Hobbs, Jean-Paul A. (2011) *Reef fishes on isolated islands: community structure, endemism and extinction.* PhD Thesis, James Cook University.

https://doi.org/10.25903/ype3%2Dkp08

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REEF FISHES ON ISOLATED ISLANDS: COMMUNITY STRUCTURE, ENDEMISM AND EXTINCTION

PhD thesis submitted by

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in April 2011

For the degree of Doctor of Philosophy

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The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *National Statement on Ethics Conduct in Research Involving Human (*1999*),* the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997), the *James Cook University Policy on Experimentation Ethics. Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001). The proposed research methodology received clearance from the James Cook University Experimentation Ethics Review Committee (approval number A976), Parks Australia North, and the Western Australia Department of Fisheries.

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STATEMENT ON THE CONTRIBUTIONS OF OTHERS

The chapters of this thesis are also manuscripts that have been published, submitted or are in preparation for submission. Several researchers have made contributions to these manuscripts and it is necessary to recognise their contributions.

Chapter 2 is a manuscript currently in review at Journal of Biogeography and is co-authored by G.P. Jones, P.L. Munday, S.R. Connolly and M. Srinivasan. Field data for this manuscript came from surveys performed by GPJ, PLM and MS. The construction, description and implementation of the null model analyses in this manuscript were done by SRC. G.R. Allen kindly provided the Indonesia species list used in the analyses. All authors provided intellectual input into this manuscript.

Chapter 3 is now published as: Hobbs, J-P.A**.**, Frisch A.J., Allen, G.R., and van Herwerden, L. (2009) Marine hybrid hotspot at Indo-Pacific biogeographic border. *Biology Letters* 5:258-261. For this publication, AJF provided funding and helped design the study. GRA provided information on hybrids from previous field surveys and LvH provided molecular data. All authors provided intellectual input.

Chapter 4 involves regression tree analysis, which I learnt through the assistance of Maya Srinivasan. This manuscript is being prepared for journal submission and GPJ, PLM and MS have provided comments.

Chapter 5 has been published as: Hobbs, J-P.A., Jones, G.P. and Munday P.L. (2010) Rarity and extinction risk in coral reef angelfishes on isolated islands: interrelationships among abundance, geographic range size and specialization. *Coral Reefs* 29:1-11. All authors provided intellectual input.

Chapter 6 is a molecular study and the manuscript is nearing submission. Adrian McMahon and Stephen Kolomyjec were employed to do some laboratory work and obtain DNA sequences for some of the samples used in this study. Comments have been provided by D. Jerry, LvH, GPJ and PLM.

I was supported by an Australian Postgraduate Award Scholarship and a Nancy Vernon Rankine write-up award from James Cook University (JCU). Funding for this study came from a JCU Competitive Research Incentive Grant to GPJ, PLM and DJ and an Envirofund Australia Natural Heritage Trust grant to J-PAH. Significant in-kind and logistical support was provided by Parks Australia. Fieldwork assistance was provided by J. Gilligan, J. Hender, J. Neilson and C. McDonald.

ACKNOWLEDGEMENTS

I thank all the people that have assisted me over the years with this PhD and I am particularly grateful to the people mentioned below. I sincerely apologise to anyone that I have forgotten to mention, and I hope that I have thanked you along the way.

Firstly, I appreciate all the time my supervisors and JCU staff members have spent providing valuable guidance and feedback. I thank my primary supervisors Geoff Jones and Philip Munday who were instrumental in my development as an independent researcher. Thanks to Lynne van Herwerden and Dean Jerry for all their help and patience with the genetics components. I also thank Maya Srinivasan and Sean Connolly for their dedicated assistance with statistical analyses and feedback on chapters. I am grateful for the valuable insights gained through discussions and advice from Howard Choat and I thank Gerry Allen for his knowledge and information on fishes of Christmas and Cocos Islands and unpublished data on fishes of Indonesia.

For assistance with molecular laboratory procedures and statistical analyses, I thank Selma Klanten, Peter Cowman, Adrian McMahon, Stephen Kolomyjec and David Jones. I would have been lost in the world of genetics without this help. Thanks to Janelle Eagle and Martial Depczynski for advice on microhabitat assessments and gut content analysis. I thank Ashley Frisch for all his valuable help in various aspects of this PhD.

For financial assistance I acknowledge the support of James Cook University and Envirofund Australia, Natural Heritage Trust. I was supported by an Australian Postgraduate Award Scholarship and also thank Mike Kingsford for providing me with the Nancy Vernon Rankine write-up award.

I would like to mention a special thanks to everyone that has helped with me with the fieldwork. There are limited people and resources at remote locations like Christmas and Cocos Islands, and this study was only made possible through the help and generosity of members of the Christmas and Cocos Islands communities. A huge thanks to all those people that gave up their time to assist, or lent me boats, fuel, equipment or gave me a meal or place to stay. I will never forget your generosity. I would like to thank all the Parks Australia staff over the years for their tremendous support of this research. The support from Alistair Graham in the early days, and more recently Marjorie Gant and Mike Misso has greatly benefited not only my research, but a greater understanding of the marine biodiversity of these Islands. I am forever grateful for the encouragement and never-ending help of Max Orchard and his offsiders Azmi Yon and Eddly Johari. Thanks to the Christmas Divers for all their help, particularly Linda Cash. A HUGE thanks to Hama and Lin (and now Leila and Lumi) of Wet ‘n’ Dry Adventures who have gone out of their way to help me in so many ways over the years.

I would like to thank the whole Cocos Islands community, and unfortunately there is not enough space mention everyone. Thanks particularly to John Cluniess-Ross, Geoff Christie and Karen and Dieter of Cocos Dive for all their logistical support. I am also

very grateful to the Cocos Island Malay community who welcomed me in and taught me so much about their culture, the Islands and their extensive knowledge of where to find (and how to eat) every marine species at the Islands. Terima kasih bunyak bunyak. Special thanks to all my Cocos Malay mates, especially Hisham Macrae (Pak Imannia) and his family for all their help and amazing hospitality.

Finally, thanks to all the friends at uni and in the field that have made this journey fun. Thanks to J. Gilligan, J. Hender, J. Neilson, C. McDonald for their assistance and adventurous nature in the field. And thanks to all those people who have been involved in the various side projects and trips to far-flung destinations. I will never forget those adventures and the discoveries we have made. It is through those experiences that I have learnt that, for me, the quest of exploring the unknown and making new discoveries is the best (and most exciting) part of science.

ABSTRACT

Ecology strives to identify the processes determining species diversity, species composition and population abundance. Island communities have served as the natural laboratories for the development and testing of ecological theories. Islands also provide the opportunity to determine whether there are differences in the ecological processes that structure mainland and isolated communities. To date, most of the theory and empirical studies of island communities have focused on terrestrial organisms. However, islands can be equally instructive about the mechanisms favouring the presence, absence and abundance of marine species. Therefore, the aim of this thesis is to determine whether the processes structuring terrestrial island communities apply in the marine environment. Ecological hypotheses spanning the fields of biogeography through to conservation biology are tested using reef fish communities at the remote Christmas Island and the Cocos (Keeling) Islands in the tropical eastern Indian Ocean.

Like small isolated terrestrial communities, the reef fish communities at Christmas and Cocos Islands were found to be species poor and contained a distinct taxonomic composition with an over-representation of species with high dispersal potential. Despite low species richness, there was no evidence of density compensation, with population densities on the islands similar to species-rich neighbouring mainland assemblages. In contrast to terrestrial communities, species at the edge of their range did not have lower abundance than species at the centre of their range, and endemic species had substantially higher abundance than widespread species. Overall, the observed patterns conform to predictions from terrestrial ecological hypotheses, indicating that similar processes are important in determining species richness and community

composition in marine and terrestrial communities on isolated islands. However, observed patterns in abundance did not conform to expectations from terrestrial theory, and this appears to be due to the different life histories of marine and terrestrial species.

Local environmental factors can also be important in structuring reef fish communities; however, few studies have examined their role on oceanic reefs. Regression tree analysis of angelfish and butterflyfish communities revealed that large physical gradients (island location, exposure, depth, habitat complexity) are more important than small-scale biotic factors (live coral cover, algal cover and habitat diversity) in determining the community structure of reef fishes at these oceanic islands.

Christmas and Cocos Islands are also situated on the Indo-Pacific biogeographic border, and in the terrestrial environment, biogeographic borders represent important areas for hybridisation. Eleven hybrid coral-reef fishes (across six families) were identified at the islands: the most recorded hybrids of any marine location. In most cases, at least one of the parent species is rare (< 3 individuals per 3000 m^2), suggesting that hybridisation has occurred due to a scarcity of conspecific partners. The Islands also represent a marine suture zone because many of the hybrids have arisen through interbreeding between Indian and Pacific Ocean species. For these species, it appears that past climate changes allowed species to diverge in allopatry, while recent conditions have facilitated contact and subsequent hybridisation at this biogeographic border.

Isolated islands often contain a high proportion of endemic species, which suffer high rates of extinction because of an association among three traits that threaten species persistence: small geographic range size, low abundance and ecological specialisation. This study found that endemic angelfishes at Christmas and Cocos Islands did not

conform to these interrelationships. Endemic angelfishes were 50-80 times more abundant than widespread species and were not more specialised than widespread congeners. High abundance and lack of specialisation by endemic reef fishes may compensate for the extinction risk posed by having an extremely small geographic range.

Endemic species, and isolated populations of widespread species, are also at risk of extinction because they tend to have low genetic diversity. Examination of angelfish mtDNA revealed that the endemic *C. joculator* exhibit high haplotype ($h > 0.98$) and nucleotide diversity (Christmas $\pi\% = 3.63$, Cocos $\pi\% = 9.99$). The isolated populations of widespread angelfishes (*C. bispinosa* and *C. flavicauda*) present at Christmas Island also had high haplotype ($h > 0.99$) and nucleotide diversity ($\pi\% = 2.81$ and $\pi\% = 5.78\%$, respectively). The genetic diversity of all three study species are among the highest reported for marine fishes and may have been caused by high abundance, relict populations, multiple clades and rapid mutation rate. High genetic diversity should reduce extinction risk in these species because it increases their evolutionary potential to adapt to the changing environmental conditions that are forecasted for coral reefs.

In summary, this study tested the generality of terrestrially-derived ecological relationships related to island communities. Some of these ecological hypotheses were found to apply to marine communities, whereas others did not. New hypotheses have been proposed to explain why marine communities do not always conform to these ecological generalisations. By combining field, laboratory and molecular studies with datasets constructed from the literature, this study has provided a thorough examination of the ecology of reef fishes on isolated islands and advances our understanding of marine ecology.

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CHAPTER 1: **General Introduction**

Ecology is the study of how species interact with each other and the environment (Haeckel, 1869). For any given biological community, ecological research strives to answer key questions about the processes determining species diversity, species composition and the abundance of species through space and time (Andrewartha, 1961; Krebs, 1978). Although these questions can be easily defined, attaining the answers has proved challenging because communities are the product of a complex interplay between a multitude of factors and the relative importance of these factors may differ between study systems and species (McIntosh, 1985; Weiner, 1995). Ultimately, ecologists seek to identify generalisations that can explain patterns in species richness, community composition and abundance across a broad range of taxa and geographic locations.

Significant advancements in the development of ecological generalisations have come through the study of island communities. The discrete nature of islands provides a natural laboratory for the development and testing of key ecological concepts (e.g. island biogeography: MacArthur and Wilson, 1967). In particular, island communities have been instrumental in elucidating the mechanisms that structure animal communities (e.g. Diamond, 1975; Simberloff, 1988) and highlighting the interplay between colonisation, speciation and extinction in determining patterns of species richness and turnover (Ricklefs and Schluter, 1993). More recently, islands have been used to test theory relating to the effects of patch size, isolation, habitat diversity and ecological interactions on species composition, abundance and body size (Fox and Fox, 2000; Lomolino, 2005, Lomolino and Brown, 2009). Even for islands communities, there can be a wide range of ecological processes at play.

The first and most notable ecological generalisation developed from island communities is the theory of “Island Biogeography” (MacArthur and Wilson, 1967). Island biogeography describes the general phenomenon whereby an equilibrium species richness increases with island size and decreases with isolation, as a function of colonisation rates and extinction rates associated with insularisation (MacArthur and Wilson, 1963, 1967; Wilcox, 1980). Lower species diversity on islands may lead to higher local abundances (density compensation) as a result of reduced interspecific competition (MacArthur *et al.*, 1972; Rodda and Dean-Bradley, 2002; Buckley and Jetz, 2007). In addition, the taxonomic composition of island communities often differs from mainland communities in that island communities typically contain a higher proportion of local endemics (Adler, 1992; Randall, 1998; Whittaker, 1998) and a greater representation of species with high dispersal abilities (Diamond *et al.*, 1976; Whittaker, 1998; Burns, 2005; Donazar *et al.*, 2005). Clearly, island size and isolation can have a predictable influence on species richness, community composition and species’ abundances in island communities. However, more recent models have abandoned the assumption of an equilibrium in species richness in favour of a pluralistic approach to the processes structuring island communities (reviewed by Brown and Lomolimo, 2000 and Lomolino and Brown, 2009).

The structure of island communities may also be determined by factors specific to the island's regional biogeographic setting. The number of species in island communities can be affected by proximity to regional centres of biodiversity (Dennis and Shreeve, 1997; Bellwood and Hughes, 2001), and the community composition on islands in different regions may reflect differences in the biogeographic pool of species (Ricklefs and Schluter, 1993; Edgar *et al.*, 2004). Islands at biogeographic borders can contain a unique mix of species from different biogeographic origins, and the composition and relative abundance of those species may depend on the position of the island on the border. For example, the Sunda Islands in South East Asia lie across Wallace's line and islands to the east of this line contain a high proportion of terrestrial species from the Australian biogeographic region whereas islands to the west of this line contain a high proportional of Oriental species (Wallace, 1860; Carlquist 1965, 1974). While the potential roles of island size and isolation have received considerable attention, the effects of these regional biogeographic factors on island communities are less well understood.

Biogeographic borders can also represent areas where regional biotas come into secondary contact resulting in communities containing a high proportion of hybridising species (Hewitt, 1988, 2000). Interbreeding between allopatric species pairs at biogeographic borders produces clusters of hybrid zones - termed a "suture zone" (Remington, 1968; Hewitt, 2000). These suture zones are considered the natural laboratories for studying hybridisation (Hewitt, 1988). Examination of the interaction of species at biogeographic borders can help elucidate the ecological conditions that promote hybridisation, such as, overlap in resource use and abundance disparities (Harrison, 1993; Arnold, 1997).

In addition to broadscale biogeographic effects, island communities can also be structured by smaller-scale local processes. For example, the presence of a competitor or predator, or the quantity and quality of habitats around the island, may influence patterns of species richness, community composition and abundances (e.g. Gilbert, 1980; Case and Cody, 1983; Whittaker, 1998; Fox and Fox, 2000; and see reviews by Brown and Lomolimo, 2000 and Lomolino and Brown, 2009). Given the widespread modification and destruction of habitat by humans, determining the role of local habitat characteristics in structuring island communities will be particularly important in predicting the response of such communities to changing environmental conditions.

Island communities generally contain a relatively high proportion of endemic species (Adler, 1992; Whittaker, 1998). Endemic species also tend to be less abundant than widespread species, which contributes to the positive relationship between abundance and geographic range size observed in most terrestrial communities (Brown, 1984, 1995; Lawton, 1993; Gaston, 1994; Blackburn *et al*. 1997; Gaston *et al*., 1997). However, the association of small range size and low abundance means that endemic species are susceptible to extinction from multiple causes, including local disturbances, the demographic attributes of small populations and habitat loss (Lawton, 1993; McKinney, 1997; Gaston, 1998; Munday, 2004). Indeed, the highest rates of extinction have been recorded for endemic species on isolated islands (Frankham, 1998; Whittaker, 1998).

Therefore, determining relationships between ecological traits that increase the threat of extinction is important to identifying, and conserving, those species most at risk.

While low abundance increases extinction risk in endemics due to demographic effects, low abundance also impinges on the genetic variability of the population. In small populations the deleterious effects of inbreeding and genetic drift become increasingly important and the deterioration of the genetic architecture of the population will result in a higher risk of extinction then predicted by abundance alone (Frankham, 1997, 1998). Isolation can also negatively influence the genetic variability of a population. Isolated populations are expected to exchange lower levels of gene flow with other populations, and this coupled with lower effective population sizes can result in lower genetic diversity and increased risk of extinction (Diamond, 1984). There is supporting evidence in the terrestrial environment that populations on isolated islands have lower genetic diversity than the populations on less isolated islands and on the mainland (Frankham, 1997, 1998). For species with small range, low abundance and isolated populations, the impact of deleterious genetic processes on genetic diversity is likely to be critical to future existence.

Although ecology aims to identify generalised patterns in nature, most ecological research has been conducted on terrestrial communities. The marine environment accounts for more than 70% of the surface of the globe, and contains some of the world's most biodiverse ecosystems (e.g. coral reefs), yet marine research currently represents only 10% of all ecological and biodiversity studies (Hendriks *et al.*, 2006; Richardson and Poloczanska, 2009). Generally, the large ecological datasets required for examining maroecological patterns are lacking for marine communities. Although some ecological relationships are often assumed to be universal, rarely have such relationships been rigorously tested for marine assemblages. There are fundamental differences between the marine and terrestrial environments (Steele, 1985; Raffaelli *et al*., 2005) and therefore it is not safe to assume that ecological patterns observed in terrestrial systems also occur in marine systems. Examining whether terrestrially derived ecological theories and relationships apply in the marine environment will be a true test of their generality (Steele, 1991).

Marine communities on isolated islands can be equally instructive as their terrestrial counterparts about the mechanisms determining species richness, community composition and species abundances (Hourigan and Reese, 1987; Kay and Palumbi, 1987; Robertson, 2001). Studying coral reef communities is likely to be especially instructive because coral reefs are associated with islands that differ in size, degree of isolation, regional biodiversity and biogeographic position. To date, biogeographic patterns in species richness and community structure of coral reefs have been largely explained by habitat area and isolation (Bellwood and Hughes, 2001; Sandin *et al*., 2008), however, most of the terrestrial ecological generalisations have not yet been tested on marine systems.

Coral reefs fishes form the most species rich vertebrate communities on Earth and are therefore an important group to include when testing the generality of ecological relationships or hypotheses. Reef fishes have been a model group in marine ecology because they represent the typical life cycle of most marine organisms (i.e. a pelagic larval phase and sedentary adult stage), their taxonomy and distribution are relatively well known, they are easily surveyed using standard techniques (e.g. underwater visual transects) and their populations are amenable to experimental manipulations. Like terrestrial communities, reef fishes associated with isolated islands tend to form communities with low species richness and a high proportion of endemics (Randall, 1998; Robertson, 2001; Jones *et al.*, 2002; Hughes *et al.*, 2002; Mora and Robertson, 2005; Allen, 2008). Islands are often located on biogeographic borders within oceanic basins (Rocha *et al.*, 2007), yet there has been little research on the role of these borders in structuring coral reef fish communities.

The Indo-Pacific biogeographic border represents the junction of the world's two largest tropical marine biogeographic provinces: the Indian and Pacific Oceans. The border extends from the western edge of Indonesia south to Christmas Island and the Cocos (Keeling) Islands (hereafter referred to at the Cocos Islands) in the eastern Indian Ocean, and most likely arose from vicariant land-bridge formations in Indonesia during historical periods of low sea level (Randall, 1998; Marie *et al.*, 2007; Rocha *et al.*, 2007; Hobbs *et al.*, 2009). While Indian and Pacific Ocean fishes are known to co-occur in this region (Hobbs and Salmond, 2008), the relative diversity, abundance and hybridisation of the two regional faunas have not been examined. The remoteness of Christmas Island and the Cocos Islands, and their position on the Indo-Pacific biogeographic border, provides the unique opportunity to examine the effects of isolation, island size, biogeographic position, and geographic range effects, on the structure of isolated reef fish communities.

Studying reef fish communities on isolated islands is a pressing issue given the limited resilience of isolated coral reefs (Ayre and Hughes 2004; Graham *et al.*, 2006), the high proportion of endemic species, and the increase in global impacts threatening coral reefs worldwide. Of the two recent reef fish extinctions, both have been island endemic species (Dulvy *et al.*, 2003) and now the challenge is to identify what increases extinction risk in endemic reef fishes. Specialisation has been linked to extinction risk (Dulvy *et al.*, 2003; Munday, 2004), and given recent phase-shifts from coral-dominated to algal-dominated reefs (phase-shifts: Hughes, 1994; Hughes *et al.*, 2003, 2007), species that rely on live coral would be expected to be among the most vulnerable to these changes (Pratchett *et al.*, 2008). In addition to ecological factors, endemic species are expected to have lower genetic diversity (Frankham, 1997, 1998) and this will limit a species' capacity to adapt to changing environmental conditions. Therefore, assessing extinction risk in vulnerable groups (e.g. endemics) will be important in determining how reef fish communities on isolated islands will be affected by the increases in impacts forecasted for coral reefs worldwide.

In this thesis, I used field-based studies of reef fishes at Christmas and Cocos Islands to test hypotheses related to island ecology and biogeography in the marine environment. In **Chapter 2**, I test biogeographical and ecological generalisations currently accepted for terrestrial biota, by comparing the reef fish communities of Christmas and Cocos Islands with communities at other locations in the Indian Ocean biogeographic region. First, I determine if species richness of reef fishes at Christmas and Cocos islands is influenced by island size or isolation. I then determine if the fish communities at these two island locations differ from what might be predicted by random colonisation from neighbouring mainland communities, or if they contain a high proportion of endemics and species with high dispersal abilities. To elucidate the effects of biogeographic borders on community structure, I examine the representation and relative abundance of species from different biogeographic regions within the fish communities at Christmas and Cocos Islands. I then determine how island location, geographic range size and position influence species abundance.

