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FROM GENES TO ECOSYSTEMS: PATTERNS, PROCESSES
AND CONSEQUENCES OF DECLINING BIODIVERSITY IN
CORAL REEF FISH COMMUNITIES

Thesis submitted by

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DU GÈNE À L'ÉCOSYSTÈME: TENDANCES, PROCESSUS ET
CONSÉQUENCES DU DÉCLIN DE LA BIODIVERSITÉ DANS
LES COMMUNAUTÉS DE POISSONS DES RÉCIFS CORALLIENS

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et

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Spécialité: Écologie / Génétique des Populations

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GENERAL ABSTRACT

Halting the global decline in biodiversity is one of the greatest challenges of the 21st century. Biodiversity is being lost at every hierarchical level of biological organisation, from ecosystems to communities to species to populations and to genes. Declining diversity at any one of these levels may have serious implications for other levels of biodiversity, either above or below it in the hierarchy. However, the common factors determining local biodiversity and the functional relationships between the different levels of biodiversity are poorly understood. This thesis explores selected relationships between different levels of diversity and the potential consequences of diversity loss for fishes in coral reef ecosystems. Specifically, the four chapters of this thesis addressed the following questions: (1) How does coral habitat diversity and composition affect the diversity, abundance and structure of fish communities? (2) How does a decline in fish diversity affect the productivity of coral reef fish communities? (3) What effect does the loss of fish diversity have on the overall abundance of coral reef fish species? (4) What is the relationship between species diversity and genetic diversity in coral reef fish?

Coral reef health is declining worldwide, with reductions in coral cover, habitat structural complexity and coral species richness commonly reported. While loss of coral cover and habitat structural complexity have been shown to have significant effects on the diversity and abundance of fish communities, the consequences of coral diversity loss on the diversity and composition of reef fish assemblages is largely unknown. **Chapter 2** describes the outcomes of manipulative experiments designed to test how coral diversity and species composition affect local fish diversity, abundance and community structure. Parallel experiments were conducted at 2 geographic locations (Kimbe Bay, PNG and Lizard Is, Australia) differing in regional species composition to identify common local processes. Replicate patch reefs of the same size and coral cover were constructed to provide two comparisons: (1) Patch reefs with three different levels of coral diversity (one, three and six species) tested the effects of coral diversity on reef fish biodiversity. (2) Single-species patch reefs made from each of the six coral species were used to test the effects of coral identity on reef fish biodiversity. Fish were allowed to colonise the patch reefs over a 12-month period, with abundance and diversity recorded at regular intervals. Fish species richness increased with increasing coral

species richness at both locations, although results were only significant for Kimbe Bay. Evenness in fish also tended to increase on patch reefs with higher coral diversity, but overall abundance was little affected by coral species richness. Some single coral treatments also had similar levels of fish diversity and abundance compared to the higher coral diversity treatments. At both geographic locations, the presence of particular coral species, rather than the diversity of coral species per se, appears to be critical in promoting high local fish diversity. Multivariate analyses illustrated that the six coral species used at each location supported very different fish communities, indicating that most coral reef fish species distinguish coral habitat at the level of coral species. Following from this, the medium and high coral diversity treatments were colonised by fish assemblages that represented a combination of the fish communities inhabiting the constituent coral species. These findings highlight the importance of coral species in explaining local reef fish biodiversity, and indicate that the loss of key coral species will have a significant negative impact on reef fish biodiversity.

Biodiversity has been hypothesised to have a positive impact on the productivity of biological assemblages, because niche complementarity and facilitation among the constituent species can result in more efficient use of resources. However, these conclusions are based almost entirely on studies with plant communities, and the relationship between diversity and productivity at higher trophic levels is largely unknown, especially in the marine environment. In **Chapter 3**, a manipulative field experiment designed to test the effects of species richness and species identity on biomass accumulation in a reef fish assemblage at Lizard Island is described. Thirty juveniles belonging to three planktivorous damselfish species (Pomacentridae) were released onto each patch reef according to three different levels of fish species richness (1, 2 and 3 species) and seven combinations of fish species. Accumulation of biomass was recorded after 18 days. Species richness had no effect on the percent increase in biomass (weight) in this assemblage. However, the percent increase in biomass differed among fish species and among the different combinations of species. Patterns of biomass were best explained by species-specific differences in growth, and differences in the intensity of both intra- and interspecific competition. Niche complementarity and facilitation do not appear to be important drivers of productivity within this guild of planktivorous fishes. As a result, overall productivity may be resilient to declining reef fish biodiversity, except for the loss of fast growing fish species.

The overall abundance of individuals in a community may be resilient to declining biodiversity if the loss of some species results in an increase in abundance of surviving species (so-called “density compensation”). However, total density may increase with increasing species richness in unsaturated communities, which can be explained by complementarity, facilitation and / or a sampling effect. **Chapter 4** provides the first experimental test of how changes in fish species richness affect patterns of abundance in a coral reef fish community. Species diversity in recruiting damselfish was manipulated on experimental patch reefs to two, four, six and eight species over a period of 10 weeks. Under a density compensation model, different treatments were predicted to reach the same total densities, and densities of individual species should decline with increasing diversity. These hypotheses were not supported. Overall density increased significantly with increasing species richness and individual species densities exhibited little variation with changing species diversity. The absence of density compensation suggests that these communities do not reach saturation over 10 weeks, despite an upper limit in species richness and in some species, individual species abundances, appears to have been reached. Results suggest that the progressive loss of species in reef fish assemblages due to habitat loss and climate change will lead to an overall decline in the abundance of reef fishes, which in turn may disrupt their role in coral reef ecosystems.

Understanding the relationship between genetic diversity and species diversity is critical for developing contemporary strategies for biodiversity conservation. While concordant large-scale clines in genetic and species diversity have been described for terrestrial organisms, whether or not these parameters co-vary in marine species is largely unknown. In **Chapter 5**, patterns of genetic diversity and composition were examined for 11 reef fish species (from 5 families) sampled at 3 locations across the Pacific Ocean species diversity gradient, from high diversity on the Great Barrier Reef, Australia (~1600 species), intermediate in New Caledonia (~1400 species), to low diversity in French Polynesia (~800 species). The combined genetic diversity for all 11 species paralleled the decline in species diversity from the West to East, with French Polynesia exhibiting lowest total haplotype and nucleotide diversity. Haplotype diversity consistently declined towards French Polynesia in all species and nucleotide diversity declined in the majority of species. Coinciding with reduced genetic diversity, the population of most species in French Polynesia also exhibited significant genetic

differentiation from the Great Barrier Reef and New Caledonia locations. The location and time of species origin, vicariance events, reduced gene flow and increasing isolation, as well as decreasing habitat area from the West to the East Pacific are all likely to have contributed to the positive correlation between genetic and species diversity across the Pacific Ocean, with isolation and habitat area likely to be most influential. The congruence between species and genetic diversity, and the large-scale patterns in species and genetic composition, suggest conservation strategies applied at one level may act as a surrogate for the other.

This thesis is an important step in developing a more comprehensive understanding of the relationships between different levels of biodiversity on coral reefs. The results will be important in predicting the likely impacts that diversity loss at any one level will have on other levels within the ecosystem. The connections between different levels of diversity have been found to be strong in some cases, but not others, and to be causally related in some cases, but not others. The study has highlighted the strong causal link between coral and fish species biodiversity, and a complex relationship between fish species and genetic diversity. In the future, these links will be important components of integrated understanding of the consequences of declining biodiversity in coral reef ecosystems.

RÉSUMÉ GÉNÉRAL

Freiner la baisse mondiale de la biodiversité est l'un des plus grands défis du 21ème siècle. La biodiversité décroît à tous les niveaux hiérarchiques de l'organisation biologique, des écosystèmes aux communautés aux espèces aux populations et aux gènes. Le déclin de la diversité pour l'un de ces niveaux peut avoir de graves conséquences pour les autres strates de la biodiversité, que ce soit au dessus ou en dessous dans la hiérarchie. Cependant, les facteurs communs qui déterminent la biodiversité locale et les relations fonctionnelles entre les différents niveaux de biodiversité sont mal comprises. Ce travail de thèse explore certaines relations entre différents niveaux de diversité et les conséquences potentielles de la perte de diversité chez les poissons dans les écosystèmes de récifs coralliens. Plus précisément, les quatre chapitres de cette thèse ont abordé les questions suivantes: (1) Comment la diversité et la composition des habitats coralliens influent sur la diversité, l'abondance et la structure des communautés de poissons ; (2) Comment un déclin de la diversité des poissons affecte la productivité des communautés de poissons récifaux coralliens ; (3) Quels sont les effets de la perte de diversité de poissons sur l'abondance globale des espèces de poissons récifaux coralliens ; (4) Quelle est la relation entre diversité spécifique et diversité génétique dans le contexte des poissons récifaux?

La santé des récifs coralliens est menacée dans le monde entier, avec des réductions de la couverture corallienne, de la complexité structurale de l'habitat et de la richesse en espèces de coraux qui sont fréquemment rapportées. Bien qu'il ait été largement démontré que la perte de la couverture corallienne et de la complexité structurale de l'habitat a des effets significatifs sur la diversité et l'abondance des communautés de poissons, les conséquences de l'appauvrissement de la diversité des coraux sur la diversité et la composition des peuplements de poissons des récifs demeurent largement inconnue. Le **chapitre 2** décrit les résultats de manipulations expérimentales visant à tester comment la diversité et la composition corallienne affectent les assemblages locaux de poissons en termes de diversité, d'abondance et de structure des communautés. Des expériences parallèles ont été menées sur 2 sites géographiques (Kimbe Bay, PNG et Lizard Island, Australie) avec des compositions régionales des espèces différentes afin d'identifier des processus locaux en commun. Des répliques de

réécifs expérimentaux de même taille et de même couverture corallienne ont été construits pour fournir deux comparaisons: (1) Des récifs de trois différents niveaux de diversité corallienne (un, trois et six espèces) ont testé l'influence de la diversité des coraux sur la biodiversité des poissons récifaux ; (2) Des récifs à espèce unique fabriqués à partir de chacune des six espèces de corail ont été utilisés pour tester la variabilité de la biodiversité des poissons récifaux dans un contexte d'habitat corallien unique. Les poissons ont colonisés les récifs sur une période de 12 mois et l'abondance et la diversité ont été reportées (par comptages visuels) à intervalles réguliers. La richesse spécifique des poissons augmentait avec la richesse spécifique des coraux aux deux endroits, mais les résultats n'étaient significatifs que pour Kimbe Bay. L'uniformité des espèces de poissons avait aussi tendance à augmenter sur les récifs de diversité corallienne plus élevée, mais l'abondance globale a été peu affectée par la richesse spécifique des coraux. Cependant, certains traitements avec une seule espèce de corail avaient des niveaux similaires de diversité de poisson. Dans les deux zones géographiques, la présence de certaines espèces de coraux, plutôt que la diversité de corail en soi, semble être particulièrement importante pour promouvoir une grande diversité locale de poissons. Les analyses multivariées ont montré que les six espèces de coraux utilisés à chaque endroit soutenaient des communautés de poissons très différentes, ce qui indique que les espèces de poissons de récifs coralliens sélectionnent l'habitat corallien principalement au niveau des espèces de coraux. Les traitements avec des diversités de coraux moyennes et hautes ont été colonisés par des assemblages de poissons qui représentent un mélange des communautés de poissons typique des espèces de corail. Ces résultats soulignent l'importance de l'espèce de corail dans l'explication de la biodiversité locale des poissons coralliens, et indiquent que la perte d'espèces de coraux aura un impact négatif significatif sur la biodiversité des poissons de récifs.

La biodiversité a été présumée avoir un impact positif sur la productivité des peuplements biologiques, dans la mesure où la complémentarité des niches et la facilitation entre espèces qui les composent peuvent conduire à une utilisation plus efficace des ressources. Cependant, ces conclusions sont presque entièrement basées sur des études sur les communautés végétales, et la relation entre la diversité et la productivité dans des niveaux trophiques supérieurs demeure largement inconnue, en particulier dans le milieu marin. Dans le **chapitre 3**, une expérience impliquant des

manipulations du terrain et visant à tester les effets de la richesse spécifique et de l'identité des espèces sur l'accumulation de la biomasse dans un assemblage de poissons de récif à Lizard Island est décrite. Trente juvéniles appartenant à trois espèces de poissons demoiselles planctophages (Pomacentridae) ont été libérés sur chaque récif avec trois niveaux différents de richesse d'espèces de poissons (1, 2 et 3 espèces) et sept combinaisons d'espèces de poissons. L'accumulation de la biomasse a été enregistrée après 18 jours. La richesse spécifique n'a eu aucun effet sur l'augmentation en pourcentage de biomasse (poids) dans cet assemblage. Toutefois, l'augmentation en pourcentage de biomasse différait entre les espèces de poissons et les différentes combinaisons d'espèces. Les tendances de la biomasse s'expliquent principalement par des différences spécifiques en termes de croissance, et des différences dans l'intensité de compétition intra- et interspécifique. La complémentarité de niches et la facilitation ne semblent pas être des moteurs importants de la productivité globale dans cette guildes des poissons planctophages. La productivité totale semble donc résiliente au déclin de la biodiversité des poissons de récif, à l'exception de la perte d'espèces de poissons de croissance rapide.

L'abondance globale d'individus dans une communauté peut être résiliente à la baisse de biodiversité si la perte de certaines espèces se traduit par une augmentation de l'abondance des espèces survivantes (on parle alors de "compensation de densité"). Cependant, la densité totale peut augmenter en même temps qu'une augmentation de la richesse spécifique dans les communautés non saturées, ce qui peut s'expliquer par la complémentarité, la facilitation et / ou un effet d'échantillonnage. Le **chapitre 4** présente le premier test expérimental pour évaluer la façon dont des changements de richesse spécifique de poissons affectent les tendances d'abondance dans une communauté de poissons des récifs coralliens. La diversité spécifique dans les recrues de poissons demoiselles (Pomacentridae) a été manipulé sur des récifs expérimentaux avec 2, 4, 6 et 8 espèces sur une période de 10 semaines. Sous un modèle de compensation de densité, différents traitements ont été simulés afin d'atteindre les mêmes densités totales, alors que la densité des espèces à proprement parler devraient diminuer avec l'accroissement de la diversité. Ces hypothèses n'ont pas été confirmées. La densité globale a augmenté de manière significative avec l'augmentation de la richesse spécifique alors que la densité des espèces affichait peu de variation avec le changement de la diversité spécifique. L'absence de compensation des densités suggère

que les modèles d'abondance dans cette communauté ne sont pas dirigés par de la compétition interspécifique. Les résultats suggèrent que la perte progressive des espèces dans les peuplements de poissons des récifs en raison de la perte d'habitat et le changement climatique entraînera une baisse globale de l'abondance des poissons de récif, ce qui peut perturber leur rôle dans les écosystèmes des récifs coralliens.

Comprendre la relation entre la diversité génétique et la diversité des espèces est essentiel au développement de stratégies contemporaines de conservation de la biodiversité. Bien que des clines concordantes entre la diversité génétique et la diversité spécifique, à grande échelle, ont été décrits pour les organismes terrestres, on ne peut pas dire si ces paramètres co-varient ou non en milieu marin. Dans le **chapitre 5**, les variations de diversité et de composition génétique ont été étudiés pour 11 espèces de poissons coralliens (appartenant à 5 familles) échantillonnés à 3 sites dans l'océan Pacifique le long d'un gradient de diversité spécifique, caractérisé par une grande diversité sur la Grande Barrière de corail, en Australie (~ 1600 espèces), une diversité intermédiaire en Nouvelle-Calédonie (~ 1400 espèces), et une faible diversité en Polynésie française (~ 800 espèces). La diversité génétique combinée pour les 11 espèces suit le déclin de la diversité spécifique de l'Ouest vers l'Est, avec la Polynésie française présentant les plus faibles valeurs en termes de diversité nucléotidique et haplotypique. La diversité haplotypique diminue de façon constante de la Grande Barrière vers la Polynésie française pour toutes les espèces et la diversité nucléotidique a diminué dans la majorité des espèces. Coïncidant avec une diversité génétique réduite, la population en Polynésie française dans la plupart des espèces a également montré une différenciation génétique significative par rapport aux populations de la Grande Barrière de Corail et de la Nouvelle-Calédonie. Le lieu et le moment de l'origine des espèces, des événements de vicariance, de flux de gènes et d'un isolement croissant, ainsi que la diminution des zones d'habitat du Pacifique Ouest à Est sont tous susceptibles d'avoir contribué à la corrélation positive entre la diversité génétique et spécifique à travers l'océan Pacifique, avec l'isolation et la zone d'habitat susceptibles d'être les plus influents. La concordance entre les diversités génétique et spécifique, et les distributions, à grande échelle des compositions spécifique et génétique, suggèrent que des stratégies de conservation visant à maximiser la protection des espèces peut également se traduire par une préservation de la diversité génétique.

Cette thèse est une étape importante dans l'élaboration d'une compréhension plus complète des relations entre les différents niveaux de la biodiversité dans les récifs coralliens. Les résultats sont importants pour prédire l'impact probable que la perte de diversité, à n'importe quel niveau, aura sur d'autres niveaux au sein de l'écosystème. Les connexions entre les différents niveaux de la diversité sont significatives et fortes dans certains cas, mais pas dans d'autres, pour être parfois sous la perspective de relation causale dans certains cas, mais pas dans d'autres. L'étude a mis en évidence le lien solide de causalité entre la biodiversité d'espèces de corail et de poisson, et une relation complexe entre la diversité génétique et spécifique de poissons. À l'avenir, ces liens seront des éléments importants pour la compréhension intégrée des conséquences du déclin de la biodiversité dans les écosystèmes des récifs coralliens.

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1 CHAPTER 1 - GENERAL INTRODUCTION

Anthropogenic impacts and climate change are threatening all ecological systems of our planet, with consequences such as biodiversity loss and disruptions to ecosystem processes (Soule 1991; Thomas *et al.* 2004; Lovejoy & Hannah 2005; Munday *et al.* 2008; Rockstrom *et al.* 2009). Few areas remain unaffected by human influence and nearly half of our earth's surface is strongly impacted by multiple drivers (Vitousek *et al.* 1997; Halpern *et al.* 2008). In particular human-induced habitat loss and degradation have already resulted in hundreds of extinctions in the terrestrial environment over the last century (Ehrlich 1995; Pimm *et al.* 1995; Vitousek *et al.* 1997; Sala *et al.* 2000; Fahrig 2001) and this trend is expected to accelerate with rapid climate change (Thomas *et al.* 2004). Growing concern about the increasing threats to biodiversity has stimulated numerous studies, but the effects of biodiversity loss on ecosystem functioning still remain poorly understood and widely debated (Chapin *et al.* 2000; Loreau *et al.* 2001; Hooper *et al.* 2005; Bracken *et al.* 2008). Increasing evidence suggests that biodiversity loss is likely to extend to declining ecosystem functions, such as productivity, stability and recovery potential (Chapin *et al.* 2000; Fridley 2001; Loreau *et al.* 2001; Cameron 2002; Hooper *et al.* 2005; Balvanera *et al.* 2006; Duffy *et al.* 2007). A recent meta-analysis of experimental studies suggests that species loss often affects the functioning of a wide variety of organisms and ecosystems, but the extent of these effects is ultimately determined by which species are lost (Cardinale *et al.* 2006).

Most studies considering the consequences of biodiversity loss address species diversity, although biodiversity can be defined and measured at many different levels, from genes and populations, to species, to communities and ultimately ecosystems (Soule 1991). Ecological studies and conservation actions usually target a particular level of biodiversity, despite the potential that the different levels of diversity are inextricably linked (Soule 1991). Genetic diversity ensures the viability and persistence of populations, different populations increase the chance of survival of a species;

species influence the stability and productivity of a community, which in turn ensure ecosystem services. In the other direction, processes that primarily degrade ecosystems may have cascading effects on constituent species, populations and their genetic composition (Franklin 1993; Tracy & Brussard 1994). Although there has been an ongoing debate about the appropriate level to target conservation actions (Franklin 1993; Tracy & Brussard 1994; Possingham *et al.* 2002; Taylor *et al.* 2005; Laikre 2010), our understanding of the relationships between any two levels of diversity, as well as how diversity loss on one level affects another, is extremely limited.

One of the primary examples of links between two levels of biodiversity is the relationship between communities of habitat-forming organisms and assemblages that are dependent upon these habitats (Bell & Galzin 1984; Jones & Andrew 1990; Chabanet *et al.* 1997; Tews *et al.* 2004; Baldi 2008; Qian *et al.* 2009). Habitat loss, degradation and fragmentation have been shown to have detrimental effects on inhabiting communities in terms of diversity and abundance (Ehrlich 1995; Vitousek *et al.* 1997; Fahrig 2001), but the effects of declining habitat biodiversity are less well known. A diverse habitat provides a wider range of resources, such as food and shelter, and is therefore assumed to offer more niches and diverse ways of exploiting environmental resources (Tews *et al.* 2004; Kadmon & Allouche 2007). As a result, species diversity is expected to increase through niche differentiation amongst inhabiting species. Positive effects of plant diversity on the faunal communities that inhabit them have been described for a number of faunal groups, particularly mammals (reviewed in (Tews *et al.* 2004)). It is therefore expected that declining habitat diversity will lead to a decline in the biodiversity of associated faunal communities, and specialised species associated with a narrow range of habitats will be vulnerable to extinction (McKinney 1997).

Species diversity loss may also affect ecosystem functioning in terms of productivity, as it has been hypothesised that productivity increases as a function of species diversity (Naeem *et al.* 1994; Naeem *et al.* 1996; Tilman *et al.* 1996; Tilman *et al.* 1997a; Tilman *et al.* 1997b; Hector *et al.* 1999). The positive effects of diversity on productivity are mostly attributed to niche differentiation, facilitation and a “sampling effect” (Naeem *et al.* 1994; Hooper 1998; Fridley 2001; Loreau *et al.* 2001; Cardinale *et*

al. 2007). A diverse community may exploit available resources more efficiently through niche specialisation and complementarity (MacArthur 1970; Tilman *et al.* 1997b; Chesson 2000; Finke & Snyder 2008). In communities characterised by positive interactions among species, the presence of certain species may also facilitate the establishment of others (Hector *et al.* 1999; Loreau & Hector 2001; Mulder *et al.* 2001; Callaway 2007). However, it has also been argued that the diversity-productivity relationship arises simply because diverse communities are more likely to include a highly productive species (the “sampling effect”) (Aarssen 1997; Huston 1997; Tilman *et al.* 1997b). Others argue that the cause-effect interpretation should be reversed, because it is highly productive environments that support greater biodiversity (Connell & Orias 1964; Leigh 1965; Waide *et al.* 1999; Huston & Wolverton 2009). There are also alternative theories that predict a negative effect of species diversity on productivity through trade-offs between competitive ability and productivity (Tilman 2000). In this case, a productive species that is competitively inferior may perform better in monocultures than in diverse mixtures. Indeed, a number of studies have found that diverse assemblages are often not more productive than the most productive monoculture (Cardinale *et al.* 2006). Hump-shaped relationships between productivity and diversity may also be observed as competitive exclusions increase with diversity (Waide *et al.* 1999). The impact of biodiversity loss on productivity depends upon which theory applies to the ecosystem under investigation.

Diversity loss at the species level may also impact on the abundance of remaining species. Some theories predict that a system supports a fixed density of ecologically similar species (Gonzalez & Loreau 2009). As a result, average population abundances are expected to be low in diverse systems and increase with decreasing diversity (density compensation) (MacArthur *et al.* 1972). This concept has recently been applied to assess if the loss of a species may be compensated for by an increase in average abundance by the remaining species (Ruesink & Srivastava 2001; Ives & Cardinale 2004; Jiang 2007; Gonzalez & Loreau 2009). Such compensatory changes in the abundance of species would have stabilising effects on ecosystem processes (Tilman *et al.* 1998; Tilman *et al.* 2006) and has been supported by some experimental evidence (Riipinen *et al.* 2010). However, the stabilising effects of density compensation will gradually deplete as diversity loss progresses (Ives & Cardinale 2004; Bunker *et al.*

2005). Evidence also suggests that overall density generally increases with species diversity and asymptotes as the system reaches saturation (Tilman 1999, 2000). Such complementarity effects suggest that diversity loss may negatively affect ecosystems by depleting the overall abundance of individuals in communities.

Ecosystem stability, resilience and dynamics have been found to generally increase both with species and genetic diversity (Loreau *et al.* 2001; Hughes & Stachowicz 2004; Reusch *et al.* 2005), but whether these two levels of diversity are causally related, or are determined by the same independent processes is largely unknown (Wehenkel *et al.* 2006). Vellend (2005) recently proposed that the concepts and processes underlying theories of species and genetic diversity are remarkably similar and identified a number of parallel processes: 1) speciation or mutation create new alleles or species respectively, 2) drift causes random changes in the relative frequencies of alleles and species, 3) migration results in the addition of alleles to a population or species to a community and 4) selection, where environmental heterogeneity can favour particular alleles or species over others (Vellend & Geber 2005). Other important driving forces include the effects of area and isolation, which similarly affect both species and genetic diversity, as described in island biogeography theories (Vellend 2003). Causal links between the two levels of diversity may also incur through increasing species extinction risk with low genetic diversity (Frankham 2005; Laikre 2010). Large-scale clines have been observed for both levels of diversity across spatial or environmental gradients, such as altitude, latitude and depth (Rosenzweig 1995; Gaston 2000; Manel *et al.* 2003; Palo *et al.* 2003a; Giordano *et al.* 2007; Palma-Silva *et al.* 2009), but are only rarely considered together. If species and genetic diversity co-vary, management strategies that target the protection at one level will be a useful surrogate for the other.

The above-mentioned theories underlying the relationships between different levels of biodiversity have been based on terrestrial environments. Links between elements of biodiversity and function in marine ecosystems are largely unknown and have seldom been investigated. Although marine extinctions appear to be few to date, dramatic declines in the extent and structure of shallow marine habitats have been widely documented (McClanahan 2002; Steneck *et al.* 2003). Coral reefs in particular are one of the most diverse and threatened of all marine ecosystems and their health is declining

on a global scale (Hoegh-Guldberg 1999; Gardner *et al.* 2003; Hughes *et al.* 2003; Wilkinson 2004). The extent of habitat loss on coral reefs is sufficient to cause dramatic reductions in fish abundance and local extinctions of some species (Jones *et al.* 2004; Munday 2004b). More extinctions are expected as threats, such as climate change induced coral bleaching, overexploitation, increasing intensity and frequency of tropical storms, as well as crown of thorns outbreaks, increasingly affect coral reefs (Sala & Knowlton 2006). Despite numerous threats to marine biodiversity, the consequences of loss of species and / or genes to the marine ecosystem remain poorly understood.

This thesis explored four selected relationships between different levels of diversity as well as the potential consequences of biodiversity loss for coral reef fish communities. While the processes establishing (Bellwood & Hughes 2001; Bellwood & Wainwright 2002; Mora *et al.* 2003) and maintaining (Bell & Galzin 1984; Sale 1991; Chabanet *et al.* 1997) species diversity have been well-studied and discussed, there have been almost no investigations into links between genetic diversity, species diversity and ecosystem parameters such as productivity and abundance for these diverse assemblages. *The overall objective of this thesis was to combine observational and experimental approaches to evaluate relationships between different levels of diversity and to assess the potential consequences of biodiversity loss on coral reef fish assemblages.* The following 4 specific questions were addressed in each chapter:

- (1) *How does habitat biodiversity (i.e. coral species richness, identity and composition) affect the diversity, abundance and structure of fish communities?*
- (2) *Does a decline in fish diversity affect the productivity of coral reef fish communities?*
- (3) *What effect does the loss of fish diversity have on the abundance of coral reef fish species and/or the total abundance of individuals in the community?*
- (4) *Are species and genetic diversity correlated in coral reef fishes and what is the basis of this relationship?*

Chapter 2 assesses the effects of coral diversity and species composition on fish communities, in terms of diversity, abundance and community structure. A decline in percent coral cover has been shown to have detrimental effects on the diversity and

abundance of fish communities in numerous studies (Syms & Jones 2000; McClanahan 2002; Jones *et al.* 2004; Munday 2004b; Graham *et al.* 2006; Wilson *et al.* 2006). However, very little is known about the effects of coral diversity loss on coral reef fish communities. Coral and fish diversity are strongly correlated across the Indian and Pacific oceans (Hughes *et al.* 2002), but it is unclear whether this large-scale correlation also applies to a local scale and whether or not the two factors are causally related. Corals are the primary habitat-forming organisms on coral reefs and can greatly influence the structure of reef fish communities (Luckhurst & Luckhurst 1978; Jones & Syms 1998; Öhman & Rajasuriya 1998). As a diverse coral community provides a wider range of resources, such as food and shelter, it is likely to support an equally diverse fish assemblage. Fewer coral species might therefore be expected to cause a decline in fish diversity, which in turn may have compounding effects on the overall abundance and productivity of the reef fish community. Furthermore, if different coral species support distinct fish communities, coral diversity loss may also result in loss of unique fish assemblages.

The effects of local coral reef fish diversity on the productivity (increase in biomass) of reef fish assemblages were determined in **Chapter 3**. Diverse plant systems are generally found to be more productive through more efficient use of available resources as a result of niche differentiation and facilitation (Fridley 2001; Loreau *et al.* 2001; Hooper *et al.* 2005; Marquard *et al.* 2009). However, very little is known about the relationship between species diversity and productivity in the marine environment. A meta-analysis of experiments assessing the effects of biodiversity on productivity in marine plants, bacteria and plankton showed an 80% increase in primary and secondary production in diverse mixtures compared to monocultures (Worm *et al.* 2006). Whether diversity positively affects productivity at higher trophic levels in the marine environment or on coral reefs has never been examined.

Chapter 4 addresses the potential impacts of fish diversity loss on the overall abundance of reef fish populations, specifically testing whether low species richness may be compensated for by higher average population densities. Evidence for density compensation is almost completely lacking for coral reef fishes, although a global study on the patterns of species richness and abundance in butterflyfish provided some

support (Findley & Findley 2001). Overall abundance declined together with species richness with distance from the diversity centre, but not as rapidly, resulting in increasing average abundance per species (Findley & Findley 2001). On a smaller scale, limited evidence for density compensation was also found in competing surfperches and gobies, although overall abundances were higher when both species were present (Holbrook *et al.* 2002; Munday 2004a). If compensatory mechanisms are a common occurrence in reef fishes, the extinction risk of remaining species should be reduced and the functional role of a species group within the community is more likely to be maintained.

