). Impacts to deeper coral communities could have important knock-on effects on the fish communities present. There has been evidence for depth to be a refuge for some reef fish species, in particular in response to fishing impacts in shallow environments (Tyler et al. 2009; Goetze et al. 2011). Most species maintained depth preferences despite habitat availability being kept constant (Chapter 4) and on reefs with reduced coral cover on the reef crest (Chapter 5). Condition in fish at deeper depths was reduced, even for species with wide depth ranges (Chapter 5). Graham et al. (2011) suggest that depth could be an important factor in the extinction risk of fish species as those species that have extended depth ranges could in fact be less impacted by disturbances to shallow reefs. These differences in depth use between species could have impacts on fish communities in the future. Shallow water specialists are likely to suffer great declines and even extinctions if impacts in shallow water increase in frequency and severity with global climate change because they are unlikely to move deeper to lessen the impact and do not have populations deeper to provide a source of juveniles to repopulate shallow environments. Depth generalist species, on the other hand, are likely to dominate communities due to the fact that they are able to use depth has a refuge and deeper populations can provide juveniles to recolonise shallow environments. Deeper specialised species will likely remain relatively unaffected but only if deeper environments remain more stable and less impacted. These deeper specialists could potentially even extend their ranges shallower to exploit habitats made free from declines in shallow specialists.

6.8 Future Studies

Despite increasing understanding of an important aspect of reef fish ecology this thesis has identified several important areas for further study. Firstly, although changes in the type and structure of the underlying habitat have significant effects on depth distributions of reef fish, it is clear that habitat cannot fully explain depth patterns and that there is most likely a range of physical factors interacting that determine spatial patterns of reef fish with depth. Further study is needed to try and quantify the true differences in physical factors with depth and to try and separate out the effects of these factors. It was identified that there may be mid-domain effect on the depth distribution of species when surveying the entire range of depths available on a reef (Chapter 3), however to confirm this further study would be needed to see if this pattern is consistent in different locations and on reefs which extend much deeper. For depth to truly provide refuge for fish, it is important for deeper habitats to be much more stable and less impacted than shallow environments. Few studies have assessed the overall stability of deeper environments and therefore it is important to investigate how deeper environments are impacted during disturbance events to see if they really are more stable. With different species abilities to use depth as a refuge being variable it would also be important to further understand the direct physiological effects of depth on fish and how this might relate to their depth distribution. Condition has been shown to decrease with depth, but there are more possible effects that could potentially impact the overall fitness of a fish including impacts on a fish's aerobic scope as well as possible impacts on reproduction and dispersal. Assessing changes in reproductive output and gonad development with depth could provide interesting and important information on the effect of depth on overall fitness. It would also be of interest to try and compare fish that can potentially use depth as a refuge to those that potentially cannot as this can help in understanding which species could be more resilient in the future and identify which species may be more at risk to future impacts. The changes in condition of reef fish studied in this thesis were short term effects; further study into longer term effects of being forced to live outside of preferred depth ranges would be important in assessing how communities could be affected in the future as well.

This thesis has further demonstrated the importance of depth in structuring coral reef fish communities and shown how habitat use and specialisation change with depth. However, there have been several findings that contrast with those from previous studies, reiterating the complex nature of depth gradient patterns and showing the need for further study. Specialisation increased with depth on reefs in the Mid-shelf GBR, showing that deeper species could potentially be just as sensitive to impacts as species in shallow environments. Deeper reef edge habitats could potentially provide refuge for coral-associated species, although overall condition of fish decreased with depth. Unusually, growth in length of coral-associated species increased at depth and may be an attempt by fish to try and gain a size advantage in unfavourable conditions. Communities as well as individual species still showed particular depth distributions and preferences despite habitat availability being kept constant. This was also the case when surveying shallow communities on reefs where the reef crest and flat had been degraded in terms of coral cover. Depth distribution and specialisation patterns can have a key influence on a fish’s sensitivity to impacts and understanding these patterns can potentially identify species that may be more vulnerable. This information would be important to future management of coral reefs as well as for predicting changes to reef fish communities in the decades to come.