For **Chapter 3**, I combine evidence from morphological and genetic studies with field observations to determine whether the interaction between Indian and Pacific Ocean species has resulted in hybridisation at the Indo-Pacific biogeographic border. In doing so, I assess the number of species that are hybridising and describe the first suture zone in the tropical marine environment. I then use field surveys to examine the ecological conditions that have facilitated hybridisation and the formation of a suture zone.

In **Chapter 4**, I use underwater visual censuses to examine the relative importance of habitat variables in determining spatial patterns of abundance and distribution within two reef fish families, angelfishes (Pomacanthidae) and butterflyfishes (Chaetodontidae), at Christmas and Cocos Islands. Six variables were investigated, including 3 large-scale variables (island location, exposure and depth) and 3 fine-scale habitat variables (microhabitat diversity, live coral cover and algal cover). Given that the recent global decline in the condition of coral reefs is causing phase-shifts from coral-dominated to algal-dominated reefs at numerous locations around the world (Hughes, 1994; Hughes *et al.,* 2003, 2007; Hoegh-Guldberg *et al.*, 2007), butterflyfishes and angelfishes are an ideal group to test how reductions in coral cover and increases in algae affect reef fish communities. Butterflyfishes are a suitable test group because many species feed on corals (Pratchett, 2005) and therefore the presence and abundance of these fishes is often determined by the amount of live coral (Pratchett *et al.*, 2006). On the other hand, the amount of algae should influence the abundance of many angelfishes because this is a major food source (Allen *et al.*, 1998). Examining the relative influence of habitat types (algae and coral) on the structure of angelfish and butterflyfish communities will be useful in predicting the affect of future habitat degradation on the assemblage structure of different reef fishes.

In the terrestrial environment, endemic species often face a high risk of extinction because of an association among three threats to species persistence: small geographic range size, low abundance and ecological specialisation. To test whether similar inter-related risk factors occur in coral reef fishes, in **Chapter 5** I compare abundance and specialisation in endemic and widespread angelfishes at Christmas and Cocos Islands. To determine the relationship between geographic range size and abundance, underwater visual surveys were conducted throughout the geographic range of angelfishes endemic to Christmas and Cocos Islands and compared to the abundance of widespread species at these locations. To determine if endemic species are habitat specialists I used underwater observations to quantify the depth range occupied by endemic and widespread angelfishes, and I also placed line-intercept transects through the territories of angelfishes to determine microhabitat use. In addition to habitat specialisation, I investigate dietary specialisation in endemic and widespread angelfishes by examining the gut contents of collected individuals.

In **Chapter 6**, I test the hypothesis that endemic species, and small isolated populations of widespread species, have low genetic diversity in the marine environment by using molecular analysis of endemic and widespread angelfishes collected from Christmas and Cocos Islands. To determine genetic diversity I calculate nucleotide and haplotype diversity indices for the sampled populations using sequences from the control region of the mitochondrial DNA.

CHAPTER 2: **Biogeography and the structure of coral reef fish communities on isolated islands**

2.1 ABSTRACT

Islands have served as the natural laboratories for the development and testing of ecological theories; however, most research has been conducted in the terrestrial environment. The aim of this study was to determine the applicability of biogeographical and ecological theory to marine species on isolated islands. This study examines how biogeography, isolation and species' geographic range size influence patterns of species richness, endemism, species composition and abundance of coral reef fishes. To do this, I examine published species lists, combined with underwater visual surveys at Christmas and Cocos Islands in the eastern Indian Ocean. These data were then statistically compared with patterns of species composition and abundance from the neighbouring "mainland" Indonesian region. Like small isolated terrestrial communities, reef fish communities at Christmas and Cocos Islands were species poor and contained a distinct taxonomic composition with an overrepresentation of species with high dispersal potential. Despite low species richness, there was no evidence of density compensation, with population densities on the islands similar to species-rich neighbouring mainland assemblages. The mix of Indian and Pacific Ocean fish species, and the proportional representation of the different regional faunas in the assemblages were not influenced by the relative proximity of the islands to different biogeographic provinces. Also, in contrast to terrestrial communities, species at the edge of their range did not have lower abundance than species at the centre of their range, and endemic species had substantially higher abundance than widespread species. Overall, the observed patterns generally conform to terrestrial ecological theory indicating that similar processes are important in determining species richness and community composition in marine communities on isolated islands. However, observed patterns in abundance did not conform to terrestrial generalisations, and these differences appeared to be due to the life history of marine organisms and the maintenance of marine populations.

2.2. INTRODUCTION

Islands often have different assemblages of plants and animals to mainland communities, a phenomenon that has been used in the development and testing of theories about how biological communities are structured (MacArthur and Wilson, 1963, 1967; Wilcox, 1980). Islands usually support fewer species in comparison to similar-sized areas in mainland communities (Whittaker, 1998). This may reflect a number of processes, including lower colonisation rates and higher extinction rates associated with insularisation (MacArthur and Wilson, 1963, 1967; Wilcox 1980), or other ecological factors, such as low habitat diversity (Williams, 1964; Gilbert, 1980; Case and Cody, 1983; Whittaker, 1998) or less frequent disturbances (Bond *et al*., 1988). Lower species diversity on islands may lead to higher local abundances as a result of reduced interspecific competition (density compensation: MacArthur *et al*., 1972; Rodda and Dean-Bradley, 2002; Buckley and Jetz, 2007). Also, island communities typically contain a higher proportion of local endemics (Adler, 1992; Randall, 1998; Whittaker, 1998) and a greater representation of species with good dispersal abilities (Diamond *et al*., 1976; Whittaker, 1998; Burns, 2005; Donazar *et al*., 2005), compared to mainland communities.

The structure of an island community may also be determined by factors specific to the island’s regional biogeographic setting. The number of species in island communities can be affected by proximity to regional centres of biodiversity (Dennis and Shreeve, 1997; Bellwood and Hughes, 2001), and the species composition on islands in different regions may reflect differences in the biogeographic pool of species (Ricklefs and Schluter, 1993; Edgar *et al*., 2004). Islands at biogeographic borders may contain a mixture of species from different biogeographic origins, and the composition and relative abundance of those species may depend on the position of the island relative to the border (e.g. Wallace's Line: Wallace, 1860; Carlquist 1965, 1974).

The relative abundance of species in island communities can also be influenced by the size of a species' range and the position of the island within this range. Species at the edge of their range often have lower abundances because environmental conditions tend to be less favourable at their range limits (Brown, 1984; Gaston *et al*., 1997; but see Sagarin and Gaines, 2002). Furthermore, small range species (endemics) tend to be less abundant than widespread species, which contributes to the positive relationship between abundance and range size observed in most terrestrial communities (Brown, 1984, 1995; Lawton, 1993; Gaston, 1994; Blackburn *et al*., 1997; Gaston *et al*., 1997). However, exceptions can occur in some isolated locations where endemics may be unusually abundant, possibly because they have become better adapted to local conditions or because there are fewer competing species in low diversity assemblages (MacArthur *et al*., 1972; Brown, 1995; Blackburn *et al*., 1997; Reif *et al*., 2006).

To date, most of the theory and empirical studies of island communities have focused on terrestrial organisms. Although marine biogeography research has been limited by a paucity of detailed datasets, the study of marine organisms can add significantly to our understanding of biogeography, particularly through the identification of differences and similarities in the processes structuring marine and terrestrial communities (Vermeij, 2004). Furthermore, isolated islands can be instructive about the mechanisms favouring the presence, absence or relative abundance of species within marine communities (Hourigan and Reese, 1987; Kay and Palumbi, 1987; Robertson, 2001). Explanations for the distribution of marine species have traditionally focused on the importance of dispersal versus vicariance (reviewed by Briggs, 2004), though it is now accepted that both are important mechanisms in the marine environment (Briggs *et al*., 2004).

Coral reef communities have proven to be particularly useful in marine biogeographical research due to the high diversity of species and their association with islands and habitat patches of varying size, degrees of isolation and biogeographic positions. Like terrestrial systems, habitat area and isolation appear to be important determinants of species richness and community structure on coral reefs (Bellwood and Hughes, 2001; Sandin *et al*., 2008); however, many of the other factors thought to be important in determining biogeographic patterns in terrestrial systems are yet to be tested in the marine environment.

Reef fishes are a suitable model group for examining marine biogeography because the majority of species have a life cycle typical of most marine organisms (i.e. high fecundity, broadcast spawning, a dispersive larval phase and sedentary adult stage), they are easily observed, and their taxonomy and distribution are relatively well known. Reef fish communities on isolated islands tend to support fewer species and have a high proportion of endemics (Randall, 1998; Robertson, 2001; Hughes *et al*., 2002; Jones *et* *al*., 2002; Mora and Robertson, 2005; Allen, 2008). Some widespread species have been reported at unusually high abundances on isolated islands (Allen *et al.*, 2007; Stevenson *et al*., 2007; Hobbs *et al*., 2008), and endemic species can also be among the most abundant species (Randall, 1998; Robertson, 2001; Jones *et al.*, 2002; DeMartini and Friedlander, 2004). Isolated islands often represent biogeographic boundaries and thus harbour a high proportion of species at the edge of their geographic range (Robertson *et al*., 2004). While the abundance of many coral reef fishes varies throughout their geographic ranges (e.g. Findley and Findley, 2001), determining whether this variation conforms to the terrestrial pattern of declining abundance towards the range edge has seldom been explored (Jones *et al*., 2002).

Although reef fishes are found throughout the tropics, species' distributions often fall within biogeographic provinces and their range edges occur along biogeographic borders that may represent historical barriers to dispersal (Randall *et al*., 1998; Bellwood and Wainwright, 2002; Rocha et al., 2007). The Indian and Pacific Ocean bioregions abut in the eastern Indian Ocean, and situated on this Indo-Pacific biogeographic border are Christmas Island and the Cocos (Keeling) Islands (Hobbs and Salmond, 2008; Hobbs *et al*., 2009). While Indian and Pacific Ocean fishes are known to co-occur in this region (Hobbs and Salmond, 2008; Hobbs *et al*., 2009), the relative diversity and abundance of the two regional faunas have not been examined.

The remoteness of Christmas Island and the Cocos Islands, and their position on this biogeographic border, provides a unique opportunity to examine the effects of isolation, biogeographic position, and geographic range effects, on the structure of isolated marine communities. This study tests whether the coral reef fish communities at Christmas Island and the Cocos Islands conform to expectations based on common patterns observed in terrestrial systems. The following questions were addressed:

(1) Are the isolated reef fish communities of Christmas Island and the Cocos Islands depauperate compared to the rest of the biogeographic region, with a high level of endemism?

(2) Does the taxonomic composition of reef fish communities at Christmas Island and the Cocos Islands differ from the composition of the closest mainland communities?

(3) Are species with greater dispersal ability disproportionately represented in the island communities?

(4) Is the composition and relative abundance of fish species at Christmas Island and the Cocos Islands influenced by the position of the island(s) relative to the different biogeographic regions?

(5) Is there evidence of density compensation? That is, do fish populations at Christmas Island and the Cocos Islands attain higher densities than mainland populations?

(6) Are species at the edge of their range less abundant than species that are at the centre of their range?

(7) Are small range species (endemics) less abundant than large range species?

2.3 METHODS

Study site

This study was conducted at Christmas Island (10’29S, 107’37E) and the Cocos (Keeling) Islands (12’04’13S, 96’48’56E) in the eastern Indian Ocean (Figure 2.1a). Christmas Island and the Cocos Islands are located approximately 400 and 1000 km (respectively) southwest of Indonesia. The Cocos Islands are situated about 1000 km west of Christmas Island and are regarded as the most isolated island group in the tropical Indian Ocean (Briggs, 1974). Christmas Island and the Cocos Islands are similar sized oceanic coral reef systems (about 20km along the longest axis); however, Christmas Island is a single high island (361 m at its highest point) whereas the Cocos Islands comprise a coral atoll with a ring of low-lying sandy islands surrounding a central lagoon (Woodroffe and Berry, 1994; Allen *et al*., 2007). Christmas Island and the Cocos Islands have approximately 20 km^2 and 110 km^2 of coral reef habitat, respectively (Robertson and Allen, 1996) and there are no estuaries at either location.

Species richness and endemism

Species richness and endemism of fish communities at Christmas Island and the Cocos Islands were estimated using published species lists (Allen and Smith-Vaniz, 1994; Allen *et al*., 2007), combined with extensive underwater visual surveys around all sides of the islands from 0 - 60 m depth (Hobbs *et al*., 2007, 2010; unpublished data). To determine if Christmas and Cocos Islands have fewer species than expected due to their isolation, a species–area curve was constructed by plotting the number of reef fishes (from published literature listed in Figure 2.1) against the area of reef habitat (from Spalding *et al*., 2001) for various Indian Ocean locations. The residual variation of Christmas and Cocos Islands on the curve was then compared with the residual variation of the other locations. The proportion of species endemic to either Christmas Island or Cocos Islands was calculated and compared with levels of endemicity at other coral reef locations (Allen, 2008). For the purposes of this study we also considered populations of two species (*Centropyge flavissima* and *Stegastes insularis*) to be endemic species. These are the only populations in the Indian Ocean and are isolated by more than 3000 km from Pacific Ocean populations. They also exhibit differences in physical appearance indicating the populations may represent separate species (Allen *et al*., 1998).

Community composition

To determine if fish communities on Christmas Island and the Cocos Islands are a random subset of the closest species-rich mainland communities, the shallow (0 – 60 m) reef fish communities at Christmas Island and the Cocos Islands (Allen and Smith-Vaniz, 1994; Allen *et al*., 2007; Hobbs *et al*., 2007, 2010) were compared with the overall community composition of Indonesia (Allen and Adrim, 2003; Allen unpublished data). The Indonesian region represents the global centre of reef fish diversity (Bellwood and Hughes, 2001; Allen and Adrim, 2003; Allen, 2008) and is the closest "mainland" source community to Christmas Island and the Cocos Islands. To test for non-randomness of community composition, a null model was constructed in which species were sampled at random from the Indonesian species pool to populate the islands. To construct the null model, only species that are present in Indonesia were included initially (2206 species:

Allen and Adrim, 2003, Allen unpublished data). That is, the 37 species that are present on Christmas or Cocos, but not in Indonesia, were excluded from the analysis. However, to verify the robustness of the results, the analysis was repeated including all species, with the species pool defined as consisting of all species present anywhere in the database (either in Indonesia, or on one of the two island locations). Results were identical, so only the former analysis is presented. Specifically, after excluding species present on either Christmas or Cocos Islands, but not part of the Indonesian species pool, 550 species remain for Christmas Island, and 497 species for the Cocos Islands, out of a total species pool of 2169 species for Indonesia. The null hypothesis is that these island faunas are random samples from the Indonesian species pools. Therefore, the null models are constructed by randomly sampling 550 species from the overall species pool for Christmas Island, and 497 species for Cocos Islands. Sampling is done without replacement, so that the same species is never sampled twice and erroneously counted as two separate species in the analysis. The null model simulations were repeated 10,000 times for each island fauna.

To test for non-random sampling of species from different families, this study takes advantage of the fact that, for each null model simulation, the taxonomic composition of an island fauna is a sample from the multivariate hypergeometric distribution. That is, the probability that a simulated island fauna consists of a particular set of species richness values for the different families, $\mathbf{k}=[k_1,k_2,...]$, is given by:

$$\Pr(\mathrm{k}) = \frac{\prod_{i-1}^{S} \binom{M_i}{k_i}}{\binom{N}{n}}$$

(Equation 1)

where M_i is the number of species in family i in the species pool, k_i is the number of species in family i in the random sample, N is the total number of species in the species pool, and n is the total number of species in the sample (equal to 550 and 497 for Christmas or Cocos Islands null model simulations, respectively). Therefore, for each null model simulation, the log-likelihood of the multivariate hypergeometric distribution is calculated (i.e., the natural logarithm of equation 1). For each island fauna, the frequency distribution of log-likelihood values across the 10,000 null model simulations is the statistical null distribution. In other words, if the real communities are, in fact, random samples of the Indonesian species pool, then the logarithm of equation 1, calculated using the observed family level species richness, should be consistent with the null model values. If, instead, it lies below that of 95% of the null model values, then it can be concluded that the multivariate hypergeometric distribution fits the real data significantly worse than expected under the null hypothesis of random sampling from the Indonesian species pool.

To determine whether isolated islands contain a greater proportion of species with high dispersal potential, the mean PLD (pelagic larval duration) for each null model simulation was computed (for those species to which PLDs could be assigned – see below). The reef fish communities at each island location were considered to have significantly longer PLDs than expected if the observed mean PLDs for Christmas and

Cocos Islands were larger than 95% of the corresponding null model values. PLD values were only used for species present in the reef fish communities and were obtained from published sources (Brothers *et al.*, 1983; Brothers and Thresher, 1985; Thresher and Brothers, 1985; Victor, 1986; Fowler, 1989; Thresher *et al.*, 1989; Wellington and Victor, 1989; Shulman, 1998; Wilson and McCormick, 1999; Victor and Wellington, 2000).

As a second test for longer PLDs, this study examined whether the PLDs of families that were under-represented on the islands was significantly lower than the PLDs of over-represented families. Under- and over-represented families were defined as those whose observed species richness fell below or above, respectively, the 95% confidence limits of the null model predictions for the corresponding family. The mean PLD was calculated for each family by taking the average value for any published estimates of PLD for species in these families (Brothers *et al.*, 1983; Brothers and Thresher, 1985; Thresher and Brothers, 1985; Victor, 1986; Fowler, 1989; Thresher *et al.*, 1989; Wellington and Victor, 1989; Tyler *et al.*, 1993; Shulman, 1998; Wilson and McCormick, 1999; Victor and Wellington, 2000; Craig *et al.*, 2007).

Christmas Island and the Cocos Islands are located 1000 km apart on the Indo-Pacific biogeographic border (Hobbs and Salmond, 2008; Hobbs *et al.*, 2009), and differences between the two locations in the composition of the fish assemblages may reflect the position of each location relative to the biogeographic border. Christmas Island is located closer to the Pacific Ocean and should contain a greater proportion of Pacific Ocean fishes compared to the Cocos Islands, and vice versa for Indian Ocean species. To test this, the proportion of shallow reef fishes (0 - 60 m depth) from different geographic distributions (Indian Ocean, Pacific Ocean, Indo-Pacific) was compared between Christmas and Cocos Islands using a Chi Square test (Zar, 1999). This test was also repeated using just Indian Ocean and Pacific Ocean species (with Yates' correction for continuity: Zar, 1999). Approximately 7.3% and 4.9% of species at Christmas and Cocos Islands (respectively) had geographic distributions that could not be classified into one of these three geographic distributions and were grouped as "other".

In addition to species composition, the relative abundance of species at the biogeographic border may be linked to their biogeographic origins. That is, Pacific Ocean species should be more abundant at Christmas Island (compared to the Cocos Islands), and vice versa for Indian Ocean species. To test this, underwater visual censuses were conducted of shallow reef fishes on the outer reefs at 14 sites at Christmas Island and 12 sites at the Cocos Islands. Censuses were conducted in November and December 2002 and focused on six common reef fish families: Acanthuridae (surgeonfish and unicornfish), Balistidae (triggerfish), Chaetodontidae (butterflyfish), Labridae (wrasse), Pomacanthidae (angelfish) and Pomacentridae (damselfish). Densities of butterflyfishes, and angelfishes were attained using 4 replicate 50 m by 6 m belt transects at each of 2 depths (5 m and 20 m) at each site. Due to their relatively high abundance, damselfish densities were estimated using 4 replicate 30 by 2 m transects at each site. The angelfish and damselfish assemblages were mainly confined to the 20 m and 5 m depth zones, respectively, and therefore the analyses for these two groups were restricted to their preferred depth. Due to the similarity in the 5 m and 20 m butterflyfish assemblages, data from the two depths were combined for all analyses. For the surgeonfishes (including unicornfish), triggerfishes and wrasses, abundance per site (estimated during a 60 minute dive between 0–20 m depth) was categorised into the following classes: 0, 1-10, 11-50, 51-100, >100. These estimates were used to calculate rank abundances rather than densities. A Wilcoxon paired-sample test (Zar, 1999) was used to examine differences in median rank abundance (combined for all 6 study families) of Indian Ocean and Pacific Ocean species common to both locations.

Abundance

To determine if island populations attain greater densities than mainland populations due to the lower number of competing species (density compensation, *sensu* MacArthur *et al*., 1972) the mean density of benthic feeding butterflyfishes (genera *Chaetodon* and *Forcipiger*) at Christmas Island and the Cocos Islands was compared to that of the Indonesian region. Butterflyfishes were chosen because this was the only group with sufficient available data on abundances for the Indonesian region, Christmas Island and the Cocos Islands. The mean density estimates for butterflyfishes in the Indonesian region were based on published density estimates obtained at 5 m depth from 8 locations across Indonesia, Malaysia and Philippines (Findley and Findley, 2001). The butterflyfish density estimates at Christmas Island and the Cocos Islands were obtained from underwater surveys conducted at 5 m depth (described above).