In the last chapter (**Chapter 5**), I tested whether species diversity and genetic diversity were correlated in coral reef fish. Large-scale patterns in genetic diversity were assessed using molecular analyses, which were then compared to the species diversity gradient across the Pacific. Species diversity in reef organisms peaks in the East Indies Triangle and gradually declines in all directions (Rosen 1981; Bellwood & Hughes 2001; Mora *et al.* 2003; Reaka *et al.* 2008; Bellwood & Meyer 2009). Limited evidence suggests that genetic diversity may parallel the species diversity decline across the Pacific. Palumbi (1996) described reduced genetic diversity in peripheral populations compared to the centre of diversity as a result of lower population sizes and greater isolation. Briggs (1999) also suggested that genetic diversity should decline with increasing distance from the East Indies Triangle basing his arguments on species origin within the centre of diversity and gradually radiating outwards with populations becoming increasingly younger. Whether or not species and genetic diversity are positively correlated has never been specifically examined for reef fish.

2 CHAPTER 2

HABITAT BIODIVERSITY AS A DETERMINANT OF LOCAL FISH COMMUNITY STRUCTURE ON CORAL REEFS

2.1 ABSTRACT

Habitat biodiversity is expected to promote the diversity of animal communities because a greater variety of habitats increases the opportunities for coexistence of species specialised on different resources. Coral reefs, which are among the most diverse ecosystems known, are under threat from climate change and other anthropogenic stresses. Hard corals, which are the primary habitat-forming organisms for most reef-associated organisms, are especially susceptible to these threats. While declines in coral biodiversity have been documented worldwide, the consequences for the diversity and community structure of other reef-associated species is largely unknown. Here the effects of coral diversity and composition on fish diversity, abundance and community structure were investigated using manipulative field experiments. Parallel experiments were conducted at two geographic locations (Kimbe Bay, PNG and Lizard Is, Australia) differing in regional species composition to identify common local processes. I tested whether coral biodiversity determines local reef fish biodiversity by constructing patch reefs differing in coral diversity and/or species composition, while controlling for reef size and coral cover. Patch reefs with three different levels of coral diversity (one, three and six species) tested the effects of coral diversity on reef fish species richness. In addition, single-species patch reefs made from each of the six coral species were used to determine the effects of coral identity on local reef fish community structure. Fish were allowed to colonise the patch reefs over a 12-month period. Fish species richness increased with increasing coral species richness in both locations, although results were only significant for Kimbe Bay. Evenness in fish

also tended to increase on patch reefs with higher coral diversity, but total abundance was not affected by coral species richness. At both geographic locations, some single coral treatments had similar levels of fish diversity and abundance compared to the higher coral diversity treatments, suggesting that particular coral species, rather than the diversity of coral species per se, are important in promoting high local fish diversity. Multivariate analyses further illustrated that the six coral species used at each location supported very different fish communities, indicating that most coral reef fish species distinguish coral habitat at the level of coral species. The medium and high coral diversity treatments were colonised by fish assemblages that represented a combination of the fish communities inhabiting the constituent coral species. These findings highlight the importance of coral species in explaining local reef fish biodiversity, and indicate that the loss of key coral species will have a significant negative impact on reef fish biodiversity.

2.2 INTRODUCTION

Understanding the causes and consequences of biodiversity loss is one of the most urgent challenges facing ecologists and a key issue for conservation planning (Soule 1991; Balmford *et al.* 2005). Habitat loss is widely recognised as one of the main drivers of declining biodiversity, particularly for terrestrial environments (Vitousek *et al.* 1997; Fahrig 2001; Laurance 2007). In many instances, habitat is transformed to a state of lower diversity and complexity, rather than being completely lost. Consequently, determining the extent to which the diversity of animal communities is dependant on habitat diversity is critical for predicting the outcome of ongoing habitat modification and degradation (Tews *et al.* 2004; Hortal *et al.* 2009). The roles of habitat heterogeneity and niche partitioning as important factors structuring ecological communities are emphasised in niche theory (Chesson 2000; Silvertown 2004; Kadmon & Allouche 2007). A diverse habitat is spatially heterogeneous and structurally complex, and therefore assumed to promote species diversity by offering greater niche space and diverse ways of exploiting environmental resources (Tews *et al.* 2004; Kadmon & Allouche 2007). Biological and physical habitat diversity is therefore predicted to play a vital role in structuring faunal communities.

In the terrestrial environment, plants are the primary habitat-forming organisms, and the relationship between plant diversity and the diversity of associated animal communities has been shown to be mostly positive (Lawton 1983; Davidowitz & Rosenzweig 1998; Tews *et al.* 2004; Hortal *et al.* 2009; Qian *et al.* 2009), although occasionally no relationship (Currie 1991) or negative relationships (Ralph 1985) have also been reported. In the marine environment, very little is known about the relationship between habitat diversity and animal diversity. Yet, coral reefs are one of the most diverse ecosystems on Earth and are well known for their extraordinary diversity of fishes, which are closely associated with the reef substratum. Scleractinian corals are the primary habitat-forming organisms on coral reefs and can greatly influence the structure of reef fish assemblages (Luckhurst & Luckhurst 1978; Jones & Syms 1998; Öhman & Rajasuriya 1998). Coral cover and topographic complexity of reef habitat, in particular, appear to have a significant influence on reef fish diversity, with numerous studies reporting positive relationships (Luckhurst & Luckhurst 1978; Bell & Galzin 1984; Roberts & Ormond 1987; McClanahan 1994; Öhman & Rajasuriya 1998). In contrast, the role of coral biodiversity in maintaining local fish diversity has received little attention.

The importance of live coral for reef fishes has been demonstrated in many studies. It has been estimated that around 9-11% of all coral reef fishes are strictly dependent on live coral for food or living space (Jones *et al.* 2004; Pratchett *et al.* 2008), and as many as two thirds of coral reef fish are only found at sites with live coral (Bell & Galzin 1984). Some coral reef fishes are associated with particular coral species (Sale 1991; Munday 2004b; Gardiner & Jones 2005) and different coral species have been shown to support different fish communities (Holbrook *et al.* 2002; Feary *et al.* 2007). The strongest associations with a particular coral species are generally found for coral reef fish with particular resource requirements, such as obligate coral dwelling (e.g. species of *Gobiodon*) (Munday *et al.* 1997) or coral feeding fishes (e.g. many species of *Chaetodon*) (Pratchett 2005; Pratchett & Berumen 2008). Other fish species may be less dependent on specific coral species, although may show a preference for certain coral species as important shelter or recruitment sites (Jones *et al.* 2004). The effect of coral biodiversity on the structure of reef fish assemblages will likely depend on the degree of habitat specialisation exhibited by the constituent fish species.

Coral reefs are one of the most threatened and vulnerable marine ecosystems and decline in coral cover and changes in habitat structure have already been demonstrated on a global scale (Hoegh-Guldberg 1999; Gardner *et al.* 2003; Hughes *et al.* 2003; Wilkinson 2004). Detrimental effects on the diversity and abundance of fish communities have been widely reported as a consequence of loss in coral cover and structural complexity, mostly affecting fish species that are dependent on live coral for shelter, food or recruitment sites (Syms & Jones 2000; McClanahan 2002; Jones *et al.* 2004; Graham *et al.* 2006; Wilson *et al.* 2006; Pratchett *et al.* 2008; Paddack *et al.* 2009). Disturbances, such as coral bleaching, storms and crown of thorn outbreaks, affect certain types of corals more strongly than others. Consequently, these stresses can lead to a shift in coral community structure and a loss of local coral diversity (McClanahan *et al.* 2007). The impacts that such a loss of coral diversity has on coral reef fish communities is unknown, but will be critical in determining the response of reef fishes to predicted increases in habitat disturbance due to global warming.

In this study, manipulative field experiments were used to assess for the first time the potential causal relationship between local coral and fish biodiversity. Specifically, I tested two hypotheses: 1) that coral species richness is a primary determinant of reef fish species richness, diversity and abundance, and 2) that different coral species support different fish communities, and fish community composition is dependent on the presence of particular coral species. Diverse coral communities are predicted to support a similarly diverse fish assemblage, as a result, a reduction in coral species is expected to cause a decline in fish diversity, which in turn may have compounding effects on the overall abundance of the reef fish community. Fish assemblages are also expected to differ between different coral species, if the majority of species are specialised on or have a preference for particular microhabitats. Furthermore, certain coral species may be preferred over others by many reef fish species and will therefore play a more important role in maintaining fish diversity and abundance and would have a greater impact on fish assemblages if lost. To determine whether local patterns are robust to regional differences in fish species composition or fish-habitat interactions, the experiment was repeated in two geographic locations; Kimbe Bay, Papua New Guinea, and Lizard Island, on the Great Barrier Reef, Australia. The two locations are characterised by similarly high levels of coral and fish diversity, but substantial differences in fish community structure.

2.3 METHODS

2.3.1 Experimental design and protocols

To test the effects of coral diversity on fish communities, manipulative experiments were set up in the lagoons of Lizard Island on the Great Barrier Reef, Australia (14° 41'S, 145° 27'E) and Schumann Island in Kimbe Bay, northern Papua New Guinea (5°31'S, 150°5'E) (Figure 2.1).

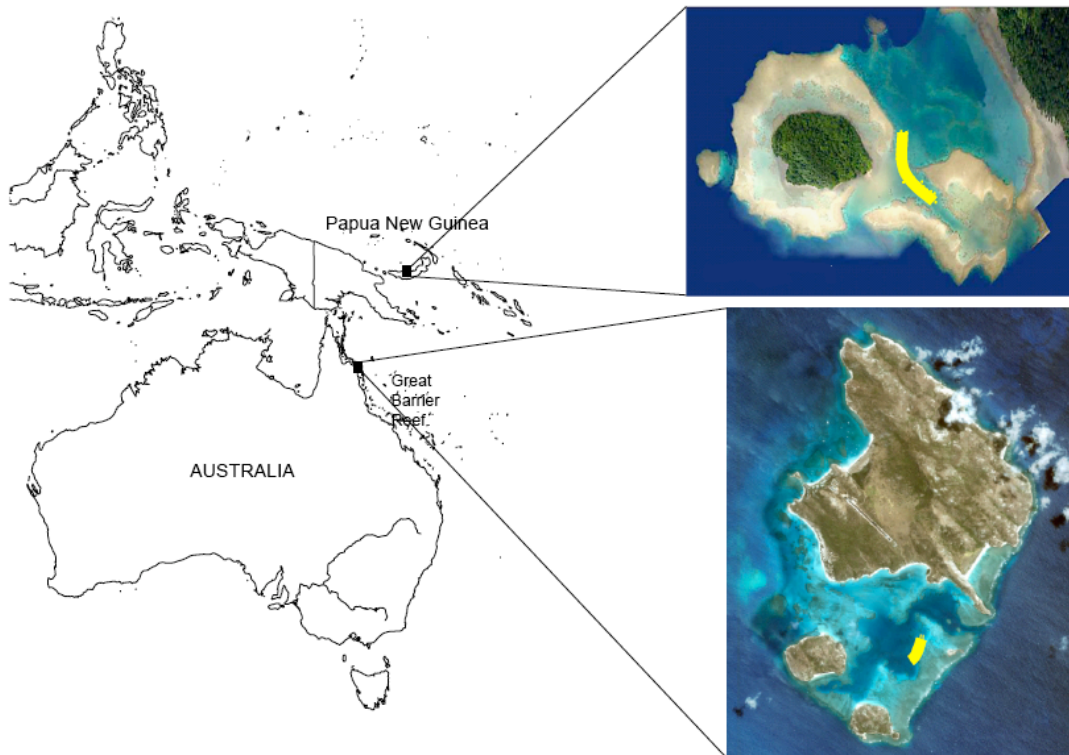


Figure 2.1: Map of the South-West Pacific showing the location of the two experimental sites Schumann Island in Kimbe Bay (Papua New Guinea) and Lizard Island on the Great Barrier Reef (Australia).

In each location, 45 patch reefs were constructed using a total of six different coral species (Table 2.1). To examine the effects of coral species richness on fish community characteristics, patch reefs consisted of: (i) one coral species, (ii) three coral species and (iii) six coral species. To examine the effects of coral species composition on fish assemblages, the single species treatment was duplicated for all of the six coral species

used in the experiment, and two medium diversity treatments were established using two different combinations of 3 coral species (see Table 2.1 for the coral species combinations). All nine treatments were replicated five times. At each location, six common reef-building coral species with a branching morphology were selected for the experiment. It was possible to use the same coral species at both locations for four of the six species: *Acropora nasuta*, *Pocillopora damicornis*, *Porites cylindrica* and *Seriatopora hystrix*. Two species as similar as possible were used to represent staghorn *Acropora* and bottlebrush *Acropora*. For staghorn *Acropora*, *Acropora muricata* was chosen at Lizard Island and *Acropora grandis* in Kimbe Bay. Bottlebrush *Acropora* was represented by *Acropora loripes* at Lizard Island and *Acropora carduus* in Kimbe Bay (Table 2.1). For simplicity, the different treatments are referred to by abbreviations: *Acropora nasuta* (An), bottlebrush *Acropora* (Bb), *Porites cylindrica* (Pc), *Pocillopora damicornis* (Pd), *Seriatopora hystrix* (Sh), staghorn *Acropora* (St), medium A (MA), medium B (MB) and high (H) (Table 2.1).

Patch reefs were built at 3-7m depth on large flat sandy areas where no other habitat structure was present. Reefs were placed 15m apart from each other and from any neighbouring reef structures to limit fish migration between reefs. The base of each patch reef consisted of dead coral rubble, which was covered with the same amount of live coral for each patch reef (90% live coral cover) according to the experimental treatment. Patch reefs were 100cm in diameter and 50cm high.

Patch reefs were established in April 2007 in Kimbe Bay and in November 2007 at Lizard Island. Commencement of the experiment at each location was timed to match the start of the respective recruitment seasons. Recruitment is highest during the dry winter season in Kimbe Bay and a distinct recruitment peak occurs over summer at Lizard Island. Fish were allowed to naturally colonise the patch reefs over a 12-month period, during which the patch reefs were surveyed four times. For each survey the abundance of every fish species present on each reef was recorded. Recorded fish species included all those associated to the patch reefs, but excluded larger mobile species that were observed to move on a regular basis between reefs. Minor repairs were carried out where necessary after each survey. As the patch reefs in Kimbe Bay were in a deteriorated state during the last survey, the results presented here are based on the survey carried out in late November 2007. The Lizard Island data represents the 12-month survey from early December 2008.

Table 2.1: List of the coral species and number of corals used in each treatment. Abbreviations used in the text and figures are also specified.

Treatment	Abbreviations	Diversity (# spp)	Lizard Island	Kimbe Bay
<i>A. nasuta</i>	An	1	<i>Acropora nasuta</i>	<i>Acropora nasuta</i>
“Staghorn”	St	1	<i>Acropora muricata</i>	<i>Acropora grandis</i>
“Bottlebrush”	Bb	1	<i>Acropora loripes</i>	<i>Acropora carduus</i>
<i>P. damicornis</i>	Pd	1	<i>Pocillopora damicornis</i>	<i>Pocillopora damicornis</i>
<i>P. cylindrica</i>	Pc	1	<i>Porites cylindrica</i>	<i>Porites cylindrica</i>
<i>S. hystrix</i>	Sh	1	<i>Seriatopora hystrix</i>	<i>Seriatopora hystrix</i>
Medium A	MA	3	<i>Acropora loripes</i> <i>Pocillopora damicornis</i> <i>Porites cylindrica</i>	<i>Acropora carduus</i> <i>Pocillopora damicornis</i> <i>Porites cylindrica</i>
Medium B	MB	3	<i>Acropora nasuta</i> <i>Acropora muricata</i> <i>Seriatopora hystrix</i>	<i>Acropora nasuta</i> <i>Acropora grandis</i> <i>Seriatopora hystrix</i>
High	H	6	<i>Acropora nasuta</i> <i>Acropora muricata</i> <i>Acropora loripes</i> <i>Pocillopora damicornis</i> <i>Porites cylindrica</i> <i>Seriatopora hystrix</i>	<i>Acropora nasuta</i> <i>Acropora grandis</i> <i>Acropora carduus</i> <i>Pocillopora damicornis</i> <i>Porites cylindrica</i> <i>Seriatopora hystrix</i>

2.3.2 Statistical analyses

The differences between the fish communities of Lizard Island and Kimbe Bay were large with only 24.2% of the recorded species shared between locations. The data was therefore analysed separately for each location. For each location, differences in overall fish diversity and abundance between coral diversity levels (treatments) and coral species were first determined. To test the effects of coral diversity on fish assemblages, the six single coral species treatments and the two three coral species treatments were averaged. To test whether different coral species affected fish assemblages differently, fish diversity and abundance were analysed separately for each treatment. Analysis of variance (ANOVA), followed by Tukey’s HSD post hoc tests, was used to compare differences for both analyses in (i) fish species richness, (ii) fish species evenness (Shannon Evenness Index, J) and (iii) total fish abundance between

treatments. Differences in the composition of fish communities between the different coral treatments were then investigated.

Canonical analyses of principal coordinates (CAP) (Anderson & Willis 2003) and multivariate regression trees (MRT) (De'Ath 2002) were used to compare the composition of fish communities according to different species of corals and levels of coral diversity. CAP were used to illustrate and examine patterns of community change between locations and between treatments at each location. CAP is a constrained ordination technique that further analyses the results of a Principal coordinates analysis (PCO), for which the type of ecological distance can be chosen. CAP enables statistical testing of significant grouping structure within the ordination by using permutation tests to assign a *p*-value to the a-priori hypothesis that the probability of the grouping found in the analysis could be due to chance alone by 'leave-one-out' allocations. MRTs were then conducted to test the differences and similarities between groups. This multivariate discrimination technique constructs a hierarchical tree by creating splits, which minimise the dissimilarity of groups within clusters.

Both CAP and MRT analyses were based on the Bray-Curtis dissimilarity measure of log-transformed abundance data ($\ln(x+1)$). A lognormal transformation reduces the emphasis of highly abundant species, which would otherwise drive most of the observed patterns. Bray-Curtis distances are generally considered well suited for abundance data, as they ignore variables that have zeros for both objects (joint absences). As apogonids are known to obscure patterns in fish communities, these were excluded from CAP and MRT analyses to highlight differences in fish communities between treatments. Rare species, where the overall number of sightings over the 12-month period was below five individuals, were also excluded.

The number of permutations in the CAP analyses was set to 100. The default was selected for the number of meaningful PCO axes (*m*), which chooses the optimal number of axes in order to provide the best distinction between groups and maximises the proportion of correct allocations to the grouping variable and minimises misclassification error (Anderson & Willis 2003). The first two axes, which explained most of the variation, were illustrated in an ordination plot. Dispersion ellipses using 0.9 confidence limits of the standard deviation of point scores were also plotted. Species showing the strongest indication of change between treatments (i.e. correlation with axis one and/or axis two exceeds 0.2) were plotted separately and listed in Table 2.2. In

the MRT analyses, the best tree size was chosen by cross-validation and the 1-SE rule. The relative error corresponds to the amount of variation among samples not explained by the tree (De'Ath 2002). All analyses and plots were coded in R 2.10.0 (R Foundation for Statistical Computing, Vienna, Austria) using the R statistical packages *vegan*, *BiodiversityR*, *MASS* and *mvpart*.

2.4 RESULTS

2.4.1 *Regional difference in local species composition*

The fish communities that colonised the patch reefs at Lizard Island were composed of a total of 150 species, whereas 122 species were recorded in Kimbe Bay, totalling to 219 species. Fifty-three of these species were shared between locations (24.2%), representing ~ 35% of the Lizard Island fish community and ~ 43% of the Kimbe Bay communities. CAP analyses revealed strong differences in the composition of fish communities between the two locations (Figure 2.2). The two clusters were strongly supported with 71.04% correct allocations ($p = 0.001^{**}$). The best result contained seventeen PCO axes and accounted for 84.72% of the total variation. The separation between locations (first PCO axis) explained 35.08% of the total variation, whereas the second PCO axis only explained 7.59% of the total variation.

2.4.2 *Effects of coral species richness on fish species richness and abundance*

Fish species richness significantly increased with increasing coral species richness in Kimbe Bay ($p < 0.001^{***}$), with low coral diversity supporting significantly lower fish species richness (13.6) than medium (17.7) and high (20.0) coral diversity (Figure 2.3b, Table 2.2). At Lizard Island, fish species richness increased from a mean of 21.0 to 25.0 species with increasing coral species richness, but the results were not significant ($p = 0.183$) (Figure 2.3a, Table 2.2). Evenness did not differ significantly between different levels of coral species richness at either location (Lizard: $p = 0.168$; Kimbe: $p = 0.400$), but tended to be highest in the 6-species treatment (Figures 2.3c and 2.3d, Table 2.2).

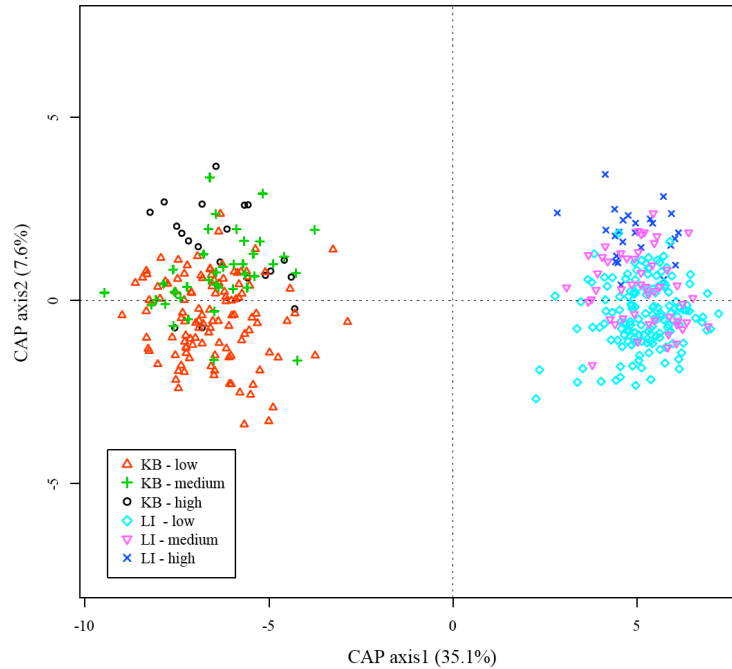


Figure 2.2: Canonical analysis of principal coordinates ordination plot (based on Bray-Curtis of log-transformed fish abundances) of fish assemblage data showing differences between sites. Each point represents a separate patch reef.

No significant changes in mean total fish abundance were observed between different levels of coral species richness. At Lizard Island, mean fish abundance varied between 298.0 individuals in the medium coral diversity and 199.8 individuals in the high coral diversity treatments ($p = 0.425$) (Figure 2.3e, Table 2.2). Total fish abundance in Kimbe Bay ranged from 138.9 in the medium coral diversity to 71.0 individual fish in the high coral diversity treatments ($p = 0.726$) (Figure 2.3f, Table 2.2). Mean abundances of fish were higher at Lizard Island (mean = 273.73) than in Kimbe Bay (mean = 120.04; $p < 0.001^{***}$), which was primarily driven by large schools of apogonids present on the patch reefs at Lizard Island. Distributions of *Chromis viridis* were very patchy, as this species was either absent or occurred in large schools (see below in section 2.4.3). Pooled mean fish abundances excluding apogonids and *Chromis viridis* were more similar between both locations, although still significantly higher at Lizard Island (mean = 82.09) than in Kimbe Bay (mean = 60.82; $p < 0.001^{***}$). Although fish abundance tended to be higher in the 6-coral species treatment at Lizard Island, results were not significant at either location (Lizard: $p = 0.168$; Kimbe: $p = 0.400$) (Figures 2.3g and 2.3h, Table 2.2).

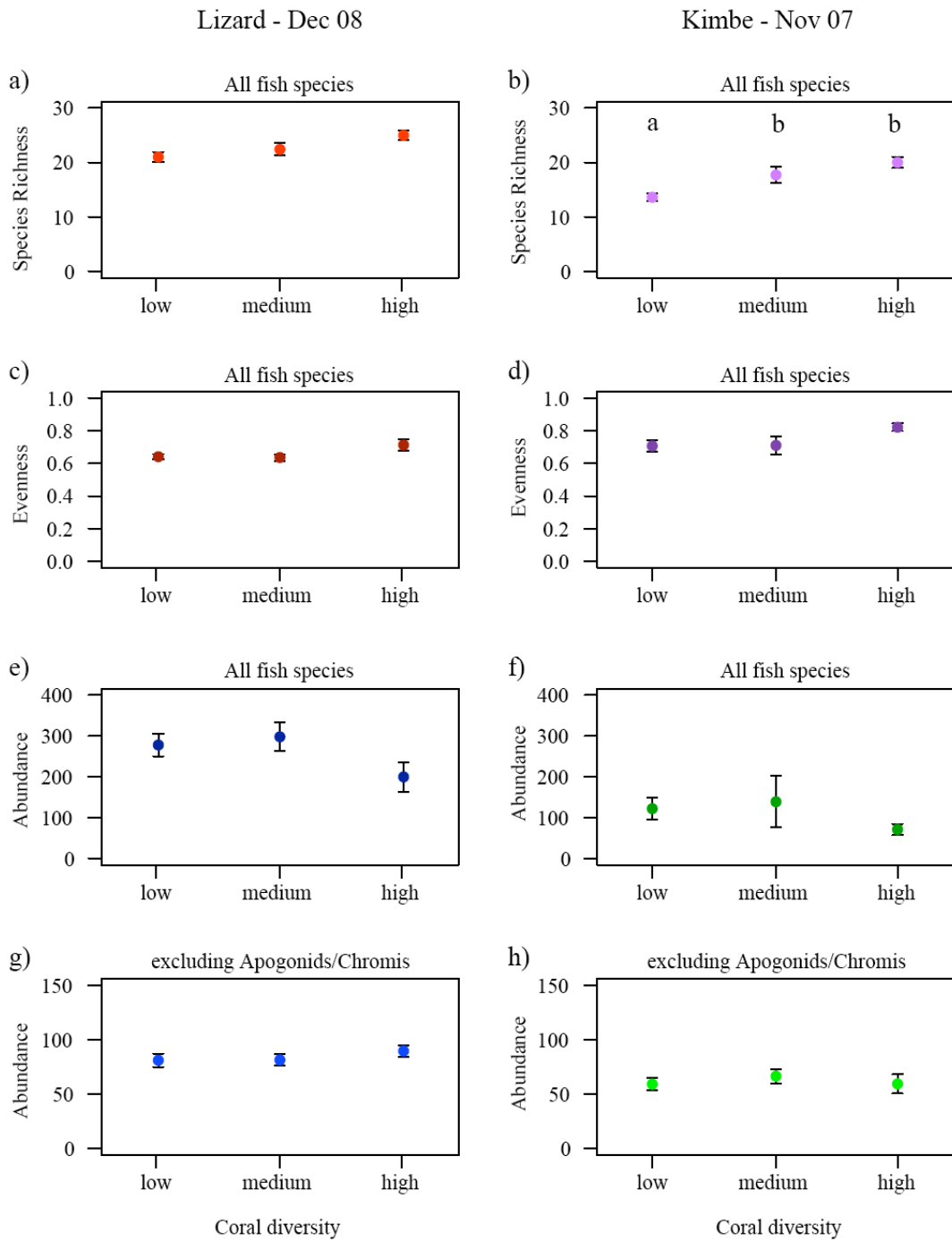


Figure 2.3: Effects of coral species richness on fish species richness and abundance: mean (\pm SE) fish species richness (a,b), Shannon Evenness Index (c,d) total fish abundance (e,f) and total fish abundance excluding apogonids and *Chromis viridis* (g,h), for each level of coral diversity (low (1 species), medium (3 species), high (6 species)) for Lizard Island and Kimbe Bay respectively (Table 2.2). Letters indicate significantly different treatments identified by Tukey’s HSD post hoc-tests.

2.4.3 Effects of coral species composition on fish species richness and abundance

Fish species richness differed between treatments at both locations (Lizard: $p < 0.001^{***}$, Kimbe: $p < 0.001^{***}$) (Figure 2.4, Table 2.2). The High diversity (H) and MediumB treatments supported the highest number of fish species in both locations. However, some single coral treatments supported equal or similar fish species richness. At Lizard Island, fish species richness was significantly higher on the High, MediumB and An treatments than on Pc and St. Sh, Bb and Pd also supported high fish diversity, but the values were not statistically higher than those found on Pc and St (Figure 2.4a, Table 2.2). In Kimbe Bay, the High and MediumB treatments supported significantly more diverse fish assemblages than Bb, Pd and St. Fish species richness was also significantly higher on the MediumB than the MediumA and Pc treatments. An and Sh attracted high species richness in Kimbe Bay, but differences were not statistically significant (Figure 2.4b, Table 2.2). Both An and Sh are present in the MediumB treatment, which likely explains the similarly high diversity between these single species treatments and the Medium B treatment in both locations. In contrast, other coral species tended to attract low species richness. For example, Pc and St showed low values at both locations. Bb and Pd also attracted low species diversity in Kimbe Bay. These two species together with Pc form the MediumA treatment, where species richness was similarly low in both locations.

Evenness was similar across treatments at Lizard Island, with no significant differences between treatments ($p = 0.701$) (Figure 2.4c, Table 2.2). In contrast, evenness differed between treatments in Kimbe Bay ($p < 0.001^{***}$) (Figure 2.4d, Table 2.2). Evenness was lowest for An and MediumB, with results from Tukey's HSD post hoc test showing that An was significantly lower than Pc, Sh, St, MediumA and the High diversity treatments. Low evenness in An and MediumB was driven by the presence of large schools of *C. viridis* on some replicates of these treatments, as mentioned below in relation to mean abundance. Removal of *C. viridis* from the analysis caused evenness in An and MediumB to be similar to other treatments, with only Pd showing significantly lower values than Pc, Sh and the High diversity treatments ($p = 0.008^{**}$) (not shown on graph). In contrast to the low abundances and species richness observed in the treatments St and Pc, values of evenness were amongst the highest in these corals.