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Appendix

A-1 Species list showing the family, species, mean abundance and standard error for fish observed on different reef profiles at both shallow and deep depths during surveys in Chapter 2

Table A 1 Species list showing the family, species, mean abundance and standard error for fish observed on different reef profiles at both shallow and deep depths during surveys in Chapter 2

Family	Species	Shallow					
		Shelf (n=23)		Slope (n=31)		Wall (n=22)	
		Mean abundance	Standard error	Mean abundance	Standard error	Mean abundance	Standard error
Acanthuridae	*Acanthochromis polyacanthus*	0.696	0.323	0.387	0.152	0.455	0.157
Acanthuridae	*Acanthurus gammoptilus*	0.000	0.000	0.000	0.000	0.000	0.000
Acanthuridae	*Acanthurus nigrofuscus*	0.000	0.000	0.032	0.032	0.000	0.000
Acanthuridae	*Acanthurus olivaceus*	0.000	0.000	0.065	0.065	0.000	0.000
Acanthuridae	*Acanthurus pyroferus*	0.174	0.136	0.097	0.071	0.000	0.000
Acanthuridae	*Ctenochaetus binotatus*	0.783	0.226	0.194	0.086	0.045	0.045
Acanthuridae	*Ctenochaetus striatus*	1.391	0.265	0.226	0.076	0.045	0.045
Acanthuridae	*Ctenochaetus tominiensis*	0.652	0.232	1.129	0.261	1.591	0.320
Acanthuridae	*Pygoplites diacanthus*	0.174	0.081	0.161	0.082	0.045	0.045
Acanthuridae	*Zebrasoma scopas*	0.130	0.072	0.032	0.032	0.045	0.045
Apogonidae	*Apogon compressus*	0.130	0.095	0.065	0.045	0.000	0.000
Apogonidae	*Apogon fragilis*	0.000	0.000	5.000	3.629	0.000	0.000
Apogonidae	*Apogon lepacanthus*	0.000	0.000	3.548	2.953	0.000	0.000
Apogonidae	*Archamia zosterophora*	0.000	0.000	2.097	1.793	0.318	0.318
Apogonidae	*Cheilodipterus artus*	0.261	0.220	0.097	0.071	0.000	0.000
Balistidae	*Balistapus undulatus*	0.348	0.149	0.065	0.045	0.000	0.000
Balistidae	*Pseudobalistes flavimarginatus*	0.174	0.136	0.000	0.000	0.000	0.000
Balistidae	*Sufflamen bursa*	0.043	0.043	0.032	0.032	0.000	0.000
Balistidae	*Sufflamen chrysopterum*	0.000	0.000	0.032	0.032	0.000	0.000
Caesionidae	*Pterocaesio pisang*	1.000	1.000	1.710	0.961	0.909	0.909
Cheatodontidae	*Chaetodon baronessa*	0.478	0.165	0.129	0.077	0.136	0.100
Cheatodontidae	*Chaetodon kleinii*	0.087	0.060	0.000	0.000	0.000	0.000
Cheatodontidae	*Chaetodon melannotus*	0.000	0.000	0.032	0.032	0.000	0.000
Cheatodontidae	*Chaetodon octofasciatus*	0.696	0.222	0.355	0.109	0.500	0.183