Because Christmas Island and the Cocos Islands are located on the Indo-Pacific biogeographic border, the islands represent the eastern or western edge of the geographic distributions of a number of species and the abundances of these edge species are predicted to be low. For widespread (Indo-Pacific) species, these islands are located in the middle of their range and, therefore, might be expect to have higher abundances than edge species. To test this hypothesis, density estimates from the underwater visual censuses were used to compare the mean densities of edge (Pacific and Indian Ocean edge species combined) and mid-range species (Indo-Pacific species) for angelfishes, butterflyfishes and damselfishes using *t*-tests (Zar, 1999). For surgeonfishes and wrasses, medians from the rank abundance data were compared using a Mann-Whitney *U*-test. Tests were conducted separately for each family and at each location (Christmas Island and the Cocos Islands). Where the assumptions of the *t*-test were not met the Mann-Whitney *U*-test was used (Zar, 1999). The triggerfish assemblages at both locations and the angelfish assemblage at the Cocos Islands were not included in the analysis due to insufficient numbers of edge species.

The underwater visual censuses may have missed some of the rare species, and this group of species may contain a high proportion of edge species. To determine whether rare species as a group had a greater proportion of edge species, qualitative abundance estimates published for Christmas Island fishes were examined (Allen *et al.*, 2007), supplemented with underwater observations for new records identified in 2002, 2004, 2005 and 2008 (Hobbs *et al.*, 2007, 2010). Fishes were grouped into three abundance categories: 1. “common species” = on average more than three individuals seen per 60 minute dive (includes species described as “abundant, common or moderately common” by Allen *et al.*, 2007); 2. “uncommon” = on average 0.2 to three individuals seen per dive (includes species reported as “uncommon or occasionally seen” by Allen *et al*., 2007); and 3. “rare” = on average less than 0.2 individuals seen per dive (includes species referred to as “rarely seen, seldom seen or rare” by Allen *et al*., 2007). The proportions of species whose range was classed as Pacific Ocean, Indian Ocean, Indo-Pacific or “other” (described above) were compared across the three abundance categories (common, uncommon and rare) using a Chi Square contingency test (Zar, 1999). Open-water pelagic, deepwater (> 60 m depth) and highly cryptic species were not included in the analysis due to inaccuracies associated with estimating their abundance using underwater visual censuses. Insufficient data on the abundance of fishes at the Cocos Islands prevented a similar analysis for this location.

Underwater visual censuses were also used to determine whether reef fishes at Christmas Island and the Cocos Islands conform to the terrestrial pattern of endemics having lower abundance than widespread species (Lawton, 1993; Gaston, 1994). Study species included the endemic *Centropyge joculator* and endemic populations of *C. flavissima* and *Stegastes insularis* (Allen *et al*., 1998, 2007; Froese and Pauly, 2010). *C. joculator* only occurs at Christmas Island and the Cocos Islands. The Indian Ocean population of *C. flavissima* is found only at Christmas Island and the Cocos Islands and is separated from the Pacific Ocean population by over 3000 km and therefore the two populations do not interbreed or exchange larvae. This lack of gene exchange, combined with different facial markings and colouration, suggests the two populations are separate species (Allen *et al*., 1998) and in this study *C. flavissima* is treated as endemic to Christmas Island and the Cocos Islands. Similarly, *Stegastes insularis* is only found at Christmas Island and

Marcus Island (which is in the Pacific Ocean and more than 3000 km from Christmas Island); therefore, in this study it is referred to as an endemic of Christmas Island. Endemic species in other families were too cryptic to accurately estimate abundance.

2.4 RESULTS

Species richness and endemism

The species richness of shallow reef fishes at Christmas Island (618 species) and the Cocos Islands (550) was the lowest across a range of Indian Ocean locations (Figure 2.1a). Christmas and Cocos Islands conform to the species–area relationship for the Indian Ocean region, indicating that the relatively small area of reef habitat, and not isolation, has a greater influence on the low species richness at the Islands (Figure 2.1b). The number of shallow reef fishes at Christmas and Cocos Islands was generally less than half that of neighbouring mainland fish communities of the Indonesian region. The proportion of endemic reef fishes was relatively low in both the Christmas and Cocos Islands communities. There were only seven endemic species and recognised sub-species at Christmas Island and two at the Cocos Islands, and overall, these species comprised 1.1% and 0.4% (respectively) of the total reef fish species richness at each location.

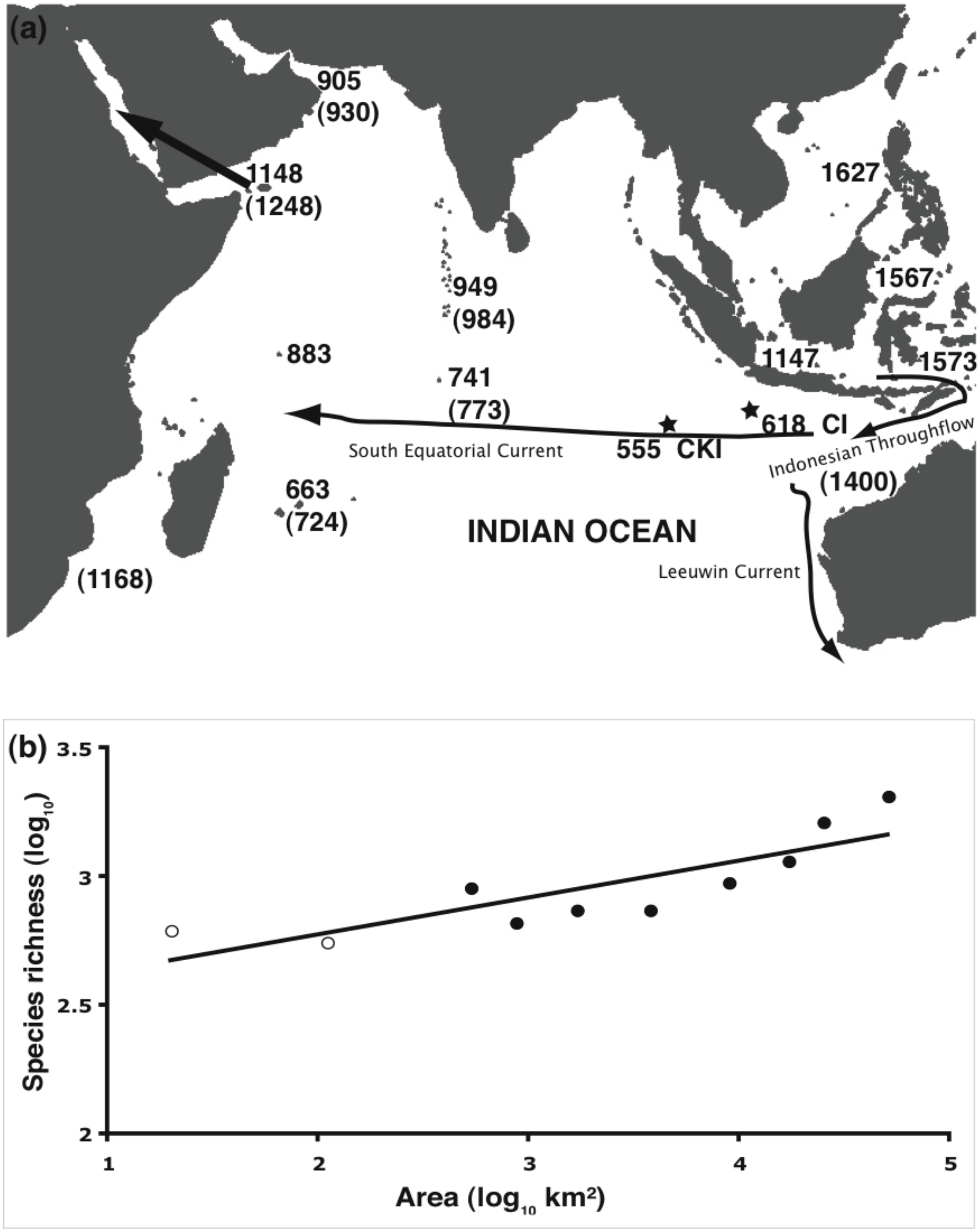

Figure 2.1 (a) Species richness and (b) species – area relationship (y = 0.14x + 2.49, R^2 = 0.71) for shallow reef fishes at locations across the Indian Ocean and Indonesian region. Only those places where reef fishes estimates were available were plotted on the species – area relationship, and the open circles represent Christmas Island and the Cocos Islands (in increasing order of area). Area of reef habitat calculated from Spalding *et al.*, 2001.

Species richness values on the map are estimates for shallow reef fishes, and estimates for all marine fishes (including deepwater and pelagic) are presented in brackets. Christmas Island (618 species, CI) and the Cocos Islands (555, CKI), located in the eastern Indian Ocean, are represented by stars. Locations from west to east and north to south are: Red Sea (1148), South Africa (1168), Oman (905), Seychelles (883), Mauritius (663), Maldives (949), Chagos (741), Cocos Islands (555), Christmas Island (618), Java (Indonesia) (1147), central Philippines (1627), Western Australia (1400), northern Sulawesi (Indonesia)(1567) and the Molucca Islands (Indonesia)(1573). Data sources are as follows: Indonesia and Philippines (Allen, 2008); Western Australia (Allen and Swainston, 1988); Christmas Island and the Cocos Islands (Allen and Smith-Vaniz, 1994; Allen *et al.*, 2007; Hobbs *et al.*, 2007, 2010); all other locations (Randall, 1998 and the references therein). Information on oceanographic currents is from Condie and Dunn, 2006.

Community composition

The taxonomic composition of the fish communities at Christmas and Cocos Islands was significantly different from that of the mainland fish community of neighbouring Indonesia (P<0.0001 in each case; Figure 2.2, Figure 2.3). Specifically, both island locations had an overrepresentation of Muraenidae, Acanthuridae, Chaetodontidae, Scaridae, Holocentridae, Labridae and Balistidae. Families underrepresented at both Christmas and Cocos Islands were: Syngnathidae, Pseudochromidae, Nemipteridae, Opistognathidae and Gobiidae (Table 2.1).

Table 2.1 Under- and over-represented families in the reef fish communities of Christmas Island and the Cocos Islands when compared to the Indonesian reef fish community. Cut-off limits for under- and over-representation were determined using 95% confidence limits based on null model predictions.

Location	**Under-represented**	**Over-represented**
Christmas Island	Syngnathidae Pseudochromidae Opistognathidae Apogonidae Lethrinidae Nemipteridae Callionymidae Gobiidae	Muraenidae Holocentridae Scorpaenidae Serranidae Kyphosidae Chaetodontidae Pomacanthidae Labridae Scaridae Acanthuridae Balistidae
Cocos Islands	Syngnathidae Pseudochromidae Opistognathidae Nemipteridae Gobiidae	Muraenidae Holocentridae Cirrhitidae Chaetodontidae Labridae Scaridae Acanthuridae Balistidae

Examination of pelagic larval duration (PLD) revealed that families over-represented at Christmas or Cocos had a longer PLD (mean PLD = 45.4 days ± 3.6 SE), and thus greater dispersal potential, than taxa that were under-represented (mean PLD = 28.7 days ± 6.1 SE) (t = 2.55, d.f. = 26, P = 0.02). In addition, 63% of the under-represented families brood or lay demersal eggs (which potentially limits dispersal: Munday and Jones, 1998), whereas only 1 (9%) of the over-represented families lay demersal eggs and the rest are broadcast spawners. Similarly, the overall mean PLDs across the whole communities at Christmas and Cocos are significantly greater than null model predictions (Christmas: P = 0.0002, Cocos: $P < 0.0001$)(Figure 2. 4).

Christmas Island and the Cocos Islands are situated on the Indo-Pacific biogeographic border and the reef fish assemblages contained a mix of species from different biogeographic regions. At both locations the assemblages typically contained 72% Indo-Pacific species, 17% Pacific Ocean species and 5% Indian Ocean species. Although Christmas Island is closer to the Pacific Ocean biogeographic region and the Cocos Islands are closer to the Indian Ocean biogeographic region, there was no significant difference in the proportions of species from different geographic distributions between Christmas Island and the Cocos Islands (χ^2 = 5.485, d.f. = 3, P = 0.14). The large number of Indo-Pacific species could potentially mask differences in the proportions of Pacific and Indian Ocean species between the two locations. However, restricting the analysis to comparing just the proportions of Pacific and Indian Ocean species still resulted in no significant difference between Christmas Island and the Cocos Islands (χ^2 with Yates' correction = 1.97, d.f. = 1, $P = 0.16$).

Not only were the proportions of Indian and Pacific Ocean species similar between the two locations, but the relative abundances of those species was also similar between locations. There were no significant differences between Christmas Island and the Cocos Islands in the rank abundances of Pacific Ocean species observed at both locations for the 6 study families ($Z = -1.065$, $P = 0.287$, $n = 11$). Similarly, there were no significant differences in the rank abundance of Indian Ocean species between Christmas Island and the Cocos Islands for the 6 study families ($Z = -1.461$, $P = 0.144$, $n = 4$).

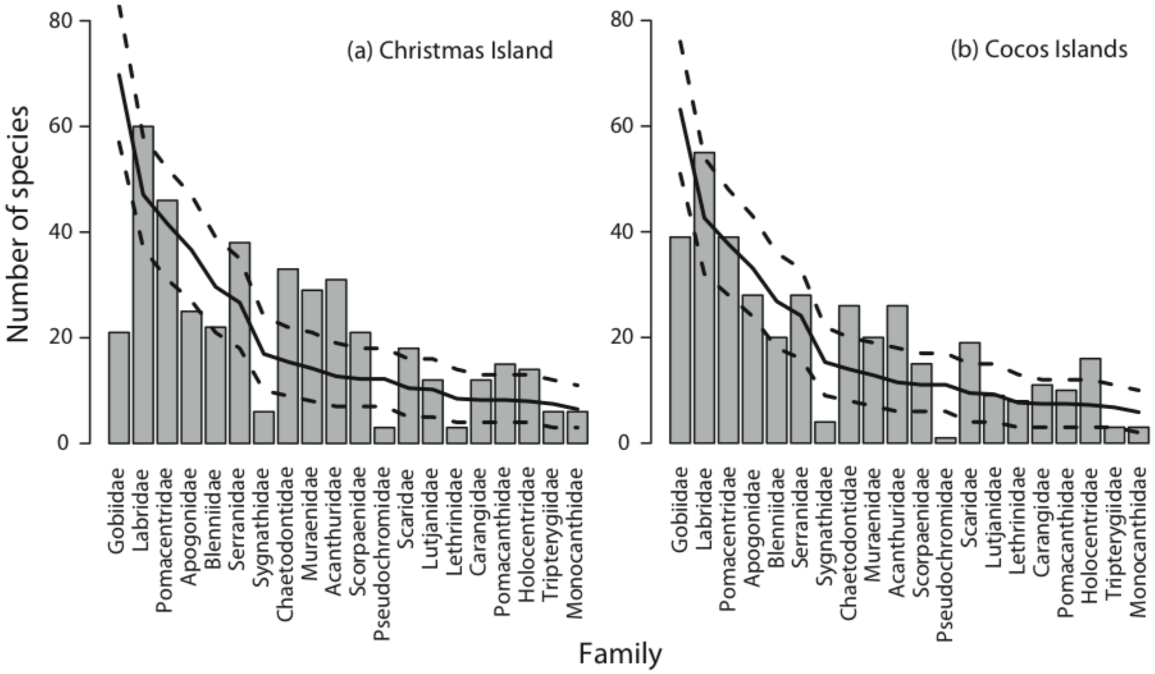

Figure 2.2 Comparison of observed and expected taxonomic composition of reef fish communities at (a) Christmas Island and (b) the Cocos Islands. Bars show the observed taxonomic composition. The expected distribution (shown as solid lines with 95% confidence limits indicated by dotted lines) is based on a null model in which species were sampled at random from the Indonesian species pool. Although the analysis was conducted on all families, the plot shows only the 20 most species rich families, shown in descending order of species richness (based on the Indonesian species pool) from left to right. The total number of species in each community is: Indonesia (2169), Christmas Island (550) and the Cocos Islands (497).

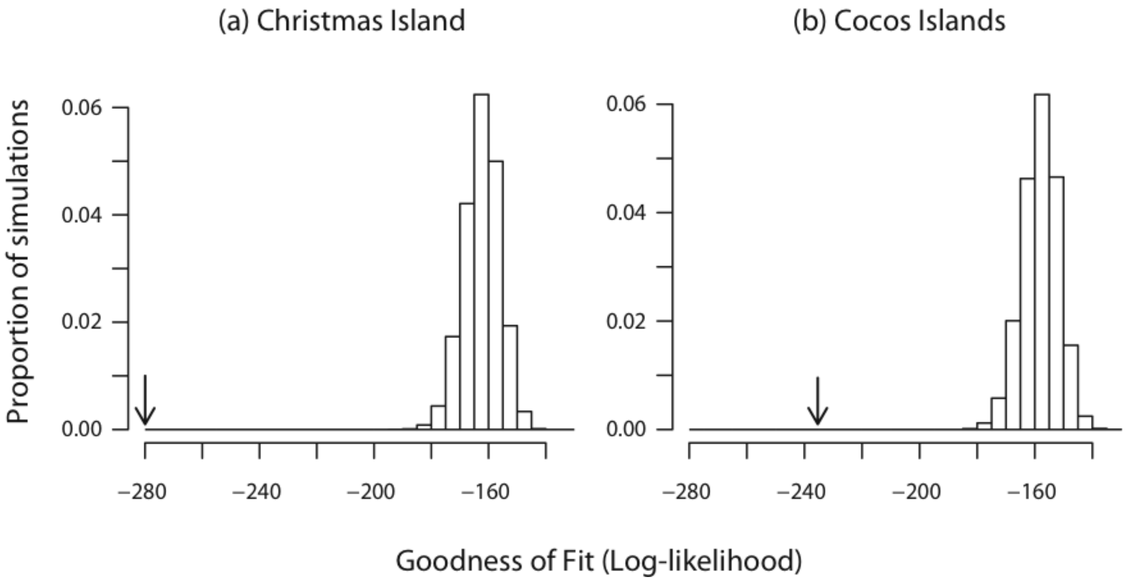

Figure 2.3 Goodness of fit of the null model of taxonomic composition for (a) Christmas Island and (b) Cocos Islands. The goodness of fit statistic is the log-likelihood of the multivariate hypergeometric distribution (i.e., the natural logarithm of equation 1). The histograms show the expected distribution of this statistic, based on a null model in which species were sampled at random from the Indonesian species pool. The downward arrows show the value of the statistic for the observed data.

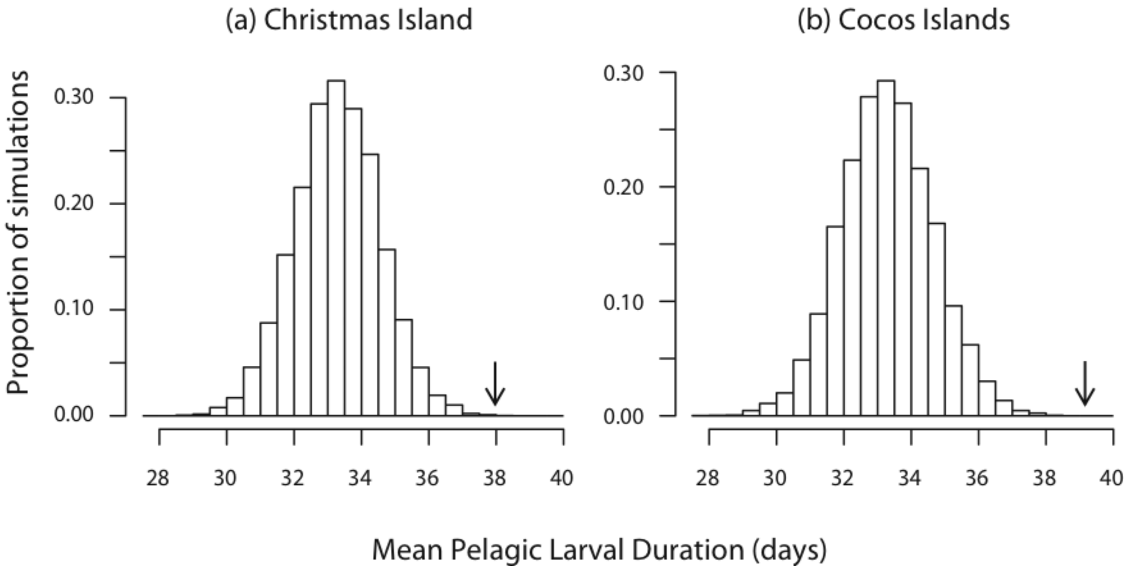

Figure 2.4 Null model test of mean pelagic larval durations (PLDs) of reef fishes at (a) Christmas Island and (b) the Cocos Islands. The histogram shows the expected distribution of mean PLDs for each island (obtained from the same null model as was used to generate Figure 2.2). The downward arrows show the mean PLD calculated from the actual data. See methods for information on published data sources for PLDs.

Abundance

Although Christmas Island and the Cocos Islands have relatively depauperate shallow reef fish communities, there was no evidence of density compensation. Christmas Island and the Cocos Islands have approximately half the number of butterflyfish species as the neighbouring Indonesian region. However, there was no significant difference in the mean density of butterflyfishes at Christmas Island and the Cocos Islands (0.26 per $300m^2$ ± 0.05 SE) compared to the mean density recorded from locations in the Indonesian region (0.21 per $300m^2$ ± 0.06 SE, Findley and Findley, 2001) ($t = 0.67$, d.f. = 43, $P = 0.50$).