Total fish abundance including all fish species per reef did not differ between treatments at Lizard Island, ($p = 0.731$) (Figure 2.4e, Table 2.2). Mean values were highest for the treatments An, Pd, Sh and MediumB and lowest for the treatments Pc and St, but these differences were not statistically significant. In Kimbe Bay, total abundances including all species differed between treatments ($p = 0.001^{**}$) and were found to be markedly higher on patch reefs of the treatments An and MediumB (Figure 2.4f, Table 2.2). Fish abundances on An were significantly different to all other treatments except for MediumB. The high variation in the An and MediumB treatments in Kimbe, as well as An, Pd, Sh and MediumB at Lizard were driven by large schools of *Chromis viridis*. At Lizard Island, *Chromis viridis* colonised only three of the six coral species used in the experiment, which included *Acropora nasuta*, *Pocillopora damicornis* and *Seriatopora hystrix*. In Kimbe Bay, *Chromis viridis* only occurred on the coral *Acropora nasuta*, which is a coral species also present in the MediumB treatment. When excluding apogonids and *Chromis viridis*, mean abundances per reef at Lizard Island were significantly lower in the Pc and St treatments than Bb, Pd and Sh ($p = 0.002^{**}$) (Figure 2.4g, Table 2.2). In Kimbe Bay, mean fish abundances were also significantly lower in Pc and St than in the An, Bb, Pd and MediumB treatments ($p < 0.001^{***}$) (Figure 2.4h, Table 2.2).

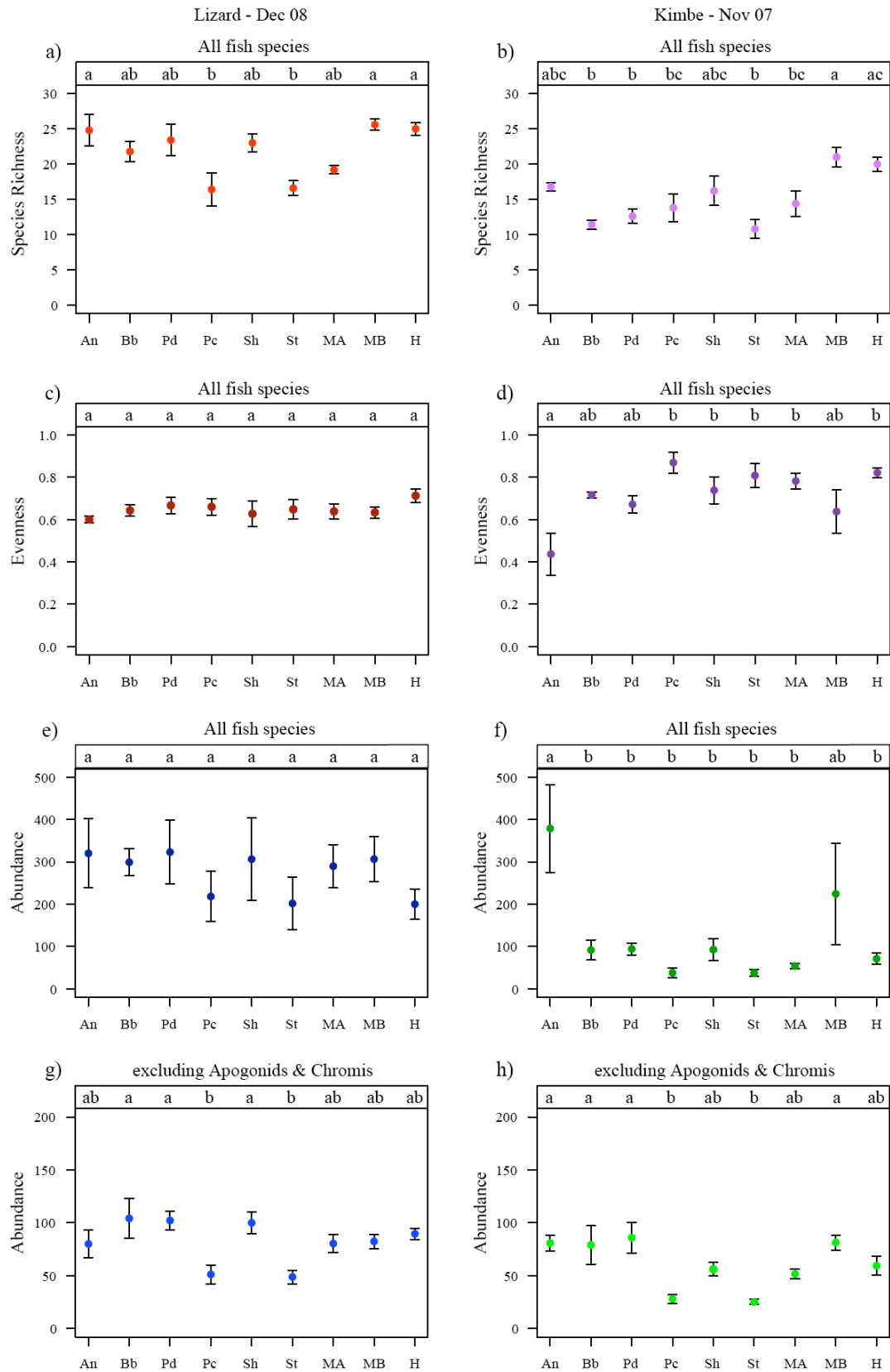


Figure 2.4: Effects of coral species composition on fish species richness and abundance. Mean (\pm SE) fish species richness (a,b), Shannon Evenness Index (c,d) total

fish abundance (e,f) and total fish abundance excluding apogonids and *Chromis viridis* (g,h), for each treatment for Lizard Island and Kimbe Bay respectively (Table 2.2). Letters above the graphs show the results of significantly different treatments identified by Tukey's HSD post hoc-tests.

Table 2.2: Summary of one-way ANOVA results for means of species richness (Figure 2.3a, 2.3b), Shannon Evenness Index (Figure 2.3c, 2.3d) total abundance (Figure 2.3e, 2.3f) and total abundance excluding apogonids and *Chromis viridis* (Figure 2.3g, 2.3h), for Lizard Island and Kimbe Bay respectively by level of coral species richness (1, 3 and 6 species).

	SS effect	df effect	SS residuals	df residuals	F	p
<i>LI – Species richness</i>	73.9	2	876.4	42	1.77	0.183
<i>KB – Species richness</i>	254.5	2	619.3	42	8.63	< 0.001 ***
<i>LI – Evenness</i>	0.0	2	0.3	42	1.86	0.169
<i>KB – Evenness</i>	0.1	2	1.3	42	0.94	0.400
<i>LI – Abundance</i>	33757	2	812250	42	0.87	0.425
<i>LI – Abundance excl.</i>	318	2	35929	42	0.19	0.831
<i>KB – Abundance</i>	15689	2	1027759	42	0.32	0.728
<i>KB – Abundance excl.</i>	415	2	36976	42	0.24	0.791

Table 2.3: Summary of one-way ANOVA results for means of species richness (Figure 2.4a, 2.4b), Shannon Evenness Index (Figure 2.4c, 2.4d) total abundance (Figure 2.4e, 2.4f) and total abundance excluding apogonids and *Chromis viridis* (Figure 2.4g, 2.4h), for Lizard Island and Kimbe Bay respectively by treatment.

	SS effect	df effect	SS residuals	df residuals	F	p
<i>LI – Species richness</i>	503.1	8	447.2	36	5.06	< 0.001 ***
<i>KB – Species richness</i>	517.0	8	356.8	36	6.52	< 0.001 ***
<i>LI – Evenness</i>	0.0	8	0.3	36	0.69	0.701
<i>KB – Evenness</i>	0.7	8	0.7	36	4.44	< 0.001 ***
<i>LI – Abundance</i>	106774	8	739233	36	0.65	0.731
<i>LI – Abundance excl.</i>	16701	8	19547	36	3.84	0.002 **
<i>KB – Abundance</i>	502680	8	540768	36	4.18	0.001 **
<i>KB – Abundance excl.</i>	21217	8	16173	36	5.90	< 0.001 ***

2.4.4 Effects of coral species on composition of fish community

Strong differences in the composition of fish communities between treatments were observed for both locations. For the experiment carried out at Lizard Island CAP groupings were strongly supported with 66.67% correct allocations ($p = 0.001^{**}$) (Figure 2.5i). The best result contained six PCO axes and accounted for 67.97% of the total variation. The first and second PCO axes explained 22.79% and 12.95% of the total variation respectively. The six single species treatments (An, Bb, Pc, Pd, Sh and St) formed clusters in the ordination graph with very little overlap between each other, indicating that the fish communities inhabiting each coral species are very different. MediumA overlapped largely with Bb, which constitutes one of its species. Similarly, An and Sh are both part of MediumB, which was embedded within their clusters. The high diversity treatment was located in the middle of the plot overlapping with most treatments, suggesting that the fish communities found on the high diversity treatment represent a mixture of those found on each of the coral species it contained.

The distinction between fish communities of different treatments using CAP was even stronger in Kimbe Bay (Figure 2.6i). Groupings were strongly supported with 93.33% correct allocations ($p = 0.001^{**}$). The best result consisted of 13 PCO axes, accounting for 96.14% of the variation. The first and second axes explained 19.75% and 14.07% of the variation respectively. The only two single species treatments that overlapped slightly in their distribution were Bb and Pd. All other single species treatments (An, Pc, Sh and St) formed unique clusters, again indicating that the fish communities inhabiting each coral species are very different. MediumA slightly overlapped with Pd, which constitutes one of its species. An and Sh are part of the MediumB treatment. The An cluster overlapped to some degree with MediumB and the Sh cluster was situated in close proximity, indicating similarities in fish community structures between MediumB and its constituent coral species. The high diversity treatment only overlapped partially with Pd and Sh, but the relatively central location and dispersed spread of this cluster in the ordination plot suggest that the fish communities found on the high diversity treatment represent a mixture of those found on each of the coral species it contained.

At Lizard Island, 66% of the species used in the analysis were strongly correlated (>0.2) with one or both of the CAP axes, indicating preferences in many fish species for particular coral species (Table 2.3). The differences between clusters of coral species

were driven by a variety of fish species covering a range of reef fish families, but consisted in particular of gobies and damselfish. For example among the damselfish species, *Dascyllus* spp clearly preferred Pd, *Chromis viridis* was mostly found on An and Sh, *Pomacentrus molluccensis* tended to select Pd and An, whereas larger numbers of *P. amboinensis* were usually found on Bb and Pd. Many goby species were exclusively found on a single coral species. For example, *Paragobiodon xanthosomus* only occurred on Sh, *P. echinocephalus* on Pd, *Pleurosicya micheli* on Pc and *Gobiodon citrinus* on St. In the other fish families, butterflyfish preferred to recruit to An, Sh and Pd, although *Chaetodon trifascialis* was only found on St. Scarid recruits showed a preference for St, Pc and An, whereas the labrid *Choris batuensis* was mostly found on St (Figure 2.5ii, Table 2.3).

In Kimbe Bay, 62% of the species used in the analysis were strongly correlated with one or both of the CAP axes, again indicating that many species show preferences for particular coral species (Figure 2.6ii, Table 2.3). A considerable proportion of the species driving the differences in fish communities between treatments were again accounted for by gobies, whereas only few damselfish species showed a preference for particular coral species. In contrast to the results for Lizard Island, only a couple of species showed a preference for Pc, including the triggerfish *Pseudobalistes flavimarginatus* and two pufferfish species. The distinction of the fish communities on St seemed to be largely driven by the absence or low abundances of many species, as no fish species preferred this coral species. Butterflyfish recruits were again mostly found on An and Sh.

The MRT for Lizard Island supported these findings with 46.8% of the total variation explained by treatments (Figure 2.5iii). Pc and St formed together the first split of the tree, therefore explaining most of the variation between groups and were most different from all the other treatments. The second split based on the remaining variation separated Pd and Ma, Pd being part of Ma. Next, An split from the remaining treatments and the final split distinguished Pd from the cluster Sh, Mb and H, Sh being part of Mb.

The MRT for Kimbe Bay also supported these findings and presented many similarities with the MRT for Lizard Island (Figure 2.6iii). 46.8% of the total variation was explained by the treatments. Pc and St, as well as Bb formed together the first split of the tree, therefore explaining most of the variation between groups and distinguishing

themselves more from all the other treatments. Each treatment split into its own leaf with St and Pc being more similar. The first split within the other major branch of the tree separated Pd together with Ma and H, Pd being part of Ma. Of the remaining treatments, Sh split from the cluster An and Mb, An being part of Mb.

Table 2.4: Species used in the canonical analysis of principal coordinates (CAP) that had correlations with either ordination axis exceeding 0.2. Correlations over 0.5 are highlighted in bold.

ID	Lizard	Scores	Kimbe	Scores
Chaetodontidae				
C1	<i>Chaetodon plebius</i>	-0.41 / 0.22	<i>Chaetodon ephippium</i>	-0.21 / 0.00
C2	<i>Chaetodon ephippium</i>	-0.28 / 0.12	<i>Chaetodon octofasciatus</i>	0.35 / -0.23
C3	<i>Chaetodon trifascialis</i>	0.31 / -0.07	<i>Chaetodon baronessa</i>	0.56 / -0.35
C4	<i>Chaetodon lunulatus</i>	-0.23 / -0.06	<i>Chaetodon lunulatus</i>	0.28 / -0.33
Gobiidae				
G1	<i>Paragobiodon echinocephalus</i>	-0.27 / 0.26	<i>Gobiodon sp C</i>	-0.49 / 0.07
G2	<i>Istigobius rigilius</i>	0.01 / 0.27	<i>Eviota nigriventris</i>	-0.31 / 0.12
G3	<i>Gobiodon okinawae</i>	0.32 / 0.36	<i>Amblygobius phaelaena</i>	0.26 / 0.06
G4	<i>Fusigobius duospilus</i>	0.32 / 0.03	<i>Gobiodon albofasciatus</i>	0.39 / -0.01
G5	<i>Pleurosicya micheli</i>	0.28 / -0.07	<i>Gobiodon quinquestrigatus</i>	0.54 / -0.40
G6	<i>Amblygobius phaelaena</i>	0.25 / -0.15	<i>Gobiodon histrio</i>	0.25 / -0.43
G7	<i>Gobiodon citrinus</i>	0.52 / -0.23	<i>Paragobiodon xanthosomus</i>	0.23 / -0.77
G8	<i>Gobiodon brochus</i>	-0.14 / -0.26	<i>Gobiodon ceramensis</i>	0.16 / -0.62
G9	<i>Gobiodon ceramicus</i>	-0.38 / -0.27	<i>Valenciennesa muralis</i>	-0.02 / -0.21
G10	<i>Asteropteryx semipunctatus</i>	-0.21 / -0.22	<i>Gobiodon oculolineatus</i>	-0.35 / -0.15
G11	<i>Paragobiodon xanthosomus</i>	-0.62 / -0.33	<i>Paragobiodon echinocephalus</i>	-0.68 / -0.07
G12	<i>Gobiodon histrio</i>	-0.27 / -0.18		
G13	<i>Gobiodon quinquestrigatus</i>	-0.27 / -0.15		
Labridae				
L1	<i>Thalassoma lunare</i>	-0.29 / 0.22	<i>Halichoeres scapularis</i>	-0.05 / 0.21
L2	<i>Choris batuensis</i>	0.39 / -0.26	<i>Oxycheilinus bimaculatus</i>	0.24 / -0.04
L3	<i>Halichoeres trimaculatus</i>	-0.07 / -0.23	<i>Pseudocheilinus hexataenia</i>	0.02 / -0.33
L4	<i>Stethojulis strigiventer</i>	-0.15 / -0.25		
Pomacentridae				
P1	<i>Dascyllus aruanus</i>	-0.72 / 0.49	<i>Chromis viridis</i>	0.36 / -0.47
P2	<i>Dascyllus reticulatus</i>	-0.37 / 0.57	<i>Stegastes lividus</i>	0.14 / -0.30

P3	<i>Pomacentrus amboinensis</i>	-0.30 / 0.47	<i>Dascyllus melanurus</i>	0.05 / -0.39
P4	<i>Pomacentrus pavo</i>	-0.32 / 0.35	<i>Dascyllus reticulatus</i>	-0.14 / -0.37
P5	<i>Pomacentrus moluccensis</i>	-0.56 / 0.18	<i>Pomacentrus pavo</i>	-0.26 / -0.19
P6	<i>Pomacentrus nagasakiensis</i>	-0.25 / 0.21		
P7	<i>Amblyglyphidodon curacao</i>	0.27 / 0.36		
P8	<i>Pomacentrus chrysurus</i>	-0.08 / -0.23		
P9	<i>Pomacentrus grammorhynchus</i>	-0.28 / -0.27		
P10	<i>Stegastes lividus</i>	-0.32 / -0.26		
P11	<i>Pomacentrus adelus</i>	-0.16 / -0.24		
P12	<i>Chromis viridis</i>	-0.59 / -0.27		
P13	<i>Dascyllus trimaculatus</i>	-0.24 / -0.08		

Fish from other families

O1	<i>Pseudochromis marshallensis</i>	-0.25 / 0.15	<i>Pseudochromis fuscus</i>	-0.14 / -0.23
O2	<i>Pseudochromis fuscus</i>	-0.04 / -0.35	<i>Cephalopholis cyanostigma</i>	-0.06 / -0.20
O3	<i>Cypho purpurascens</i>	0.02 / 0.35	<i>Cephalopholis microprion</i>	-0.36 / -0.38
O4	<i>Ogilbyina queenslandiae</i>	-0.04 / -0.25	<i>Pseudobalistes flavimarginatus</i>	0.02 / 0.23
O5	<i>Epinephelus maculatus</i>	-0.03 / -0.31	<i>Pseudobalistes viridescens</i>	0.27 / 0.05
O6	<i>Canthigaster bennetti</i>	0.29 / -0.38	<i>Canthigaster papua</i>	0.26 / -0.15
O7	<i>Neoniphon samara</i>	-0.32 / 0.09	<i>Canthigaster valentini</i>	0.03 / 0.23
O8	<i>Siganus punctatus</i>	0.02 / 0.34	<i>Canthigaster bennetti</i>	0.02 / 0.31
O9	Scarid recruit A	0.36 / -0.22	<i>Neoniphon</i> sp.	0.39 / -0.17
O10	Scarid recruit B	-0.30 / -0.36	<i>Cirrhitichthys falco</i>	0.19 / -0.28
O11	Lionfish	0.11 / -0.20	<i>Paracanthurus hepatus</i>	0.35 / -0.22
O12			Scarid recruit A	0.20 / -0.29
O13			Lionfish	0.26 / 0.09

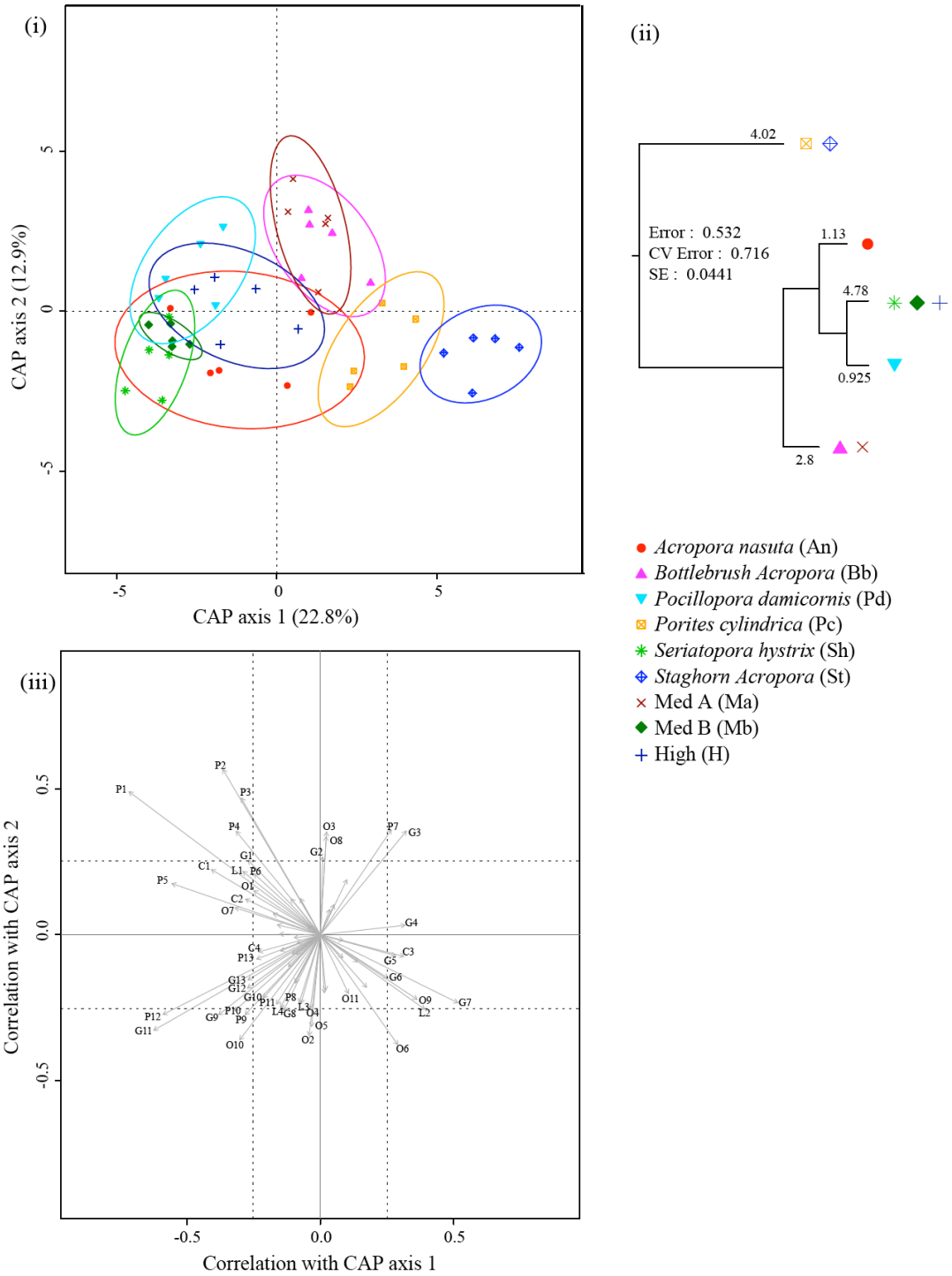


Figure 2.5: Lizard Island – December 08, (i) Canonical analysis of principal coordinates (CAP) ordination plot (Bray-Curtis) of fish assemblage data showing overlap between treatments. Each point represents a separate patch reef; (ii) Multivariate Regression Tree (MRT) constructed on a Bray-Curtis dissimilarity matrix of log-transformed fish abundance data, using treatments as groupings; (iii) species scores for CAP plots.

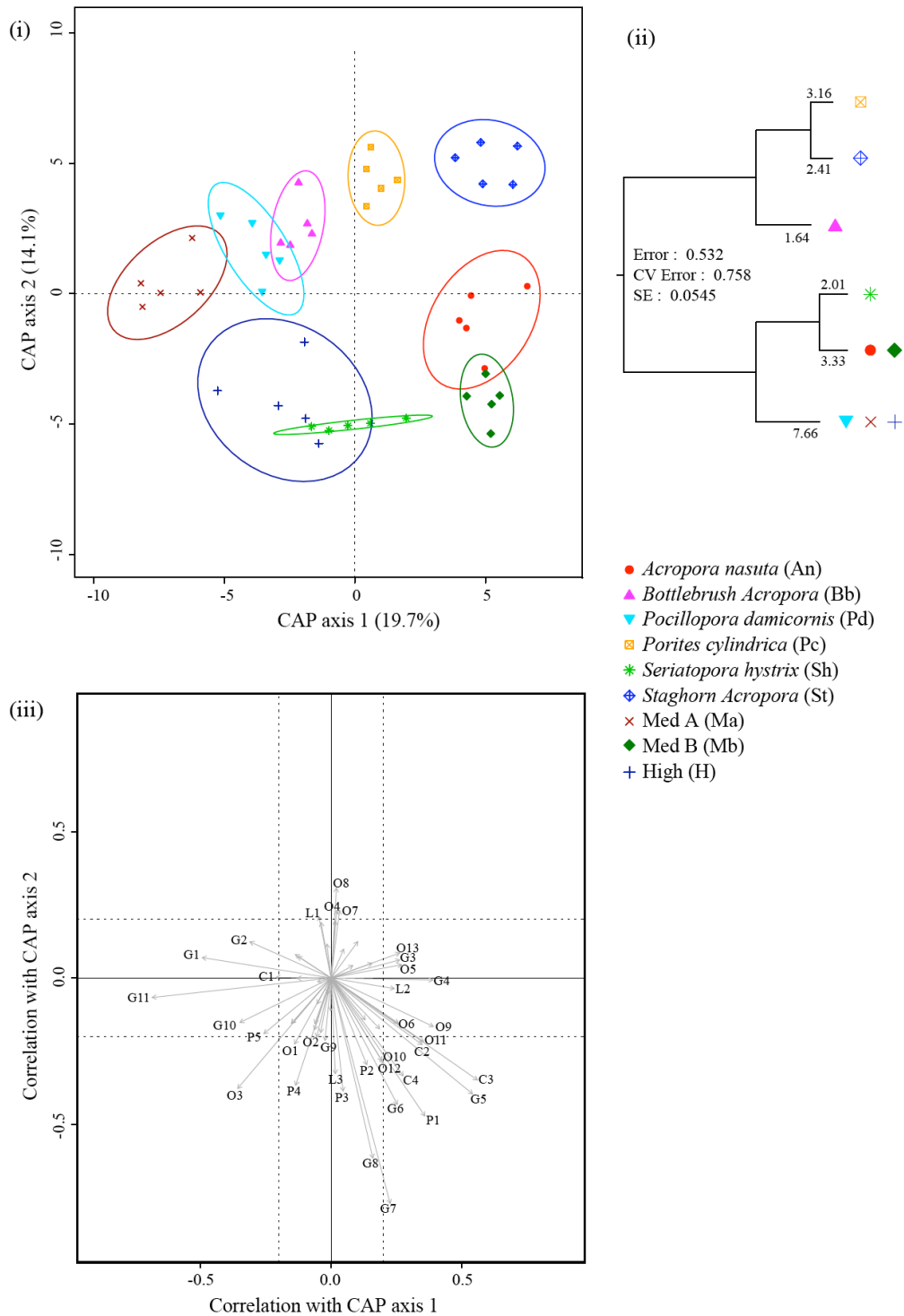


Figure 2.6: Kimbe Bay – November 2007, (i) Canonical analysis of principal coordinates (CAP) ordination plot (Bray-Curtis) of fish assemblage data showing treatment effects. Each point represents a separate patch reef; (ii) Multivariate Regression Tree (MRT) constructed on a Bray-Curtis dissimilarity matrix of log-transformed fish abundance data, using treatments as groupings; (iii) species scores for CAP plots.

2.5 DISCUSSION

This study experimentally demonstrates for the first time the importance of coral diversity and species composition, to the local diversity, composition and abundance of reef fish communities. It shows not only that fish species richness is promoted by coral diversity, but also that certain coral species support more abundant and diverse fish assemblages than others. Importantly, the results indicate that the presence of particular species in coral communities is important for maintaining the diversity of fish communities. There were substantial differences in the composition of fish communities associated with different coral species, whereas habitats composed of several coral species supported combinations of fish species that reflected the coral composition. These results were remarkably consistent across geographic locations, despite having only ~24% of all the fish species shared between locations. The consistency in the response of fish communities to coral identity and diversity, regardless of differences in the regional species composition or differences in the environment, highlight the importance of diversity in habitat-forming species and habitat diversity in promoting fish diversity.

The results are congruent with the generally positive relationship between habitat diversity and animal species richness found in the terrestrial environment (Lawton 1983; Tews *et al.* 2004; Hortal *et al.* 2009). A more diverse habitat provides a wider range of resources and has been recognised as an important factor structuring ecological communities through niche partitioning (Chesson 2000; Silvertown 2004; Kadmon & Allouche 2007). Habitat diversity, in this case coral species richness, provides a wider range of microhabitats or niches, which seem to be exploited by different fish assemblages presumably through niche partitioning. Similarly, different plant species have also been found to act as different habitat niches for associated terrestrial fauna, leading to an increase in animal species richness (Davidowitz & Rosenzweig 1998; Kissling *et al.* 2007; Qian *et al.* 2009). Reduced coral diversity is therefore expected to extend to a decline in fish species richness, in particular specialised species with distinct resource requirements are expected to be the first ones to disappear.

The vital role of corals in structuring fish communities is well known due to the close association between corals and many reef fishes (Bell & Galzin 1984). 9-11 % of reef fish species are believed to be directly dependent on live coral (Jones *et al.* 2004;

Pratchett *et al.* 2008), although the percentage is higher in some families (Munday *et al.* 1997; Wilson *et al.* 2008). Live coral cover and structural complexity have been demonstrated to be crucial in maintaining abundant and diverse fish communities (Luckhurst & Luckhurst 1978; McClanahan 1994; Jones & Syms 1998; Graham 2007), but the relationship between coral diversity and fish diversity is less well known. However, the relatively few studies that have examined the relationship between coral and fish diversity using correlative data (Luckhurst & Luckhurst 1978; Bell & Galzin 1984; Roberts & Ormond 1987; McClanahan 1994; Öhman & Rajasuriya 1998; Komyakova 2009), have generally found the relationship to be positive, which is supported by the present experiment.

Even though fish species richness and evenness were found to be correlated with coral diversity, the relationship between habitat (coral) and animal (fish) diversity was also clearly dependent on the particular corals included in the density treatments. As coral species vary in structure and many fish seem to preferentially associate with certain coral species (Hixon & Menge 1991; Munday *et al.* 1997; Holbrook *et al.* 2002), fish diversity is expected to vary between coral species. In this experiment, *Porites cylindrica* and staghorn *Acropora* were characterised by consistently low fish diversity. In Kimbe Bay, bottlebrush *Acropora* and *Pocillopora damicornis*, which together with *Porites cylindrica* form the Medium A treatment, displayed similarly low fish diversity. The MediumA treatment also did not support high fish diversity, presumably because its constituent coral species did not individually support high fish diversity. In contrast, the MediumB treatment supported equal diversity to the High diversity treatment because it contained the same individual coral species that supported high fish diversity. This discrepancy therefore likely reflects the ‘performance’ of the constituent coral species of both treatments in terms of fish diversity.

Although overall fish abundance did not appear to be affected by coral species richness, it varied significantly depending on coral identity and composition. Patterns of mean abundance after excluding apogonids and *Chromis viridis* were strikingly similar between locations. Coral identity played an important role in maintaining abundant fish communities, with *Porites cylindrica* and staghorn *Acropora* consistently supporting lowest fish abundances. At both sites, mean fish abundances were high in the medium and high coral diversity treatments, but not more so than the ‘good’ coral species, such as *Acropora nasuta*, bottlebrush *Acropora*, *Pocillopora damicornis* and *Seriatopora*

hystrix. These results suggest that particular coral species and not coral diversity per se are critical for sustaining abundant reef fish communities. The similarities in patterns of both fish abundance and fish diversity on different coral species across locations clearly suggest that some coral species play a more important role in promoting coral reef fish biodiversity than others.