Cheatodontidae	*Chaetodon rafflesi*	0.000	0.000	0.000	0.000	0.091	0.091
Cheatodontidae	*Chaetodon trifasciatus*	0.000	0.000	0.000	0.000	0.091	0.091
Cheatodontidae	*Chaetodon vagabundus*	0.000	0.000	0.032	0.032	0.000	0.000
Cheatodontidae	*Heniochus monoceros*	0.000	0.000	0.000	0.000	0.000	0.000
Cheatodontidae	*Heniochus varius*	0.000	0.000	0.032	0.032	0.091	0.091
Ephippidae	*Platax pinnatus*	0.000	0.000	0.000	0.000	0.000	0.000
Holocentridae	*Neoniphon sammara*	0.000	0.000	0.000	0.000	0.000	0.000
Holocentridae	*Squirrel fish sp. 1*	0.000	0.000	0.097	0.071	0.091	0.063
Holocentridae	*Squirrel fish sp. 2*	0.087	0.060	0.032	0.032	0.364	0.140
Labridae	*Bodianus diana*	0.000	0.000	0.000	0.000	0.000	0.000
Labridae	*Bodianus mesothorax*	0.130	0.095	0.161	0.094	0.091	0.063
Labridae	*Cheilinus celebicus*	0.522	0.242	0.839	0.174	0.955	0.250
Labridae	*Cheilinus fasciatus*	0.043	0.043	0.161	0.082	0.136	0.075
Labridae	*Chlorurus bleekeri*	0.391	0.249	0.000	0.000	0.000	0.000
Labridae	*Cirrhilabrus punctatum*	0.043	0.043	0.000	0.000	0.000	0.000
Labridae	*Diprotacanthus xanthurus*	0.217	0.108	0.323	0.163	0.000	0.000
Labridae	*Halichoeres argus*	0.000	0.000	0.032	0.032	0.000	0.000
Labridae	*Halichoeres chloropterus*	0.043	0.043	0.000	0.000	0.000	0.000
Labridae	*Halichoeres melanurus*	4.913	0.397	5.323	0.487	3.318	0.380
Labridae	*Halichoeres prosopeion*	0.217	0.108	0.129	0.101	0.273	0.117
Labridae	*Halichoeres purpurescens*	0.348	0.135	0.903	0.214	0.636	0.283
Labridae	*Halichoeres richmondii*	0.739	0.237	0.645	0.210	0.545	0.183
Labridae	*Hemigymnus melapterus*	0.000	0.000	0.032	0.032	0.000	0.000
Labridae	*Labrichtys unilatus*	0.304	0.098	0.484	0.185	0.045	0.045
Labridae	*Labroides dimidiatus*	0.435	0.138	0.387	0.120	0.500	0.171
Labridae	*Labroides pectoralis*	0.000	0.000	0.032	0.032	0.000	0.000
Labridae	*Labropsis alleni*	0.043	0.043	0.000	0.000	0.045	0.045
Labridae	*Paracheilinus filamentosus*	0.130	0.095	0.161	0.115	0.000	0.000
Labridae	*Pseudocheilinus hexataenia*	0.565	0.225	0.161	0.082	0.091	0.063
Labridae	*Scarus flavipectoralis*	0.000	0.000	0.000	0.000	0.000	0.000

Labridae	*Scarus niger*	0.043	0.043	0.000	0.000	0.000	0.000
Labridae	*Thalassoma hardwickii*	0.130	0.130	0.032	0.032	0.000	0.000
Labridae	*Thalassoma lunare*	1.087	0.266	0.935	0.258	0.000	0.000
Lethrinidae	*Monotaxis grandoculis*	0.087	0.087	0.032	0.032	0.045	0.045
Lutjanidae	*Caesio teres*	0.130	0.130	0.710	0.496	1.455	0.960
Lutjanidae	*Lutjanus biguttatus*	0.000	0.000	0.000	0.000	0.000	0.000
Lutjanidae	*Lutjanus gibbus*	0.000	0.000	0.000	0.000	0.000	0.000
Lutjanidae	*Macolor macularis*	0.043	0.043	0.000	0.000	0.000	0.000
Nemipteridae	*Scolopsis margaritifer*	0.043	0.043	0.065	0.045	0.045	0.045
Pomacanthidae	*Centropyge bicolor*	0.043	0.043	0.032	0.032	0.045	0.045
Pomacanthidae	*Centropyge nox*	0.000	0.000	0.097	0.097	0.045	0.045
Pomacanthidae	*Centropyge vroliki*	0.261	0.144	0.129	0.077	0.000	0.000
Pomacanthidae	*Chaetodontoplus mesoleucus*	0.087	0.087	0.161	0.082	0.000	0.000
Pomacanthidae	*Pomacanthus sexstriatus*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Amblyglyphidodon aureus*	0.000	0.000	0.000	0.000	0.182	0.142
Pomacentridae	*Amblyglyphidodon curacao*	0.304	0.222	0.129	0.129	0.364	0.203
Pomacentridae	*Amblyglyphidodon leucogaster*	0.217	0.177	0.226	0.089	0.318	0.274
Pomacentridae	*Amphiprion clarkii*	0.000	0.000	0.194	0.108	0.000	0.000
Pomacentridae	*Amphiprion percular*	0.043	0.043	0.065	0.065	0.091	0.091
Pomacentridae	*Chromis amboinensis*	0.739	0.340	1.516	0.585	3.864	1.064
Pomacentridae	*Chromis delta*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Chromis elerae*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Chromis retrofasciata*	3.435	0.688	4.774	1.046	5.136	1.035
Pomacentridae	*Chromis ternatensis*	7.435	2.417	3.613	0.957	2.091	1.044
Pomacentridae	*Chromis xanthura*	0.000	0.000	0.032	0.032	0.045	0.045
Pomacentridae	*Chrysiptera parasema*	7.783	4.643	2.806	1.099	2.864	1.366
Pomacentridae	*Chrysiptera rollandi*	5.435	0.871	6.968	1.224	6.000	1.170
Pomacentridae	*Chrysipterus talboti*	0.652	0.348	0.968	0.355	4.455	0.647
Pomacentridae	*Dascyllus melanurus*	0.739	0.617	0.806	0.806	0.000	0.000
Pomacentridae	*Dascyllus reticulatus*	0.348	0.248	0.000	0.000	0.000	0.000