Species at the edge of their range (Indian and Pacific Ocean species) did not have significantly lower mean densities or median rank abundance compared to closely related mid-range species (Indo-Pacific species). There were no significant differences in edge and mid-range species' densities for 8 of the 9 families ($P > 0.05$, Table 2.2) and in the remaining family (Cocos Island butterflyfishes), edge species exhibited a greater mean density than mid-range species ($t = 0.266$, d.f. = 19, $P = 0.015$, although this was not significant after Bonferroni correction for multiple comparisons). Similarly, there was no significant difference in the proportions of Indian Ocean, Pacific Ocean and Indo-Pacific species that comprised the common, uncommon or rare species groups at Christmas Island ($\chi^2 = 9.82$, d.f. = 6, $P = 0.13$). That is, the rare species group did not contain a significantly higher proportion of species at the edge of their range.

Table 2.2 Comparisons of abundance between edge and mid-range species at Christmas Island and the Cocos Islands. Mean densities were compared using *t*-tests for chaetodontids, pomacanthids and pomacentrids and Mann-Whitney *U*-tests were used to compare median rank abundance for acanthurids and labrids. Bonferroni correction for multiple comparisons means significance level is adjusted to $P = 0.0056$.

Location	**Family**	**Test statistic**	***P***
Christmas Island	Labridae	$U = 152.0$	0.39
Christmas Island	Acanthuridae	$U = 63.0$	0.26
Christmas Island	Pomacanthidae	$t = 0.67$	0.52
Christmas Island	Pomacentridae	$U = 36.5$	0.65
Christmas Island	Chaetodontidae	$t = 0.65$	0.52
Cocos Islands	Labridae	$U = 88.0$	0.78
Cocos Islands	Acanthuridae	$U = 33.0$	0.60
Cocos Islands	Pomacentridae	$t = 0.24$	0.82
Cocos Islands	Chaetodontidae	$t = 2.66$	0.02

Finally, endemic fishes of Christmas Island and the Cocos Islands had high abundances compared to their widespread relatives. The mean density of *Stegastes insularis* at Christmas Island (15.4 per 60 m^2) was more than double the overall mean density of widely distributed damselfishes (6.1 per 60 m^2) (Figure 2.5a). The mean densities of endemic angelfishes (*Centropyge joculator* and *C. flavissima*) at both Christmas Island and the Cocos Islands were more than 45 times greater than the overall mean densities for widespread angelfishes (Figure 2.5b).

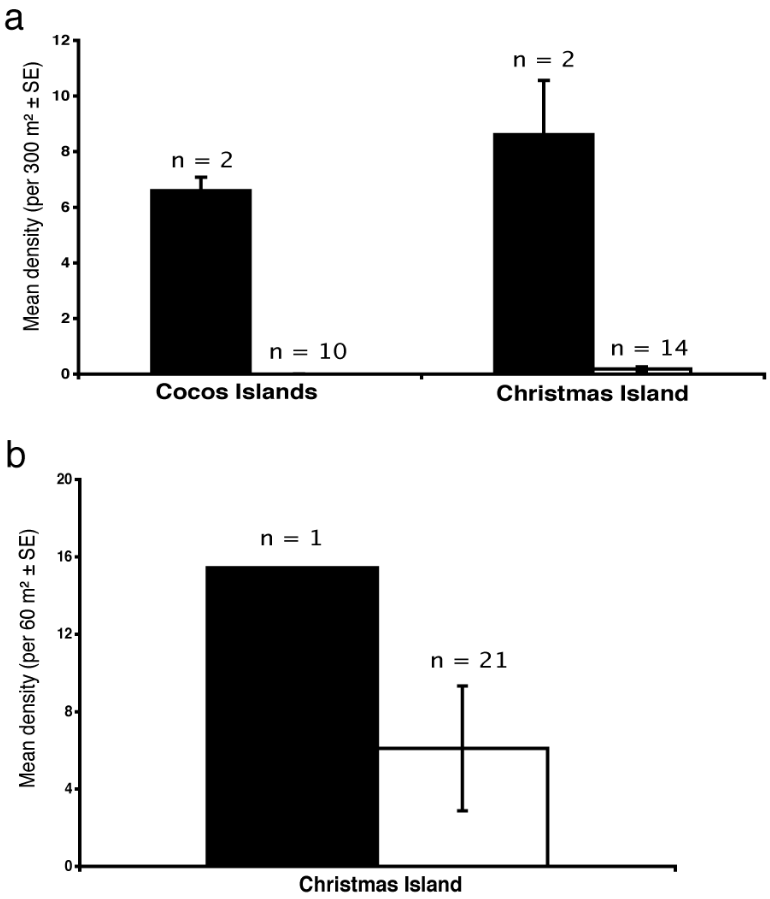

Figure 2.5. a) The mean density (per $300 m^2$ ± SE) of endemic (black bars) and widespread (white bars) angelfishes from surveys at 20 m depth at Christmas Island and the Cocos Islands. b) The mean density (per $60 m^2$ ± SE) of endemic (black bars) and widespread (white bars) damselfishes from surveys at 5 m depth at Christmas Island. Mean density is pooled across species, n = number of species.

2.5 DISCUSSION

Patterns of species richness, composition and relative abundance of fishes at Christmas Island and the Cocos Islands conform to some, but not all, of the terrestrially-derived ecological and biogeographical generalisations examined in this study.

Species richness and endemism

According to island biogeography theory (MacArthur and Wilson, 1967), small isolated islands should be the most species depauperate. Christmas Island and the Cocos Islands are the smallest, and among the most isolated, islands in the tropical Indian Ocean and thus it is not surprising that these islands have the lowest species richness in the region. The species-area relationship revealed that area was more important than isolation in determining species richness of reef fishes at Christmas and Cocos; a pattern found elsewhere for reef fishes (Bellwood and Hughes, 2001). While small area is theorised to be associated with lower rates of speciation, higher extinction rates and lower colonisation rates (target effect)(MacArthur and Wilson, 1967; Gilpin and Diamond, 1976; Rosenzweig, 1995, 1999), the relative importance of these processes in limiting species richness at Christmas and Cocos has not been determined. Low habitat diversity is another common explanation for low richness on small islands (Williams, 1964) and this effect is noticeable at the study locations. This is most evident at Christmas Island, which lacks estuaries, bays, mangrove coasts, seagrass meadows and lagoons and consequently many reef fishes that use these shallow sheltered habitats, as juveniles or adults, are noticeably absent (Allen *et al.*, 2007; Hobbs *et al.*, 2010).

Isolated island communities typically contain a high proportion of endemic species (Whittaker, 1998), and this pattern also holds for reef fishes (Randall, 1998; Jones *et al*., 2002; Allen, 2008). The communities of Christmas and Cocos Islands only contain 1.1% and 0.4% endemism, respectively, which is well outside the world's top ten locations for percent reef fish endemism (3.8-23% endemism: Allen, 2008). However, Christmas Island only contains a narrow fringe of coral reef and once habitat area has been accounted for, Christmas Island ranks sixth in the world for the number of endemic coral reef fishes per km^2 of coral reef habitat (Allen *et al*., 2007; Allen, 2008). The evolution and persistence of endemic fishes at the Cocos Islands may have been limited by the relatively recent origins of the Islands (3000 years old: Woodroffe and McLean, 1994), and the high temporal variability in the amount and diversity of shallow water habitats in the lagoon (Woodroffe and Berry, 1994).

Community composition

Terrestrial communities on islands tend to differ from mainland communities in that they contain a relatively high proportion of species with high dispersal potential (Diamond *et al*., 1976; Whittaker, 1998). Similarly, the reef fish communities of Christmas and Cocos Islands had longer PLDs, on average, than the Indonesian species pool; moreover, at the higher taxonomic level, families that were over-represented on these islands had greater dispersal potential (longer PLDs and broadcast spawning), compared to under-represented families. Although PLD generally does not correlate strongly with range size for many marine taxa (Lester *et al*., 2007), it does appear that longer PLDs are important for colonising remote locations (Mora *et al*., 2003; Lester and Ruttenberg, 2005; Paulay and Meyer, 2006). For example, the Hawaiian Islands are one of the most remote locations in the Pacific Ocean and groups of fishes that are over-represented at this location tend to have longer PLDs (Hourigan and Reese, 1987). The results from this study support the hypothesis that reef fishes whose larvae have the greatest dispersal potential are more likely to colonise isolated islands and thus become over-represented in the community.

The location of an island relative to different biogeographic regions can influence the composition and structure of its animal communities (e.g. “Wallace’s Line”: Wallace, 1860; Carlquist 1965, 1974). Christmas Island and the Cocos Islands are situated on the Indo-Pacific marine biogeographic border, resulting in a mix of Indian and Pacific Ocean species (Hobbs and Salmond, 2008; Hobbs *et al*., 2009), as well as widespread Indo-Pacific species. In contrast to patterns in terrestrial communities located near biogeographic borders (Wallace, 1860; Carlquist 1965, 1974), there were no differences in the proportions and mean abundance of Pacific and Indian Ocean species between Christmas and Cocos, even though these locations are separated across this border by 1000 km. The similarity in fish assemblages at Christmas and Cocos Islands may be due to the hydrodynamics of the area. Oceanic currents in this area generally flow east to west (Southern Equatorial Current), which would mean that even though the Cocos Islands are closer to the Indian Ocean bioregion, the Islands mainly receive immigrants from the east (that is, from Christmas Island and Indonesia). Higher proportions of Pacific Ocean species (17%) than Indian Ocean species (5%) were observed at both locations, supporting the notion that east to west currents are bringing larvae of Pacific Ocean species to both locations and inhibiting eastward dispersal by Indian Ocean species. A similar scenario has been reported for the East Pacific Barrier where colonisation of reef fishes across the barrier has been greater in one direction largely due to the role of prevailing currents in facilitating unidirectional larval dispersal (Robertson *et al*., 2004). It appears that the effect of prevailing currents on larval dispersal means that biogeographic edges are not as well defined as those in the terrestrial environment. For marine communities that rely on larval dispersal, species composition will be determined not only by the location of an island relative to different biogeographic regions but also by the prevailing currents.

Abundance

One consequence of the low species richness typical of island communities is that there are potentially fewer competing species, which is thought to allow populations on isolated islands to attain higher abundances than mainland populations (density compensation: MacArthur *et al*., 1972). At Christmas Island and the Cocos Islands, the mean density of butterflyfish species was not higher than that of mainland populations. Butterflyfish densities at Christmas and Cocos may not have been as high as expected because they were constrained by the availability of resources. Corals are a food source for many butterflyfishes (Pratchett, 2005), with butterflyfish densities often reflecting the availability of live hard corals (e.g. Pratchett *et al*., 2006), and at Christmas and Cocos, live hard coral cover was generally low (Christmas: mean cover = 45%, n = 9 sites; Cocos: mean cover = 20%, n = 8 sites; Hobbs unpublished data). Furthermore, Christmas and Cocos Islands have low species richness of corals (99 and 88, respectively: Done and Marsh 1988, Veron, 1994) and the relatively low diversity of coral food resources may have limited butterflyfish abundance. Other widespread reef fishes have been reported at high abundances on isolated islands (Allen *et al.*, 2007; Stevenson *et al.*, 2007; Hobbs *et al.*, 2008), indicating a possible density compensation effect; however, further studies are required before generalisations can be made about the role of density compensation in isolated marine communities.

In terrestrial ecology a species' abundance is often reported to be greatest near the centre of its range and decreases towards the edge (Brown, 1984; Gaston *et al.*, 1997). This pattern was not observed for the fish assemblages examined at either Christmas Island or the Cocos Islands, where centre and edge species were equally abundant. Similarly, reef fishes studied in other locations do not necessarily have low abundances at their range edge (Jones *et al.*, 2002; Tuya *et al.*, 2008). It is now apparent that reef fishes do not conform to the terrestrial pattern of low abundance at the range edge, and the next step is to determine why this is the case. In terrestrial studies, exceptions to the rule may be explained by abrupt changes in the physical or biological environment (Brown, 1984; Caughley *et al.*, 1988; Case *et al.*, 2005). However, in the marine environment it is probably more likely due to the high variation in recruitment typical of most marine species (Doherty and Williams, 1988; Doherty, 1991; Ripley and Caswell, 2006 and the references therein). Given that isolation and variable recruitment increase the likelihood of a population or species going extinct (Diamond, 1984; Pimm, 1991; McKinney, 1997; Thrall *et al.*, 2000), it would be difficult for small populations of a marine species with highly variable recruitment to persist at isolated locations on the edge of their range. Therefore, high abundance at the edge of the range is required for population persistence and this may be achieved through local adaptation and increased self-recruitment (discussed below).

Small-range endemics are expected to have low abundance resulting in a positive relationship between range size and abundance (Gaston, 1994; Brown, 1995). This relationship has been observed throughout terrestrial communities and is considered "one of the most general and robust patterns in nature" (Gaston *et al*., 1997). The three endemic reef fishes examined in this study had considerably higher abundances than widespread relatives. This also appears to be the case for reef fishes in other isolated locations (Randall, 1998; Jones *et al.*, 2002; DeMartini, 2004; DeMartini and Friedlander, 2004). It has been suggested that endemic species on isolated islands are often the exception to the range size-abundance rule, and may achieve high local abundances, either because of the lack of competitors or through adaptation to local conditions (Blackburn *et al*., 1997; Reif *et al*., 2006). Although the low species richness of fishes at Christmas Island and the Cocos Islands means species may have fewer potential competitors, there is no evidence that this leads to higher densities (see density compensation above). Therefore, this study concludes that a more likely explanation is that endemic reef fishes achieve high abundances through adaptation to the local environment (Hourigan and Reese, 1987; Randall, 1998), which may be facilitated by effective self-recruitment mechanisms in island locations (Swearer *et al*., 2002). For example, endemic reef fishes in Hawaii tend to have restricted dispersal (Eble *et al*., 2009), exhibit consistently high recruitment (DeMartini, 2004), and are generally very abundant (DeMartini and Friedlander, 2004).

In conclusion, species richness and community composition of reef fish communities at Christmas Island and the Cocos Islands generally conformed to terrestrial biogeographical theory. The Islands' reef fish communities had low species richness and an over-representation of species with a high dispersal potential which are signatures characteristic of terrestrial communities on small isolated islands. Island size, the likelihood of receiving colonists, and species dispersal ability are fundamental parameters in the theory of island biogeography. The results of this study suggest that similar processes are determining species richness and community composition in marine communities on isolated islands. However, patterns in abundance did not conform to terrestrial generalisations, and this was evident by the lack of density compensation, the high abundance of endemics, and range-edge species not having low abundance. These differences appear to be due to the life history of marine organisms (dispersal larval stage) and the maintenance of marine populations with inherently high recruitment variability. By determining the similarities and differences between marine and terrestrial communities, this study contributes to the development of a more unified theory on the processes structuring island communities.

CHAPTER 3: **Marine hybrid hotspot at Indo-Pacific biogeographic border**

3.1 ABSTRACT

Studying hybridisation is crucial to understanding speciation and almost all our knowledge comes from terrestrial and freshwater environments. Marine hybrids are considered rare, particularly on species-rich coral reefs. This study reports on a significant marine hybrid zone at Christmas and Cocos Islands (eastern Indian Ocean) with eleven hybrid coral-reef fishes (across six families). This represents the most recorded hybrid marine fishes of any location in the world. In most cases, at least one of the parent species is rare (< 3 individuals per 3000 m^2), suggesting that hybridisation has occurred because individuals of the rare species have mated with another species due to a scarcity of conspecific partners. These islands also represent a marine suture zone where many of the hybrids have arisen through interbreeding between Indian and Pacific Ocean species. For these species, it appears that past climate changes allowed species to diverge in allopatry, while recent conditions have facilitated contact and subsequent hybridisation at this Indo-Pacific biogeographic border. The discovery of the Christmas-Cocos hybrid zone refutes the notion that hybridisation is lacking on coral reefs and provides the natural laboratory for testing the generality of terrestrially derived hybridisation theory in the marine environment.

3.2 INTRODUCTION

A wide range of plants and animals hybridise, and these hybrids provide the key to understanding barriers to gene flow and the speciation process (Arnold, 1997; Seehausen, 2004; Mallet, 2005). Central to the study of hybridisation are hybrid zones – areas where species or subspecies interbreed (Hewitt, 1988; Harrison, 1993). These zones often arise where there is secondary contact between allopatric species (Hewitt, 1988, 2000). When regional biotas come into secondary contact at biogeographic borders many species pairs may interbreed, forming a cluster of hybrid zones termed a “suture zone” (Remington, 1968; Hewitt, 2000).

Almost all our knowledge and theories of hybridisation, hybrid zones and suture zones comes from research in the terrestrial and freshwater environments (Harrison, 1993; Arnold, 1997; Hewitt, 2000; Seehausen, 2006). Even though the marine environment covers more than 70% of the planet and contains some of world’s most diverse ecosystems, hybridisation has seldom been explored in the sea and this has led to the belief that marine hybridisation is rare and insignificant (Arnold, 1997).

Coral reef fishes comprise the most species-rich vertebrate communities on earth, attaining their greatest diversity in the Indonesia-Philippines region. Yet “the seeming lack of hybridization in the swarming reef fauna of the Indo-Pacific region is amazing” (Hubbs, 1955), especially given the prevalence of hybridisation in freshwater fishes (Hubbs, 1955; Arnold, 1997; Gardner, 1997; Seehausen, 2006). Similarly, suture zones have not been reported in the tropical marine environment (Gardner, 1997), despite obvious boundaries between major biogeographic provinces, such as, the region surrounding Christmas and Cocos (Keeling) Islands in the eastern Indian Ocean where the Indian and Pacific Ocean regional biotas abut (Marie *et al.*, 2007; Rocha *et al.*, 2007).

This study presents findings from the investigation of hybrid coral reef fishes at Christmas Island (10°30'S 105°40'E) and the Cocos (Keeling) Islands (12°12'S 96°54'E), which challenges the long-held belief that hybridisation is rare in the marine environment. This study describes the first suture zone in the tropical marine environment (Figure 3.1), determines the number of species that are hybridising, and examines the conditions that have facilitated hybridisation and the formation of a suture zone.

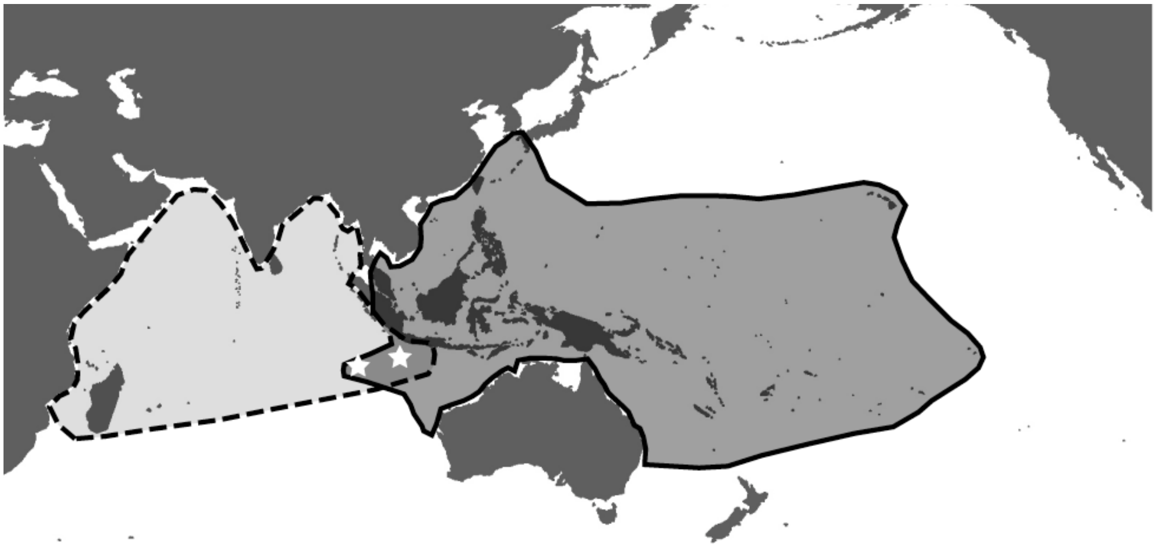

Figure 3.1 Christmas and Cocos Islands (represented by stars) represent a tropical marine suture zone located in the eastern Indian Ocean on the Indo-Pacific marine biogeographic border. At these islands Indian (represented by the lightly shaded area with dashed outline) and Pacific Ocean species (darker shaded area with solid outline) have come into contact and interbreed.

3.3 METHODS

Hybrid coral reef fishes were first identified underwater based on obvious intermediate coloration whilst SCUBA diving on fieldtrips to Christmas and/or Cocos Islands in 1978, 1986, 1987, 1989, 2006 by G.R. Allen and by myself in 2001, 2002, 2005 and 2008. To confirm hybrid status, individuals were photographed and/or collected and compared to published accounts, verified by expert fish taxonomists or examined genetically. Underwater observations of heterospecific groups or breeding pairs and interspecific spawnings at Christmas Island in 2005 and 2008 provided additional evidence of hybridisation. To determine if heterospecific pairs and groups had a reproductive basis (i.e. contained mature heterosexual individuals), members of the heterospecific butterflyfish pairs and angelfish groups were captured and the sex and maturity of their gonads were determined.

To ascertain the role of abundance disparities in promoting hybridisation the density of parent species was determined through underwater surveys. The mean density (per 3000 m^2) of the 11 parent species pairs was estimated from 4 sites at Christmas Island in 2005, 2006 and 2008. The mean density was calculated based on the number of individuals encountered during a 40 min swim covering depths of 0 - 40 m at each site. This equates to an approximate survey area of 3000 m^2 per site. Species were considered rare if their mean density was less than 3 individuals per 3000 m^2 and if their mean abundance did not differ significantly from zero (one sample, one tailed *t*-test, Zar, 1999). For abundant species, counts stopped once 30 individuals were encountered at a site.