Beside the already clear differences in fish diversity and abundance on particular coral species, the CAP and MRT analyses also revealed that fish assemblages were strikingly different between the six coral species investigated. Corals represent the primary habitat-forming organisms on coral reefs with over two thirds of coral reef fish only found at sites with live coral (Bell & Galzin 1984). Specialised fish species are known to be highly selective in their habitat choice (Munday *et al.* 1997; Pratchett 2005), although less specialised species also often exhibit preferences for certain coral species (Munday *et al.* 1997; Gardiner & Jones 2005; Wilson *et al.* 2008). Such strong associations of many fish species with certain coral types were also found in the present study. At both locations the species scores of nearly two thirds of the species (62% for Kimbe and 66% for Lizard) used in the CAP analysis (apogonids and extremely rare species excluded) presented a strong correlation with one or both of the two axes (>0.2). This shows that many reef fish species show a clear preference for particular coral species. For example, the often highly specialised coral-dwelling gobies showed strong preferences for a particular species of coral, as previously described by (Munday 2000). Certain species of planktivorous pomacentrids also clearly preferred certain corals for shelter over others. *Chromis viridis*, *Dascyllus* spp, *Pomacentrus molluccensis* mostly preferred *Acropora nasuta*, *Seraiatopora hystrix* and *Pocillopora damicornis*. Coral feeders, such as *Chaetodon* spp., which are known to be very selective (Pratchett & Berumen 2008), also distinctly preferred the same three types of corals over others.

The MRTs illustrated that staghorn *Acropora* and *Porites cylindrica* were the two treatments most different from all the others at both locations, although bottlebrush *Acropora* was also grouped with these in Kimbe Bay. These species appeared to be actively avoided by a number of coral reef fish, especially the majority of gobies and damselfishes. However, a small number of gobies (e.g. *Gobiodon citrinus*, *Pleurosicya micheli*) were exclusively found on these coral species, and a few other fish species preferred these corals as well. The avoidance of staghorn *Acropora* and *Porites cylindrica* by some fish species may be due to the open branching structure of these

coral species, compared with other species. As a result, these corals are likely to attract adults or larger species, for which the habitat size of the patch reefs may have been too small.

The results clearly show that each coral species used in this study provided a preferred microhabitat for a number of coral reef fish species either as resource of food, shelter or living space. Other fish species were found across treatments and may be considered more generalist habitat users. These results are consistent with previously recorded differences in fish community structure between coral species (Holbrook *et al.* 2002; Feary *et al.* 2007). Another important aspect that emerged from these analyses was that the medium and high diversity treatments supported fish communities that were a mixture of fish communities found on the constituent coral species. Therefore, even if habitats characterised by higher coral diversity do not necessarily support more diverse or abundant fish communities than some single coral species patches, a diverse habitat contains more microhabitats, which are likely to be preferred or strongly selected for by a significant number of different coral reef fishes and should overall increase animal diversity.

As the health of coral reefs is declining at a global scale (Hoegh-Guldberg 1999; McClanahan 2002; Gardner *et al.* 2003; Hughes *et al.* 2003; Wilkinson 2004), more coral species are expected to go extinct at least at a local scale. The clear preference of many fish species for particular types of coral in addition to the consistently higher fish abundance and diversity found on *Acropora nasuta* and *Seriatopora hystrix* in both locations indicate that these coral species play a more important role in promoting diverse local fish communities. However, these two coral species have been found to be particularly susceptible to disturbances, such as coral bleaching, crown of thorn outbreaks, and storms (McClanahan *et al.* 2007). Loss of these species would be expected to have a strong impact on local fish communities with reductions in many fish species. In contrast, *Porites cylindrica*, which is more resistant to disturbances, supported much lower levels of fish diversity and abundance. A shift in coral community structure from reefs dominated by *Acropora nasuta* and *Seriatopora hystrix* to *Porites cylindrica* would likely result in less diverse and abundant fish communities. These results indicate that significant alterations in fish communities may be expected if the corals providing important habitats are the first ones to disappear due to anthropogenic disturbances, such as global warming.

The remarkable congruence in the response of fish communities to coral diversity and identity between the two locations highlights the strength and nature of the relationship between fish and corals. The effects of coral diversity and identity on fish composition, diversity and abundance were similar, despite the differences in the fish communities and overall higher diversity and abundance at Lizard Island. The overall lower total species richness recorded in Kimbe Bay (122 species as opposed to 150 species at Lizard Island) in spite of higher regional fish diversity in Papua New Guinea than on the GBR may be attributed to environmental differences between the sites. Mid-shelf or off-shore reefs on the GBR generally exhibit higher species diversity than inshore reefs, which may have been driving differences here as well. Schumann Island in Kimbe Bay is an inshore island, whereas Lizard Island is further offshore. The difference in overall fish abundances between both locations was mostly attributed to the presence of large schools of apogonids on the patch reefs at Lizard Island. These differences in apogonid densities between locations may be attributed to tidal currents at the experimental site in Kimbe Bay, whereas the site at Lizard Island was more sheltered.

The use of a manipulative field experiment enabled us to investigate for the first time the specific influence of coral species and coral diversity on the structure of coral reef fish communities, the nature of the relationship between coral diversity and fish diversity and the potential consequences coral diversity loss could incur. Our results highlight the importance that each coral species plays in coral reef ecosystems in maintaining the species richness and community structure of the associated reef fish assemblages. Although many coral reef fish may be able to use a number of microhabitats, selective preference for specific coral species by others were clearly demonstrated. Thus, there is a strong potential for a positive relationship between coral diversity and fish diversity and the declining health of corals worldwide is likely to pose a serious threat to the diversity and structure of coral reef fish communities.

3 CHAPTER 3

EXPERIMENTAL EVALUATION OF DIVERSITY-PRODUCTIVITY RELATIONSHIPS IN CORAL REEF FISH ASSEMBLAGES

3.1 ABSTRACT

The global decline in biodiversity is causing increasing concern about the effects of biodiversity loss on ecosystem services such as productivity. Biodiversity has been hypothesised to be important in maintaining productivity of biological assemblages, because niche complementarity and facilitation among the constituent species can result in more efficient use of resources. However, these conclusions are primarily based on studies with plant communities, and the relationship between diversity and productivity at higher trophic levels is largely unknown, especially in the marine environment. Here, I used a manipulative field experiment to test the effects of species richness and species identity on biomass accumulation in coral reef fish assemblages at Lizard Island. Small patch reefs were stocked with a total of thirty juveniles belonging to 3 planktivorous damselfish (*Pomacentrus* sp.) according to three different levels of fish species richness (1, 2 and 3 species) and seven different combinations of fish species. Accumulation of biomass was recorded after 18 days. Species richness had no effect on the percent increase in biomass in this assemblage. However, the percent increase in biomass differed among individual fish species and among the different combinations of species. Patterns of biomass were best explained by species-specific differences in growth, and variable effects of intra- and interspecific competition on growth. These results suggest that niche complementarity and facilitation are not important drivers of total productivity within this guild of planktivorous fishes and that total productivity may be resilient to declining reef fish biodiversity, but will depend on the life history traits of remaining species.

3.2 INTRODUCTION

There is growing concern about the impacts of accelerating biodiversity loss on ecosystem services (Vitousek *et al.* 1997; Scheffer *et al.* 2001; Folke *et al.* 2004; Thomas *et al.* 2004; Sala & Knowlton 2006; Rockstrom *et al.* 2009), because diversity can affect important ecosystem parameters, such as biomass and productivity (Loreau *et al.* 2001; Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2007). Although the risk of species loss is proportionally greater in higher trophic levels (Duffy 2003; Petchey *et al.* 2004), most studies addressing the effects of diversity on productivity have been based on plant communities (Huston 1997; Loreau *et al.* 2001; Balvanera *et al.* 2006; Cardinale *et al.* 2006; Cardinale *et al.* 2007; Long *et al.* 2007). The relationship between diversity and productivity has often been found to be positive in primary producers (Naeem *et al.* 1996; Tilman *et al.* 1996; Hector *et al.* 1999; Loreau & Hector 2001; Loreau *et al.* 2001; Hooper *et al.* 2005; Marquard *et al.* 2009), but the relatively few studies considering other trophic levels show variable results (Norberg 2000; Downing & Leibold 2002; Cardinale *et al.* 2003; Duffy 2003; Downing 2005). Consequently, the nature and shape of the diversity-productivity relationship remains controversial and largely unknown at higher trophic levels.

Positive effects of diversity on productivity have mostly been attributed to mechanisms such as niche complementarity and/or facilitation (Naeem *et al.* 1994; Tilman *et al.* 1997b; Hooper 1998; Fridley 2001; Loreau *et al.* 2001). Higher productivity in diverse communities may arise through more efficient use of available resources through niche partitioning and **complementarity** (MacArthur 1970; Tilman *et al.* 1997b; Chesson 2000; Finke & Snyder 2008). That is, resource differentiation among consumers may lead to more complete exploitation of available resources (Finke & Snyder 2008), which is likely to increase with greater functional diversity between species (Cadotte *et al.* 2008; Marquard *et al.* 2009). However, few studies have been able to demonstrate that resources are used more efficiently when more species are present (Balvanera *et al.* 2006; Cardinale *et al.* 2006; Worm *et al.* 2006), as it is often difficult to distinguish complementarity effects from other processes, such as facilitation (Loreau & Hector 2001). **Facilitation** may have a positive effect on productivity in diverse assemblages through positive interactions among species. For example, some plant species have been found to facilitate the establishment of more

productive plants (Hector *et al.* 1999; Loreau & Hector 2001; Mulder *et al.* 2001; Callaway 2007). Another study also showed that biomass accumulation in *Echinacea purpurea* was favoured by the increase in nutrients available in the soil in more diverse communities (Dybzinski *et al.* 2008).

Despite growing evidence for the importance of biodiversity in maintaining ecosystem function especially in plant communities or lower trophic levels, the causal mechanisms and extrapolation to multi-trophic-level system remains subject to considerable debate (Loreau *et al.* 2001; Duffy 2002; Thebault & Loreau 2003; Hooper *et al.* 2005). Diverse communities may simply be more productive as the probability of containing a highly productive species increases with the number of species present, a process referred to as the “**sampling effect**” (Aarssen 1997; Huston 1997; Tilman *et al.* 1997b). Scale of sampling and species identity may also account for the observed variation in the diversity-productivity relationship (Mittelbach *et al.* 2001; Covich *et al.* 2004; Hector & Loreau 2005). Others also argue that productivity is driving species richness and not vice versa (Connell & Orias 1964; Leigh 1965; Grime 1973; Waide *et al.* 1999; Mittelbach *et al.* 2001). The controversy of cause and effect in the diversity-productivity relationship and what processes influence it may best be resolved using experimental manipulations.

Although the diversity-productivity relationship has received relatively little attention in the marine environment, increasing evidence that a range of human impacts negatively affect the biodiversity of shallow marine habitats (Alongi 2002; Duarte 2002; McClanahan 2002; Steneck *et al.* 2003; Bellwood *et al.* 2004) has made this issue a priority research area. A meta-analysis by Worm *et al.* (2006) concluded that restoring diversity resulted in a fourfold increase in primary and secondary productivity in marine ecosystems. However, the experiments used in the analysis involved only marine plants, plankton and bacteria (Worm *et al.* 2006). The effect of diversity on productivity at higher trophic levels in the marine environment has never been examined.

Coral reefs are particularly diverse, but threatened, marine ecosystems (McClanahan 2002; Gardner *et al.* 2003; Hughes *et al.* 2003; Pandolfi *et al.* 2003; Wilkinson 2004). Assemblages of coral reef fishes at some locations have exhibited dramatic reductions in abundance and local extinctions in some species in response to reduced coral cover and structural complexity (Syms & Jones 2000; Jones *et al.* 2004; Wilson *et al.* 2006; Graham 2007). Although global extinctions in reef fish are few to

date (Jones *et al.* 2002; Jones *et al.* 2004; Munday 2004b), population declines and local extinctions are expected to increase dramatically in coming decades due to widespread habitat degradation from coral bleaching and other disturbances (Roberts & Hawkins 1999; Jones *et al.* 2004; Munday 2004b; Sala & Knowlton 2006; Wilson *et al.* 2006; Jackson 2008; Pratchett *et al.* 2008). Yet the potential effects of biodiversity loss on the productivity of coral reef ecosystems are unknown, because the diversity-productivity relationship has never been examined.

Reef fish communities offer an ideal opportunity to examine the relationship between species diversity and productivity, as many species are sedentary and closely associated with the coral reef substratum, which facilitates observations of biomass accumulation. Biomass accumulation rates would be expected to increase with diversity if food resources are exploited more efficiently. More diverse reef fish communities may be expected to accumulate biomass more rapidly through faster individual growth. However, growth rates are likely to vary among species, therefore total productivity might depend on species composition. Growth rates will also be affected by the relative importance of competitive interactions versus complementarity effects, as intra- and interspecific competition has been shown to negatively influence growth rates (Jones 1987a; Jones & McCormick 2002; McCormick 2006).

The aim of this study was to experimentally test the effects of species richness and species identity on biomass accumulation in a guild of three planktivorous damselfishes (Pomacentridae). Fish diversity was manipulated to 1, 2 or 3 species on equally sized patch reefs while maintaining density constant. Competitive interactions are likely to vary within species as well as between different combinations of species, therefore all possible combinations of species were replicated in the diversity manipulations. Specifically, I tested if: (i) overall growth rates increase with increasing species richness, (ii) if species-specific growth rates change with species richness and identity and (iii) if intra- and inter-specific aggression may explain differences in intra-specific growth rates.

3.3 METHODS

3.3.1 Patch reef experiment

Thirty five identical patch reefs were constructed at a depth of 3-5m in the lagoon of Lizard Island on the Great Barrier Reef, Australia (14° 41'S, 145° 27'E). Each patch reef consisted of a coral rubble base of 70cm in diameter onto which live colonies of *Pocillopora damicornis* and *Acropora loripes* coral were placed. Patch reefs were set up on large flat sandy areas with no other habitat structure. To limit fish migration between reefs, these were placed 10m apart from each other and from any neighbouring reef structures.

Three abundant damselfishes that inhabit lagoonal patch reefs were chosen for the experiment: *Pomacentrus amboinensis*, *P. moluccensis* and *P. nagasakiensis*. These three species are similar sized planktivores that coexist in natural reef fish assemblages. A total of seven treatments representing three levels of diversity (1, 2 and 3 species) were established. The single species treatment was repeated for all three species and all combinations of 2 species were used in the two-species treatment. Each treatment was replicated five times. For simplicity, the different treatments will be referred to by abbreviations: *Pomacentrus amboinensis* (A), *P. moluccensis* (M), *P. nagasakiensis* (N), *P. amboinensis* with *P. moluccensis* (AM), *P. amboinensis* with *P. nagasakiensis* (AN), *P. moluccensis* with *P. nagasakiensis* (MN) and all three species (AMN) (Table 3.1).

A total of 1050 newly settled recruits (350 of each species) were collected on the reefs surrounding Lizard Island using clove oil anaesthetic and hand nets. Each individual was measured (0.1mm), weighed (0.001g) and tagged using subcutaneous injections of coloured elastomer. The tag enabled any movement of individuals between patch reefs to be identified. Each patch reef was then stocked on the same day with a total of 30 recruits according to their treatment and diversity level, i.e. 30 individuals per species for the single species treatments, 15 individuals per species for the two-species treatments and 10 individuals per species for the three-species treatment. After two days, additional recruits were added where required in order to maintain similar densities on all patch reefs, as many fish were lost to predation during the first two days of acclimation on the patch reefs. Subsequently, the patch reefs were monitored every two days and any new individuals that naturally colonised the patch reefs, were caught

and removed. After 18 days, all remaining fish were collected and the length and weight of each fish remeasured.

Table 3.1: List of fish species and number of species used in each treatment. Abbreviations used in the text and figures are also specified.

Treatment	Diversity	Fish species
Abbreviation	(# spp)	
A	1	<i>Pomacentrus amboinensis</i>
M	1	<i>Pomacentrus moluccensis</i>
N	1	<i>Pomacentrus nagasakiensis</i>
AM	2	<i>Pomacentrus amboinensis</i> <i>Pomacentrus moluccensis</i>
AN	2	<i>Pomacentrus amboinensis</i> <i>Pomacentrus nagasakiensis</i>
MN	2	<i>Pomacentrus moluccensis</i> <i>Pomacentrus nagasakiensis</i>
AMN	3	<i>Pomacentrus amboinensis</i> <i>Pomacentrus moluccensis</i> <i>Pomacentrus nagasakiensis</i>

Increase in biomass was measured using the percent increase in biomass per reef (overall and per species), i.e. $(T2-T1)/T1$, where $T1$ = mean initial weight per reef and $T2$ = mean final weight per reef. As densities declined on some reefs over the experimental period, a linear regression was used to examine the influence of density on growth. Since no effect of density on the percent increase in biomass (slope = -0.006, R^2 = 0.014) was observed, density was discarded from further analyses. One-way ANOVA followed by Tukey's HSD post-hoc tests (where applicable) was used to test if the overall percent increase in biomass differed between diversity levels, as well as between treatments. One-way ANOVAs were also used to test whether the percent increase in biomass for each species separately varied between diversity levels.

3.3.2 Interaction observations

Intra- and inter-specific agonistic interactions between individuals were examined to determine if they might explain differences in growth rates observed in the experiment. A total of 12 small juveniles were released into an aquarium containing a single coral head (*Pocillopora damicornis*). The 12 individuals belonged to the same three species of pomacentrids (*Pomacentrus amboinensis*, *P. moluccensis* and *P. nagasakiensis*) used in the field experiment and groups were constructed using the same seven species combinations. Therefore, for the three single species treatments, the 12 individuals consisted of the same species. In the combinations of two species, each species was represented by 6 individuals and the three-species treatment included 4 individuals of each species.

After an acclimation period of one hour, all interactions where one individual chased another individual were recorded during three replicate observations of 5 minutes. These observations were repeated for each group after another hour. Observation series were replicated three times for each treatment. Repeated observations were averaged for each replicate and standardised to represent attacks per fish. One-way ANOVA followed by Tukey's HSD post-hoc tests were used to test whether: (1) the total number of interactions varied between treatments, (2) the number of intra-specific interactions varied between species in the single species treatment, (3) the number of intra- and inter-specific interactions varied between species in the two-species treatments, and whether these were dependent on species combinations, and (4) the number of intra- and inter-specific attacks varied between species in the three-species treatments.

3.4 RESULTS

3.4.1 Patch reef experiment (Table 3.2)

Percent increase in total biomass showed no significant differences with changing fish species richness ($p = 0.076$) (Figure 3.1a), but differed significantly between individual treatments ($p = 0.032^*$) (Figure 3.1b). Tukey's HSD post hoc test revealed no significant differences between any of the pairwise comparisons. However, there were two general trends in aggregate growth rates. The lowest aggregate growth rates

occurred in the treatments containing just *P. amboinensis* (A) (43.95%), *P. amboinensis* with *P. moluccensis* (AM) (39.33%) and *P. moluccensis* with *P. nagasakiensis* (MN) (44.86%). High growth rates were observed in the treatments including just *P. nagasakiensis* (N) (64.74%), *P. amboinensis* with *P. nagasakiensis* (AN; 59.11%), all three species (AMN, 68.34%) and were highest containing just *P. moluccensis* (69.61%) (Figure 3.1b, Table 3.2).

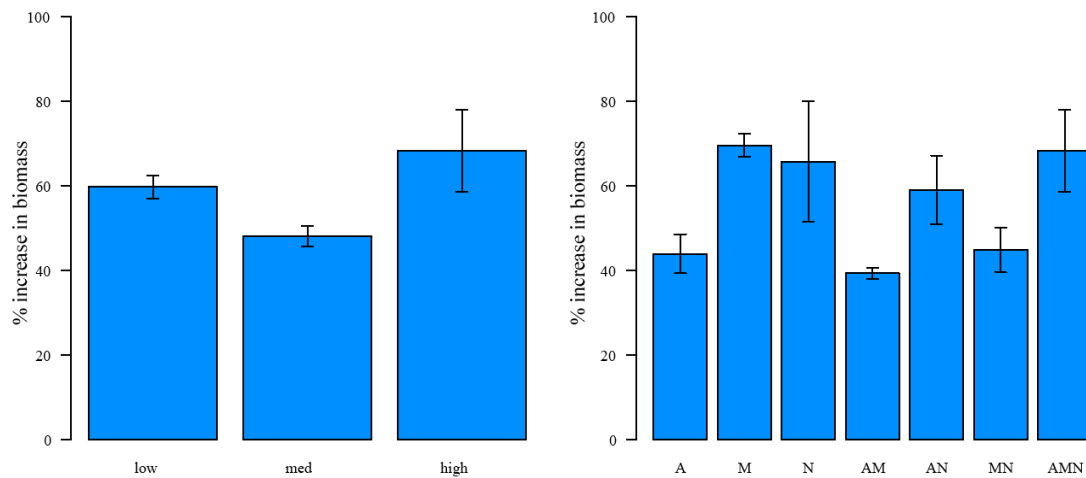


Figure 3.1: Mean percent increase in fish biomass (T2-T1)/T1 over 18 days per (a) diversity level and (b) treatment (Table 3.2). Error bars represent SE.

The overall density at the end of the experiment was 16.5 individuals per patch reef. Although the average density per treatment varied between 13.8 for AMN and 20.4 for AN, density was not found to affect the percent increase in biomass ($r^2 = 0.021$; Figure 3.2).

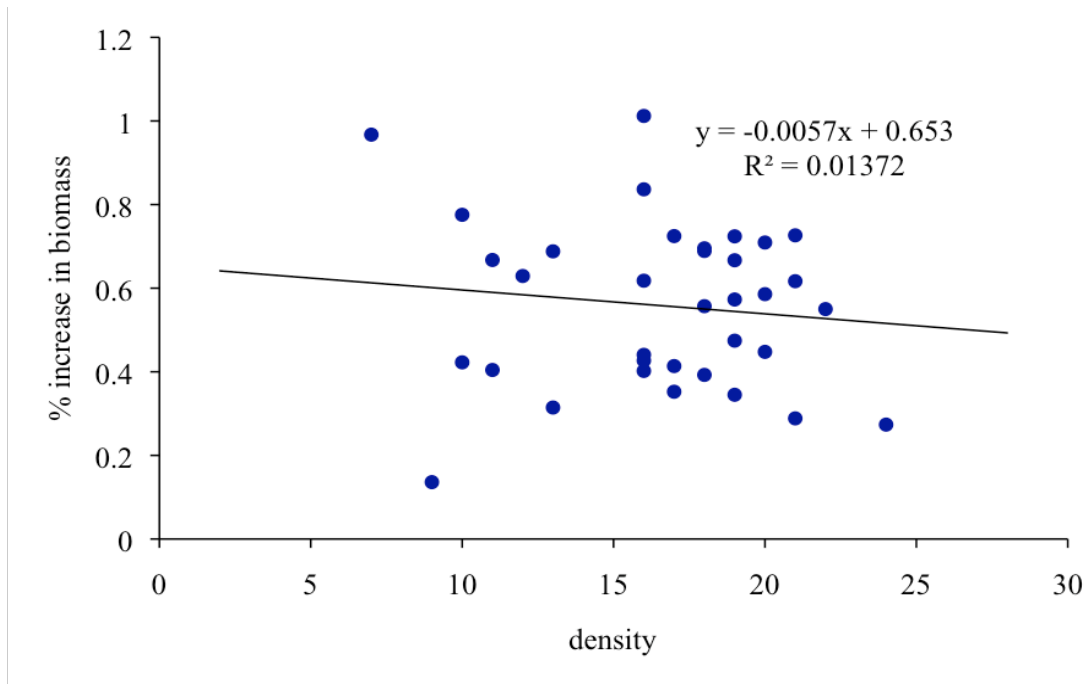


Figure 3.2: Scatterplot of the percent increase in biomass per patch reef against density with linear regression line.

At the species level, the increase in biomass differed significantly between treatments for *P. amboinensis* ($p = 0.021^*$; Figure 3.3a) and *P. moluccensis* ($p < 0.001^{***}$; Figure 3.3b). For *P. amboinensis*, growth rates increased with increasing diversity (43.95%, 48.25%, 74.08% respectively) (Figure 3.3a). In contrast, growth rates were highest in the low diversity treatment for *P. moluccensis* (69.61%), lowest in the medium diversity treatments (33.13%) and intermediate in the high diversity treatment (46.91%) (Figure 3.3b). Growth in *P. nagasakiensis* did not change with increasing diversity ($p = 0.851$) and varied between 63.09% and 74.05% (Figure 3.3c).

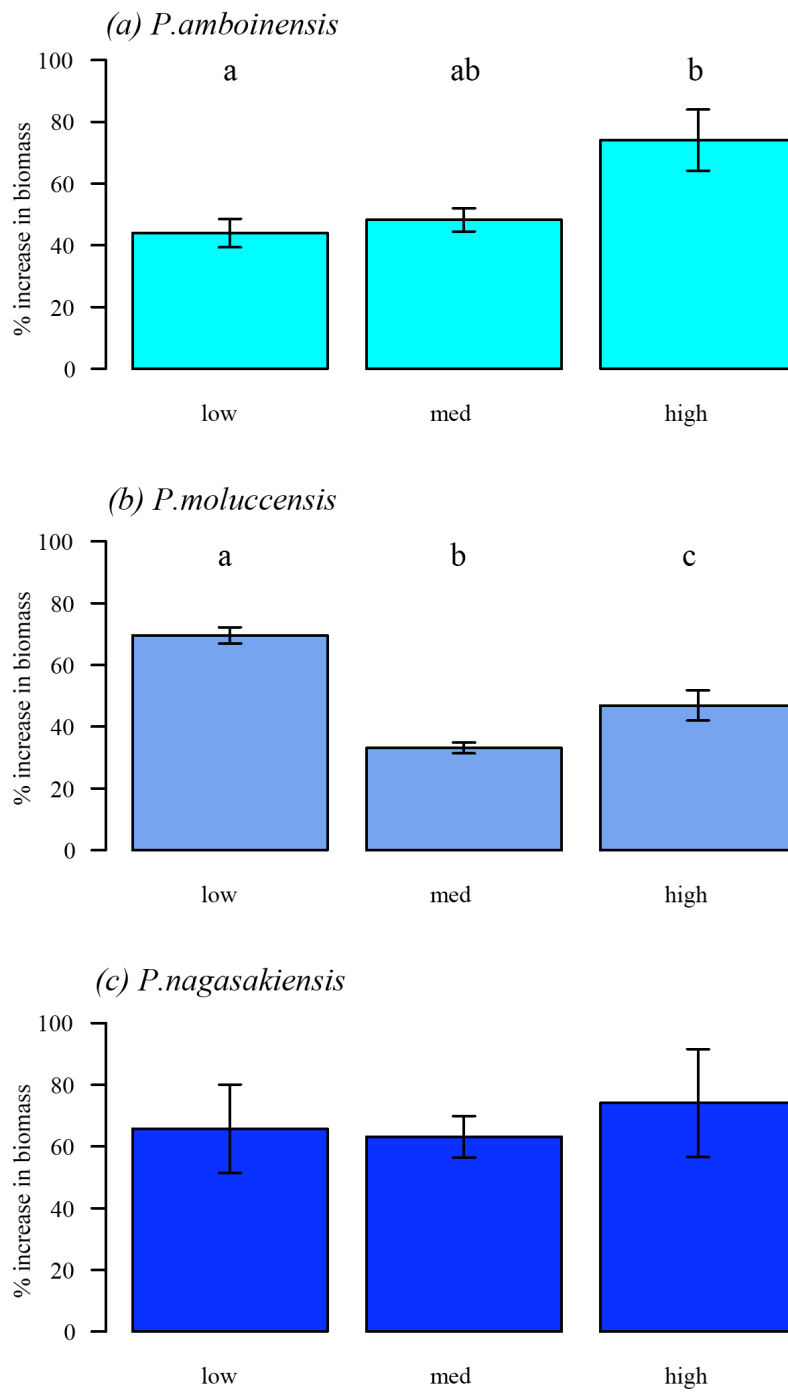


Figure 3.3: Mean percent increase in fish biomass (T2-T1)/T1 for each species over 18 days per diversity level: (a) *Pomacentrus amboinensis* (b) *P. moluccensis* and (c) *P. nagasakiensis*. Error bars represent SE. Letters above the graphs show the results of significantly different treatments identified by Tukey's HSD post hoc-tests.

Table 3.2: Summary of one-way ANOVA results for mean differences in percent increase in biomass for species combined by diversity level (Figure 3.1a) and treatment (Figure 3.1b), and for each individual species by diversity level (Figure 3.3a to 3.3c).

	SS	df	SS	df	F	p
	effect	effect	residuals	residuals		
Growth rates - species combined						
<i>By species richness</i>	0.2	2	1.1	32	2.79	0.076
<i>By treatment</i>	0.5	6	0.8	28	2.74	0.032*
Growth rates - individual species						
<i>P. amboinensis</i>	0.3	2	0.3	12	5.41	0.021*
<i>P. moluccensis</i>	0.3	2	0.1	11	29.54	< 0.001***
<i>P. nagasakiensis</i>	0.0	2	1.2	12	0.16	0.851

3.4.2 Interaction observations (Table 3.3)

For the three single species treatments, aggressive interactions per fish varied significantly between species. *P. moluccensis* were significantly more aggressive towards each other than *P. nagasakiensis* ($p = 0.019^*$) (Figure 3.4a), whereas intra-specific aggressions in *P. amboinensis* were intermediate. In the two-species treatments, inter-specific interactions varied between species combinations. In the AM treatment, *P. amboinensis* was on average nearly 10 times more aggressive towards *P. moluccensis* than vice versa ($p = 0.022^{**}$) (Figure 3.4b). In the AN treatment, *P. amboinensis* was this time attacked nearly 5 times more frequently by *P. nagasakiensis* than vice versa ($p = 0.010^{**}$) (Figure 3.4c). Inter-specific interactions between *P. moluccensis* and *P. nagasakiensis* (MN) were relatively rare, but again *P. moluccensis* tended to be attacked more frequently than showing aggressive behaviour towards *P. nagasakiensis* (0.37 and 0.70 attacks per fish respectively; $p = 0.507$) (Figure 3.4d). In contrast to the single diversity treatment, intra-specific aggressions in the high diversity treatment were lowest in *P. moluccensis* (0.90) and highest in *P. nagasakiensis* (2.15; $p = 0.012^*$) (Figure 3.4e). Similarly to the inter-specific interactions in the two-species treatments, *P. moluccensis* was the most frequent target of aggression (2.26; $p = 0.111$) and was responsible for the least number of inter-specific aggressions (0.5; $p = 0.044^*$).