Pomacentridae	*Dascyllus trimaculatus*	0.000	0.000	0.065	0.045	0.000	0.000
Pomacentridae	*Neoglyphidodon nigrorus*	0.087	0.060	0.548	0.222	3.045	0.434
Pomacentridae	*Neoglyphidodon thoracotaeniatus*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Neopomacentrus azysron*	3.913	1.532	3.871	1.797	0.091	0.063
Pomacentridae	*Plectroglyphidodon lacrymatus*	0.348	0.162	0.226	0.120	0.091	0.091
Pomacentridae	*Pomacentrus amboinensis*	0.000	0.000	0.290	0.155	0.000	0.000
Pomacentridae	*Pomacentrus aurifrons*	15.913	5.581	21.097	6.349	1.500	1.087
Pomacentridae	*Pomacentrus bankanensis*	0.043	0.043	0.000	0.000	0.000	0.000
Pomacentridae	*Pomacentrus burroughi*	4.391	0.602	2.226	0.439	0.773	0.360
Pomacentridae	*Pomacentrus moluccensis*	3.870	1.113	2.355	0.686	2.000	0.603
Pomacentridae	*Pomacentrus nigromarginatus*	4.783	1.012	6.000	1.004	7.091	0.800
Pomacentridae	*Pomacentrus reidi*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Pomacentrus simsiang*	0.000	0.000	0.097	0.097	0.000	0.000
Pomacentridae	*Pomacentrus smithi*	0.000	0.000	0.032	0.032	0.000	0.000
Pomacentridae	*Pomacentus adelus*	1.087	0.371	0.452	0.190	0.227	0.185
Psuedochromidae	*Pictichromis paccagnellae*	0.000	0.000	0.000	0.000	0.000	0.000
Ptereleotridae	*Ptereleotris evides*	0.000	0.000	0.000	0.000	0.091	0.091
Serranidae	*Cephalopholis argus*	0.000	0.000	0.000	0.000	0.045	0.045
Serranidae	*Cephalopholis cyanostigma*	0.130	0.072	0.065	0.045	0.000	0.000
Serranidae	*Cephalopholis microprion*	0.087	0.060	0.097	0.054	0.000	0.000
Serranidae	*Plectropomus leopardus*	0.043	0.043	0.032	0.032	0.000	0.000
Serranidae	*Plectropomus oligacanthus*	0.000	0.000	0.000	0.000	0.000	0.000
Serranidae	*Pseudanthias tuka*	0.391	0.286	8.065	3.403	5.045	2.732
Siganidae	*Siganus vulpinus*	0.304	0.159	0.065	0.065	0.045	0.045
Sphyraenidae	*Sphyraena putnamae*	0.435	0.435	0.000	0.000	0.000	0.000
Tetradontidae	*Arothron nigropunctatus*	0.000	0.000	0.000	0.000	0.000	0.000
Tetradontidae	*Canthigaster solandri*	0.000	0.000	0.000	0.000	0.091	0.063
Zanclidae	*Zanclus cornutus*	0.000	0.000	0.000	0.000	0.000	0.000