The parent species examined in this study are not polymorphic but represent unique and separate species. Phylogenetic studies confirm that *Chaetodon guttatissimus*, *C. lunulatus, C. punctatofasciatus*, *C. trifasciatus*, *Naso elegans*, *N. litaratus*, *Thalassoma jansenii* and *T. quinquevittatum* are distinct species (McMillan and Palumbi, 1995; Klanten *et al*., 2004; Yaakub *et al*., 2006; Fessler and Westneat, 2007; Hsu *et al*., 2007). Published phylogenies are not available for the other parent species, however, fish taxonomy guides have long recognised theses species as distinct (Allen *et al*., 1998; Froese and Pauly, 2007; Kuiter and Debelius, 2006).

3.4 RESULTS

The field studies of reef fishes at Christmas and Cocos Islands identified ten hybrids in addition to a previously reported hybrid (Yaakub *et al.*, 2006). The eleven recorded hybrids belong to six reef fish families: *Acanthurus leucosternon* × *A. nigricans, Naso elegans* × *N. lituratus* (Acanthuridae); *Melichthys indicus* × *M. vidua* (Balistidae); *Chaetodon guttatissimus* × *C. punctatofasciatus, C. ornatissimus* × *C. meyeri, C. lunulatus* × *C. trifasciatus* (Chaetodontidae); *Thalassoma jansenii* × *T. quinquevittatum* (Labridae)(Yaakub et al. 2006); *Centropyge flavissima* × *C. eibli* (Figure 3.2), *C. eibli* × *C. vrolikii, C. flavissima* × *C. vrolikii* (Pomacanthidae); *Arothron nigropunctatus* × *A. mappa* (Tetraodontidae). In six of these cases, the hybrids were formed via interbreeding between Pacific and Indian Ocean species (Table 3.1). The underwater surveys revealed that in nine cases either one or both parent species were rare (abundances did not differ significantly from zero: $t_{0.05\,(1),\,3} < 2.35$, $p > 0.05$; Table 3.1).

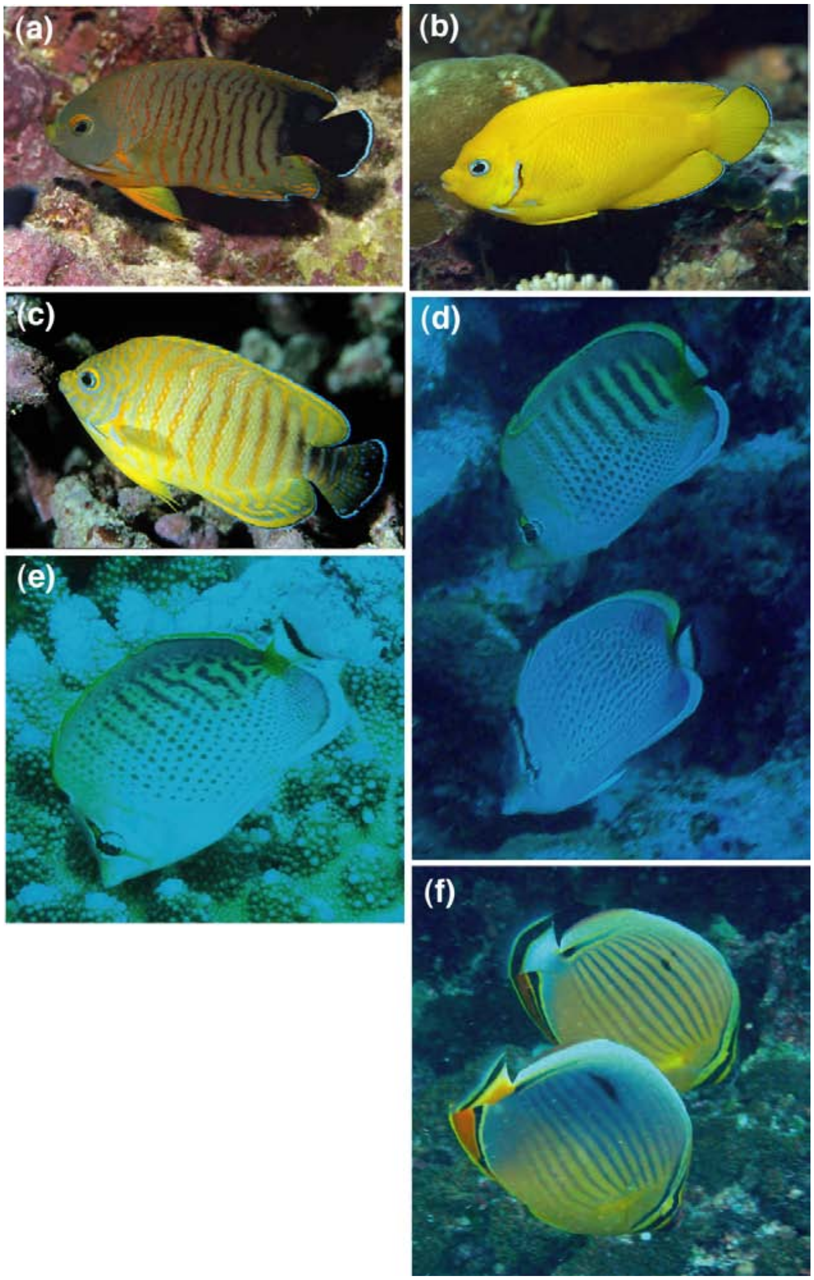

Figure 3.2 Christmas and Cocos Islands constitute a marine suture zone where (a) Indian Ocean (*Centropyge eibli*) and (b) Pacific Ocean species (*C. flavissima*) come into contact and interbreed to produce hybrids (c). Heterospecific breeding pairs (d) of *Chaetodon guttatissimus* (Indian Ocean - bottom) and *Ch. punctatofasciatus* (Pacific Ocean - top) produce hybrids (e). Heterospecific breeding pair of Indian (*Ch. trifasciatus* – bottom) and Pacific Ocean (*Ch. lunulatus* – top) butterflyfishes (f).

Table 3.1 The occurrence of parent species and hybrids at Christmas (CI) and Cocos Islands (CKI). The presence of the parental species (denoted by the first letter of the species name) and hybrids (H) at each location is listed. The estimated mean densities (individuals per 3000 m^2) of parent species are presented for Christmas Island where parent species 1 is the species listed first in the hybrid column and parent species 2 is listed second. An asterisk denotes rare species whose abundance was not significantly different from zero ($t_{0.05\ (1),\ 3} < 2.35$, $p > 0.05$). Geographic range of parent species is based on published reports (Allen et al. 1998; Froese and Pauly 2007). Support for each hybrid is listed as: heterospecific social groups (HS), heterospecific breeding pair (HP), interspecific spawning (IS), genetic confirmation (G), morphological evidence (M), intermediate colouration (C). [1] = Yaakub *et al*., 2006 and Marie *et al.*, 2007, [2] = Selma Klanten unpublished data, [3] = Pyle and Randall, 1994.

	Occurrence		mean density (per 3000 m^2)		geographic range		Hybrid support
hybrid	CI	CKI	species 1	species 2	species 1	species 2	
Acanthurus leucosternon × *A. nigricans*	L, N, H	L, N, H	2*	23.75	Indian Ocean	Pacific Ocean	HS, G[1], C
Naso elegans × *N. lituratus*	E, L, H	E, L, H	2.75*	12	Indian Ocean	Pacific Ocean	HS, G[2], C
Melichthys indicus × *M. vidua*	I, V, H	I, V, H	11.5	23.25	Indian Ocean	Indo-Pacific	HS, C
Chaetodon guttatissimus × *C. punctatofasciatus*	G, P, H	G, P	7.75	0.75*	Indian Ocean	Pacific Ocean	HP, C
C. trifasciatus × *C. lunulatus*	T, L, H	T	0.5*	0*	Indian Ocean	Pacific Ocean	HP, C
C. ornatissimus × *C. meyeri*	O, M, H	O, M	11.5	14.5	Indo-Pacific	Indo-Pacific	HP, C
Thalassoma jansenii × *T. quinquevittatum*	J, Q, H	J, Q, H	1.75*	9.5	Indo-Pacific	Indo-Pacific	HS, IS, G[1], C
Centropyge eibli ×	E, F, H	E, F, H	0.5*	> 30	Indian	Pacific	HS, IS, M[3],

C. flavissima					Ocean	Ocean	C
Centropyge eibli × *C. vrolikii*	E, V, H	E	0.5*	0.5*	Indian Ocean	Pacific Ocean	HS, M[3], C
Centropyge flavisssima × *C. vrolikii*	F, V, H	F, H	> 30	0.5*	Pacific Ocean	Pacific Ocean	HS, IS, M[3], C
Arothron nigropunctatus × *A. mappa*	N, H	N	4*	0*	Indo-Pacific	Indo-Pacific	C

3.5 DISCUSSION

The identification of eleven hybrid fishes at Christmas and Cocos Islands represents the greatest number of hybrids reported from any marine location (Gardner, 1997) and the first recorded suture zone in tropical seas. Genetic and/or morphological studies so far confirm or support hybridisation between six of these species pairs (Table 3.1). Furthermore, genetic analyses of two hybridising species pairs confirm introgression has occurred (Yaakub *et al*., 2006; Marie *et al*., 2007), signifying that some hybrids are fertile and backcross with the parent species.

Contact between typically allopatric species appears to be the most plausible reason for hybridisation in six of the eleven cases. These hybrids generally represent interbreeding between recently diverged Pacific and Indian Ocean species (Pyle and Randall, 1994; McMillan and Palumbi, 1995; Klanten *et al*., 2004; Marie *et al*., 2007) and phylogenetic studies show that a concordant genetic division occurred in this region 1-3 mya (McMillan and Palumbi, 1995; Benzie, 1999; Hewitt, 2000). This timing coincides with sea level changes that formed land bridges across the Indonesian region, thereby restricting gene flow between the Indian and Pacific Oceans (Benzie, 1999; Hewitt, 2000). Christmas and Cocos Islands are apparently a tropical marine equivalent of terrestrial suture zones (Remington, 1968; Hewitt, 2000) where hybridisation has subsequently occurred due to recent contact between allopatric species that diverged as a result of past (probably Pleistocene) climate changes. Divergence time may have been insufficient to establish pre- or post zygotic barriers thus enabling hybridisation following secondary contact.

In five cases, sympatric species have hybridised indicating that factors other than secondary contact are important. Hybridisation can also be promoted by low abundance (Hubbs, 1955; Arnold, 1997; Yaakub *et al*., 2006) and our field surveys at Christmas Island revealed that either one or both parent species were rare in nine of the eleven cases. Consequently, individuals of the rare species may choose to mate with another closely related species due to a scarcity of conspecific partners. However, in two cases, the parent species were abundant, occupied the same habitat, and importantly Christmas and Cocos Islands are the only locations where hybrids of these sympatric species have been reported. It is unclear why these species are hybridising at this location. It may represent accidental hybridisation, which has been suggested for other reef fish hybrids where groups of two species have spawned in the vicinity of each other and their gametes have come into contact (Frisch and van Herwerden, 2006; Yaakub *et al*., 2007). It appears that even within the Christmas-Cocos zone, hybrids can arise due to different processes. Further exploration in other marine taxa and locations is required to determine what factors are most commonly responsible for hybridisation in the marine environment.

The occurrence of hybridisation is usually underestimated (Mallet, 2005) and more cases are likely at Christmas and Cocos Islands. Hybrid individuals of many reef fishes often go undetected because they exhibit the physical appearance of one of the parent species (McMillan *et al*., 1999; Yaakub *et al*., 2006; Marie *et al*., 2007). More importantly, this study only examined reef fish, and hybridisation is likely in other marine groups. Christmas and Cocos Islands lie on the largest marine biogeographic border in the tropical Indo-Pacific (Bay *et al*., 2004; Rocha *et al*., 2007) and phylogenetic studies of a wide range of marine taxa, including invertebrates and plants, consistently report a phylogenetic break in this region (Benzie, 1999; Hewitt, 2000). At these islands many tropical marine species are at the edge of their range, are low in abundance, and come into contact with allopatric sister species or subspecies (Wells, 1994; Hobbs and Salmond, 2008); all factors that promote hybridisation (Mayr, 1979; Hewitt, 1988; Arnold, 1997).

The discovery of the Christmas-Cocos suture zone is significant because it refutes the notion that hybridisation is rare in the marine environment and lacking on coral reefs (Hubbs, 1955, Arnold, 1997). These islands now provide the natural laboratory for testing the generality of terrestrially derived hybridisation theory in the marine environment. Furthermore, these studies will provide unique insights and contribute to our understanding of evolutionary processes in the sea, such as barriers to gene flow, insular speciation processes and the formation of hybrid lineages. Finally, the location of this suture zone close to the global centre of coral reef diversity (Indonesia-Philippines) helps to explain this extraordinary diversity by identifying Pleistocene sea level changes as a significant biodiversity contributor to this region.

CHAPTER 4: **Physical factors determine community structure of coral reef fishes on oceanic islands**

4.1 ABSTRACT

The structure of coral reef fish communities varies across gradients occurring over different spatial scales. Most studies on factors influencing species richness and community structure along these gradients have focused on communities in mainland regions or island archipelagos, and few have examined oceanic islands, even though these islands originate differently and have different physical characteristics. This study used regression tree analysis to examine the relative importance of six explanatory factors (island location, exposure, depth, microhabitat diversity, live coral cover and algal cover) in determining spatial variation in angelfish and butterflyfish community structure at two oceanic locations in the Indian Ocean: Christmas Island and the Cocos Islands. For angelfishes, depth explained the greatest percentage of the spatial variation in total abundance, species richness and species composition/relative abundance. Species richness and total abundance of angelfishes was higher at 20 m than at 5 m, which appeared to be related to the availability of shelter sites. Spatial variation in the total abundance and species richness of butterflyfishes was best explained by exposure, with both being lower at sites with high wave exposure. Island location accounted for the greatest variation in the species composition/relative abundance of butterflyfishes, probably due to differences in physical characteristics (degree of isolation and presence/absence of a lagoon) between the two island locations. A relatively small

proportion of the spatial variation in total abundance, species richness and community composition of the two fish families was explained by the three biotic habitat factors. This study indicates that large-scale physical gradients associated with a location’s physical characteristics as well as exposure, depth and habitat complexity are more important than small-scale biotic factors (live coral cover, algal cover and microhabitat diversity) in determining the community structure of reef fishes on oceanic islands.

4.2 INTRODUCTION

The structure of animal communities is determined by the interplay of many biotic and abiotic factors that operate on a range of spatial and temporal scales (Haeckel, 1869; Andrewartha, 1961; Krebs, 1978; Begon *et al.*, 2006). The combination of factors affecting community structure on isolated islands have attracted considerable theoretical attention, beginning with island biogeography theory, which predicts that equilibrium species richness is a balance between large-scale colonisation and long-term extinction events (MacArthur and Wilson 1963, 1967). More recently, the roles of other factors such as local non-equilibrium dynamics, disturbance, local-scale biotic interactions and the historic and current characteristics of the local habitat have received increased attention (Brown and Lomolino, 2000, Fox and Fox, 2000; Graham *et al.*, 2006; Parent *et al.*, 2008; Hortal *et al.*, 2009; Lomolino and Brown, 2009). Islands often support reduced faunal diversity and favour species with particular life history characteristics, such as high dispersal ability (Paulay, 1994; Whittaker, 1998). As such, they represent a useful system for examining the relative importance of regional versus local factors, and abiotic versus biotic factors that affect the distribution and abundance of species.

Coral reef fishes are the most diverse vertebrate communities on earth and the factors affecting the distribution and abundance of species are known to be complex (Jones, 1991). A variety of physical and habitat-related factors have been shown to influence the structure of reef fish communities at a range of spatial and temporal scales (Jones, 1991), including wave exposure (Depczynski and Bellwood, 2005; Fulton *et al.*, 2005), depth

(Srinivasan, 2003), microhabitat availability (Munday *et al.*, 1997; Munday, 2002) and habitat complexity (Hixon and Jones, 2005). Biological processes such as predation (Hixon, 1991; Almany and Webster, 2004), competition (Robertson, 1996; Schmitt and Holbrook, 1999; Munday *et al.*, 2001; Holbrook and Schmitt, 2002) and larval supply (Doherty and Williams, 1988; Doherty, 1991) are important in structuring reef fish communities, and can interact with physical and habitat-related factors. Furthermore, historical factors such as plate tectonics, the development of reefs and islands, and vicariance events can also be important determinants of community structure (Randall, 1998; Bellwood and Wainwright, 2002; Robertson *et al.*, 2004; Renema *et al.*, 2008). Although numerous studies have investigated the relative roles of physical and biological factors in determining reef fish communities on coastal reefs or island archipelagos, few have used isolated oceanic systems to test theory predicting the determinants of local distribution, abundance and diversity (Friedlander and Parish 1998a,b; Friedlander *et al.*, 2003).

As the physical and biological environments of reefs surrounding oceanic islands are different to reefs associated with continents or island archipelagos, there is likely to be a difference in the relative importance of the factors influencing spatial patterns in fish community structure. Wave energy is likely to have a disproportionate influence on reef fish communities on oceanic islands because of the constant exposure to large ocean swells. High wave energy can affect fishes directly (Friedlander and Parish 1998a; Depczynski and Bellwood, 2005; Fulton *et al.*, 2005), or indirectly by causing reduced habitat complexity (Friedlander and Parish 1998b; Friedlander *et al.*, 2003; Madin and

Connolly, 2006) and differences in the quality and availability of food resources (Purcell and Bellwood, 2001; Depczynski and Bellwood, 2005, Tuya and Haroun, 2006). The reefs around oceanic islands are often characterised by steep drop-offs, therefore depth may have a greater impact on reef fish communities on oceanic islands compared to continental reefs with less steep reef slopes and narrower depth ranges. Another feature of oceanic islands is that there are often fewer species present and therefore, interspecific competition is expected to be less intense (Diamond, 1970a,b; MacArthur *et al*., 1972; May, 1975)

There are also differences in the geological origins and ecological history of reefs around oceanic islands compared to those associated with mainlands or archipelagos. Oceanic islands rise from the abyssal plain through volcanic activity and, as they have never been connected to continents, their ecological communities develop through colonisation from distant locations and *in situ* speciation (Wallace, 1902; Paulay, 1994; Whittaker and Fernandez-Palacios, 2007). Colonisation success can be determined theoretically by the location of an island, the dispersal potential of larvae and the presence of suitable habitat. Long distance dispersal is essential to colonisation success on oceanic islands and can be an important factor in structuring communities (Diamond *et al*., 1976; Brothers and Thresher, 1985; Paulay and Meyer, 2006).

Extinction is the main process by which species are removed from islands, and for reef fish communities, historical events and habitat loss are common causes of island extinctions (Dulvy *et al*, 2003; Renema *et al*., 2008). Recently, shifts in the structure of benthic communities from coral-dominated reefs to algae-dominated reefs have had profound impacts on reef fish communities, especially for specialist species that rely on live coral for food or shelter (Jones *et al.*, 2004; Munday, 2004; Bellwood *et al.*, 2006; Wilson *et al.*, 2006; Pratchett *et al.*, 2008). The impact of such habitat changes can be particularly severe on oceanic reefs, resulting in significant reductions in species richness and local extinctions of reefs fishes (Graham *et al.*, 2006). Habitat loss is especially detrimental at oceanic locations because recovery is slow due to the isolation and the limited amount of larvae received from other locations (Ayre and Hughes, 2004; Graham *et al.*, 2006). Increasing habitat loss may result in reefs becoming dominated by generalist species that are resilient to fluctuating abiotic and biotic interactions, and local scale changes in habitat structure (Wilson *et al.*, 2008). Therefore, determining the relative importance of the factors structuring reef fish communities on oceanic islands will be important in predicting the response of such communities to changing environmental conditions.

This study investigates the relative importance of factors determining spatial patterns of abundance, species richness and community structure of two coral reef fish families, angelfishes (Pomacanthidae) and butterflyfishes (Chaetodontidae), at two isolated locations in the Indian Ocean: Christmas Island and the Cocos Islands. Six factors were investigated, including a macro-scale factor (island location), 2 meso-scale gradients (wave exposure, depth) and 3 fine-scale habitat factors (microhabitat diversity, live coral cover and algal cover). Although variation in fine-scale biotic habitat characteristics have been found to strongly influence the composition and abundance of reef fishes in less remote locations (Bouchon-Navaro and Bouchon, 1989; Carpenter *et al.*, 1981; Munday, 2002; Jones *et al.*, 2004; Gardiner and Jones, 2005; Cheal *et al.*, 2008), the isolation and oceanic exposure of Christmas Island and the Cocos Islands may mean that large-scale physical factors are more important than fine-scale biotic factors in structuring reef fish communities at these remote islands.