Although showing relatively little intra- and inter-specific aggression in the single and two-species treatments, *P. nagasakiensis* was responsible for the highest number of intra- and inter-specific aggressions (2.15 and 1.93 attacks per fish respectively) and only rarely subject to inter-specific aggression (0.58) (Figure 3.4e). Overall aggression rates across treatments varied from 1.56 attacks per fish in the AN treatment to 3.62 attacks in M. Treatments containing *P. nagasakiensis* generally showed reduced aggression rates (Figure 3.4f).

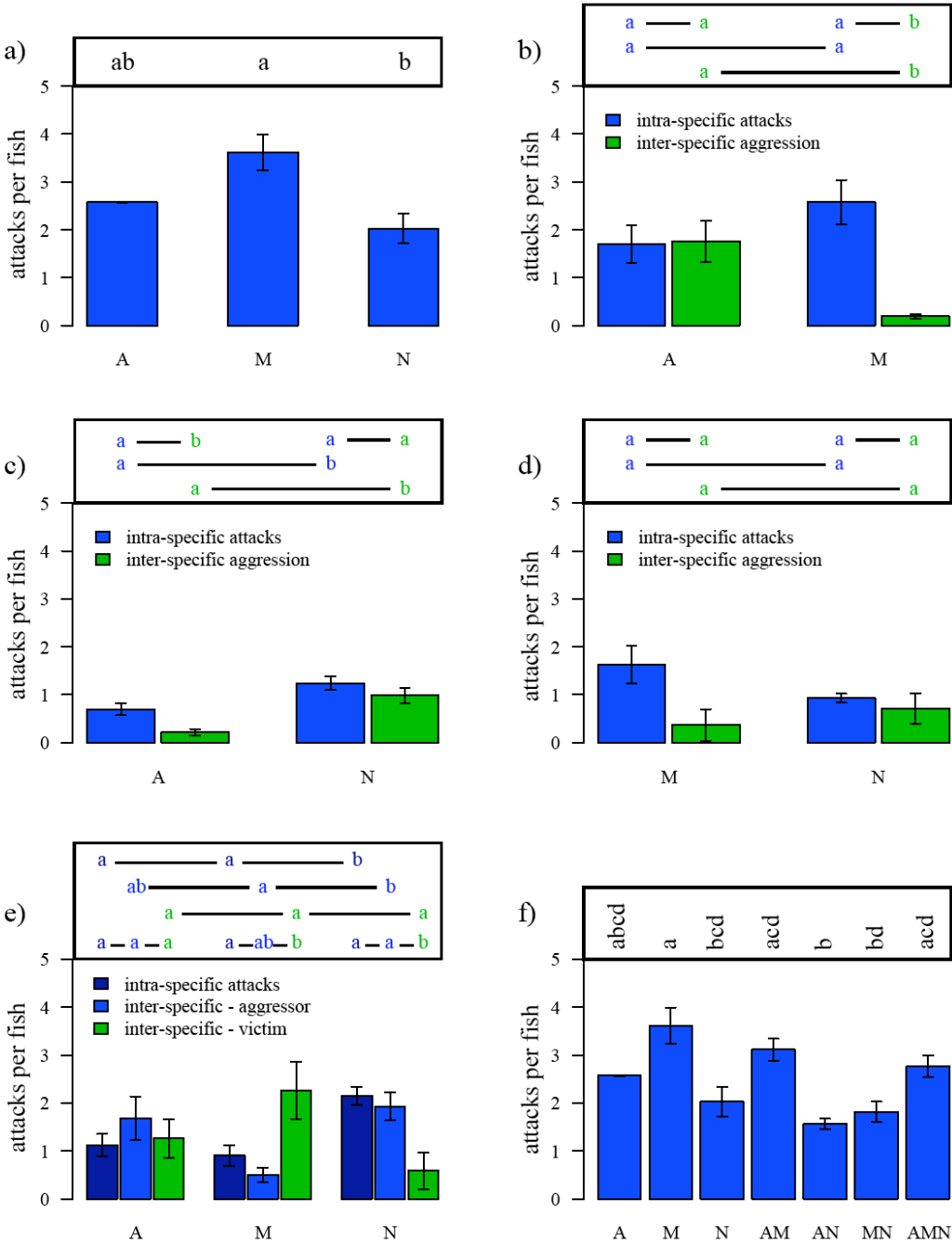


Figure 3.4: (a) Mean number of intra-specific aggressions per fish for each species in the single-species treatments. (b-d) Mean number of intra- and inter-specific aggressions per fish for each species in the two-species treatments (in order: AM, AN and MN). (e) Mean number of intra-specific aggressions, inter-specific aggressor and victim for each species in the high diversity treatment. (f) Mean number of overall attacks per fish per treatment (Table 3.3). All error bars represent SE. Letters above the graphs show the results of significantly different treatments identified by Tukey’s HSD post hoc-tests. Connecting lines specify which values were compared.

Table 3.3: Summary of one-way ANOVA results for fish observations (Figure 3.4): (a) Mean number of intraspecific aggressions per fish for each species in the single-species treatments. (b-d) Mean number of intra- and interspecific aggressions per fish for each species in the 2-species treatments (in order: AM, AN and MN). (e) Mean number of intraspecific aggressions, interspecific aggressor and victim for each species in the high diversity treatment. (f) Mean number of overall attacks per fish per treatment.

	SS	df	SS	df	<i>F</i>	<i>p</i>
	effect	effect	residuals	residuals		
a) Single species treatment						
<i>Intraspecific aggression</i>	2.9	2	1.4	6	8.20	0.019*
b) Two-species treatment - AM						
<i>Intraspecific attacks</i>	1.1	1	2.2	4	2.02	0.228
<i>Interspecific aggression</i>	3.6	1	1.1	4	13.33	0.022*
<i>A : Intra- vs inter</i>	0.0	1	2.0	4	0.01	0.929
<i>M : Intra- vs inter</i>	8.5	1	1.3	4	25.86	0.007**
c) Two-species treatment – AN						
<i>Intraspecific attacks</i>	0.4	1	0.2	4	8.09	0.047*
<i>Interspecific aggression</i>	0.9	1	0.2	4	21.33	0.010**
<i>A : Intra- vs inter</i>	9.3	1	0.1	4	11.51	0.027*
<i>M : Intra- vs inter</i>	0.1	1	0.3	4	1.51	0.286
d) Two-species treatment - MN						
<i>Intraspecific attacks</i>	0.7	1	0.9	4	3.11	0.153

<i>Interspecific aggression</i>	0.2	1	1.3	4	0.53	0.507
<i>A: Intra- vs inter</i>	2.4	1	1.6	4	6.13	0.069
<i>M: Intra- vs inter</i>	0.4	1	0.7	4	2.35	0.200
e) Three-species treatment - AMN						
<i>Intraspecific attacks</i>	2.7	2	0.8	6	10.08	0.012*
<i>Interspecific aggressor</i>	3.5	2	1.9	6	5.52	0.044*
<i>Interspecific victim</i>	4.3	2	4.0	6	3.24	0.111
<i>A: Intra- vs inter</i>	0.5	2	2.5	6	0.59	0.582
<i>M: Intra- vs inter</i>	5.1	2	2.5	6	6.05	0.036*
<i>N: Intra- vs inter</i>	4.3	2	1.6	6	8.15	0.019*
e) All combined per treatment						
<i>All attacks</i>	9.8	6	2.4	14	9.51	< 0.001***

3.5 DISCUSSION

The results of this study provide no evidence for an overall positive effect of diversity on productivity (in terms of increase in biomass) within an assemblage of three small coral reef fish. Although growth rates between diversity levels ranged from 48% to 68% and between treatments from 39% to 70%, the increase in biomass was not related to species richness. The highest increase in biomass was observed in the single species treatment of *P. moluccensis*, whereas the lowest growth rates occurred in the 2-species treatment that included *P. amboinensis* and *P. moluccensis*. Although the percent increase in biomass in the 3-species treatment was overall high, the values were no different from the two highest values in the single-species treatments and one of the 2-species treatments. In the individual species treatments, *P. moluccensis* exhibited the highest increase in growth and *P. amboinensis* the lowest. However, these patterns changed at the species level with species richness and different species combinations. The percent increase in biomass in *P. amboinensis* increased with increasing diversity and *P. moluccensis* grew most in the single-species treatment and the least when paired with one other species. Growth rates in *P. nagasakiensis* were very similar across treatments and were overall higher than in the other two species.

Although overall productivity in terms of growth was not found to be affected by species richness in this guild of planktivorous damselfish, the intrinsic differences in growth between species suggest that this relationship is likely to change depending on which species is lost from an assemblage. Overall productivity would decline if the fastest growing species was lost. However, the results also showed that growth rates within a species varied with species richness and different species combinations. Individual growth rates may be affected by intra- and interspecific competitive interactions, density and complementarity effects, such as differential resource use and facilitation. Competition-induced stress has been shown to negatively influence growth rates (Jones & McCormick 2002; McCormick 2006) and may explain some of the differences in growth observed within species. However, as overall density did not appear affect growth rates, as also previously reported for *P. nagasakiensis* (Pitcher 1992), dynamics of intra-versus interspecific interactions are believed to have mostly shaped patterns in growth rates.

The tank experiments suggest a hierarchical dominance in inter-specific aggressions, where *P. moluccensis* is persistently subject to aggression by *P. amboinensis* and *P. nagasakiensis*. *P. amboinensis* on the other hand is subject to inter-specific aggression from *P. nagasakiensis*. It has been suggested, that differences in body size between individuals can create highly asymmetrical intra-specific competition (Webster & Hixon 2000; Webster 2004), but may also affect inter-specific interactions. Differences in body size between the three species are consistent with these observations, as *P. nagasakiensis* was on average larger and *P. moluccensis* smaller than the other two species. *P. nagasakiensis* is therefore less likely to suffer physiological stress through inter-specific interactions, which is reflected in the constant growth rates across treatments.

Differences in growth rates may also have been affected by intra-specific interactions, but the relative importance between intra- versus inter-specific interactions is subject to variation, depending on the species and different species combinations. For example, intra-specific aggression appears to affect growth in *P. amboinensis*, as growth rates improved with decreasing intra-specific density in the more diverse treatments. In contrast, growth rates in *P. moluccensis* were highest in the single species treatment and decreased with increasing species richness, suggesting inter-specific aggressions play a more important role affecting growth in this species.

Differential growth rates between species in the single species treatment therefore suggest differences between facilitative versus territorial behaviour between species.

Although facilitation between species has been shown to positively affect productivity in more diverse plant communities (Hector *et al.* 1999; Loreau & Hector 2001; Mulder *et al.* 2001; Cardinale *et al.* 2002), it does not appear to have an overall positive effect on growth in this study, but might have an influence at the individual species level. For example, new recruits are found to be attracted to conspecific resident fish in some reef fish species (Sweatman 1983; Jones 1987c; Booth 1992; Steele 1997), but not others (Jones 1987c). Benefits to growth in larger groups may also be due to the reduced cost of predator avoidance (Booth 1995; Jones & McCormick 2002). Intra-specific interactions in *P. moluccensis* are likely to be facilitative, as growth rates were high in the monospecific treatment and this species has a natural tendency to aggregate (Brunton & Booth 2003). Growth rates within this species are therefore more likely to be affected by interspecific interactions, as suggested above. In contrast, poor growth rates in the single species treatment for *P. amboinensis* indicate a lack of intra-specific facilitation. Indeed, competitive interactions in *P. amboinensis* have previously been shown to increase physiological stress, leading to reduced growth rates (McCormick 2006). The increase in growth rates in *P. amboinensis* with increasing diversity suggests that intra-specific competition in this species is likely to decrease in more diverse assemblages and be more influential than inter-specific effects.

The absence of species richness effects on productivity indicates that complementarity effects, such as differential resource use, were less influential than inter- and intraspecific interactions. Although complementarity has previously been observed within functional groups (Marquard *et al.* 2009) and is a central aspect of coexistence theory (Colwell & Fuentes 1975), resource requirements, such as food and shelter, in these three *Pomacentrus* species may strongly overlap and the relative importance of competitive interactions seems to have outweighed potential complementarity effects. Differences in food requirements are hard to observe as all three species feed on plankton and gut content analyses would be necessary to discern any differences in diet. However, differences in feeding rates and diet composition have previously been observed within a single species of damselfish as a result of social rank and size (Forrester 1991). Such hierarchical behaviour regarding access to food could have taken place, particularly since *P. nagasakiensis* was generally the largest species

and *P. moluccensis* the smallest. Additionally, *P. nagasakiensis* overall showed a greater increase in biomass than the other two species. Some degree of niche partitioning is therefore likely, but the effects may be too weak to be reflected in higher growth rates with increasing species richness and were probably masked by interspecific differences.

The strong decrease in density during the first couple of days after release onto the patch reefs could potentially also indicate that shelter was a limiting factor. However, reduction in density showed no correlation with species diversity, suggesting that habitat use is similar between species. Alternatively, the loss in density at the beginning of the experiment could also suggest that the fish were initially disoriented and easy prey for predators. Even though individuals grew bigger over the experimental period and thus were likely to increasingly defend their territories, only relatively few fish were lost after the initial two days and no tagged individuals were found on the surrounding reefs.

The absence of species richness effects on productivity here may also partially be the result of the scale of the experiment. Due to the difficulty associated with manipulating mobile species in their natural environment, only three planktivorous damselfish belonging to the same trophic level were used. As biomass accumulation is reported to be greater with increasing functional diversity through greater complementarity (Marquard *et al.* 2009), the relationship between fish diversity and biomass is likely to change at a larger scale and using an evolutionary more diverse assemblage.

In conclusion, the results suggest that productivity in a small assemblage of similar reef fish species may be resilient to diversity loss. Although, intra- versus interspecific interactions are likely to affect growth rates in this guild of damselfish species, they do not entirely explain the variation in growth rates observed between treatments. Instead the results suggest that biomass accumulation in coral reef fish is a complex process subject to a number of mechanisms, including species identity and species-specific interactions. These interactions are most likely to change in more diverse systems, which include species with less similar resource requirements and belonging to different trophic levels. Processes such as complementarity, facilitation and sampling effect are expected to play a more important role in more diverse assemblages. Further studies are

therefore crucial to assess the potential impacts of fish diversity loss on the productivity of fish communities.

4 CHAPTER 4:

NO EVIDENCE FOR DENSITY COMPENSATION IN PATCH REEF ASSEMBLAGES OF CORAL REEF FISHES

4.1 ABSTRACT

The overall abundance of individuals in a community may be resilient to declining biodiversity if lower diversity communities support higher population densities. This *density compensation* is expected to arise as a result of competitive release in communities regulated by interspecific competition. However, total abundance may increase with increasing species richness in unsaturated communities and may even increase exponentially with species number in communities characterised by mutualistic interactions. Communities of coral reef fishes on patch reefs often exhibit high diversity and abundance, and there is accumulating evidence that inter-specific competitive interactions can be important in regulating abundances of some species. However, the potential relationship between species richness and abundance has not been investigated. This chapter provides the first experimental test of how changes in fish species richness affect patterns of abundance in a coral reef fish community. Species diversity of damselfish recruiting to experimental patch reefs was manipulated to two, four, six and eight species over a period of 10 weeks. Under a density compensation model, different treatments were predicted to reach the same total abundance, and densities of individual species should decline with increasing diversity. These hypotheses were not supported. Overall abundance increased significantly with increasing species richness and individual species densities exhibited little variation with changing species diversity. The absence of density compensation suggests that these communities do not reach saturation over 10 weeks, despite an upper limit of species richness and in some species, individual species abundances, appears to have been reached. Results suggest that the progressive loss of species in reef fish

assemblages due to habitat loss and climate change will lead to an overall decline in the abundance of reef fishes with subsequent effects on the productivity of fish assemblages.

4.2 INTRODUCTION

The rapidly accelerating loss of biodiversity due to increasing human domination of natural habitats is causing growing concern about ecosystem resilience and stability (Soule 1991; Tilman *et al.* 1998; Chapin *et al.* 2000; Loreau *et al.* 2001; Thomas *et al.* 2004; Rockstrom *et al.* 2009). However, the hypothesised relationships between biodiversity and ecosystem parameters such as productivity and numerical abundance are highly debated in the literature (Naeem *et al.* 1994; Chapin *et al.* 2000; Ives & Cardinale 2004; Hooper *et al.* 2005; Srivastava & Vellend 2005). In particular, the consequences of biodiversity loss on the abundance of remaining species within a community are uncertain and several different outcomes have been predicted (Naeem & Li 1997; Ives & Cardinale 2004; Gonzalez & Loreau 2009).

Recently the concept of density compensation has been applied to predict the consequences of declining biodiversity through human-impacts. Density compensation provides a mechanism of ecosystem resilience, assuming that the loss or decline of stress-intolerant species can be compensated for by population growth on other species (Ruesink & Srivastava 2001; Ives & Cardinale 2004; Jiang 2007; Gonzalez & Loreau 2009). Such interspecific interactions resulting in compensatory changes in the abundance of species would have stabilising effects on ecosystem processes (Tilman *et al.* 1998; Tilman *et al.* 2006) and there is some experimental support for this concept (Riipinen *et al.* 2010). However, it has also been suggested that the stabilising effect of density compensation will gradually be depleted as extinctions progress (Ives & Cardinale 2004; Bunker *et al.* 2005).

The concept of density compensation was first proposed to explain a commonly described phenomenon where relative population densities in species-poor island communities can be higher than their species-rich mainland counterparts (MacArthur *et al.* 1972; Case 1975). The underlying mechanism of density compensation is interspecific competition and theory predicts that resources made available by the lack

of one species are taken up by another species through niche expansion (Case *et al.* 1979; Gonzalez & Loreau 2009). As a consequence, similar total densities of island communities to mainland communities have been reported for a wide range of organisms and ecosystems (MacArthur *et al.* 1972; Case 1975; Nilsson 1977; Rodda & Dean-Bradley 2002; Sara & Morand 2002; Buckley & Jetz 2007). On the other hand, not all studies have found evidence for density compensation (Vaughn 1997; Oberdorff *et al.* 1998; Mesquita *et al.* 2007) and there is relatively little experimental support for this concept.

A wide range of studies has reported diversity-abundance relationships that differ from those expected under a density compensation model. Many studies show that overall abundance of individuals in communities tends to increase with increasing diversity (Tilman 1999, 2000). This may arise in under-saturated communities where the dynamics of constituent species are completely independent. It may also arise as a result of niche partitioning and more efficient exploitation of resources, which may increase overall carrying capacity (Naeem *et al.* 1994; Tilman 1999; Finke & Snyder 2008). Total abundance may also increase as a function of diversity if highly diverse communities are characterised by symbiotic interactions, such as facilitation or mutualism (Berkowitz *et al.* 1995; Hector *et al.* 1999; Mulder *et al.* 2001; Cardinale *et al.* 2002). Loss of biodiversity is predicted to have its greatest negative effect on ecosystem resilience in such communities.

Most of the research into diversity-abundance relationships has concentrated on terrestrial or freshwater communities (Tilman 1996; Walker *et al.* 1999; McGrady-Steed & Morin 2000; Ives & Cardinale 2004; Jiang 2007). The accelerating loss of terrestrial biodiversity has stimulated a new wave of studies on the potential consequences for ecosystem processes (Ruesink & Srivastava 2001; Elmqvist *et al.* 2003; Gonzalez & Loreau 2009). Much less attention has been given to diversity-abundance relationships in the marine environment. Although recorded marine extinctions to date are few (Jones *et al.* 2002; Jones *et al.* 2004; Munday 2004b), extensive reductions in the extent and structure of marine habitats have been observed in most coastal environments (Alongi 2002; Duarte 2002; McClanahan 2002; Steneck *et al.* 2003), resulting in dramatic population declines and local extinctions (Carlton *et al.* 1999; Roberts & Hawkins 1999; Dulvy *et al.* 2003; Dulvy *et al.* 2004; Jones *et al.* 2004; Sala & Knowlton 2006; Graham 2007; Jackson 2008). It seems inevitable that more

species will go extinct, but we have limited ability to predict the consequences of such extinctions for marine ecosystems.

Reef fish assemblages are the most diverse concentrations of vertebrate biodiversity on Earth, yet surprisingly little is known on the consequences of species loss in these communities. Density compensation has been observed for competing species of coral gobies (Munday 2004a) and surfperches (Holbrook & Schmitt 1995), although overall densities in the absence of the competitor were lower than combined densities for the surfperch (Holbrook & Schmitt 1995). Only limited density compensation was observed in a large-scale study on patterns of abundance in butterflyfish assemblages (Findley & Findley 2001) and no evidence for density compensation was found in reef fish communities on isolated islands characterised by low species richness (Hobbs, pers. comm.). Given the potential for confounding factors in comparative studies on diversity and abundance, and the difficulty in separating cause-and effect in this relationship, conclusions as to the importance of density compensation await studies in which diversity is experimentally manipulated.

This study is the first attempt to experimentally assess the consequences of diversity loss within patch reef communities of coral reef fishes. It examines the effect of increasing species richness on total abundance and the average density of constituent species. In order to achieve this, species richness in planktivorous damselfish (Pomacentridae) was manipulated on experimental patch reefs to two, four, six and eight species. Firstly, I tested whether increasing species richness resulted in: 1) no change in total abundance (as predicted by the density compensation hypothesis), 2) an increase in total abundance towards an asymptote (no or weak competitive interactions) or an exponential increase in total abundance (facilitation) (Fig. 1a). Secondly, I tested whether densities of individual species 1) declined with increasing species richness (density compensation), 2) were unaffected by species richness (no interactions) or 3) increased with increasing species richness (facilitation) (Fig. 1b). Given that the effects of competition and facilitation are likely to depend on how close communities are to their carrying capacity, I also monitored the rates of accumulation of species and individuals within species to examine evidence of how close populations and communities were to saturation.

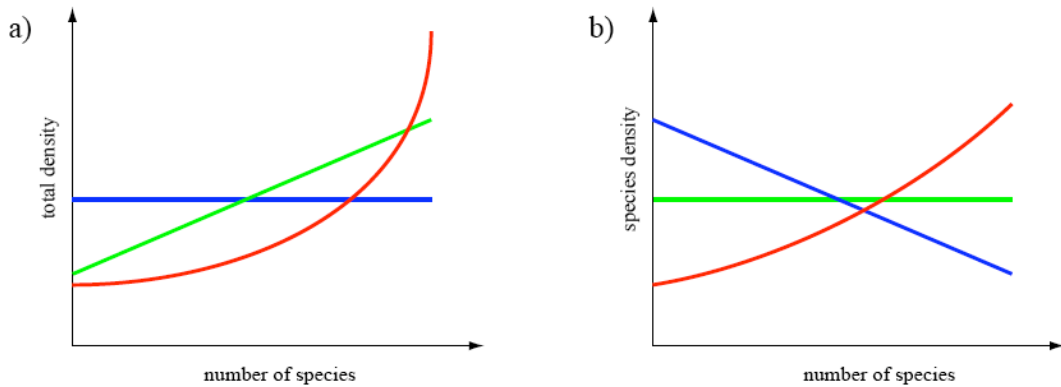


Figure 4.1: Predicted a) total density and b) average density for species, under three different scenarios: Blue: density compensation; green: no interaction between species; red: facilitation

4.3 METHODS

4.3.1 Study group

Planktivorous damselfishes (Pomacentridae) were chosen as the study group because of their diversity, abundance, and suitability to manipulative experiments. Damselfish are one of the most diverse families of coral reef fishes and many species coexist in the same area of reef. Damselfish readily colonise small isolated patch reefs and due to their sedentary and territorial nature are easily manipulated in field-based experiments. For the experimental manipulations I used 6 species belonging to a guild of planktivorous damselfishes that commonly coexist on lagoonal patch reefs of the Great Barrier Reef: *Pomacentrus amboinensis*, *P. bankanensis*, *P. moluccensis*, *P. nagasakiensis*, *Dascyllus aruanus* and *D. reticulatus*

4.3.2 Experimental design

To determine the influence of fish diversity on the overall abundance of coral reef fishes, 40 identical patch reefs were constructed on a sandy flat in the shallow lagoon of Lizard Island on the Great Barrier Reef, Australia (14° 41'S, 145° 27'E). Patch reefs

were approximately 70cm in diameter and consisted of a rubble base and a live colony each of *Acropora nasuta*, *A. horrida* and *Pocillopora damicornis*. They were positioned 10m apart from each other or any other reef structure at a depth of 4m to 6m.

The patch reefs were set up early December 2008 at the beginning of the recruitment season. Fish were allowed to naturally recruit to the patch reefs, but the composition and diversity was manipulated according to one of the eight different treatments (Table 4.1). Diversity levels included two, four, six and all pomacentrid species. The 2-species treatment consisted of three combinations of two pomacentrid species (*Pomacentrus amboinensis* with *P. bankanensis*; *P. moluccensis* with *Dascyllus aruanus*; *P. nagasakiensis* with *D. reticulatus*). Three treatments were characterised by combinations of four species (*Pomacentrus amboinensis* with *P. bankanensis*, *P. moluccensis* and *Dascyllus aruanus*; *P. amboinensis* with *P. bankanensis*, *P. nagasakiensis* and *D. reticulatus*; *P. moluccensis* with *D. aruanus*, *P. nagasakiensis* and *D. reticulatus*). One treatment included all six species, and in the last treatment all pomacentrid species that naturally settled onto the patch reefs were included. Each treatment was replicated five times and the treatments were randomly distributed between patch reefs.

Table 4.1: List of fish species and number of species used in each treatment. Abbreviations used in the text and figures are also specified.

Treatment Abbreviations	Diversity (# spp)	Fish species
A	2	<i>Pomacentrus amboinensis</i> + <i>Pomacentrus bankanensis</i>
M	2	<i>Pomacentrus moluccensis</i> + <i>Dascyllus aruanus</i>
N	2	<i>Pomacentrus nagasakiensis</i> + <i>Dascyllus reticulatus</i>
AM	4	<i>Pomacentrus amboinensis</i> + <i>Pomacentrus bankanensis</i> <i>Pomacentrus moluccensi</i> + <i>Dascyllus aruanus</i> s
AN	4	<i>Pomacentrus amboinensis</i> + <i>Pomacentrus bankanensis</i> <i>Pomacentrus nagasakiensis</i> + <i>Dascyllus reticulatus</i>
MN	4	<i>Pomacentrus moluccensis</i> + <i>Dascyllus aruanus</i> <i>Pomacentrus nagasakiensis</i> + <i>Dascyllus reticulatus</i>
AMN	6	<i>Pomacentrus amboinensis</i> + <i>Pomacentrus bankanensis</i> <i>Pomacentrus moluccensis</i> + <i>Dascyllus aruanus</i> <i>Pomacentrus nagasakiensis</i> + <i>Dascyllus reticulatus</i>
ALL	8	All pomacentrid species that settled to the patch reef

All fish present on each reef were counted and recorded at 5 day intervals for 2.5 months. Fish that were not part of the treatments were removed using clove oil anaesthetic and hand nets after each census. The experiment was terminated at the end of the recruitment season, at which time it had been running for 2.5 months. At the end of the experiment, a total of 10 different pomacentrid species had colonised the “all pomacentrid” patch reefs, with an average of 8 species per patch reef. For clarity and simplicity, this treatment is referred to as the ‘8 species’ treatment.

4.3.3 Analyses

To investigate if total abundance (all species combined) is affected by species richness, differences in mean densities of all pomacentrids at the end of the experiment were compared between diversity levels (two, four, six and all pomacentrid species) and tested using a one-way ANOVA followed by Tukey’s HSD post-hoc tests. For this purpose, the three 2-species treatments were grouped together, as well as the three 4-species treatments. Similarly, to investigate if density compensation could be observed at the species level, a one-way ANOVA followed by Tukey’s HSD post-hoc tests was used to detect differences in mean densities per species between diversity levels. Due to the schooling nature of *Chromis viridis*, results excluding this species are also presented to distinguish between facilitation and complementarity. The effects of species richness on differences in average population densities for each of the six species used in the experimental design (*Pomacentrus amboinensis*, *P. bankanensis*, *P. moluccensis*, *P. nagasakiensis*, *Dascyllus aruanus* and *D. reticulatus*) were also tested using ANOVA and Tukey’s HSD post-hoc tests.

To assess whether the mean total number of species and mean overall density per treatment approach carrying capacity, these parameters were plotted across the 13 censuses between the 13.12.08 and the 23.2.09. Furthermore, cumulative (sum total) densities for each species in the 8-species treatment were plotted against time to observe patterns of density accumulation for each species.

4.4 RESULTS

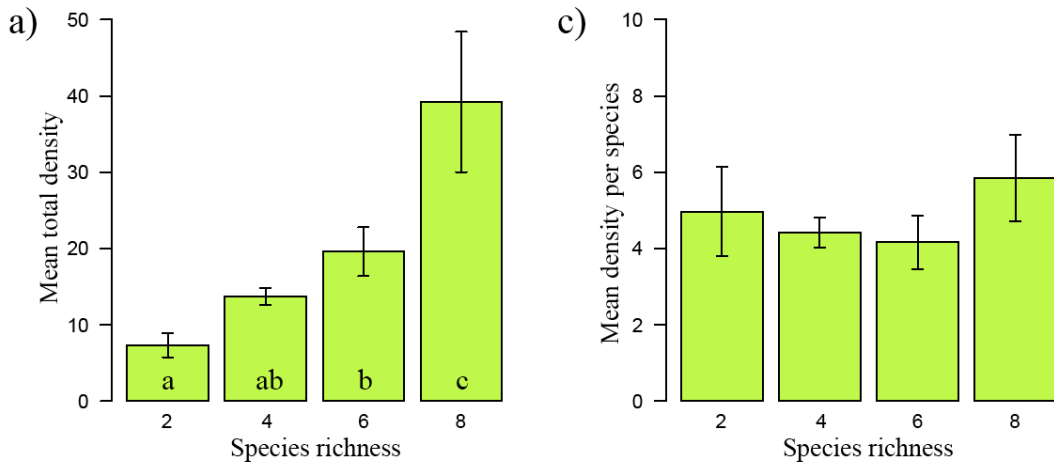
4.4.1 Diversity-abundance relationships

Mean total density (total number of individuals per reef, regardless of species) significantly increased with increasing pomacentrid diversity ($p < 0.001^{***}$) (Table 4.2, Figure 4.2a). Mean density for the 8-species treatment was significantly higher than the 2-, 4- and 6-species treatments ($p_{8,2} < 0.001^{***}$, $p_{8,4} < 0.001^{***}$, $p_{8,6} = 0.005^{**}$). The 6-species treatment was also significantly higher than the 2-species treatment ($p_{6,2} = 0.033^*$) (Figure 4.2a). The rate of increase in abundance with species richness was not linear, with a doubling of the population abundance between 6 and 8 species per reef. Excluding *Chromis viridis*, which was present in a large school on one of the 8-species treatments, resulted in a more linear increase in abundance (Figure 4.2b). The mean total number of individuals on the 8-species treatment was reduced to 30.0 without *C. viridis*. As above, the mean density for the 8-species treatment was significantly higher than the 2-, 4- and 6-species treatments ($p_{8,2} < 0.001^{***}$, $p_{8,4} < 0.001^{***}$, $p_{8,6} = 0.023^*$). The 2-species treatment was also significantly lower than the 4- and 6-species treatments ($p_{2,4} = 0.007^{**}$, $p_{2,6} < 0.001^{***}$) (Figure 4.2b).