Family	Species	Deep					
		Shelf (n=15)		Slope (n=18)		Wall (n=18)	
		Mean abundance	Standard error	Mean abundance	Standard error	Mean abundance	Standard error
Acanthuridae	*Acanthochromis polyacanthus*	0.133	0.133	0.389	0.282	0.000	0.000
Acanthuridae	*Acanthurus gammoptilus*	0.067	0.067	0.056	0.056	0.000	0.000
Acanthuridae	*Acanthurus nigrofuscus*	0.000	0.000	0.056	0.056	0.000	0.000
Acanthuridae	*Acanthurus olivaceus*	0.000	0.000	0.000	0.000	0.000	0.000
Acanthuridae	*Acanthurus pyroferus*	0.000	0.000	0.056	0.056	0.000	0.000
Acanthuridae	*Ctenochaetus binotatus*	0.000	0.000	0.111	0.111	0.000	0.000
Acanthuridae	*Ctenochaetus striatus*	0.133	0.133	0.333	0.162	0.000	0.000
Acanthuridae	*Ctenochaetus tominiensis*	2.467	0.413	1.444	0.398	1.500	0.406
Acanthuridae	*Pygoplites diacanthus*	0.200	0.107	0.222	0.173	0.111	0.076
Acanthuridae	*Zebrasoma scopas*	0.267	0.206	0.056	0.056	0.000	0.000
Apogonidae	*Apogon compressus*	0.467	0.401	0.056	0.056	0.000	0.000
Apogonidae	*Apogon fragilis*	0.000	0.000	0.000	0.000	0.000	0.000
Apogonidae	*Apogon lepacanthus*	0.000	0.000	0.000	0.000	0.000	0.000
Apogonidae	*Archamia zosterophora*	0.800	0.800	0.000	0.000	0.000	0.000
Apogonidae	*Cheilodipterus artus*	0.333	0.232	0.111	0.111	0.167	0.167
Balistidae	*Balistapus undulatus*	0.200	0.107	0.056	0.056	0.056	0.056
Balistidae	*Pseudobalistes flavimarginatus*	0.000	0.000	0.000	0.000	0.000	0.000
Balistidae	*Sufflamen bursa*	0.000	0.000	0.056	0.056	0.000	0.000
Balistidae	*Sufflamen chrysopterum*	0.000	0.000	0.056	0.056	0.000	0.000
Caesionidae	*Pterocaesio pisang*	0.000	0.000	0.000	0.000	3.333	2.425
Cheatodontidae	*Chaetodon baronessa*	0.267	0.206	0.167	0.121	0.000	0.000
Cheatodontidae	*Chaetodon kleinii*	0.000	0.000	0.000	0.000	0.000	0.000
Cheatodontidae	*Chaetodon melannotus*	0.000	0.000	0.000	0.000	0.000	0.000
Cheatodontidae	*Chaetodon octofasciatus*	0.933	0.330	0.500	0.218	0.111	0.111
Cheatodontidae	*Chaetodon rafflesi*	0.000	0.000	0.000	0.000	0.000	0.000