The life history characteristics of angelfishes and butterflyfishes are typical of most reef fishes, i.e. they are broadcast spawners with a pelagic larval stage of about 20 – 50 days (Brothers *et al.*, 1983; Brothers and Thresher, 1985; Thresher and Brothers, 1985), they are relatively sedentary as adults, and form a breeding group that occupies a discrete territory. Angelfishes and butterflyfishes are found on coral reefs around the world and they occupy a broad range of depths and habitats (Allen *et al.*, 1998). Many butterflyfishes feed on corals (Pratchett, 2005) and therefore their presence and abundance is often influenced by live coral cover (Pratchett *et al.*, 2006). In contrast, the major food source of most angelfishes is algae (Allen *et al.*, 1998). Coral cover on reefs in many parts of the world is in decline (Gardner *et al.*, 2003, Bruno and Selig, 2007) due to a variety of anthropogenic impacts including sedimentation, pollution, overfishing, and global warming-induced coral bleaching (Hughes *et al.*, 2003). Declines in coral cover are usually followed by increases in algal cover (e.g. Hughes, 1994; Jones *et al.*, 2004; Graham *et al.*, 2006), sometimes resulting in phase-shifts from coral-dominated to algal-dominated reefs (Hughes *et al.*, 2003; Hughes *et al.*, 2007). Therefore, examining the relative influence of habitat types (coral and algae) on the structure of angelfish and butterflyfish communities will be useful in determining the affect of continued habitat degradation (Hoegh-Guldberg *et al*., 2007) on the structure of different reef fish assemblages.

4.3 METHODS

Study location

Christmas Island and the Cocos (Keeling) Islands are located 350 km and 1000 km southwest of Indonesia, respectively. The Indonesian Archipelago lies within the centre of diversity for coral reef fishes (Bellwood and Hughes, 2001), with species richness declining with increasing distance from this region. Christmas Island is closer to this source of diversity than the Cocos Islands. Both locations are volcanic seamounts that rise steeply from 4000-5000 m of water, with no other islands or reef systems nearby. Christmas Island is a single high island that rises to 361 m above sea level. A narrow (0-100 m wide) coral reef surrounds the island then drops steeply to the abyssal plain. The Cocos Islands lie 1000 km west of Christmas Island and consist of 26 low-lying sandy islands distributed around the perimeter of a central lagoon. The coral reef on the outside of the atoll drops off steeply to the ocean floor. Both locations receive relatively constant oceanic swell from the south, and trade winds blow from the southeast for most of the year. Consequently, the southern coastline at each location is very exposed, the eastern and western coastlines are moderately exposed, while the northern coastline is relatively well protected from the swell and wind.

Underwater visual surveys

Underwater visual surveys were conducted from February to May 2008 to estimate the abundance, species richness and spatial distributions of angelfishes (Pomacanthidae) and butterflyfishes (Chaetodontidae) at both locations. Fish surveys were conducted whilst

SCUBA diving at 16 sites at Christmas Island and 16 sites at the Cocos Islands (Figure 4.1). The 16 sites at each location were divided equally among the north, south, east and west coasts, which differ in their level of exposure (south > east and west > north). At each site, surveys were conducted using three 50 x 5m belt transects at each of two depths (shallow = 5 m and deep = 20 m) on the outer reef slope, which is similar in area and structure at both locations. The abundance of all angelfish and butterflyfish species was recorded whilst swimming slowly and simultaneously laying out a 50 m tape.

To determine the importance of microhabitat in structuring the butterflyfish and angelfish communities, two 2m^2 quadrats were randomly placed within each of the fish transects (after the fish were counted) and the percent benthic cover of different substrata within the quadrat was visually estimated. Quadrats are a commonly used approach for quantifying marine benthos (Bakus, 2007), and because data can be collected relatively quickly they were ideal for this study given the time constraints associated with SCUBA diving at depth. Although only 2 replicate quadrats were conducted on each fish transect, this equated to 12 transects per site, which represents ample replication given that site was the scale used for the data analyses. For calculations of microhabitat diversity, benthic substrata were divided into 14 categories: 7 live scleractinian coral morphologies (corymbose, branching, foliose, massive, submassive, plate and encrusting), soft corals, calcareous coralline algae, turf algae, sand, rubble, dead hard coral and "other" (rare benthic organisms with a combined cover of about 1%, e.g. fungid corals, sponges, anemones, zooanthids, gorgonians, seagrasses and macroalgae). Microhabitat diversity was calculated for each replicate using the Shannon-Weiner diversity index, $H' = -\sum p_j$

log p_j (where p is the proportion of each substrate category). This index was used because it accounts for both the number and evenness of substrate types.

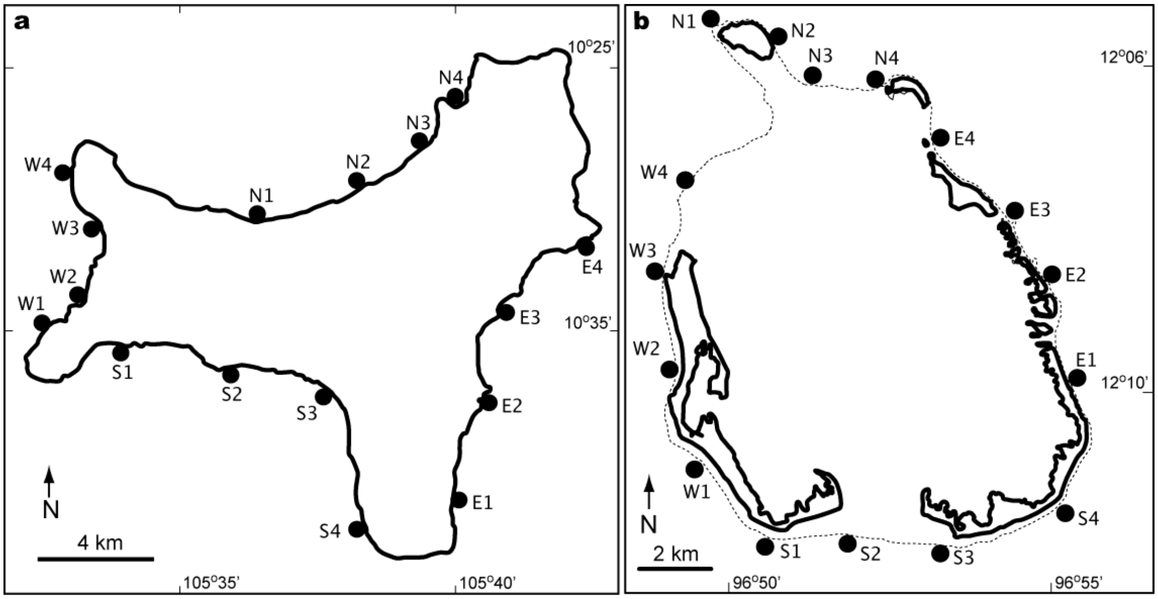

Figure 4.1 Position of the survey sites located on the outer reef drop-offs around a) Christmas Island and b) the Cocos Islands. Sites are denoted by N, S, E and W to indicate the side of the island(s). The dotted line on the Cocos Islands map represents the approximate position of the outer reef drop-off.

Regression tree analyses

Regression trees were used to examine the relative importance of the six explanatory factors (island location, exposure, depth, microhabitat diversity, live coral cover and algal cover) in determining spatial patterns in the structure of angelfish and butterflyfish communities. Regression trees are ideal for describing meaningful patterns in large, complex ecological datasets and quantifying the relative importance of different explanatory factors (De'ath and Fabricius, 2000). Regression tree analyses partition the variation in one or more response variables according to the explanatory variables in a series of binary splits (De'ath and Fabricius, 2000). Another advantage of regression trees is that both continuous and category explanatory variables can be included in the same analysis (De'Ath and Fabricius, 2000; De'Ath, 2002).

Univariate regression trees were used to examine the relative importance of each of the six factors in explaining (i) total abundance (all species pooled) and (ii) species richness of each of the two fish families. Total abundance data were pooled across transects for each depth at each site due to the low densities of many species and data were log10 (x+1) transformed to reduce the effect of patchiness in abundance. The explanatory variable 'live coral cover' included all scleractinian coral morphologies, and 'algal cover' included turf algae and macroalgae but not crustose coralline algae. As the values of both variables are percentages, the data were arcsine transformed prior to analyses.

Multivariate regression trees were used to examine the relative importance of each of the six factors on the community structure of the angelfish and butterflyfish assemblages. Of the 12 angelfish species surveyed, 2 were extremely abundant and dominated preliminary analyses (even after transformations); therefore, the multivariate regression tree for the angelfish community was based on presence-absence data. This reduced the influence of the two most common species whilst still preserving some information on relative abundance. For example, species with high abundance had a high frequency of occurrence (i.e. present in many transects).

Butterflyfishes were examined using two separate multivariate regression trees, one with the 12 most abundant species (with mean densities > 0.3 per 250 m^2). The rare species were examined separately to avoid the analysis being dominated by the most abundant species. Densities were pooled across transects at each depth and log10 (x+1) transformed.

Analyses were conducted using TreesPlus software (De'ath, 2002). For each tree, 50 sets of 10-fold cross-validations were carried out, and the modal tree size was selected using the 1SE rule, i.e. where the smallest tree with an error value within 1 SE of the minimum error is chosen (De'Ath and Fabricius, 2000; De'Ath, 2002).

4.4 RESULTS

A total of 12 species of angelfish were recorded in transects, with all species (451 individuals) observed at Christmas Island and just 4 species (580 individuals) at the Cocos Islands. The most abundant species at both locations was *Centropyge flavissima*, with mean densities (pooled across all sites and both depths at each location) of 3 to 4 individuals per 250m^2, followed by *C. joculator,* with mean densities of 1 to 2 individuals per 250m^2 (Figure 4.2). The other angelfish species occurred at much lower densities (Figure 4.2). Twenty-eight butterflyfish species were recorded in the surveys, with 24 species (877 individuals) at Christmas Island and 22 species (697 individuals) at the Cocos Islands (Figure 4.3). Eighteen of the butterflyfish species were found at both locations. Patterns of relative abundance among the butterflyfishes differed between the two locations. At Christmas Island the most abundant species (mean density > 0.77 per 250m^2) were *Forcipiger flavissimus*, *Chaetodon trifascialis*, *C. ornatissimus*, and *C. guttatissimus*. At the Cocos Islands, the most abundant species (mean density > 0.85 per 250m^2) were: *C. trifasciatus*, *C. ulietensis*, *Hemitaurichthys polylepis* and *C. auriga*.

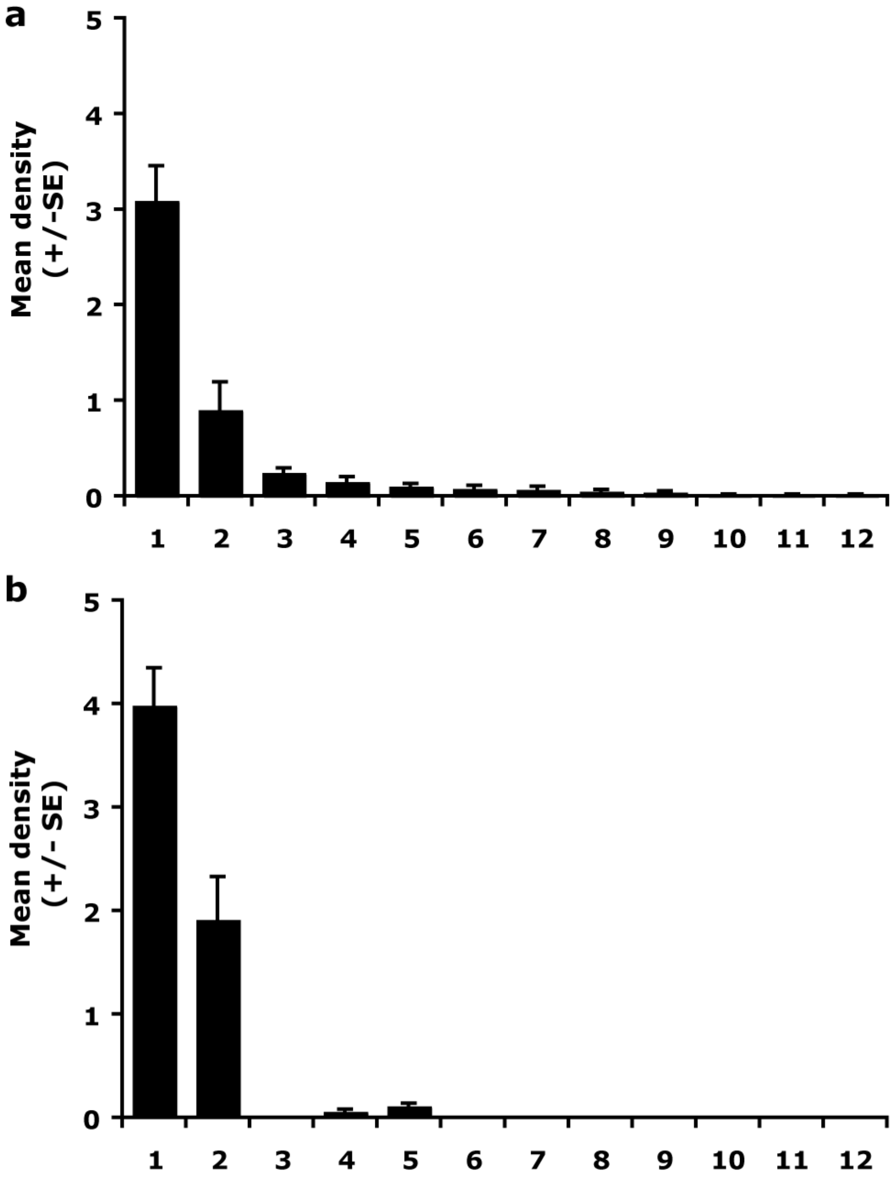

Figure 4.2 The mean density per 250m^2 (±SE) of angelfishes at a) Christmas Island and b) Cocos Islands. Species ranked in order of density at Christmas Island. 1 = *C. flavissima*, 2 = *C. joculator*, 3 = *Pygoplites diacanthus*, 4 = *Apolemichthys trimaculatus*, 5 = *Pomacanthus imperator*, 6 = *C. eibli*, 7 = *C. bicolor*, 8 = *C. bispinosa*, 9 = *C. flavicauda*, 10 = *C. tibicen*, 11 = *C. vrolokii*, 12 = *Pomacanthus semicirculatus.*

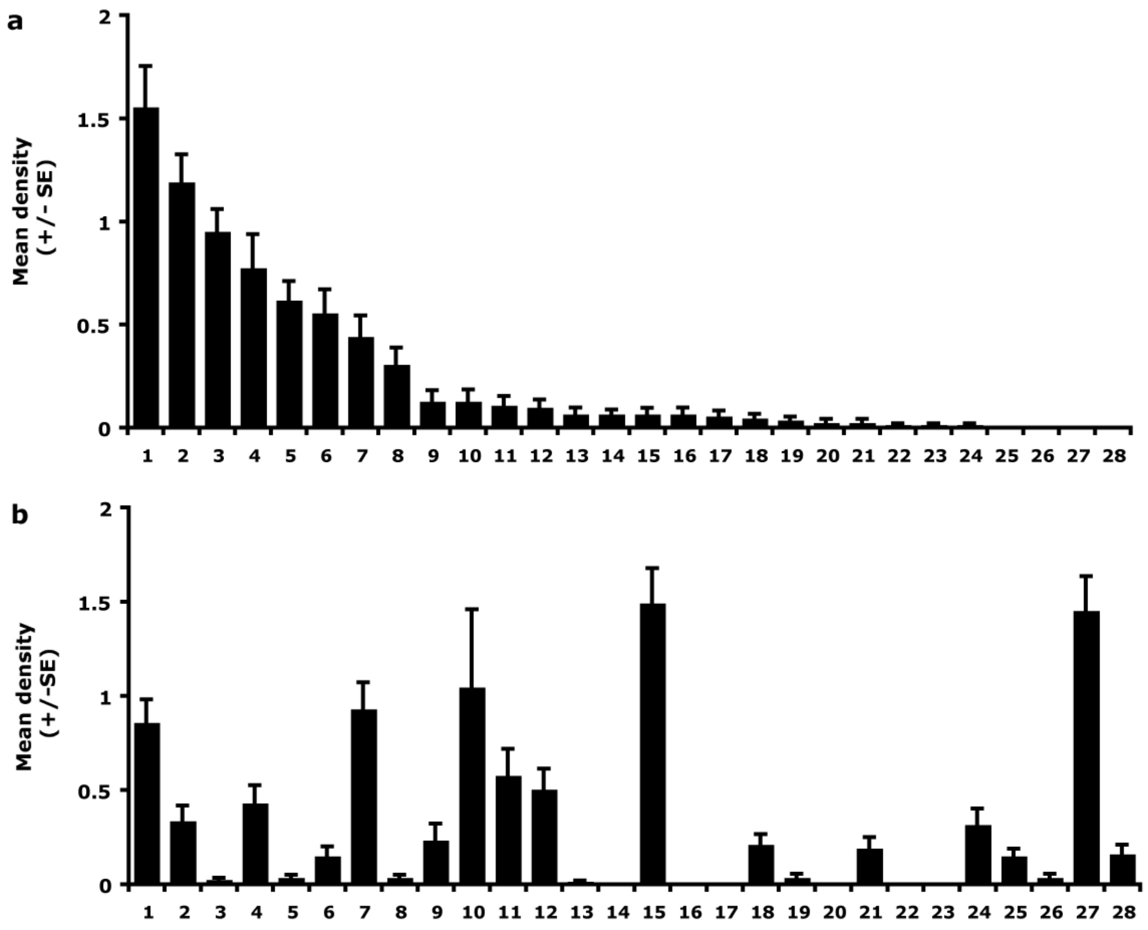

Figure 4.3 The mean density per 250m^2 (±SE) of butterflyfishes at a) Christmas Island and b) Cocos Islands. Species ranked in order of density at Christmas Island. Species in numerical order are: 1 = *Forcipiger flavissimus* , 2 = *Chaetodon trifascialis*, 3 = *C. ornatissimus*, 4 = *C. guttatissimus*, 5 = *C. meyeri*, 6 = *C. lunula*, 7 = *C. auriga*, 8 = *F. longirostris*, 9 = *C. kleinii*, 10 = *Hemitaurichthys polylepis*, 11 = *C. unimaculatus*, 12 = *C. citrinellus*, 13 = *C. lineolatus*, 14 = *C. punctatofasciatus*, 15 = *C. trifasciatus*, 16 = *Heniochus singularius*, 17 = *Heniochus varius*, 18 = *C. ephippium*, 19 = *C. vagabundus*, 20 = *C. speculum*, 21 = *Heniochus chrysostomus*, 22 = *C. adiergastos*, 23 = *C. collare*, 24 = *C. madagascariensis*, 25 = *C. melannotus*, 26 = *C. semeion*, 27 = *C. ulietentsis*, 28 = *Heniochus monoceros*.

Species richness and total abundance

Univariate regression tree analysis of spatial patterns in species richness of angelfishes resulted in a 3-leaf tree explaining 61.4% of the variation (Figure 4.4a). The first split, explaining 46.5% of the variation, was determined by depth, with a greater number of species at 20 m than at 5 m. The second split explained 14.9% of the variation and was determined by microhabitat diversity. In this split, the 20 m data were separated according to microhabitat diversity, with higher species richness of angelfishes at the sites where microhabitat diversity was high.

For spatial patterns in butterflyfish species richness, a 4-leaf tree explained 42.4% of the variation (Figure 4.4b). The greatest percentage of spatial variation in butterflyfish species richness was explained by exposure (33.2%), which determined the first two splits. The first split explained 23.5% of the variation in species richness and separated the sites on the north coast, which were the least exposed and had the highest species richness, from the other sites. The second split, explaining 9.7% of the variation, separated the sites on the south coast, which were the most exposed and had the lowest species richness, from sites on the east and west coasts. The third split, explaining 9.2% of the variation, divided the sites on the east and west coasts according to algal cover, with higher species richness at sites with lower algal cover.

Univariate regression tree analysis of spatial patterns in the total abundance of angelfishes resulted in a 2-leaf tree with a single split determined by depth, which explained 44.8% of the variation (Figure 4.5a). The total abundance of angelfishes was greater at 20 m than at 5 m. Spatial variation in the total abundance of butterflyfishes was also best explained by a 2-leaf tree (accounting for 37.6% of the variation), with exposure determining the split (Figure 4.5b). The total abundance of butterflyfishes at both island locations was lower at sites on the exposed south coasts than at sites on the other coasts.

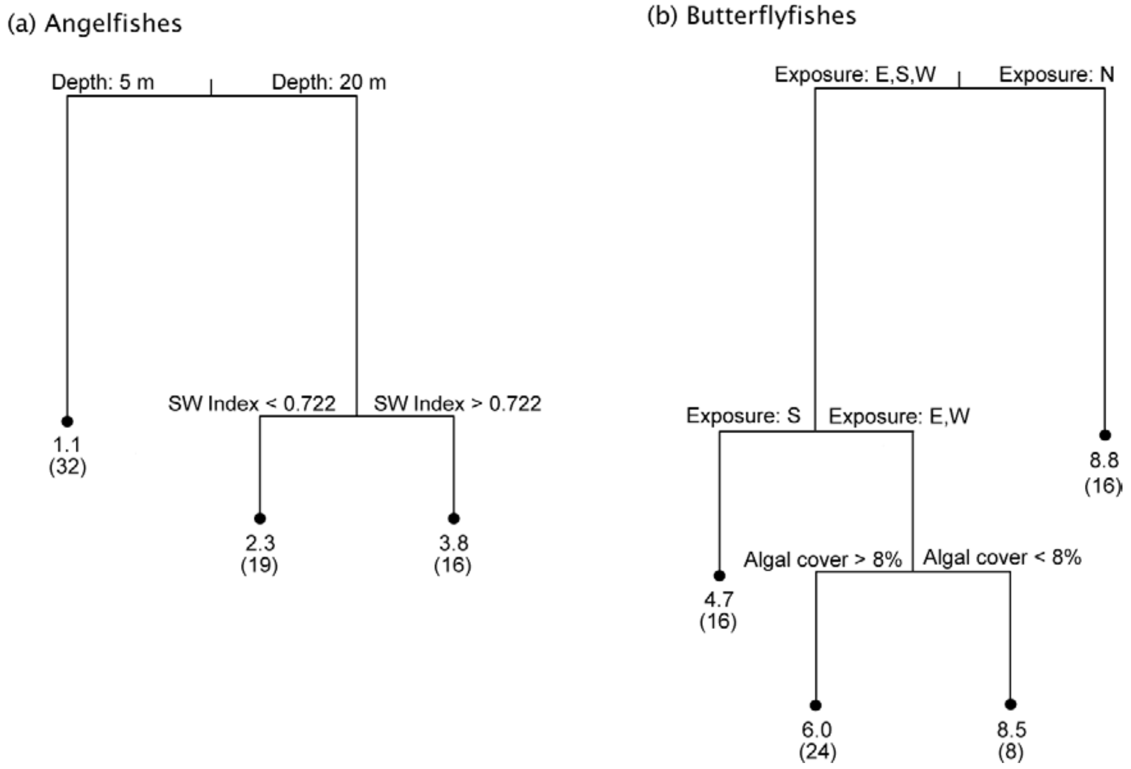

Figure 4.4 Univariate regression trees of variation in species richness of a) angelfishes and b) butterflyfishes from Christmas Island and the Cocos Islands. SW = microhabitat diversity represented by Shannon-Weiner index. The value below each node represents the mean species richness per replicate and the value in brackets is the number of replicates.