The mean number of individuals per species was not significantly different across species diversity levels ($p = 0.779$) (Figure 4.2c). Mean number of individuals per species varied between 4.2 individuals for the 6-species treatment and 5.8 for the 8-species treatment (Figure 4.2c). Excluding *C. viridis* from the calculations reduced mean density per species on the 8-species treatment to 4.8 ($p = 0.943$) (Figure 4.2d). There was no evidence that species had higher densities at low species richness.

Mean number of individuals for each of the six species used in the lower diversity treatments (*Pomacentrus amboinensis*, *P. bankanensis*, *P. moluccensis*, *P. nagasakiensis*, *Dascyllus aruanus* and *D. reticulatus*) was also non-significantly different across all diversity levels for any of the species (Figure 4.3). Mean population densities for *P. amboinensis*, *D. aruanus*, and *D. reticulatus* were relatively similar ranging from 4.6 to 6.4, 3.8 to 5.6 and 4.0 to 7.5 respectively (Figure 4.3a, 4.3d and 4.3f). Densities for *P. bankanensis* were lower varying between 1.8 and 4.4 (Figure 4.3b). *P. moluccensis* and *P. nagasakiensis* both had very low mean population densities with on average less than one individual per patch reef for *P. moluccensis* and an average of 0.5 to 1.7 individuals per reef for *P. nagasakiensis* (Figure 4.3c and 4.3e).

All species



Excluding *Chromis viridis*

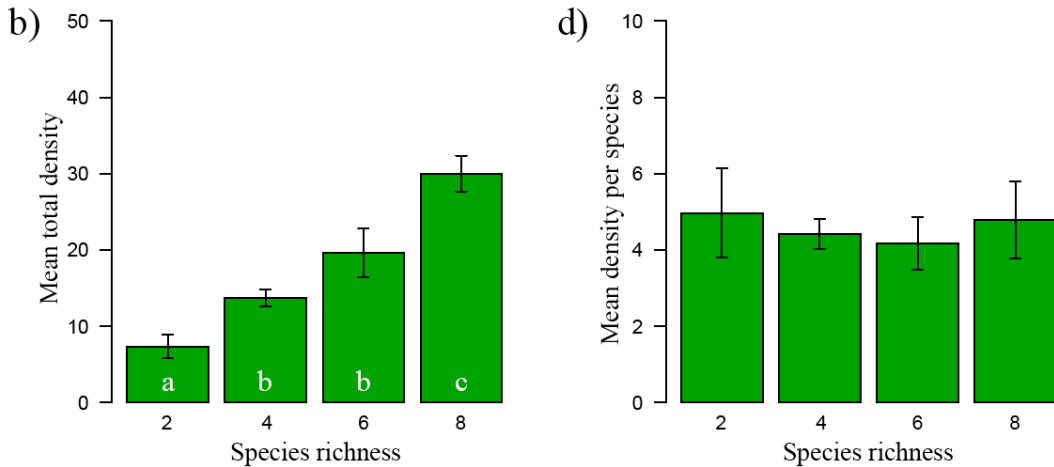


Figure 4.2: (a) Overall mean number of individuals per patch reef, (b) overall mean number of individuals excluding *Chromis viridis* per patch reef, (c) overall mean number of individuals per species per patch reef and (d) overall mean number of individuals per species excluding *Chromis viridis* per patch reef characterised by two, four, six and eight damselfish (Table 4.2). Letters above the graph show the results of significantly different treatments identified by Tukey's HSD post hoc-tests.

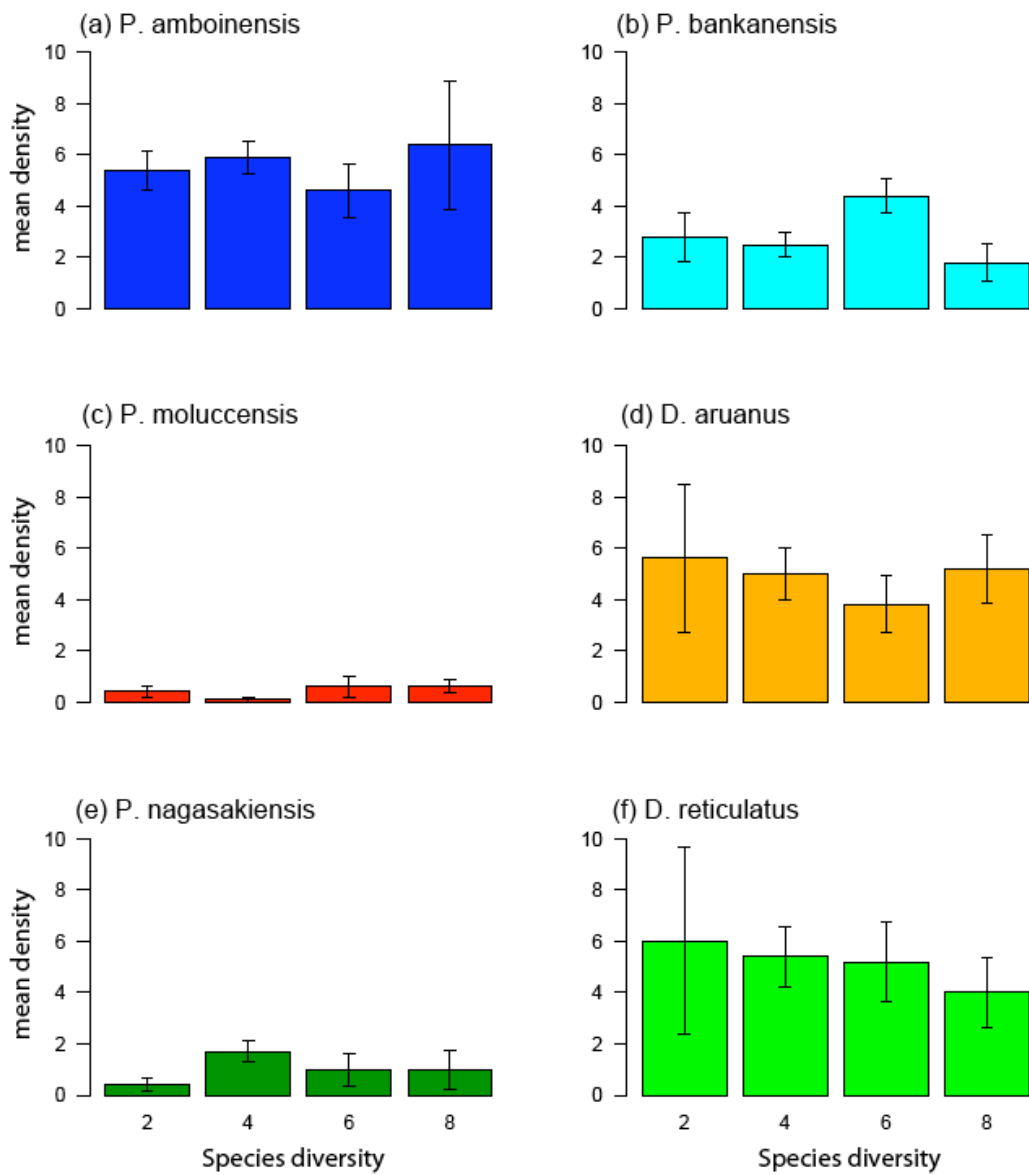


Figure 4.3: Mean population density for each species in the two, four, six and eight damselfish species treatments: (a) *Pomacentrus amboinensis*, (b) *P. bankanensis*, (c) *P. moluccensis*, (d) *Dascyllus aruanus*, (e) *P. nagasakiensis*, (f) *D. reticulatus* (Table 4.2).

Table 4.2: Summary of the one-way ANOVA results of means for total density and average species density including all species and excluding *Chromis viridis* (Figure 4.2), as well as for densities of each individual species (Figure 4.3).

	SS effect	df effect	SS residuals	df residuals	F	p
All species						
<i>Total density</i>	4050.1	3	2646.7	36	18.36	< 0.001***
<i>Avg species density</i>	9.9	3	317.7	35	0.36	0.7788
Excluding <i>Chromis viridis</i>						
<i>Total density</i>	2200.9	3	1063.9	36	24.83	< 0.001***
<i>Avg species density</i>	3.4	3	312.5	35	0.13	0.9433
Individual species						
<i>P. amboinensis</i>	14.2	4	191.6	20	0.37	0.828
<i>P. bankanensis</i>	19.6	4	60.4	20	1.62	0.208
<i>P. moluccensis</i>	1.4	4	6.4	20	1.06	0.401
<i>D. aruanus</i>	9.4	4	322.4	20	0.15	0.963
<i>P. nagasakiensis</i>	6.2	4	37.2	20	0.83	0.523
<i>D. reticulatus</i>	17.2	4	472.8	20	0.18	0.945

4.4.2 Colonization of reefs over time

Mean total density across all species reached an asymptote after 30 days (7.1.09) in all treatments except the 8-species (“ALL”) treatment (Figure 4.4a). When *Chromis viridis* are excluded, total density in the 8-species treatment (“ALL b”) also asymptotes after approximately 2 months. Mean total densities were similar between the three 2-species treatments, as well as the three 4-species treatments, increased in the 6-species treatment and were highest in the 8-species treatment (Figure 4.4a).

The target number of species per treatment was reached in most treatments within 25 days (2.1.09). Treatment “A” (*Pomacentrus amboinensis* + *Pomacentrus bankanensis*) reached the number of species already after 5 days (at first census) (Figure 4.4b). Species richness was reached later, after 1 month, in the 8-species and 6-species treatments. The average number of species was slightly lower than those predicted by the treatment because not all patch reefs reached the number of species designated by their treatment.

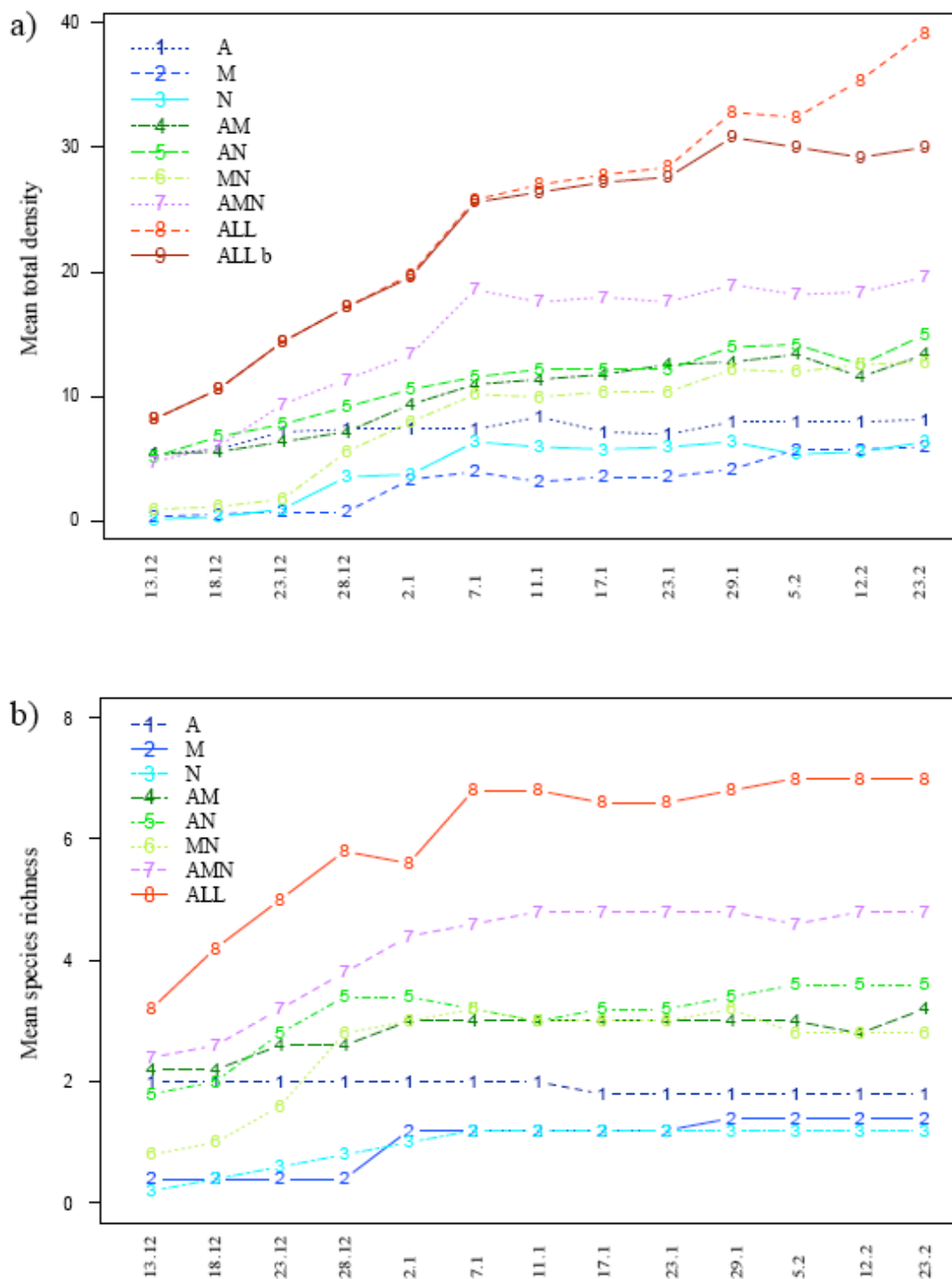


Figure 4.4: (a) Mean density per treatment over time. In “ALL b”, *Chromis viridis* is removed. (b) mean species richness per treatment over time. See Table 4.1 for treatment abbreviations.

The sum total of individuals for each species in the 8-species treatment shows that the timing of the recruitment peak differed between species (Figure 4.5). For *P. bankanensis*, *D. reticulatus* and *D. aruanus*, most individuals recruited to the patch reefs between the 18.12.08 and the 2.1.09, whereas *Chromis viridis* experienced a recruitment peak towards the end of the experiment. Except for *P. bankanensis*, no species showed a decline in total numbers during the experiment.

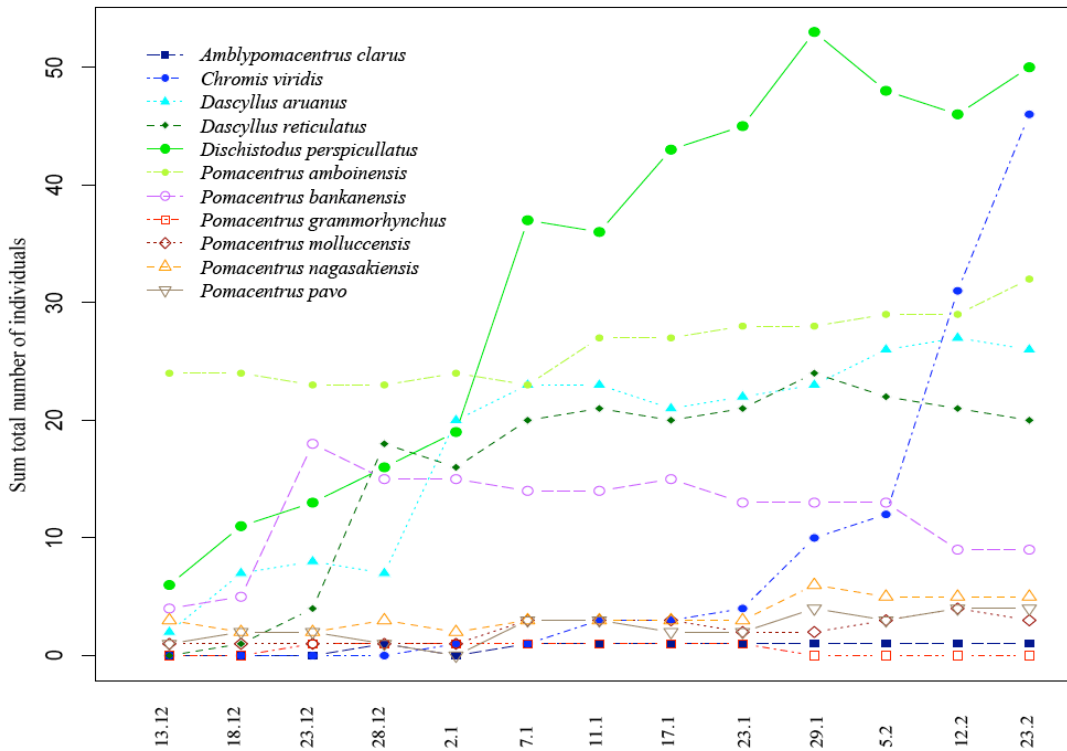


Figure 4.5: Cumulative number of individuals for each species in the “All” treatment.

4.5 DISCUSSION

This study is the first to experimentally test the diversity-abundance relationship in a guild of coral reef fishes common in patch reef habitats. No evidence for density compensation was found, either for total density or for the densities of individual species. Total density did not remain constant with increasing species richness (as predicted by density compensation), but instead increased with increasing species richness. Furthermore, average densities of individual species did not decline with increasing diversity (as predicted by density compensation) but remained constant. The results are not consistent with the idea that interspecific interactions are controlling the abundance of species in these habitats, despite some evidence that densities reach a maximum in just 10 weeks. The absence of density compensation is important as it suggests that these populations have no natural resilience to declining biodiversity.

The results of this study are in contrast with studies providing empirical support for density compensation in a wide range of terrestrial or freshwater organisms and ecosystems (MacArthur *et al.* 1972; McGrady-Steed & Morin 2000; Rodda & Dean-Bradley 2002; Jiang 2007; Gonzalez & Loreau 2009). In the marine environment, studies addressing density compensation are few. Density compensation was found to influence the community structure in a global study of butterflyfish (Findley & Findley 2001) and two competing surfperches (Holbrook & Schmitt 1995), although in both cases overall density was found to be higher in the species rich communities. On the other hand, Hobbs *et al.* (in press), reported no density compensation in butterflyfish on species-poor isolated islands compared to mainland populations. Similarly, some studies have demonstrated that interspecific competition can limit the abundance of species within guild of coral reef fishes (Robertson 1996; Munday 2001, 2004a), whereas many others have not detected effects of interspecific competition on population abundance (Doherty 1982; Jones 1987b; Roberts 1987; Jones 1988, 1991)

The absence of the competition-driven density compensation has also been described in other organisms (Vaughn 1997; Oberdorff *et al.* 1998; Mesquita *et al.* 2007) and may be explained by opposing hypotheses, where an increase in biomass or abundance in more diverse systems is attributed to non-interactive processes. Complementarity may lead to higher overall abundance through processes such as niche partitioning or facilitation (Tilman *et al.* 1997b; Loreau & Hector 2001). Niche

partitioning can lead to higher abundances through more efficient use of limited resources in diverse systems (Cardinale *et al.* 2006; Finke & Snyder 2008). Potentially limiting resources on the patch reefs are most likely to be food and shelter. With all the pomacentrid species here being primarily plankton feeders it is difficult to assess to what degree food was a limiting factor. Future studies could shed light on the degree of dietary overlap between species to determine if they use different components of the available planktonic food resource. However, (Limbourn *et al.* 2007) did not detect any evidence for dietary niche partitioning between two closely related species of *Dascyllus* (*D. aruanus* and *D. melanurus*) in locations where they coexisted. Therefore it seems unlikely that dietary partitioning was responsible for the observed increase in total abundance with increasing species richness.

Differences in habitat use between pomacentrid species on the other hand may be responsible for the increase in total abundance in the higher diversity treatments. Each of the species used in this experiment seems to have a slightly different microhabitat preference. *Dischistodus perspiculatus* tends to prefer the sandy edge of the patch reefs. *Dascyllus aruanus* and *D. reticulatus* tend to inhabit the top part of live coral, with *Pocillopora damicornis* being the preferred coral substratum (Jones 1987c). *Pomacentrus nagasakiensis* and *P. bankanensis* seem to prefer the rubble base of corals, whereas *P. moluccensis* is closely associated with live coral branches (Öhman & Rajasuriya 1998). *P. amboinensis* is often found in areas with sand and rubble near live coral (Öhman & Rajasuriya 1998; McCormick *et al.* 2010). These differences in microhabitat preference may enable populations of the various species to coexist on the same patch reef without competing for habitat space.

Facilitation may also have a positive effect on density and would be expected to result in an exponential increase in abundance with increasing species richness. In plant communities, the presence of certain species may favour the establishment or persistence of other species (Berkowitz *et al.* 1995; Mulder *et al.* 2001). In the marine environment, resident fish have been found to enhance the recruitment of conspecifics. This positive influence of conspecifics on recruitment patterns has previously been described for the pomacentrids *Dascyllus albisella* (Booth 1992), *D. aruanus* (Jones 1987c) and *D. reticulatus* (Sweatman 1983), as well as the temperate goby *Lythrypnus dalli* (Steele 1997). However, facilitation does not seem to positively influence the settlement in other species (e.g. *Pomacentrus amboinensis*, Jones 1987) or congenics

(Sweatman 1985), although no negative effects were observed either. In this experiment, recruitment facilitation of conspecifics was primarily observed in *Chromis viridis*, which was either absent from a patch reef or occurred in large numbers and accounted for the near exponential increase in total density with increasing diversity. Removing *C. viridis* from the analysis resulted in a linear increase of total density suggesting that non-interactive complementarity mechanisms were primarily controlling total abundance and species densities.

The “sampling effect” has also been proposed as a mechanism to positively affect total abundance with increasing diversity (Huston 1997; Loreau 2000; Loreau & Hector 2001; Cardinale *et al.* 2006). This may be the case if the likelihood of including a numerically abundant or schooling species increases with higher diversity. The schooling and patchy distribution of *Chromis viridis*, of which 41 individuals recruited to a single patch reef of the 8-species (all pomacentrid) treatment, may indicate that the sampling effect could have contributed to the high overall abundance in the 8-species treatment. Another species that recruited in high numbers to the 8-species patch reefs compared to any other species was *Dischistodus perspiculatus*, but in contrast to *C. viridis* its density distributions were less patchy. However, sampling effects alone have been found to be insufficient to explain positive effects of diversity on abundance in ecosystems (Loreau & Hector 2001; Yachi & Loreau 2007). Although the presence of a numerically abundant (*D. perspiculatus*) and a schooling species (*C. viridis*) in the high diversity treatment indicate that this mechanism is contributing to the higher abundance with increasing fish species richness, niche complementarity allows the coexistence of these species.

The temporal dynamics of density and species richness accumulation both reached an asymptote after one month, potentially indicating that the community is approaching carrying capacity in both species richness and abundance. If this was the case, we would expect competitive interactions to prevent further individuals from settling to the patches. However, some theories predict that larval supply is insufficient for total population size to ever reach carrying capacity determined by resource limitation (Victor 1986; Doherty & Williams 1988; Doherty & Fowler 1994). At an individual species level, the temporal dynamics show that recruitment patterns differed between species, in terms of timing as well as accumulation. A number of species experienced a recruitment peak after which only very few individuals of the same species colonised

the patch reefs. This pattern may reflect one of two things, either carrying capacity for individual species was reached or recruitment was limited and the system never reached saturation. Rapid recruitment to a noticeable asymptotic abundance seem to suggest the first alternative for *P. amboinensis*, *Dascyllus aruanus* and *D. reticulatus*, whereas steadily increasing numbers for *Dischistodus perspiculatus* and consistently low numbers throughout the study for *P. moluccensis* and *P. nagasakiensis*, indicate that recruitment was limited for these species

Although this study found no evidence for density compensation, but rather an increase in overall abundance with increasing species richness, further investigations are needed to confirm the generality of these results. Regulatory processes, such as intra- and inter-specific competition for food and shelter, are likely to increase as the recruits and juveniles grow older and larger. It would therefore be important to investigate if these patterns persist in well-established assemblages. Another potential reason for the complete lack of density compensation could be insufficient recruitment. If the patch reefs have not reached the population densities they are able to support, then the addition of new species would be likely to lead to the observed increase in density with species richness. The low recruitment levels in *Pomacentrus moluccensis* and *P. nagasakiensis* in this study suggest that not all species had reached attainable densities and may have contributed to the absence of compensatory dynamics. However, if the lack of density compensation in coral reef fish were to be confirmed by further research, this would have important consequences for understanding the effects of diversity loss on coral reef communities, because compensatory processes are thought to be a key mechanisms promoting ecosystem stability resilience.

5 CHAPTER 5:

CONCORDANCE BETWEEN GENETIC AND SPECIES DIVERSITY IN CORAL REEF FISHES ACROSS THE PACIFIC OCEAN BIODIVERSITY GRADIENT

5.1 ABSTRACT

The relationship between genetic diversity and species diversity provides insights into historic patterns of evolution and biogeography, and is critical for developing contemporary strategies for biodiversity conservation. While concordant large-scale clines in genetic and species diversity have been described for terrestrial organisms, whether or not these parameters co-vary for marine species remains largely unknown. Here, patterns of genetic diversity and composition were examined for 11 coral reef fish species (from 5 families) sampled at 3 locations across the Pacific Ocean species diversity gradient, from high diversity on the Great Barrier Reef, Australia (~1600 species), intermediate in New Caledonia (~1400 species), to low diversity in French Polynesia (~800 species). The overall genetic diversity for all 11 species paralleled the decline in species diversity from the West to East, with French Polynesia exhibiting lowest total haplotype and nucleotide diversity. Haplotype diversity consistently declined towards French Polynesia in all species and nucleotide diversity declined in the majority of species. Coinciding with reduced genetic diversity, the French Polynesian population of most species also exhibited significant genetic differentiation from the Great Barrier Reef and New Caledonia locations. The location and time of species origin, vicariance events, reduced gene flow and increasing isolation, as well as decreasing habitat area from the West to the East Pacific might have contributed to the general positive correlation between genetic and species diversity, but isolation and habitat area may be most influential. The congruence between species and genetic

diversity, and the large-scale patterns in species and genetic composition, suggest conservation strategies applied at one level may act as a surrogate for the other.

5.2 INTRODUCTION

Global biodiversity, of which species richness and genetic diversity represent two important components, is distributed heterogeneously across the planet. Recurring patterns exist in species richness, such as clines with latitude (Willig *et al.* 2003; Hillebrand 2004; Sizing *et al.* 2009), altitude (Heaney *et al.* 2001; McCain 2007, 2009) and depth (Rex 1981; Grassle & Maciolek 1992; Brokovich *et al.* 2008; Doherty *et al.* 2010). A wide variety of historic evolutionary and ecological factors have been implicated in explanations of these patterns and none have been attributed to a single cause (Gray 2001; Heaney *et al.* 2001; Willig *et al.* 2003; McCain 2009). Historic patterns of speciation and extinction (Gaston 2000; He *et al.* 2005), physical environmental gradients (Willig *et al.* 2003; Hillebrand 2004; McCain 2009) and the effects of habitat area (Rosenzweig 1995; Gaston 2000; Hillebrand 2004; Sizing *et al.* 2009) are all potentially important. Although biodiversity clines have mostly focussed on species richness, similar patterns have recently emerged for genetic diversity, which has been shown to decrease with increasing latitude (Hewitt 1996; Palma-Silva *et al.* 2009), altitude (Palo *et al.* 2003b; Giordano *et al.* 2007) and depth (Vonlanthen *et al.* 2009). Explanations for these clines parallel those for species diversity, including environmental gradients of temperature, light, seasonal fluctuations (Palo *et al.* 2003a; Giordano *et al.* 2007; Vonlanthen *et al.* 2009) and historic factors, such as range contractions during Pleistocene climate oscillations and subsequent range expansions (Hewitt 1996; Palma-Silva *et al.* 2009). Patterns in species diversity and genetic diversity are potentially explained by the same processes, yet are usually examined in isolation. A full understanding of the relationship between them is important, not only for evaluating threats to biodiversity and the consequences of biodiversity loss, but also for management strategies that are effective in protecting biodiversity from genes to species.

Antonovics (1976) first recognised that “the forces maintaining species diversity and genetic diversity are similar”. More recently, Vellend & Geber (2005) suggested that a

positive relationship between species diversity and genetic diversity may arise in two fundamentally different ways: firstly, through parallel effects, where both genetic and species diversity have been influenced by the same or equivalent processes; or secondly, as a result of direct causal relationships between the two levels of diversity (Vellend 2005, 2006). Most of the research into these two factors has focussed on terrestrial systems. Examples of positive relationships between species and genetic diversity caused by parallel processes include positive effects of speciation/mutation and migration, negative impacts of drift or selection (Vellend 2005; Sei *et al.* 2009), the same historical processes, variation in habitat area, or environmental gradients (Vellend 2003; Magurran 2005; He *et al.* 2008). Similar patterns in species and genetic diversity may also be the result of causal effects, such as competition (Booth & Grime 2003; Vellend 2008), but also species extinctions as a result of reduced genetic diversity (Frankham 2005; Bouzat 2010; Caballero *et al.* 2010; Laikre 2010). Variable relationships have been linked to differential responses to habitat characteristics (Karlín *et al.* 1984; Odat *et al.* 2004) or environmental changes (Puscas *et al.* 2008).