Cheatodontidae	*Chaetodon trifasciatus*	0.000	0.000	0.000	0.000	0.000	0.000
Cheatodontidae	*Chaetodon vagabundus*	0.000	0.000	0.000	0.000	0.000	0.000
Cheatodontidae	*Heniochus monoceros*	0.200	0.145	0.000	0.000	0.056	0.056
Cheatodontidae	*Heniochus varius*	0.000	0.000	0.167	0.121	0.056	0.056
Ephippidae	*Platax pinnatus*	0.000	0.000	0.000	0.000	0.056	0.056
Holocentridae	*Neoniphon sammara*	0.000	0.000	0.000	0.000	0.056	0.056
Holocentridae	*Squirrel fish sp. 1*	0.000	0.000	0.056	0.056	0.000	0.000
Holocentridae	*Squirrel fish sp. 2*	0.133	0.091	0.000	0.000	0.000	0.000
Labridae	*Bodianus diana*	0.000	0.000	0.000	0.000	0.056	0.056
Labridae	*Bodianus mesothorax*	0.200	0.107	0.056	0.056	0.278	0.226
Labridae	*Cheilinus celebicus*	1.400	0.335	2.167	0.430	1.278	0.278
Labridae	*Cheilinus fasciatus*	0.200	0.145	0.222	0.101	0.000	0.000
Labridae	*Chlorurus bleekeri*	0.133	0.133	0.056	0.056	0.000	0.000
Labridae	*Cirrhilabrus punctatum*	0.000	0.000	0.333	0.333	0.000	0.000
Labridae	*Diprotacanthus xanthurus*	0.133	0.091	0.500	0.202	0.167	0.167
Labridae	*Halichoeres argus*	0.000	0.000	0.000	0.000	0.000	0.000
Labridae	*Halichoeres chloropterus*	0.000	0.000	0.056	0.056	0.000	0.000
Labridae	*Halichoeres melanurus*	2.000	0.447	2.222	0.358	1.833	0.316
Labridae	*Halichoeres prosopeion*	0.200	0.145	0.333	0.162	0.833	0.283
Labridae	*Halichoeres purpurescens*	0.933	0.284	0.889	0.254	0.833	0.218
Labridae	*Halichoeres richmondii*	0.533	0.215	0.556	0.202	0.389	0.200
Labridae	*Hemigymnus melapterus*	0.000	0.000	0.000	0.000	0.000	0.000
Labridae	*Labrichtys unilatus*	0.133	0.091	0.000	0.000	0.000	0.000
Labridae	*Labroides dimidiatus*	0.067	0.067	0.222	0.152	0.333	0.140
Labridae	*Labroides pectoralis*	0.000	0.000	0.000	0.000	0.000	0.000
Labridae	*Labropsis alleni*	0.000	0.000	0.167	0.167	0.111	0.076
Labridae	*Paracheilinus filamentosus*	0.000	0.000	0.000	0.000	0.000	0.000
Labridae	*Pseudocheilinus hexataenia*	0.000	0.000	0.000	0.000	0.000	0.000
Labridae	*Scarus flavipectoralis*	0.000	0.000	0.056	0.056	0.000	0.000
Labridae	*Scarus niger*	0.000	0.000	0.000	0.000	0.000	0.000

Labridae	*Thalassoma hardwickii*	0.000	0.000	0.000	0.000	0.000	0.000
Labridae	*Thalassoma lunare*	0.000	0.000	0.000	0.000	0.000	0.000
Lethrinidae	*Monotaxis grandoculis*	0.000	0.000	0.056	0.056	0.000	0.000
Lutjanidae	*Caesio teres*	0.000	0.000	0.000	0.000	5.056	2.035
Lutjanidae	*Lutjanus biguttatus*	0.467	0.165	0.222	0.129	0.167	0.090
Lutjanidae	*Lutjanus gibbus*	0.133	0.091	0.000	0.000	0.000	0.000
Lutjanidae	*Macolor macularis*	0.000	0.000	0.000	0.000	0.000	0.000
Nemipteridae	*Scolopsis margaritifer*	0.067	0.067	0.000	0.000	0.000	0.000
Pomacanthidae	*Centropyge bicolor*	0.000	0.000	0.111	0.076	0.167	0.090
Pomacanthidae	*Centropyge nox*	0.133	0.091	0.167	0.090	0.167	0.090
Pomacanthidae	*Centropyge vroliki*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacanthidae	*Chaetodontoplus mesoleucus*	0.200	0.200	0.000	0.000	0.056	0.056
Pomacanthidae	*Pomacanthus sexstriatus*	0.000	0.000	0.056	0.056	0.000	0.000
Pomacentridae	*Amblyglyphidodon aureus*	0.000	0.000	0.111	0.111	0.333	0.114
Pomacentridae	*Amblyglyphidodon curacao*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Amblyglyphidodon leucogaster*	1.000	0.425	0.389	0.335	0.167	0.167
Pomacentridae	*Amphiprion clarkii*	0.000	0.000	0.000	0.000	0.111	0.111
Pomacentridae	*Amphiprion percular*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Chromis amboinensis*	2.000	0.647	1.111	0.427	3.000	0.808
Pomacentridae	*Chromis delta*	0.000	0.000	0.000	0.000	1.556	0.764
Pomacentridae	*Chromis elerae*	0.000	0.000	0.000	0.000	0.389	0.200
Pomacentridae	*Chromis retrofasciata*	6.600	1.753	1.611	0.750	4.667	2.140
Pomacentridae	*Chromis ternatensis*	7.067	2.912	0.000	0.000	0.833	0.833
Pomacentridae	*Chromis xanthura*	0.000	0.000	0.000	0.000	0.111	0.076
Pomacentridae	*Chrysiptera parasema*	19.800	4.423	5.889	1.490	3.778	1.940
Pomacentridae	*Chrysiptera rollandi*	3.133	0.833	6.889	1.143	6.889	0.796
Pomacentridae	*Chrysipterus talboti*	0.000	0.000	0.056	0.056	0.056	0.056
Pomacentridae	*Dascyllus melanurus*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Dascyllus reticulatus*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Dascyllus trimaculatus*	0.000	0.000	0.000	0.000	0.000	0.000