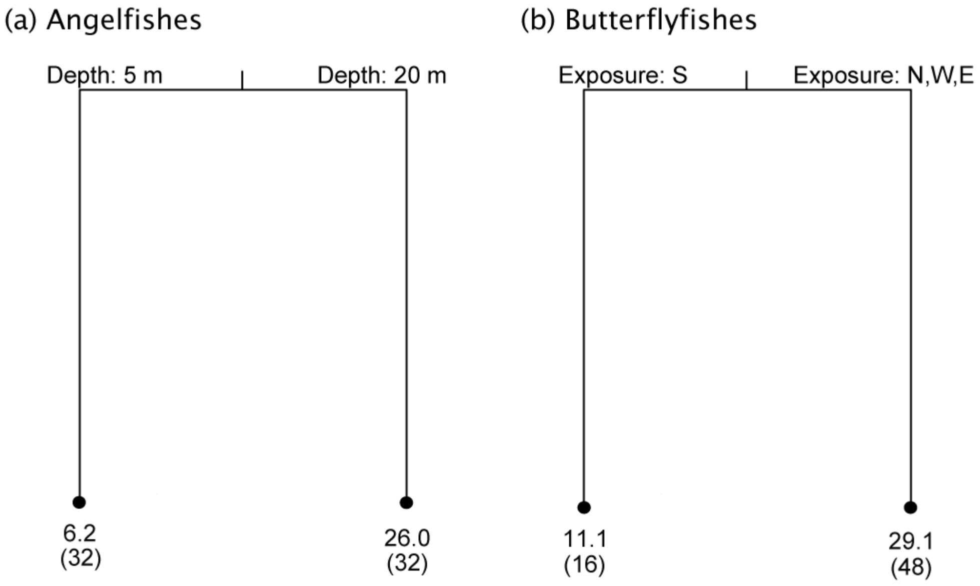

Figure 4.5 Univariate regression trees of variation in total abundance of a) angelfishes and b) butterflyfishes from Christmas Island and the Cocos Islands. The value below each node represents the mean total abundance (untransformed data) per replicate and the value in brackets is the number of replicates.

Species composition and relative abundance

Multivariate regression tree analysis of spatial patterns in the species composition of angelfishes resulted in a 3-leaf tree, which explained 33.8 % of the variation (Figure 4.6). The first split explained 15.3% of the variation and was determined by depth. This split was influenced most by *C. joculator* and *Pomacanthus imperator,* which were seldom encountered at 5 m depth, but were common at 20 m depth (Figure 4.6, Table 4.1). The second split explained 9.8% of the variation and divided the 20 m data between sites on the exposed south coast from sites on the other coasts. This split was mostly determined by *C. joculator*, which was noticeably absent on the south coast at both locations, and *Apolemichthys trimaculatus*, which occurred more frequently on the south coasts (Table 4.1). The north, east and west coast sites were further divided by island in the third split, which explained 8.7% of the variation. This split was mostly influenced by *Pygoplites diacanthus* (Table 4.1), which was the third most abundant species at Christmas Island but was not recorded in any transects at the Cocos Islands (Figure 4.2).

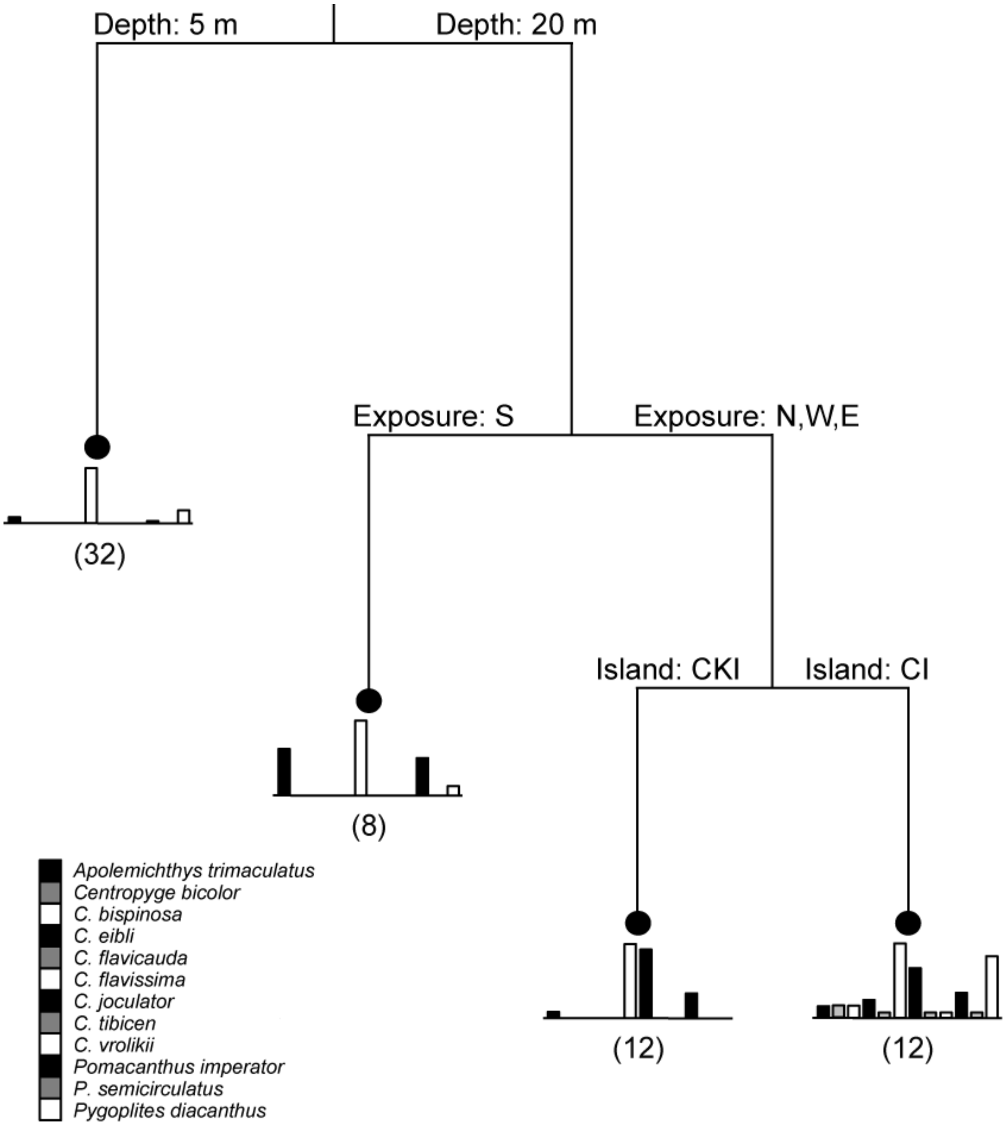

Figure 4.6 Multivariate regression tree of variation in the species composition and frequency of occurrence of angelfishes at Christmas Island (CI) and the Cocos Islands (CKI). The bar plots show presence/absence patterns of each species listed in the legend and represented by black, grey and white bars running from left to right. The number of depth by site replicates that comprise each node is provided in brackets.

Table 4.1 Summary of the splits in the multivariate regression tree for angelfishes showing the contribution of each species to the variation explained by each split. The species contributing the most to each split are presented in bold. Abbreviations are: CI = Christmas Island, CKI = Cocos Islands, A.Po = *Apolemichthys trimaculatus*, C.bc = *Centropyge bicolor*, C.bs = *C. bispinosa*, C.ei = *C. eibli*, C.fc = *C. flavicauda*, C.fv = *C. flavissima*, C.jo = *C. joculator*, C.ti = *C. tibicen*, C.vr = *C. vrolokii*, P.im = *Pomacanthus imperator*, P. se = *P. semicirculatus*, and P.di = *Pygoplites diacanthus*.

Nature of split	A.po	C.bc	C.bs	C.ei	C.fc	C.fv	C.jo	C.ti	C.vr	P.im	P.se	P.di	Split total
Depth: 5 vs 20 m	0.62	0.10	0.10	0.22	0.02	1.59	**8.96**	0.02	0.02	**3.00**	0.02	0.62	15.31
Exposure: S vs E,N,W	**2.38**	0.07	0.07	0.15	0.02	0.00	**5.97**	0.02	0.02	0.26	0.02	0.81	9.77
Island: CI vs CKI	0.07	0.26	0.26	0.60	0.07	0.00	0.60	0.07	0.07	0.00	0.07	**6.62**	8.67
Tree total	3.07	0.43	0.43	0.97	0.11	1.59	15.52	0.11	0.11	3.27	0.11	8.05	33.75

Multivariate regression tree analysis of spatial variation in species composition and relative abundance of the 12 most common butterflyfishes resulted in a 5-leaf tree, which accounted for 42.4% of the variation (Figure 4.7). The first split, explaining 24.2% of the variation, was determined by island and was most strongly influenced by *Chaetodon ulietensis, C. trifasciatus* and *C. ornatissimus* (Table 4.2). *C. ulietensis* and *C. trifasciatus* were the 2 most abundant butterflyfish species at the Cocos Islands but both species had very low densities at Christmas Island (Figure 4.2). *C. ornatissimus* was the third most abundant species at Christmas Island but had very low densities at the Cocos Islands (Figure 4.2). The second split explained 6.3% of the variation and separated the south coast sites at Cocos Island from sites on the other coasts and was largely influenced by the low abundance of *C. ulietensis* and *C. trifasciatus* on the south coast. The third split explained 6.1% of the variation and split the north, west and east sites at the Cocos Islands by depth and was largely due to the relatively high abundance of *H. polylepis* and *F. flavissimus* at 20 m depth (Table 4.2). The fourth split explained 5.8% of the variation in butterflyfish community structure and separated sites at Christmas Island based on live coral cover (Table 4.2, Figure 4.7).

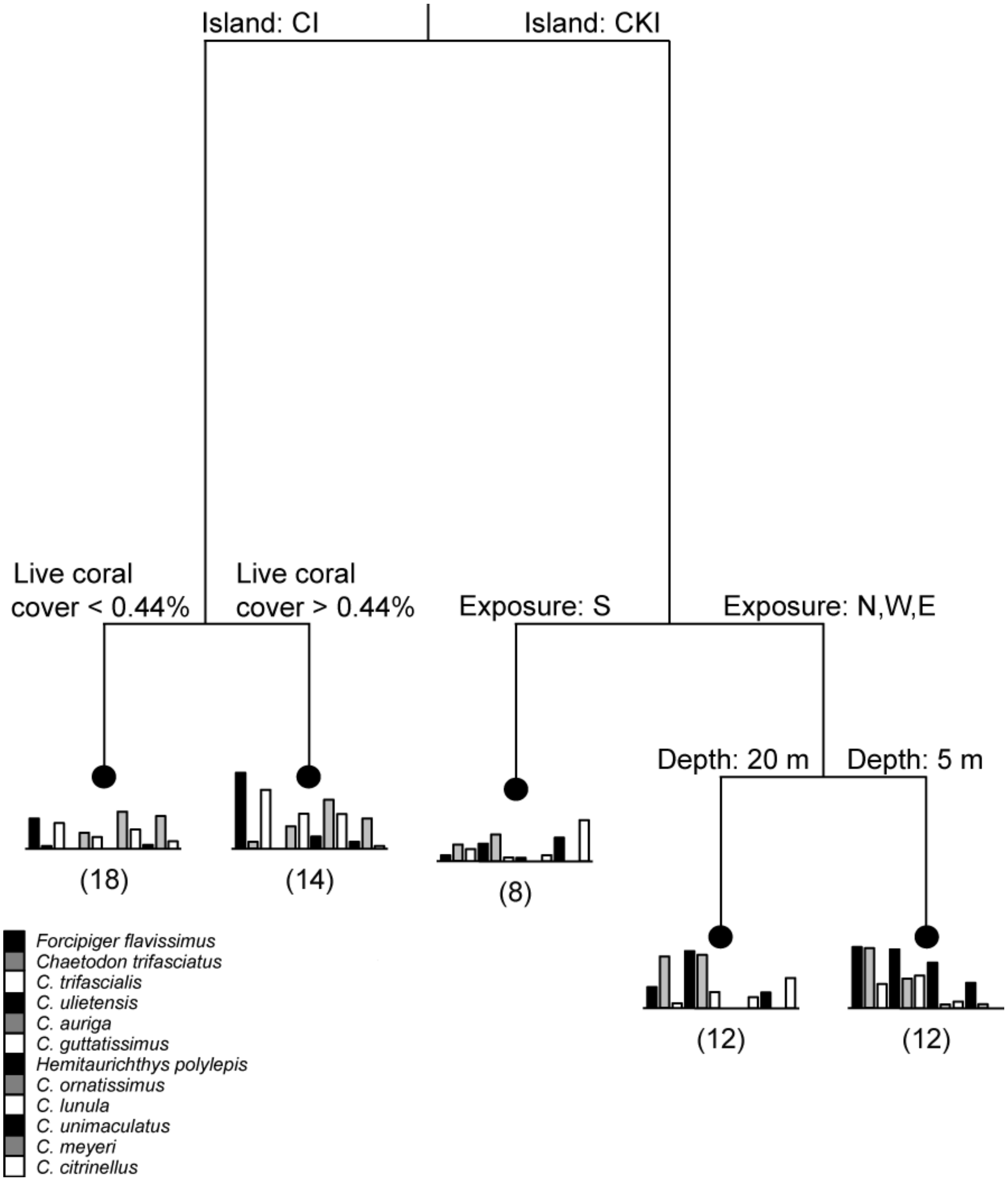

Figure 4.7 Multivariate regression tree of variation in the species composition and relative abundance of 12 common butterflyfishes at Christmas Island (CI) and the Cocos Islands (CKI). The bar plots show the relative abundance of each species, indicated using cyclical shading (black, grey and white) running from left to right. The number of depth × site replicates that comprise each node is provided in brackets.

Table 4.2 Summary of the splits in the multivariate regression tree for the 12 most common butterflyfishes showing the contribution of each species to the variation explained by each split. The species contributing the most to each split are presented in bold. Abbreviations are: CI = Christmas Island, CKI = Cocos Islands, F.fl = *Forcipiger flavissimus,* C.tt = *Chaetodon trifasciatus,* C.tf = *C. trifascialis,* C.ul = *C. ulietensis,* C.au = *C. auriga*, C.gu = *C. guttatissimus,* H.po = *Hemitaurichthys polylepis*, C.or = *C. ornatissimus*, C.lu = *C. lunula*, C.un = *C. unimaculatus*, C.me = *C. meyeri*, C.ci = *C. citrinellus*.

Nature of split	F.fl	C.tt	C.tf	C.ul	C.au	C.gu	H.po	C.or	C.lu	C.un	C.me	C.ci	Split total
Island: CI vs CKI	0.86	**4.85**	1.82	**6.20**	0.97	0.01	0.42	**4.46**	0.83	0.72	2.29	0.75	24.20
Exposure: S vs E,N,W	1.25	**1.56**	0.01	**1.70**	0.24	0.48	0.39	0.00	0.01	0.01	0.01	0.68	6.33
Depth: 5 vs 20 m	**1.63**	0.07	0.38	0.00	0.57	0.27	**2.10**	0.02	0.02	0.10	0.00	0.94	6.10
Live coral cover: < 44%	**2.74**	0.05	**1.46**	0.00	0.05	0.71	0.20	0.21	0.33	0.02	0.01	0.04	5.81
Tree total	10.31	11.96	10.82	11.18	8.00	9.75	8.70	7.02	5.19	6.62	4.91	5.53	42.44

For the 16 rarer butterflyfishes, spatial variation in species composition was best described by a 4-leaf tree, explaining 22.2% of the variation (Figure 4.8). The first split was determined by island location and explained 8.2% of the variation. This was mostly influenced by the relative high abundance of *C. madagascariensis* at the Cocos Islands and *Forcipiger longirostris* at Christmas Island (Table 4.3). The second split (explaining 8.8% variation) was determined by wave exposure (north coast sites were separated from sites on the other coasts) and was influenced by the relatively high abundance of *C. kleinii* and *C. madagascariensis* on the sheltered north coast (Table 4.3). The third split was determined by depth and explained 5.1% of the variation. The relative high abundance of *Heniochus chrysostomus* and *C. kleinii* in deeper waters (20 m) was an important contributor to the third split (Table 4.3).

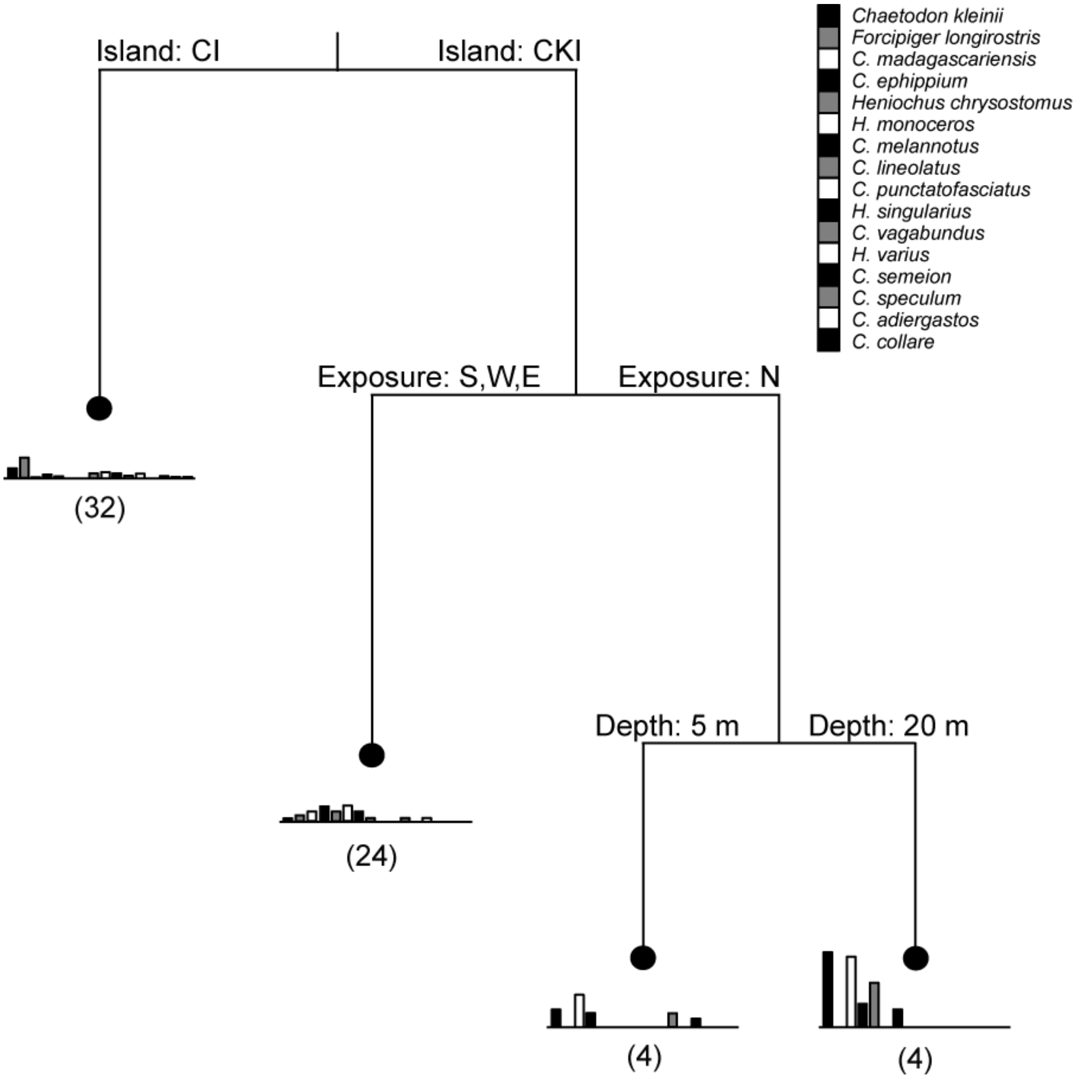

Figure 4.8 Multivariate regression tree of variation in the species composition and relative abundance of 16 rare butterflyfishes at Christmas Island (CI) and the Cocos Islands (CKI). The bar plots show the relative abundance of each species, indicated using cyclical shading (black, grey and white) running from left to right. The number of depth × site replicates that comprise each node is provided in brackets.