In the marine environment, the relationship between species and genetic diversity remains largely unexplored. Although the marine habitat provides the capacity for high dispersal and species often exhibit little genetic differentiation across large geographic ranges, species diversity patterns are not homogeneous across ocean basins. Geographic patterns in marine species diversity, similar to those in terrestrial organisms, are relatively well-known and include increases in species diversity with declining latitude (Gray 2001; Mora & Robertson 2005) and increasing depth (Gray 2001). There is also some preliminary evidence that genetic diversity mirrors clines in species diversity along latitudinal (Hickerson & Ross 2001; Martin & McKay 2004; McMillen-Jackson & Bert 2004; Hickerson & Cunningham 2005; Hickey *et al.* 2009) or depth gradients (Hickey *et al.* 2009) for some groups of marine organisms.

The distribution of most coral reef organisms follows a bulls-eye pattern, with a prominent hotspot in the Indo-Australian Archipelago (IAA) and latitudinal and longitudinal declines in species richness from the IAA (Rosen 1981; Briggs 2000; Bellwood & Hughes 2001; Hughes *et al.* 2002; Roberts *et al.* 2002; Mora *et al.* 2003; Briggs 2005; Reaka *et al.* 2008; Bellwood & Meyer 2009). Despite the congruent pattern in species diversity common to many groups of marine organisms, the underlying processes are widely debated (Bellwood & Wainwright 2002; Mora *et al.*

2003). Although molecular tools are increasingly applied to elucidate biogeographic patterns and provide valuable information on the evolutionary history of coral reef organisms in the oceans, the relationship between genetic and species diversity on coral reefs has rarely been mentioned (Palumbi 1997; Briggs 2004) and never specifically investigated. While some studies indicate that genetic diversity is high in the IAA (Palumbi 1997; Benzie *et al.* 2002) and low genetic diversity has been recorded in the east Pacific (Nishida & Lucas 1988), these studies mostly only address one or few species.

Once the relationship between species and genetic diversity is established, the next stage is to discern if other processes are important or if direct cause effect links exist between genetic and species diversity. Variation in genetic diversity in the marine environment have been primarily attributed to: (i) historic events, such as species origin and the geological history of the region; (ii) gene flow or connectivity, which are influenced by geographic isolation, sea surface currents and larval dispersal; and (iii) population size and area. The trans-pacific decline in species diversity from East to West offers a unique opportunity to examine relationships between genetic and species diversity along a relatively uniform environmental gradient. A positive correlation between species and genetic diversity in coral reef organisms across the Pacific Ocean may for example arise from the IAA acting as a centre of origin from where species radiate outwards resulting in increasingly younger populations (Briggs 1999, 2000; Mora *et al.* 2003; Briggs 2004) or habitat area being highest in the IAA, reducing eastwards and becoming increasingly isolated (Bellwood & Hughes 2001). Examining the roles of these factors requires more detailed phylogeographic studies of the underlying patterns in the genetic structure of populations.

As both species and genetic diversity are argued to affect ecosystem stability, resilience and dynamics (Loreau *et al.* 2001; Hughes & Stachowicz 2004; Reusch *et al.* 2005) and both levels of diversity are often observed to decline in strongly disturbed environments (Vellend 2004; Cleary *et al.* 2006; Evanno *et al.* 2009), a better understanding of the relationship between species and genetic diversity may be critically important for conservation strategies, such as site selection for protected areas. The aim of the present study is therefore to specifically investigate for the first time large-scale patterns of genetic diversity in coral reef fish along the Pacific species diversity gradient to determine if there are congruent patterns between species richness

and genetic diversity, and between species composition and the genetic structuring of populations. The regional species richness of coral reef-associated fishes declines from 1600 to 800 species across 65 degrees of longitude from the Great Barrier Reef, Australia to French Polynesia (Allen 2008). By examining the genetic diversity of widespread representatives of different reef fish families at three locations across the Pacific species diversity gradient, I first tested if patterns in genetic diversity are correlated with patterns of species diversity. I then used molecular analyses to examine if any of the following questions might explain the observed correlation between species and genetic diversity from east to west across the Pacific Ocean: (1) Do species originate in the IAA and radiate outwards? (2) Did the geological history of the Pacific (e.g. sea level fluctuations) cause greater population reduction, hence reduced genetic diversity, as one moves east across the Pacific? (3) Is gene flow reduced towards the east Pacific through increasing isolation of suitable habitat? and (4) Is population size reduced towards the east as a result of smaller coral reef habitat area? Analyses of historical demography provide insights into changes in population size over time, such as potential expansions and bottlenecks. Genetic diversity analyses may help identify ancestral populations and more recent colonisations. Population differentiation may indicate areas subject to restricted gene flow and greater isolation, whereas coalescent analyses estimate population sizes and migration rates.

5.3 METHODS

5.3.1 *Study species and locations*

Patterns in genetic diversity and differentiation were examined for 11 widely distributed coral reef fish species from 5 common reef fish families. These included *Zebrasoma veliferum* and *Z. scopas* (Acanthuridae); *Chaetodon vagabundus*, *C. trifascialis*, *C. lunulatus* and *C. citrinellus* (Chaetodontidae); *Paracirrhites forsteri* and *P. arcatus* (Cirrhitidae); *Chromis viridis*, and *C. atripectoralis* (Pomacentridae); and *Gobiodon quinquestrigatus* (Gobiidae). These species were chosen from a limited number of relatively abundant species that occur at all the locations sampled, and include species with a range of different life history traits (Table 5.1).

Table 5.1: Life history traits for each species, including reproductive mode (demersal or pelagic spawners) and habitat use.

Family	Species	Reproductive mode		Habitat
		Demersal	pelagic	
Gobiidae	<i>Gobiodon quinquestrigatus</i>	√		Shallow protected reefs, lagoons
Pomacentridae	<i>Chromis viridis</i>	√		Shallow protected reefs, lagoons
	<i>Chromis tripteralis</i>	√		Shallow protected reefs, lagoons
Chaetodontidae	<i>Chaetodon vagabundus</i>		√	Various
	<i>Chaetodon citrinellus</i>		√	Shallow reef
	<i>Chaetodon lunulatus</i>		√	Coral-rich reefs, , lagoons
	<i>Chaetodon trifascialis</i>		√	Crest
Cirrhitidae	<i>Paracirrhites forsteri</i>		√	Outer slopes
	<i>Paracirrhites arcatus</i>		√	Outer slopes
Acanthuridae	<i>Zebrasoma veliferum</i>		√	Various
	<i>Zebrasoma scopas</i>		√	Various

Samples were collected at 3 locations along the trans-Pacific biodiversity gradient that lie roughly along a similar latitude and encompass the extremes in terms of regional species richness: (1) Lizard Island on the Great Barrier Reef, Australia (14° 41'S, 145° 27'E), (2) Nouméa, New Caledonia (22° 23'S, 166° 22'E) and (3) Moorea, French Polynesia (17° 29'S, 149° 51'W) (Figure 5.1). Estimates of regional species diversities are as follows: 1600 (GBR, Australia), 1400 (New Caledonia), 800 (French Polynesia) reef-associated fish species respectively (Allen 2008).

The fish were collected on SCUBA using hand spears for the larger species and an anaesthetic (clove oil) and hand nets for smaller individuals. A small section of the caudal fin (fin clip) was removed using scissors and preserved in 95% ethanol. A total of 1089 individuals were sampled, including a minimum of 25 individuals of each species from each location (Table 5.2).

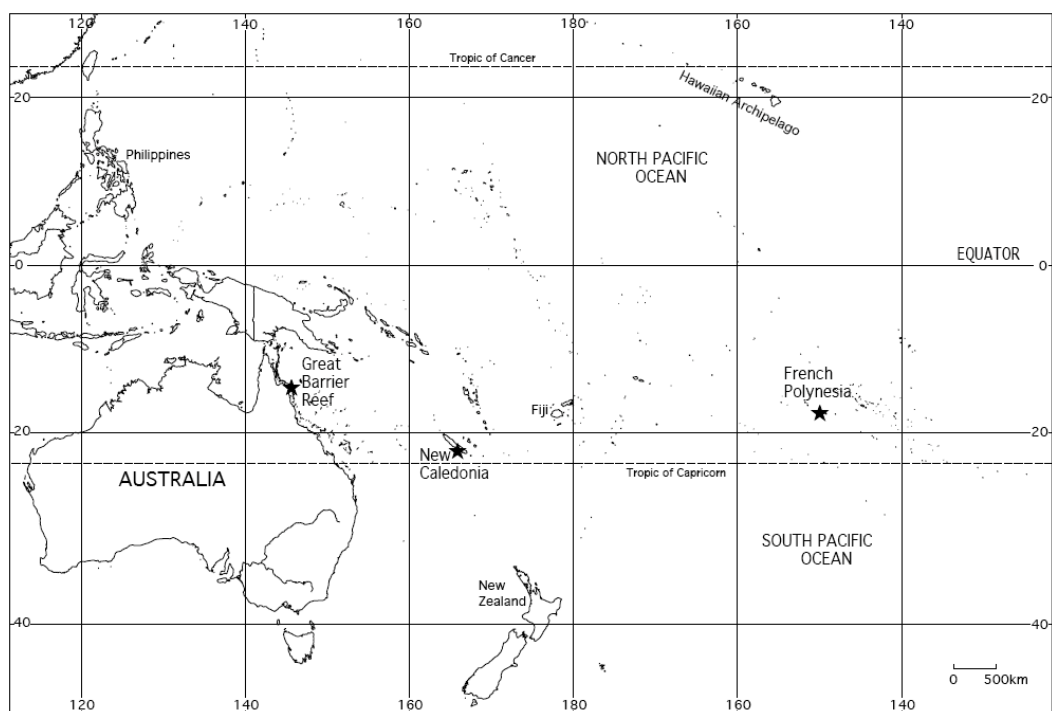


Figure 5.1: Map of the South Pacific Ocean. Sampling locations are indicated by stars: Lizard Island, Great Barrier Reef; Noumea, New Caledonia; Moorea, French Polynesia.

Table 5.2: Number of individuals collected per species from the Great Barrier Reef, Australia (GBR), Noumea in New Caledonia and Moorea in French Polynesia. Sequence lengths are specified for each species. The best fitting evolutionary model and gamma corrections were estimated in jModeltest.

Species	GBR	Noumea	Moorea	Seq length	Model selected	Gamma
<i>Gobiodon quinquestrigatus</i>	25	26	28	393	HKY+G	0.120
<i>Chromis viridis</i> - all	37	27	26	404	TPM2uf+I+G	0.476
<i>Chromis viridis</i> – sep	29/8	27	26	404	HKY+I+G	0.594
<i>Chromis atripectoralis</i> - all	28	27	51	396	TPM2+G	0.100
<i>Chromis atripectoralis</i> - sep	28	26/1	24/27	396	TPM3uf+I+G	0.607
<i>Chaetodon vagabundus</i>	25	25	25	405	TPM2uf+I+G	0.665
<i>Chaetodon citrinellus</i>	26	25	26	399	TrN+I+G	0.463
<i>Chaetodon lunulatus</i>	27	26	26	375	TPM3uf+I+G	0.456
<i>Chaetodon trifascialis</i>	28	26	25	377	TVM+G	0.244
<i>Paracirrhites arcatus</i>	26	25	26	471	TPM2uf+I+G	0.838
<i>Paracirrhites forsteri</i>	26	28	26	454	TVM+I+G	0.735
<i>Zebrasoma veliferum</i>	26	26	21	389	TIM2+I+G	0.588
<i>Zebrasoma scopas</i>	27	25	26	387	TIM3+I+G	0.650

5.3.2 Laboratory procedures

Total genomic DNA was extracted using the Puregene genomic DNA purification kit based on the protocol of DNA purification from 5 to 10 mg of fresh or frozen tissue. DNA was isolated by isopropanol precipitation, washed in 70% ethanol and resuspended in 50µl DBA Hydration Solution. The 5' end of the mitochondrial control region I (Dloop) was PCR amplified with the primers CRA (5'-TTC CAC CTC TAA CTC CCA AAG CTA g-3') and CRE (5'-CCT GAA GTA GGA ACC AGA TG-3') (Lee *et al.* 1995). Alternative forward primers were designed for *Gobiodon quinquestrigatus*: Gquin1 (5'-CCA AAG CTA GRR TTC TAG GCT-3') and Gquin2 (5'-TCA CCC CTA GCT CCC AAA GCT A-3'). Amplification was performed on an Eppendorf Mastercycler Gradient in a 25µl reaction volume containing: 2.5µl of 10x Buffer (1.5mM Mg²⁺), 200µM of each dNTP, 0.5mM MgCl₂, 0.5µM of each primer, 1U Taq DNA Polymerase (Eppendorf) and 1µl genomic DNA template. A modified hot-start PCR with an initial soak at 94°C for 5min was followed by 40 cycles consisting of denaturation at 94°C for 1 min, annealing at 51°C for 1min 15sec and extension at 68°C for 2min. The PCR was ended by a final extension at 68°C for 5min. The quality and quantity of the PCR products were determined on a 2% TBE (0.5x) agarose gel with 2% EtBr. PCR purifications and sequencing were carried out on an ABI 3730xl at GATC Biotech (Constance, Germany).

A few individuals were also sequenced in reverse directions to test the reliability of the sequences. The consensus of forward and reverse sequences was entirely congruent. As a result, most individuals were only sequenced in forward direction, except for *G. quinquestrigatus*, which was sequenced in reverse direction due to mutations in the region of the forward primer. Sequences were edited and aligned by comparing chromatograms in the computer software SequencherTM v.4.2.2 (Gene Codes Corporation, Ann Arbor, MI, USA). Alignments were adjusted by eye and trimmed to be of same length. All sequences will be submitted to GenBank.

5.3.3 Estimates of genetic diversity

Genetic diversity was estimated using nucleotide diversity (π) and haplotype diversity (h) measurements for each location and each species. Haplotype diversities (h) were calculated in DnaSP v5 (Librado & Rozas 2009). Nucleotide diversities (π) were estimated using gamma corrections as well as the (Tamura & Nei 1993) parameter as a

distance measurement in Arlequin ver 3.11 (Excoffier *et al.* 2005) . Gamma corrections were obtained through a likelihood approach implemented in jModeltest 0.1.1 (Quindon & Gascuel 2003; Posada 2008) that determines which evolutionary model best fits the data using the Aikake information criterion (Table 2). Total nucleotide and haplotype diversities were plotted for each species against location as a representative for regional species diversity. The sums of π and h across all species were also plotted against locations. Differences between mean π and h were tested using one-way ANOVA using location as factor. ANOVAs were run in R version 2.9.0 including and excluding *Gobiodon quinquestrigatus*, as this species accounted for a large proportion of the variation.

5.3.4 Population genetic analyses

Relatedness of haplotypes, as well as geographic and historical partitioning were assessed for each species using the molecular-variance parsimony technique (Excoffier & Smouse 1994), also called Minimum Spanning Networks (MSN) (Rohlf 1973). MSNs of haplotypes were computed under a distance model of haplotype pairwise differences in Arlequin ver 3.11 (Excoffier *et al.* 2005), showing the number of mutational steps between haplotypes. Networks are appropriate representations of intraspecific genetic variation and the MSN method presents the solution in the form of a set of (near) optimal networks (Posada & Crandall 2001). Networks were drawn by hand in Adobe Illustrator CS to show spatial and historical patterns of haplotype distributions.

Population genetic structures for each species were investigated by an analysis of molecular variance (AMOVA) implemented in Arlequin using the nucleotide substitution model of (Tamura & Nei 1993) and the gamma correction calculated by Modeltest. As our study involves only three geographic locations, the simple hierarchical analysis of variance calculated the fixation index F_{ST} . The significance of the fixation index was tested using a non-parametric approach of 1023 permutations as described in (Excoffier *et al.* 1992). To further assess spatial population genetic partitioning, population pairwise genetic distances (F_{ST}) were estimated. Their significance was tested by performing 10 000 permutations.

5.3.5 Historical demography

Historical demography provides insights into population expansion and potential bottlenecks and was investigated for each species using the mismatch distribution of pairwise nucleotide differences among individuals in Arlequin v3.0 (Excoffier *et al.* 2005). The past demographic parameters τ , Θ_0 and Θ_1 which were integrated into an expansion model and compared to the observed distribution were calculated. As mismatch distributions were found to be very conservative (Ramos-Onsins & Rozas 2002), the demographic history of each species was further investigated using other statistics, including Tajima's D-Test and Fu's F_S test. These tests were performed in Arlequin v3.0 (Excoffier *et al.* 2005). Tajima's D-test is used to test the neutral mutation hypothesis under the assumption that a population is at equilibrium (Tajima 1989; Rand 1996). Fu's F_S test was used to test for evidence of recent population expansion. These tests are based on rare mutations (recent) and singletons respectively compared to the average number of nucleotide differences (Ramos-Onsins & Rozas 2002).

Population size theta ($\Theta = N_e\mu$; N_e : effective population size, μ : mutation rate per site per generation) and migration rates M ($M=m/\mu$; m : immigration rate) between populations and directionality were estimated using the coalescent program Migrate 3.0.8 (Beerli & Felsenstein 1999, 2001; Beerli 2006). The program was run in Bayesian mode using a Markov chain Monte Carlo algorithm initially based on default setting to obtain priors of parameters. Three separate runs were then carried out for each of two different methods used to check the consistency of the estimates: 1) combining chains for estimates, where a single long chain was replicated 10 times; 2) "heating", which allows swapping between chains that run in parallel at 12 temperatures, the "colder" chain exploring less genealogy space than the "hotter" one. 100'000 steps every 1'000 genealogies were recorded for both techniques. Theta (Θ) priors were set to 0.0, 0.1 and 1.0. Migrate analyses were carried out using the High Performance Computing Unit (HPC) at James Cook University.

5.4 RESULTS

5.4.1 Species-genetic diversity correlation

The sums of nucleotide and haplotype diversities across all species for each location were highest at Lizard Island ($\pi=53.37\%$, $h=10.88$), intermediate at Noumea ($\pi=45.90\%$, $h=10.86$) and lowest in Moorea ($\pi=29.75\%$, $h=9.94$) (Figure 5.2), matching the decline in coral reef fish species diversity from 1455, to 1060 and 599. Overall nucleotide diversity declined by 14.0% in Noumea and by 44.3% in Moorea compared to Lizard Island, whereas haplotype diversity declined by 0.1% and 8.6% respectively. The one-way analyses of variance (ANOVA) for nucleotide diversities of each location were not significant ($p=0.265$), but haplotype diversities were significantly different between locations ($p=0.003$).

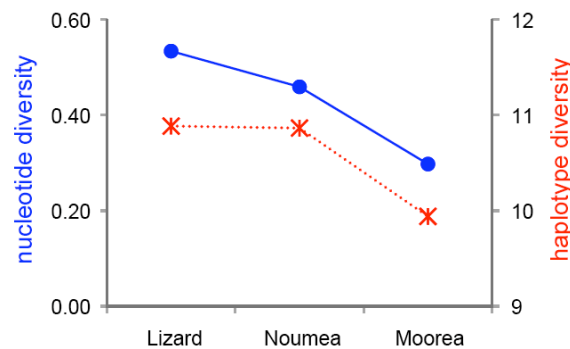


Figure 5.2: Sums of nucleotide (blue solid lines) and haplotype diversities (red dotted lines) for all species combined (divergent lineages in both *Chromis* species removed due to potentially different species):

At the species level, nucleotide diversity was highest on the GBR for *C. viridis*, *G. quinquestrigatus*, *C. citrinellus*, *C. trifascialis* and *Z. veliferum* and in New Caledonia for *C. atripectoralis*, *P. forsteri*, *C. lunulatus*, and *C. vagabundus*. *P. arcatus* and *Z. scopas* were the only two species for which nucleotide diversity increased in French Polynesia (Figure 5.3). The largest proportion of species with highest values of nucleotide diversity was recorded for Lizard Island, followed by Noumea and only a small proportion in Moorea (Figure 5.4). Haplotype diversity was consistently lowest in French Polynesia except for *P. arcatus*, where haplotype diversity equalled 1 for all locations (Figure 5.3).

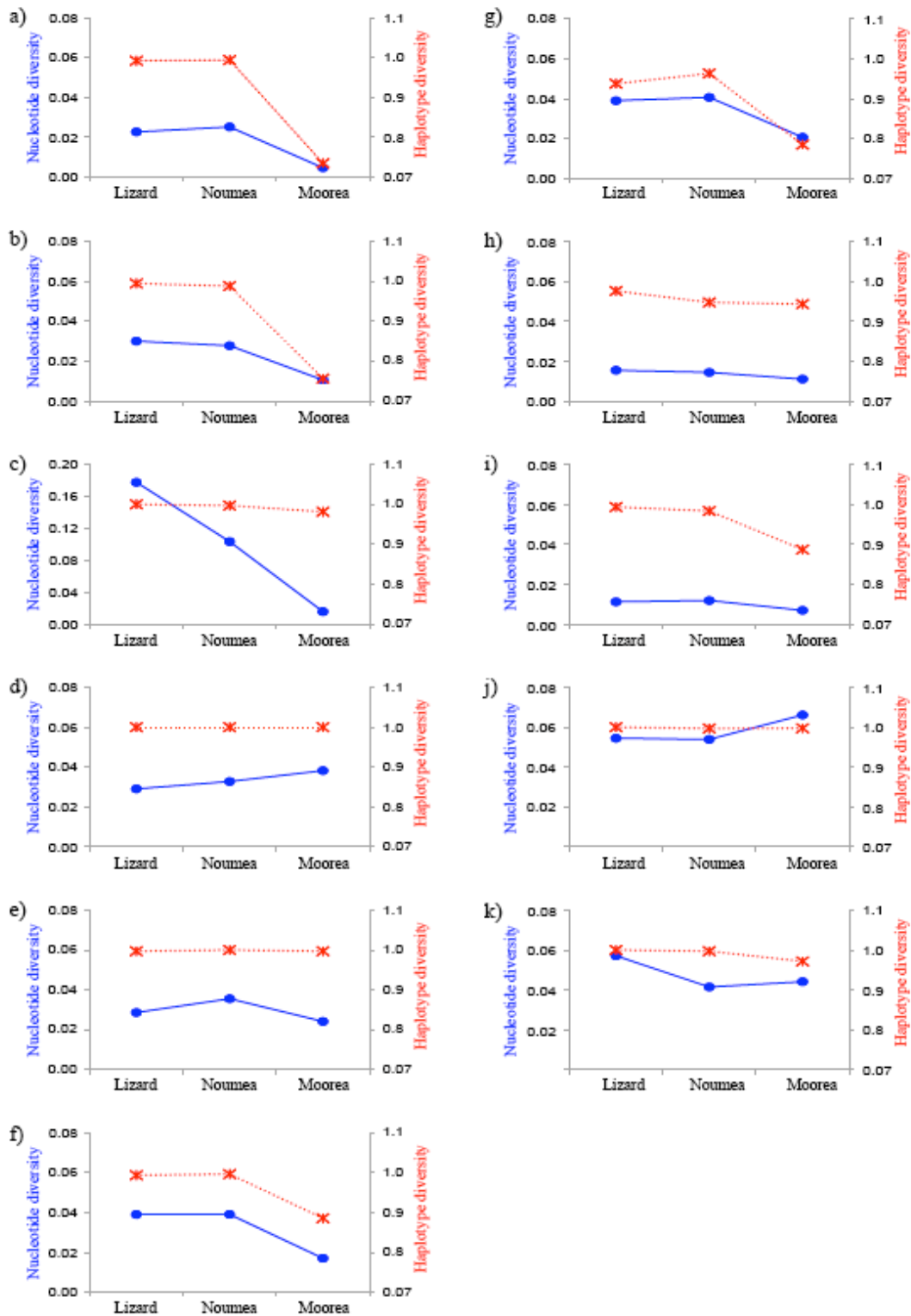


Figure 5.3: Nucleotide and haplotype diversities for each species: a) *C. atripectoralis*, b) *C. viridis*, c) *G. quinquestrigatus* (note difference in scale for nucleotide diversity), d) *P. arcatus*, e) *P. forsteri*, f) *C. citrinellus*, g) *C. lunulatus*, h) *C. trifascialis*, i) *C.*

vagabundus, j) *Z. scopas*, k) *Z. veliferum*. Blue solid lines stand for nucleotide diversities, red dotted lines for haplotype diversity

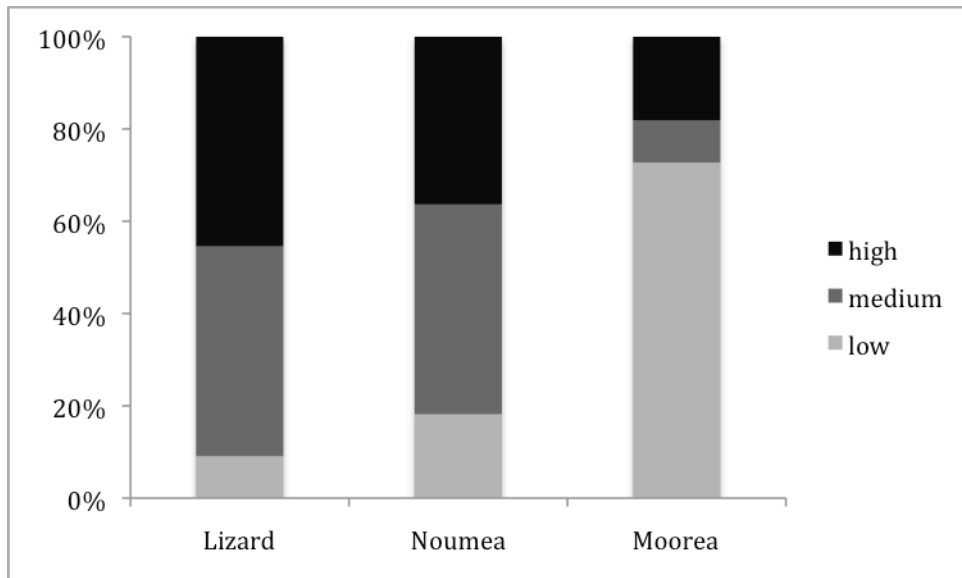


Figure 5.4: Proportions of species displaying highest, medium and lowest values of nucleotide diversity for each location

5.4.2 Population genetic differentiation

Values of nucleotide and haplotype diversities were consistently high for all species (Figure 5.5). Nucleotide diversity varied from 1.0721% in *C. vagabundus* to 18.9722% in *G. quinquestrigatus*, whereas haplotype diversity ranged from 0.97468 in *C. trifascialis* to 0.99932 in *P. arcatus*.

Overall, shapes of the haplotype network were unique to each species and show little similarities even between congeners (Figure 5.5). *Paracirrhites forsteri* exhibited a single starlike network, typical of a species that has undergone a recent population expansion, although some more ancient lineages persist. Less pronounced starlike patterns are also found in *C. trifascialis* and to some degree in *P. arcatus* and *C. lunulatus*. Some of the other species also display starlike patterns, but they are more numerous and therefore restricted to fewer individuals, possibly indicating that different lineages may have undergone population expansions at different times. On the other hand, *Z. scopas* displays a very different pattern, with numerous mutations between

haplotypes and no evidence of groupings, suggesting a long evolutionary history. Few mutations between haplotypes are only found in *C. vagabundus* and *C. trifascialis*.

The analyses of molecular variance (AMOVA) were significant for all species except for *P. arcatus* and *P. forsteri*, indicating genetic differentiation between populations (Table 5.3). The percent variation attributed to differences between populations varied between -0.71% in *P. arcatus* and 73.13% in *C. viridis* (Table 5.3). Pairwise F_{ST} calculations showed that the Moorea population was significantly different from the populations of the Lizard Island and Noumea in all species except *P. arcatus* and *P. forsteri* (Table 5.3). Additionally, the Moorea population of *C. atripectoralis* formed two distinct lineages and similarly *C. viridis* was characterised by two deeply divergent lineages in the Lizard population. Further divergent lineages were found within the Lizard Island and Noumea populations of *G. quinquestrigatus* (Table 5.3, Figure 5.5).