Pomacentridae	*Neoglyphidodon nigrorus*	0.067	0.067	0.056	0.056	0.167	0.090
Pomacentridae	*Neoglyphidodon thoracotaeniatus*	0.200	0.107	0.000	0.000	0.000	0.000
Pomacentridae	*Neopomacentrus azysron*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Plectroglyphidodon lacrymatus*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Pomacentrus amboinensis*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Pomacentrus aurifrons*	4.267	2.152	0.000	0.000	0.000	0.000
Pomacentridae	*Pomacentrus bankanensis*	0.000	0.000	0.000	0.000	0.222	0.222
Pomacentridae	*Pomacentrus burroughi*	2.200	0.656	1.167	0.316	0.111	0.076
Pomacentridae	*Pomacentrus moluccensis*	0.067	0.067	0.000	0.000	0.000	0.000
Pomacentridae	*Pomacentrus nigromarginatus*	5.733	1.465	6.389	1.473	10.833	1.294
Pomacentridae	*Pomacentrus reidi*	0.000	0.000	0.000	0.000	0.056	0.056
Pomacentridae	*Pomacentrus simsiang*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Pomacentrus smithi*	0.000	0.000	0.000	0.000	0.000	0.000
Pomacentridae	*Pomacentus adelus*	0.200	0.145	0.000	0.000	0.000	0.000
Pseudochromidae	*Pictichromis paccagnellae*	0.000	0.000	0.000	0.000	0.722	0.341
Ptereleotridae	*Ptereleotris evides*	0.000	0.000	0.000	0.000	0.000	0.000
Serranidae	*Cephalopholis argus*	0.000	0.000	0.056	0.056	0.056	0.056
Serranidae	*Cephalopholis cyanostigma*	0.067	0.067	0.000	0.000	0.111	0.076
Serranidae	*Cephalopholis microprion*	0.133	0.091	0.167	0.090	0.167	0.090
Serranidae	*Plectropomus leopardus*	0.133	0.091	0.056	0.056	0.111	0.111
Serranidae	*Plectropomus oligacanthus*	0.067	0.067	0.000	0.000	0.000	0.000
Serranidae	*Pseudanthias tuka*	0.067	0.067	0.000	0.000	8.056	2.515
Siganidae	*Siganus vulpinus*	0.000	0.000	0.000	0.000	0.000	0.000
Sphyraenidae	*Sphyraena putnamae*	0.000	0.000	0.000	0.000	0.000	0.000
Tetradontidae	*Arothron nigropunctatus*	0.000	0.000	0.000	0.000	0.056	0.056
Tetradontidae	*Canthigaster solandri*	0.133	0.091	0.000	0.000	0.056	0.056
Zanclidae	*Zanclus cornutus*	0.000	0.000	0.056	0.056	0.111	0.111