Table 5.3: AMOVA Φ_{ST} values and pairwise Φ_{ST} values. *C.atripectoralis* all and *C. viridis* all include the deeply divergent lineages. *C. atripectoralis* w/out and *C. viridis* w/out do not include the deeply divergent lineages. * $p<0.05$; ** $p<0.01$; *** $p<0.00$

	AMOVA		Pw Φ_{ST}					
	Φ_{ST}		LI-NC	sig	LI-FP	Sig	NC-FP	Sig
<i>G. quinquestrigatus</i>	0.59035	***	0.34870	***	0.58169	***	0.77890	***
<i>C. atripectoralis – all</i>	0.70195	***	<i>FP – FP sep :</i>		0.89532	***		
<i>C. viridis - all</i>	0.73128	***	<i>LI – LI sep :</i>		0.90195	***		
<i>C. atripectoralis w/out</i>	0.34701	***	0.01717	ns	0.48492	***	0.50863	***
<i>C. viridis w/out</i>	0.16794	***	-0.01011	ns	0.25603	***	0.27935	***
<i>P. arcatus</i>	0.00487	Ns	0.00732	ns	0.01733	ns	-0.00989	ns
<i>P. forsteri</i>	-0.00705	Ns	-0.01451	ns	-0.01197	ns	0.00475	ns
<i>C. citrinellus</i>	0.08888	***	-0.02466	ns	0.16420	***	0.14135	***
<i>C. lunulatus</i>	0.30789	***	-0.01502	ns	0.43496	***	0.42311	***
<i>C. trifascialis</i>	0.06122	**	0.02839	ns	0.05880	**	0.10334	**
<i>C. vagabundus</i>	0.10404	***	-0.00918	ns	0.14435	***	0.17968	***
<i>Z. scopas</i>	0.02455	*	0.00339	ns	0.05968	**	0.00413	ns
<i>Z. veliferum</i>	0.06505	***	0.00744	ns	0.10403	***	0.09267	**

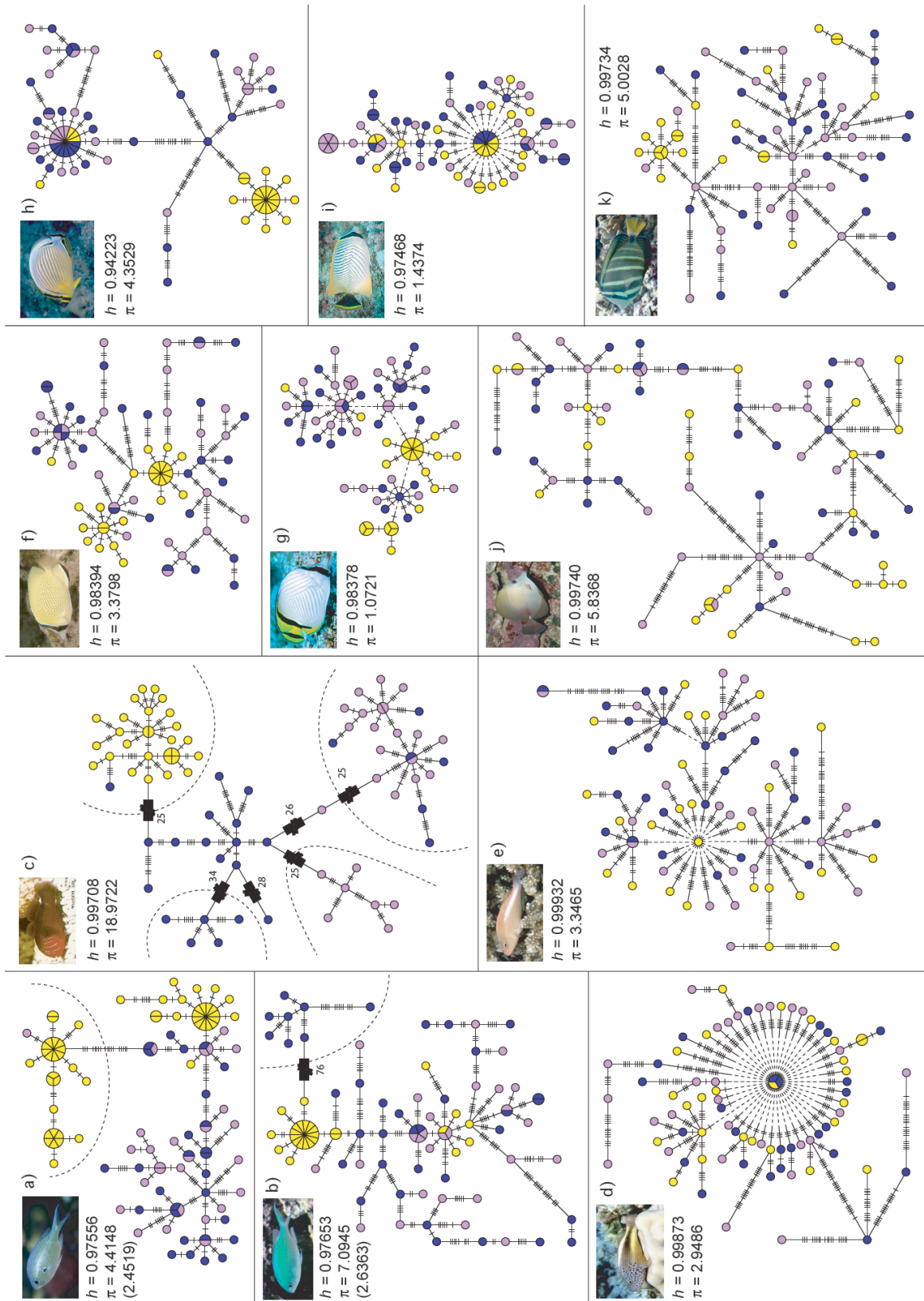


Figure 5.5: Minimum spanning networks (MSN), haplotype diversity (h) and nucleotide diversity (p) for a) *Chromis atripectoralis*; b) *Chromis viridis*; c) *Gobiodon quinquestrigatus*; d) *Paracirrhites forsteri*; e) *Paracirrhites arcatus*; f) *Chaetodon*

citrinellus; g) *Chaetodon vagabundus*; h) *Chaetodon lunulatus*; i) *Chaetodon trifascialis*; j) *Zebrasoma scopas* and k) *Zebrasoma veliferum*.

These clusters of haplotypes that can be distinguished from the rest of the population in the MSN for *C. atripectoralis*, *C. viridis* and *G. quinquestrigatus* are separated by high numbers of mutations (Figure 5.5). In *C. atripectoralis* this clade was differentiated by 18 mutations and included 27 individuals from Moorea and one from Noumea. In *C. viridis*, the separate clade consisted exclusively of individuals from Lizard Island and is separated from the rest by 76 mutations. In *G. quinquestrigatus*, numerous clades are separated by 25 to 34 mutations. All individuals from Moorea are grouped into one clade in this species. Clusters of individuals from Moorea were also observed in *C. atripectoralis*, *C. viridis*, *C. citrinellus*, *C. lunulatus*, *C. vagabundus* and to some degree in *C. trifascialis* and *Z. veliferum*. No geographic groupings could be observed in the MSNs in *P. forsteri*, *P. arcatus* and *Z. scopas* (Figure 5.5).

5.4.3 Historical demography

Unimodal mismatch distributions indicative of population expansions were found in *C. vagabundus*, *C. trifascialis*, *P. arcatus* and *P. forsteri* (Figure 5.6). Tajima's D and Fu's F tests were both significantly negative for these four species, confirming that they have experienced a spatial or demographic population expansion event (Figure 5.6). The remaining species were characterised by non-unimodal to multimodal distributions. Although Fu's F test was significantly negative for all species, the more conservative Tajima's D test was not significant for *G. quinquestrigatus*, *C. viridis*, *C. atripectoralis*, *C. citrinellus*, *C. lunulatus*, *Z. scopas* and *Z. veliferum* (Figure 5.6). This suggests that their populations are stable through time.

The six separate runs using the coalescent program Migrate 3.0.8 were consistent for all species. Results for *P. arcatus* and *P. forsteri* are not provided as the analyses were unable to provide estimates due to the lack of any population genetic structure. Population estimates across all six runs did not converge in the Lizard and Noumea populations of *C. citrinellus*, *Z. scopas* and *Z. veliferum*, the Lizard population of *C. trifascialis*, as well as the Moorea population for *C. lunulatus*. These estimates are therefore represented by the maximum value of 1 (Table 4). Population estimates only

converged to some degree in the Lizard and Noumea populations of *C. vagabundus*, the Lizard population of *C. viridis* and the Noumea populations of *C. atripectoralis* and *C. trifascialis* (fixed at $\Theta = 0.75$). Population size estimates for Moorea were mostly very low (Figure 1). Migration rates varied between locations and species. The highest migration rate was estimated in *C. trifascialis* (529.4), whereas the lowest was recorded for *Z. veliferum* from Lizard to Noumea (25.2). The overall highest mean rates were observed from Noumea to Lizard (303.8). Intermediate overall mean migration rates were recorded from Lizard to Noumea and to Moorea (194.4 and 196.8 respectively). Migration rates from Noumea to Moorea and from Moorea to Lizard and to Noumea were similarly low (151.2, 146.6 and 138.9 respectively).

Table 5.4: Estimated population size theta ($\Theta=N_e\mu$; N_e : effective population size, μ : mutation rate per site per generation) and migration rates M ($M=m/\mu$; m : immigration rate) between locations based on coalescent analyses in MIGRATE. Population size estimates not quite converging are highlighted in bold, whereas $\Theta > 1$ are populations with non-converging results. Direction of migration rate estimates between any two populations is indicated by arrows between the 2 location abbreviations: LI = Lizard Island, NC = Noumea, New Caledonia, FP = Moorea, French Polynesia.

Species	Θ LI	Θ NC	Θ FP	LI->NC	LI->FP	NC->FP	NC->LI	FP->LI	FP->NC
<i>C. atripectoralis</i>									
<i>w/out</i>	0.1966	0.5038	0.0078	479.5	134.6	161.2	124.8	141.0	144.7
<i>C. viridis w/out</i>	0.4776	0.5661	0.0108	51.6	159.4	332.7	78.7	80.8	56.2
<i>C. citrinellus</i>	0.5091	0.3724	0.0190	120.3	177.9	482.4	56.2	98.7	42.2
<i>C. lunulatus</i>	> 1	> 1	0.0059	81.5	289.4	140.3	266.8	260.3	244.6
<i>C. trifascialis</i>	0.2519	0.0681	> 1	305.2	183.0	529.4	426.3	135.8	415.0
<i>C. vagabundus</i>	> 1	0.4951	0.0081	356.6	354.2	442.6	102.4	326.6	97.6
<i>Z. scopas</i>	> 1	> 1	0.1728	135.0	149.3	97.5	107.5	80.6	79.4
<i>Z. veliferum</i>	> 1	> 1	0.0388	25.2	127.0	244.2	47.0	49.4	32.3

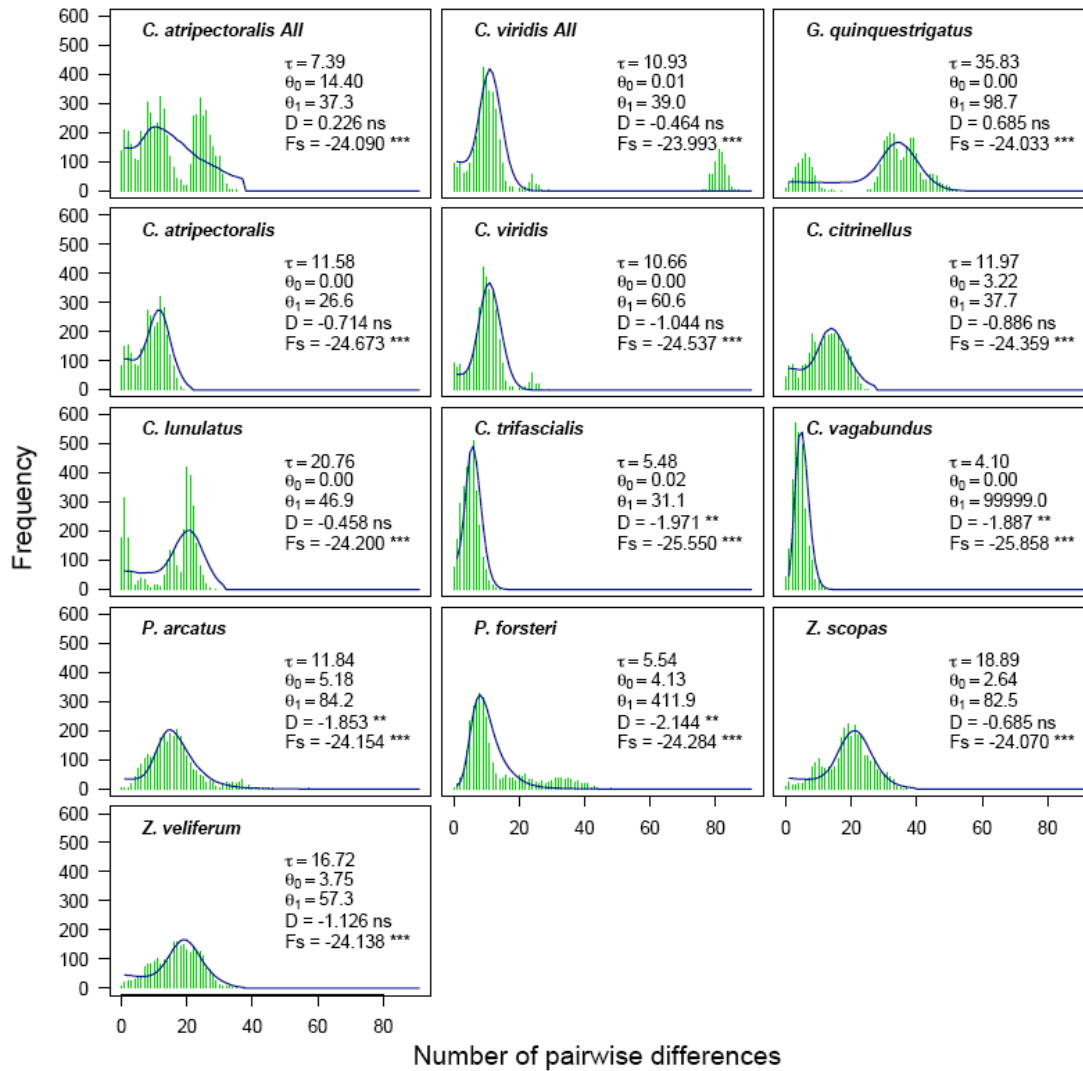


Figure 5.6: Mismatch distributions, observed distributions (green bars), simulated distributions (blue line). Mismatch distributions for *C. atripectoralis* and *C. viridis* are displayed including and excluding the highly divergent lineages.

5.5 DISCUSSION

Our results show that there is an overall trend for genetic diversity to decline in coral reef fish across the Pacific that parallels the widely studied Pacific gradient in species richness. Nucleotide diversity was reduced by 14.0% in Noumea and by 44.3% in Moorea compared to Lizard Island. Species diversity declines similarly by 27.2% and 58.3% respectively. The decline in haplotype diversity was significant, but less steep,

because very few haplotypes were shared between individuals and haplotype diversity was therefore consistently high. The decline in haplotype diversity was observed in all species across the Pacific, except for *P. arcatus*, for which haplotype diversity equalled 1 for all populations. Whilst nucleotide diversity was lowest in Moorea for most species (8 out of 11), this pattern was not congruent across all species. As a result, patterns between the two genetic diversity measures were inconsistent in a few species, suggesting that not all species are influenced in the same way through evolutionary history. Nevertheless, the combined results across all species indicate that factors shaping genetic diversity over space in time do act in such a way that overall genetic diversity parallels the decline in species diversity across the Pacific in coral reef fishes.

The greatest decline in genetic diversity was observed in French Polynesia, whereas values in the Lizard Island population were only slightly higher than in the Noumea population. Similarly, species richness is not much lower in New Caledonia than on the Great Barrier Reef compared to French Polynesia. The generally positive correlation between genetic diversity and species richness across the Pacific suggests that similar processes shaped both diversity levels at large spatial scales, but influence Lizard Island and Noumea more similarly than Moorea. These patterns coincide with the geographic proximity of the Great Barrier Reef and New Caledonia, whereas French Polynesia is situated at the eastern limit of the Central Pacific with relatively few stepping-stones in between. In contrast to latitudinal diversity gradients, the longitudinal Pacific diversity gradient is not subject to strong environmental clines, such as temperature, light and seasonal variation. Therefore, other factors must influence genetic diversity and species diversity patterns in similar ways. These factors are likely to include the biogeographic history of regions (species origin, vicariance events, demographic history), patterns of connectivity (gene flow, isolation, larval dispersal) and habitat area, of which isolation of and reduced habitat area in French Polynesia are likely to play the most important role.

Life history traits do not seem to strongly affect the nature of the relationship. For example, similar levels of genetic differentiation between the western and eastern Pacific were found between damselfishes and butterflyfishes, despite differences in pelagic larval durations (PLD) and reproductive modes. Butterflyfish are pelagic spawners with PLDs of around 30-40 days, whereas damselfish are demersal spawners with PLDs of only about 20 days. Furthermore, species from the same genus did not

necessarily display more similar patterns of genetic diversity and structure than those found across families. The only consistent pattern observed was the presence of potentially cryptic species in the demersal spawners.

Assuming the genetic patterns of a species bear the genetic signature of its origin and subsequent expansions, the decline in genetic diversity towards French Polynesia observed in the majority of species I tested suggests that most species originated (diverged) in the centre of diversity and radiated outwards as proposed by the centre of origin theory (Briggs 2000). However, since genetic diversity is not consistently highest on the GBR, species formation in the centre of origin is not exclusive and some species may have originated outside the IAA, including peripheral areas. Potential evidence for species arising throughout the Pacific is further provided by the likely presence of cryptic species across the trans-Pacific diversity gradient. Two distinct clades were found in *Chromis viridis* at Lizard Island, whereas *C. atripectoralis* was characterised by two distinct populations in Moorea. Furthermore, *Gobiodon quinquestrigatus* may represent a complex of cryptic species with deep evolutionary lineages occurring both at Lizard Island and in Noumea. Cryptic species are increasingly described through advances in molecular techniques (see (Knowlton 2000; Rocha *et al.* 2007) for review) and deep genetic breaks have already been previously recorded for *Chromis viridis* in the Indo-Malay Archipelago and the Red Sea (Froukh & Kochzius 2008). Contrary to the initial belief that most species arise in allopatry, recent theories and studies indicate that sympatric and ecological speciation are also important drivers in diversity (Schluter 2001; Munday *et al.* 2004; Messmer *et al.* 2005; Rocha *et al.* 2005), which may also be the case here. Alternatively, these deeply divergent lineages may represent surviving relics of ancestral populations that have gone extinct elsewhere. These results support the increasing evidence that species diversity patterns cannot be explained by a single model, but rather are the result of complex and multiple processes (Palumbi 1997; Malay & Paulay 2010).

Speciation is the primary process creating species diversity (Hubbell 2001), but local species richness as well as genetic diversity are shaped by biogeographic processes. Species richness and genetic diversity build up through diversification and immigration, and are countered by population declines and extinction (MacArthur & Wilson 1967; Brown & Lomolino 2000; Whittaker *et al.* 2008). Molecular phylogenetics provide important insights into these processes, which may distinguish

between historical events and present-day factors, such as connectivity and isolation. Diversification may be promoted through vicariance events, adaptive radiation through changes in environmental conditions or isolation, but these same processes may also lead to population reductions and local extinctions.

The geological history of Indo-Pacific coral reefs is likely to have had strong and potentially similar impacts on both species and genetic diversity patterns. Although no biogeographic barriers have been described between the GBR and French Polynesia, repeated rapid sea level changes during the 7 glaciation periods in the Pleistocene are likely to have had profound effects on coral reef habitats and their residents. Species ranges were restricted and patterns of connectivity disrupted, leading to local population reductions or extinctions, followed by expansion of species ranges and secondary contact (Palumbi 1994; McMillan & Palumbi 1995; Benzie 1999). Particularly affected were lagoonal habitats either in oceanic islands (such as in French Polynesia) or coastal barrier reefs (such as New Caledonia and the Great Barrier Reef). The lagoons of French Polynesia were shallower than the drop in sea levels and thus would have been completely exposed. As a result, many lagoonal reef fish species, may have disappeared and then subsequently recolonised these areas as sea levels rose again, resulting in reduced genetic variation (i.e. bottlenecks) and rapid population expansions (Fauvelot & Planes 2002). The lagoons of New Caledonia are similarly shallow and would have repeatedly dried and refilled during the Pleistocene, leading to repeated population extinctions and recolonisations. In contrast, the Great Barrier Reef may have been able to provide deeper refuges and species may have been less affected. However, the lagoonal habitat was unlikely to be the only one affected, as we observed reduced genetic diversity in lagoonal as well as non-lagoonal species. Species with particular resource requirements (e.g. shallow water for *Chaetodon citrinellus* and specific food resources for *C. trifascialis*) may have also suffered great population reductions. Such population reductions followed by population expansions could explain the often clustered star-shaped pattern for the Moorea populations (yellow) observed in the minimum spanning network (MSN). The consistently lower haplotype diversity for the Moorea population across all species further supports the hypothesis that coral reef fishes in the area have undergone more recent population expansions. Local species extinctions and population reductions followed by expansions or recolonisations could therefore have contributed to the lower biodiversity recorded in French Polynesia.

These results further strengthen the idea that island systems are more sensitive and more easily impacted due to their smaller size and greater isolation resulting in reduced genetic and species diversity (MacArthur & Wilson 1967).

Connectivity between regions plays a major role in local community composition and maintaining genetic integrity of species, but generally decreases with increasing isolation. However, a single migrant per generation has been shown to be sufficient to maintain gene flow between two populations and counteract the effects of genetic drift and declining genetic diversity (Planes 2002). The comparatively low migration rates between Moorea and Lizard Island/Noumea, suggest that long-distance dispersal is a rare occurrence. Therefore, although perhaps not sufficiently absent to produce genetic drift or speciation, immigration to French Polynesia may still be rare enough to reduce genetic diversity. This may occur despite the potential for long-distance dispersal in marine organisms, due to complex larval behaviour (Leis 2002; Cowen & Sponaugle 2009) and the potential for self-recruitment (Jones *et al.* 1999; Swearer *et al.* 2002; Jones *et al.* 2005; Jones *et al.* 2009). The tendency for more gene flow from New Caledonia to the GBR, which is consistent with present-day surface currents, may similarly contribute to the cline in genetic diversity, as immigration, in this case to Lizard Island, is generally associated with higher genetic diversity.

Significant genetic differentiation of the Moorea population from the GBR and Noumea populations observed in all but two of the species studied here (*P. forsteri* and *P. arcatus*) further indicates that French Polynesia is to some degree geographically isolated, a break that has already previously been reported (Planes 2002; Schultz *et al.* 2008). As a result, peripheral or isolated populations are more likely to be subject to strong swings in population size, which can create severe bottlenecks or species extinctions (Palumbi 1997). As French Polynesia more or less represents the range limit for all species in this study, these processes may well account for a reduction in species diversity and genetic diversity for at least some of the species.

Habitat area is another important factor generally acting similarly on species richness and genetic diversity. Larger areas support more species and more individuals, thus both species richness and population genetic diversity are expected to increase and therefore be positively correlated with habitat area (Wright 1940; MacArthur & Wilson 1967; Triantis *et al.* 2008). Although French Polynesia consists of hundreds of islands and atolls surrounded by coral reefs and the reefs of New Caledonia form one of the

largest continuous barrier reefs, the area covered by coral reefs at these locations is less extensive than on the GBR, which in addition is part of the largest area of coral reefs, the Indo-Australian Archipelago (IAA) (Bellwood *et al.* 2005). Hence, area may be responsible for the smaller population size in French Polynesia, which were estimated for most species and contribute to reduced genetic diversity and lower species richness of the region.

This study for the first time specifically investigated the overall relationship between species and genetic diversity in coral reef fish across the Pacific diversity gradient. The overall patterns of genetic diversity paralleled the decline in species richness along the trans-Pacific diversity gradient. However, since this result was not consistent across all species, it suggests that the distribution of species ranges and the distribution of genotypes within a species are the result of complex interactions of biological and physical factors that have operated through time. Processes that are likely to similarly affect both levels of biodiversity include species origin, sea-level changes in the Pleistocene, isolation, gene flow and area and population size. However, a more substantial sampling effort (species and locations) and the use of different markers are needed to confirm this positive correlation, considering more species and locations. Furthermore, this study also highlights the need for more studies addressing all levels of biodiversity, since cryptic species may be a more common occurrence than previously thought and as a result species diversity may often be underestimated. Anthropogenic impacts and climate change are threatening all ecological systems of our planet, with consequences such as biodiversity loss and disruptions to ecosystem processes (Soule 1991; Thomas *et al.* 2004; Lovejoy & Hannah 2005; Munday *et al.* 2008; Rockstrom *et al.* 2009). Considering the increasing evidence that both species and genetic diversity are crucial to the functioning, stability and resilience of ecosystems (Loreau *et al.* 2001; Hooper *et al.* 2005; Sala & Knowlton 2006; Worm *et al.* 2006; Bracken *et al.* 2008), it is important to further investigate the nature of the relationship between these two levels of diversity. The results could have important implications for conservation priorities if for example areas of low species diversity were found to be more vulnerable to disturbances. Understanding patterns of biodiversity are therefore crucial for conservation and minimizing the risks of further extinctions.

6 CHAPTER 6 - GENERAL CONCLUSIONS

This thesis represents a first step towards a more comprehensive understanding of the interrelationships between different hierarchical levels of coral reef biodiversity and also assesses the potential consequences of biodiversity loss for reef fish communities. The results show that the nature and strength of relationships between different levels of biodiversity vary, with some being stronger than others, and some being causal whereas others are not. Chapter 2 revealed strong causal links between coral and fish communities, with more diverse coral habitats playing a major role in promoting diverse and abundant fish communities. Fish diversity was not found to affect fish productivity in terms of growth, which instead seemed to be mainly influenced by the relative importance of intra- versus interspecific antagonistic interactions (Chapter 3). However, competitive interactions were not found to limit total abundance within a guild of planktivorous damselfish, which instead increased with fish species richness and showed no evidence for density compensation (Chapter 4). Parallel declines in both species diversity and overall genetic diversity were observed from the West to the East Pacific (Chapter 5).

1. Levels of biodiversity: Causal links versus parallel effects

The most significant causal link established in this thesis was the demonstrable impact of coral biodiversity on fishes. **Chapter 2** experimentally tested for the first time the effects of coral diversity and identity on reef fish communities, and showed coral diversity and community structure were major determinants of local fish diversity and community structure. It showed that certain coral species clearly play a more important role in promoting diverse and abundant fish communities than others. However, the composition of fish communities also differed between all coral species with many reef fish displaying strong habitat selectivity. As a result, the loss of any coral species is likely to result in the loss of unique fish assemblages.

The causal links and potential consequences of fish diversity loss itself on patterns and processes of fish communities were investigated in **Chapters 3** and **4**. Fish diversity was found to cause overall numerical abundance to increase, but appeared to have no effect on productivity in terms of growth rates within a guild of planktivorous damselfish. Competitive interactions did not limit the accumulation of individuals, resulting in a linear increase in total abundance with increasing diversity (**Chapter 4**). However, intra- and interspecific competitive interactions did affect individual growth rates, but overall productivity remained constant with increasing fish diversity (**Chapter 3**). It therefore appears that factors such as niche complementarity and facilitation affect the fish community as whole in terms of total density, but not at an individual level, where growth rates are determined by competitive interactions. As a result, although overall growth does not appear to be affected by fish diversity, fish species loss is likely to cause overall abundance of the fish community to decline.

The relationship between species and genetic diversity received only very recently attention (Vellend 2003, 2004; Magurran 2005; Vellend 2005; Vellend & Geber 2005; He *et al.* 2008; Sei *et al.* 2009), and the nature of it is still largely unknown, particularly in the marine environment. In **Chapter 5**, this relationship was for the first time specifically investigated in coral reef fishes of the Pacific Ocean. Overall genetic diversity was found to parallel the decline in species diversity across the Pacific, although at an individual level, the relationship was found to be variable in some of the species. No single process can account for the overall positive correlation between the two levels of diversity, as the patterns of species and genetic diversity are the results of evolutionary history and spatial mechanisms. However, reduced habitat area and increasing isolation may account for most of the reduction in species and genetic diversity in French Polynesia. Although reduced genetic diversity may cause species extinctions, the overall positive correlation between species and genetic diversity seems to be primarily the result of parallel processes rather than a causal link.

2. Implications for future conservation strategies

The strong causal relationship between coral diversity and inhabiting fish communities highlights the importance of not only preserving coral cover and structural complexity, which have already been shown to be critical for fish assemblages (Syms &

Jones 2000; McClanahan 2002; Jones *et al.* 2004; Graham *et al.* 2006; Wilson *et al.* 2006; Pratchett *et al.* 2008; Paddack *et al.* 2009), but to also ensure that coral diversity is maintained. This thesis shows that a diverse coral habitat is likely to positively affect other levels of biodiversity on coral reefs, as coral diversity was found to be crucial for maintaining diverse fish assemblages, which in turn are likely to translate into higher total fish abundance and potentially higher genetic diversity.

Considerable debate at what level efforts to preserve biodiversity should be focused on still exists and it is increasingly suggested that protecting individual species is insufficient (Brussard 1991; Franklin 1993). This thesis provides important insights into the relationships between different levels of diversity and the potential consequences of biodiversity loss for coral reef fish communities. Diversity from genes to ecosystems was found to be intimately linked, indicating that loss at one level is likely to have escalating/cascading effects to other levels. Preserving diverse habitats is likely to ensure the diversity and abundance of inhabiting fish communities, which in turn result in greater biomass and are likely to contain high genetic diversity.

These findings have important implications for conservation strategies, such as site selection for marine protected areas. Targeting resilient habitats is critical for ensuring the persistence of an ecosystem facing global threats, such as climate change. However, some of the better microhabitats (specific coral species, such as *Acropora nasuta* and *Seriatopora hystrix*) were also found to be more vulnerable, in which case local threats, such as pollution, destructive fishing methods etc, need to be minimised. Overall, the protection of diverse and complex habitats seems to provide a useful tool to simultaneously maximise species and genetic diversity, and total abundance, which in turn are likely to maintain ecosystem processes and services.

3. Knowledge gaps and future research directions

Although **Chapter 2** showed a clear and strong link between coral and fish communities, many aspects remain unanswered and require further investigations. The same experiment was therefore recently set up in French Polynesia to assess how regional diversity affects the causal relationship between corals and fish. Reduced regional diversity may result in weaker associations of many reef fish with particular

coral species, as they are likely to be less specialised. As a result, fish communities on low diversity reefs may initially be less affected by coral diversity loss. On the other hand, the scale of the study may also have resulted in an under estimate of the effects of coral diversity on fish diversity if saturation of fish species richness per habitat area was already reached in some of the single coral species treatments. Although the patch reef habitat is an important component of coral reef systems, it would also be important to explore the relationship of coral and fish diversity in different habitats types of the main reef structure.

The biomass of a fish community is ultimately driven by both total abundance, and the size and growth rate of individuals. Although the results of this thesis suggested that fish communities may be resilient to diversity loss in terms of growth, but not in terms of total abundance, more research is needed to confirm these trends. Experimental outcomes are often found to be variable due to inherent variability of the natural environment and depending on which species go extinct (Ives & Cardinale 2004; Worm *et al.* 2006). But if the lack of density compensation was to be confirmed, total abundance would be affected, resulting in reduced total biomass and consequently, ecosystem processes and stability may be further affected. Longer-term experiments, covering a wider range of ontogenetic stages and evolutionary more diverse assemblages, should therefore be considered to determine the generality of the observed relationships, as the experiments were only based on a small guild of closely related juvenile damselfish. Furthermore, it would be useful to also establish the relationship between growth and density of fish assemblages.

As both species and genetic diversity have been hypothesised to positively affect ecosystem stability and resilience (Loreau *et al.* 2001; Hughes & Stachowicz 2004; Reusch *et al.* 2005), a correlation between species and genetic diversity may put low diversity systems more at risk. However, the suggestion that a positive relationship exists between species and genetic diversity in marine reef organisms is only tentative and requires further investigations covering more species and locations. If confirmed, areas with low diversity may be more vulnerable to disturbances as a species or genotypes may be less likely to be able to adapt to environmental changes or resist to diseases. It would also be important to test whether species and genetic diversity are

positively correlated at a local scale, in which case species diversity may represent a surrogate for the preservation of genetic diversity.

4. Concluding remarks

Coral reefs form one of the most diverse ecosystems on our planet, but whether this places them more at risk or resilient to disturbances is largely unknown. This thesis provides important insights into how different levels of biodiversity relate to each other on coral reefs, which consequently allows us to better assess potential impacts of biodiversity loss at different levels and to better preserve these extraordinary systems through more effective conservation priorities and strategies. The strong causal link between coral and fish communities is particularly important, as the global decline in reef health and higher susceptibility to disturbances of certain coral species suggest that coral species will go extinct, at least at a local scale. The effects of increasing temperatures due to global warming are likely to extend to reef fish biodiversity and ecosystem functioning, either directly through intolerant fish species going extinct or indirectly through habitat diversity loss.

7 REFERENCE LIST

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