Table 4.3 Summary of the splits in the multivariate regression tree for the 16 rarer butterflyfishes showing the contribution of each species to the variation explained by each split. The species contributing the most to each split are presented in bold. Abbreviations are: CI = Christmas Island, CKI = Cocos Islands, C.kl = *Chaetodon kleinii*, F.lo = *Forcipiger longirostris*, C.ma = *C. madagascariensis*, C.ep = *C. ephippium*, H.ch = *Heniochus chrysostomus*, H.mo = *H. monoceros*, C.me = *C. melannotus*, C.li = *C. lineolatus*, C.pu = *C. punctatofasciatus*, H.si = *H. singularius*, C.va = *C. vagabundus*, H.va = *H. varius*, C.se = *C. semeion*, C.sp = *C. speculum*, C.ad = *C. adiergastos*, C.co = *C. collare*.

Nature of split	C.kl	F.lo	C.ma	C.ep	H.ch	H.mo	C.me	C.li	C.pu	H.si	C.va	H.va	C.se	C.sp	C.ad	C.co	Split total
Island: CI vs CKI	0.03	**1.80**	**1.96**	1.12	0.93	0.74	0.96	0.10	0.22	0.16	0.00	0.12	0.05	0.02	0.01	0.01	8.24
Exposure: N vs E,S,W	**4.22**	0.03	**3.71**	0.00	0.21	0.50	0.06	0.00	0.00	0.00	0.07	0.00	0.01	0.00	0.00	0.00	8.81
Depth: 5 vs 20 m	**2.23**	0.00	1.00	0.06	**1.38**	0.00	0.23	0.00	0.00	0.00	0.14	0.00	0.12	0.02	0.01	0.01	5.10
Tree total	6.48	1.83	6.67	1.18	2.53	1.24	1.25	0.11	0.22	0.16	0.21	0.12	0.12	0.02	0.01	0.01	22.15

Out of all the regression trees, depth accounted for the greatest percentage of the spatial variation in species richness, total abundance, and species composition/relative abundance of angelfishes (Table 4.4). For the butterflyfishes, exposure accounted for the greatest percentage of the spatial variation in species richness and total abundance, while island location accounted for the greatest percentage of the spatial variation in species composition/relative abundance (Table 4.4).

Table 4.4 Summary of the relative importance of each of the six factors in explaining variation in species richness, total abundance, and the species composition/relative abundance of angelfishes and butterflyfishes at Christmas Island and the Cocos Islands. The following categories were used to classify the percentage of variation explained by each variable calculated using regression tree analyses: High = >20%, Medium = 10-20%, Low = 5-10%, Negligible = 0-5% (indicated by -).

Variable	Angelfish			Butterflyfish			
	Species richness	Total abundance	Species composition and relative abundance	Species richness	Total abundance	Species composition and relative abundance (12 common species)	Species composition and relative abundance (16 rarer species)
Island	-	-	Low	-	-	High	Low
Exposure	-	-	Low	High	High	Low	Low
Depth	High	High	Medium	-	-	Low	Low
Microhabitat diversity	Medium	-	-	-	-	-	-
Coral cover	-	-	-	-	-	Low	-
Algal cover	-	-	-	Low	-	-	-

4.5 DISCUSSION

This study supports the prediction that large-scale physical factors (associated with island location, exposure and depth) have greater importance than the fine-scale biological components of the habitat (live coral cover, algal cover and microhabitat diversity) in determining the structure of two reef fish families on these oceanic islands. This is consistent with other studies that have reported the importance of physical factors in structuring reef fish assemblages at other oceanic locations (Friedlander and Parish, 1998a,b; Lecchini *et al.*, 2003; Letourneur *et al.*, 2008). These results contrast with studies on continents or island archipelagos where biotic habitat characteristics often have a strong influence on the composition and abundance of reef fish communities (Carpenter *et al.*, 1981; Bouchon-Navaro and Bouchon, 1989; Munday, 2002; Jones *et al.*, 2004; Gardiner and Jones, 2005; Pratchett *et al.*, 2006; Cheal *et al.*, 2008).

Spatial patterns among the angelfishes: depth

For angelfishes, depth explained the greatest variation in total abundance, species richness, and species composition/relative abundance at Christmas Island and the Cocos Islands. Species richness and the total abundance of angelfishes was higher at 20 m depth than 5 m. Lechinni *et al*. (2003) found a similar pattern at the oceanic Ryuku Islands, where species richness and abundance of angelfishes were much greater in deeper areas (10–15 m). In contrast, Eagle *et al*. (2001) studied angelfishes on the continental Great Barrier Reef and found that species richness and abundance were greatest at depths of 2–5m. These Great Barrier Reef angelfish species also occur at Christmas Island and the Cocos Islands, where they were most abundant at the 20 m depth. Angelfish species might have greater preferred depths at these oceanic islands, or there may be other factors causing a shift in their depth ranges to deeper water. For example, greater depths may provide a refuge for species that are incapable of inhabiting shallow areas exposed to high wave energy (Fulton *et al.*, 2001, Depczynski and Bellwood, 2005; Fulton *et al.*, 2005). Wave energy can also affect the quality and availability of resources. For example, wave energy affects algal communities (Tuya and Haroun, 2006), which are the main food source of *Centropyge* angelfishes (Allen *et al.*, 1998; Eagle and Jones, 2004) including those at Christmas Island (Chapter 5). However, both wave exposure and algal cover were included in the analysis and neither of these factors were important in explaining the spatial variation in angelfish communities. Similarly, Eagle *et al* (2001) examined sites where *Centropyge* were relatively common and found that their abundance was not correlated with the abundance of their algal food source.

The importance of depth in structuring angelfish assemblages on oceanic islands could be related to the strong depth gradient in habitat complexity on outer reefs of oceanic islands. Habitat complexity has been linked to higher abundances and species richness of reef fishes at both oceanic and continental locations (Sano *et al.*, 1987; Carpenter *et al.*, 1981; Connell and Kingsford, 1998; Friedlander *et al.*, 2003; Gratwicke and Speight, 2005; Graham *et al.*, 2006; Benfield *et al.*, 2008 and references therein); however, it appears to be particularly important on oceanic reefs (Friedlander and Parish 1998b; Friedlander *et al.*, 2003). At Christmas Island and the Cocos Islands, the 5 m depth contour represents a horizontal reef flat comprised of a solid pavement with a veneer of biotic cover (e.g. live coral, turfing algae). In contrast, the 20 m depth represents a steep slope or vertical wall, which contains an underlying “honeycomb” reef matrix, covered in various sessile organisms. Habitat complexity is important in creating refuges for small fishes, and personal observations revealed that the shelter sites used by angelfishes are abundant at 20 m and rare at 5 m. In contrast, on continental reefs, the complex reef structure preferred by angelfishes occurs in shallow water and hence angelfish abundance is greatest in the shallows (e.g. 2-5 m: Eagle *et al*., 2001).

Greater numbers of shelter sites support higher abundances of small reef fishes by providing a refuge from predation (Hixon and Beets, 1989) and the abundance of shelter sites is thought to be the most critical component of habitat complexity influencing species richness and abundance of fishes on oceanic reefs (Friedlander and Parish 1998b). Small-bodied fishes are the most reliant on the reef matrix for shelter (Munday and Jones, 1998; Wilson *et al*., 2006). Angelfishes prefer areas of high habitat complexity (Eagle *et al*., 2001 and references therein) and are reliant on shelter sites (Allen *et al*., 1998), so much so, that they do not persist on reefs when habitat complexity declines (Sano *et al*., 1987). The availability of shelter sites is likely to be an important determinant of species richness and abundance in angelfishes, especially given that mortality rates in these species can vary by an order of magnitude among locations (Aldenhoven, 1986). The availability of shelter sites can also be an important determinant of reef fish recruitment (Hixon and Beets, 1993, Almany, 2004), which can ultimately influence adult abundance (Jones *et al*., 2007). Recruits of *Centropyge* angelfishes adopt a cryptic lifestyle by hiding in shelter holes (Lecchini, 2005; Hobbs pers. obs.). Therefore, it is possible that the availability of shelter sites, rather than depth *per se,* is an important determinant of spatial patterns of angelfish abundance and community structure at Christmas Island and the Cocos Islands.

Spatial patterns among the butterflyfishes: exposure and island location

The abundance, species richness, and species composition of butterflyfishes in continental locations is largely influenced by the availability and diversity of suitable substrates (e.g. live coral cover: Bouchon-Navaro and Bouchon, 1989; Halford *et al*., 2004; Pratchett *et al*., 2006). However, in this study, fine-scale habitat factors (live coral cover, algal cover and microhabitat diversity) had little influence on the spatial structure of butterflyfish communities relative to the larger-scale factors (exposure and island location). Exposure relates directly to wave energy, and studies at both continental and oceanic locations have found wave energy has a strong influence on reef fish community structure (Friedlander and Parish, 1998a; Friedlander *et al*., 2003; Depczynski and Bellwood, 2005; Fulton *et al*., 2005). For example, the Hawaiian Islands are exposed to large swells and sheltered habitats tend to support greater abundance, species richness and diversity of reef fishes (Friedlander and Parish, 1998a; Friedlander *et al*., 2003). The lower abundances and species richness of butterflyfish species on the exposed sides of Christmas and Cocos Islands may be because they lack the locomotory abilities required to persist in high wave energy environments. Butterflyfishes use a pectoral-caudal swimming mode, which has relatively low efficiency and manoeuvrability in high wave energy environments, making it difficult for these species to seek shelter, or maintain position and obtain food from the substrate (Fulton and Bellwood, 2005).

Butterflyfish abundance and species richness are known to be positively correlated with habitat complexity (Sano *et al*., 1987; Graham *et al*., 2009). Therefore, in addition to the direct effects of high wave energy, reduced habitat complexity associated with areas of high wave energy (Madin and Connolly, 2006) may also contribute to lower abundances and species richness of butterflyfishes (Friedlander *et al*., 2003). The reduced complexity (and associated shelter holes) may explain the low species richness and abundance on the most exposed sites at Christmas Island and the Cocos Islands. In addition to habitat complexity, exposure can influence the abundance of food resources. Many butterflyfishes feed on live corals (Pratchett, 2005) and as coral community structure is strongly influenced by wave energy (Madin and Connolly, 2006), this may influence the distribution and abundance of some butterflyfishes, particularly those that have more specialised diets (Pratchett, 2005; Graham *et al*., 2009). However, live coral cover was included in the regression tree analyses and surprisingly explained relatively little of the spatial variation in butterflyfish total abundance, species richness and community structure.

Differences in butterflyfish communities between islands

Six butterflyfishes (*C. adiergastos, C. collare, C. punctatofasciatus, C. speculum, Heniochus singularius* and *H. varius*) were recorded in surveys at Christmas Island but were not observed in, or outside of, transects at the Cocos Islands. These species have never been recorded at the Cocos Islands (Allen and Smith-Vaniz, 1994) and it appears that they have not been able to colonise the Cocos Islands due to its greater isolation. Christmas Island and the Cocos Islands are likely to be colonised by larvae arriving from the nearest source populations in Indonesia. Christmas Island is just 350 km from Indonesia, whereas the Cocos Islands are 1000 km from Indonesia (and 1000 km from Christmas Island). Species capable of dispersing to Christmas Island may not be able to disperse to the Cocos Islands due to the extra distance they need to travel. In the terrestrial environment, isolation acts as a significant filter in the colonisation of islands and the dispersal capabilities of species plays a key role in determining community structure on oceanic islands (Diamond *et al.*, 1976; Whittaker, 1998). Similarly, the dispersal abilities of reef fishes appear to be important for the colonisation of isolated oceanic islands (Brothers and Thresher, 1985; Lester and Ruttenberg, 2005), and the communities at these islands differ to communities on continental reefs because they have an over-representation of species with good dispersal abilities and under-representation of species with poor dispersal abilities (Chapter 2).

There were four butterflyfish species recorded at the Cocos Islands which were not observed in transects at Christmas Island. Three of the four species (*C. melannotus, C. semion*, *Heniochus monoceros*) are present at Christmas Island (Allen *et al.*, 2007) but are rare and were not observed in the surveys. The other species, *C. ulietensis*, inhabits sheltered environments as juveniles (Froese and Pauly, 2010) and its absence from Christmas Island is probably explained by the lack of a lagoon at Christmas Island. This species is the second most abundant butterflyfish at the Cocos Islands where there is a large lagoon.

In addition to differences in species composition of butterflyfishes between Christmas Island and the Cocos Islands, there were also differences in relative abundances. Three of the four most abundant species at the Cocos Islands (*C. trifasciatus*, *C. ulietensis* and *C. auriga*) use lagoonal or sheltered environments at some stage of their life (Allen *et al*., 1998; Pratchett *et al*., 2008; Froese and Pauly, 2010), which probably explains their relatively high abundance at the Cocos Islands but not at Christmas Island. The other abundant species (*Hemitaurichthys polylepis*) does not require lagoonal environments and it is not clear why its relative abundance is much higher at the Cocos Islands than at Christmas Island, but it is atypical of butterflyfishes in that it is planktivorous (Allen *et al*., 1998).

Differences in the relative importance of spatial variables between the two families

The relative importance of each of the six variables in explaining spatial variation in total abundance, species richness and community structure differed between the two study families. This is probably due to the wide range of factors that can be involved in determining the spatial structure of reef fish communities as well as biological and ecological differences between families. For example, island location will be particularly important for taxa with poor dispersal abilities because they will have greater difficulty colonising isolated locations (Lester and Ruttenberg, 2005; Paulay and Meyer, 2006). Taxonomic differences in body size and locomotory abilities are likely to lead to differences in the importance of high wave energy in structuring different taxonomic groups (Fulton *et al*., 2001; Depczynski and Bellwood, 2005; Fulton and Bellwood, 2005; Fulton *et al*., 2005). The availability of particular habitats (e.g. lagoons) or microhabitats (e.g. species of corals) is likely to be important to taxa that are heavily reliant on these resources for either food or shelter (Munday, 2002; Allen *et al.*, 2007; Graham *et al.*, 2009). Therefore, the relative importance of different factors in determining the spatial structure of reef communities will vary depending on the resource preferences of the group examined.

Community establishment on oceanic versus continental islands

The establishment of communities on oceanic islands is largely dependent on colonisation from other source locations, and therefore an island's location and degree of isolation is an important determinant of community structure because it controls which species can disperse to that island. Island location and isolation are likely to be less important on continental margins because there are usually networks of reefs and islands in relatively close proximity (e.g. Australia's Great Barrier Reef). Successful colonisation of an oceanic island is not only dependent on the arrival of larvae but also the availability of suitable habitat (e.g. lagoon). Once a species has successfully colonised, and established itself on an oceanic island, other physical variables (exposure, depth, habitat complexity, availability of shelter sites) determine its spatial distribution and abundance around the island (Friedlander and Parish 1998a,b; Lecchini *et al.*, 2003; Letourneur *et al.*, 2008; this study). These variables are often correlated with one another, e.g. wave energy decreases with increasing depth and the physical structure of the reef habitat can differ with both depth and exposure. Compared to continental areas, wave energy is greater on oceanic islands and is therefore likely to result in stronger gradients in habitat complexity and shelter site availability among depths, and from exposed to leeward sides of islands. It appears that following successful colonisation and establishment, physical factors take precedence in the structuring of reef fish communities on oceanic islands, and biological and ecological factors play a secondary role. For example, reef fish communities on oceanic islands are generally species poor (Bellwood and Hughes, 2001), therefore competition is expected to be less intense (MacArthur *et al*., 1972) and the availability of biotic (e.g. food) resources is likely to be less influential in driving spatial patterns of community structure on oceanic reefs compared to high diversity communities typical of continental reefs.

Overall, this study demonstrates that large-scale physical gradients associated with island location, exposure and depth had greater relative importance than fine-scale biotic factors (microhabitat diversity, live coral cover and algal cover) in determining spatial patterns in the total abundance, species richness and community structure of angelfishes and butterflyfishes at the two oceanic island locations. The importance of the physical characteristics of reefs on oceanic islands means that the associated reef fish communities are likely to be impacted by destructive processes such as storms, coral bleaching and coral disease, which are predicted to increase worldwide due to climate change (Harvell *et al*., 1999; Hughes *et al*., 2003; Sheppard, 2003; Emanuel, 2005; Hoyos *et al*., 2006; Hoegh-Guldberg *et al*., 2007). Reef fish communities on oceanic islands are particularly vulnerable to disturbances and have low resilience (due to low species diversity and isolation), which means that these communities recover much slower from disturbances (Graham *et al*., 2006) than continental reefs (Halford *et al*., 2004). Recovery of reef fish communities on oceanic islands is not only dependent on larval dispersal from distant source populations, but is also reliant on the arrival of habitat forming organisms (e.g. corals), which have even more limited dispersal than reef fishes (Ayre and Hughes, 2004). The reduced potential for recovery means that management of reef fishes on oceanic islands should aim to preserve the physical characteristics of the reef and minimise human impacts that reduce habitat complexity.

CHAPTER 5: **Rarity and extinction risk in coral reef angelfishes on isolated islands: interrelationships among abundance, geographic range size and specialisation**

5.1 ABSTRACT

Determining the species most vulnerable to increasing degradation of coral reef habitats requires identification of the ecological traits that increase extinction risk. In the terrestrial environment, endemic species often face a high risk of extinction because of an association among three traits that threaten species persistence: small geographic range size, low abundance and ecological specialisation. To test whether these traits are associated in coral reef fishes, this study compared abundance and specialisation in endemic and widespread angelfishes at the remote Christmas and Cocos Islands in the Indian Ocean. The interrelationships among traits conferring high extinction risk in terrestrial communities did not apply to these fishes. Endemic angelfishes were 50-80 times more abundant than widespread species at these islands. Furthermore, there was no relationship between abundance and ecological specialisation. Endemic species were not more specialised than widespread congeners and endemics used similar resources to many widespread species. Three widespread species exhibited low abundance and some degree of specialisation, which may expose them to a greater risk of local extinction. For endemic species, high abundance and lack of specialisation on susceptible habitats may compensate for the global extinction risk posed by having extremely small geographic ranges. However, recent extinctions of small range reef fishes confirm that endemics are not immune to the increasing severity of large-scale disturbances that can affect these species throughout their geographic range.

5.2 INTRODUCTION

The causes of rarity have long intrigued biologists (Darwin, 1859) and are critical to conservation biology because rare species may experience a high intrinsic risk of extinction (Soulé, 1986; Simberloff, 1988). Rarity can be defined in terms of whether a species has a large or small geographic range, high or low abundance, or specialist or generalist pattern of resource use (Rabinowitz, 1981). Species with small geographic ranges (endemics), low abundance or specialist patterns of resource use appear susceptible to extinction from multiple causes, including local disturbances, the demographic attributes of small populations and habitat loss (Lawton, 1993; McKinney, 1997; Gaston, 1998; Munday, 2004). Indeed, the highest rates of extinction have been recorded for endemic species on isolated islands (Frankham, 1998; Whittaker, 1998). Consequently, the study of island endemics is imperative to understanding the processes that combine to increase extinction risk and directly affect global biodiversity.

Rare species face a greater intrinsic risk of extinction if two or more of the characteristics that threaten population persistence are associated. One of the most widely reported macroecological patterns is the positive relationship between geographic range size and abundance (Gaston *et al*., 1997). Widely distributed species tend to be abundant while small-range relatives are often scarce. This pattern is considered one of the few fundamental laws in ecology (Lawton, 1999) because it has been observed across a broad array of taxa and systems, and spans a variety of spatial and temporal scales (Lawton, 1993; Brown, 1995; Gaston, 1994, 1996; Gaston *et al*., 1997; McKinney, 1997). As a consequence of this relationship, endemic species are expected to face a dual threat of extinction associated with either small range size or low abundance – often referred to as a double jeopardy (Gaston, 1998).

Range size also tends to be positively correlated with niche breadth (Brown, 1995; Lawton and May, 1995; McKinney, 1997). This relationship is thought to exist because a species' geographic distribution will be constrained by the distribution of its resources, and thus on average, specialist species tend to have smaller geographic ranges than generalists (Brown, 1984; Gaston *et al.*, 1997). Generalist species can potentially persist in more locations than specialist species because they can utilise a greater variety of resources (Gaston, 1994; Lawton, 1995; Kunin and Gaston, 1997).

Not only do specialist species tend have smaller range sizes, but they also appear to have lower abundance than generalists (Brown, 1984; Hanski *et al.*, 1993). Specialists are expected to be more vulnerable to disturbances because changes in just a few resources can have profound effects on their abundance. Indeed specialisation is considered a fundamental trait that increases extinction risk (Foufopoulos and Ives, 1999; Fisher *et al.*, 2003; Julliard *et al.*, 2004) and has been linked to recent and past extinctions (McKinney, 1997). The potential for a positive association among specialisation, small range size, and low abundance means that endemic species could face a triple jeopardy risk of extinction (Munday, 2004).

The majority of published studies on extinction risk and macroecology have focussed on terrestrial communities. Determining the generality of terrestrial based patterns and theories in the marine environment is crucial for identifying marine species that are most at risk of extinction (Jones *et al*., 2002; Dulvy *et al*., 2003, 2004); an urgent priority given the recent global changes that are occurring in this system (Hughes *et al*., 2003; Orth *et al*., 2006; Bruno and Selig, 2007). For example, an estimated 20% of the world's coral reefs have recently been seriously degraded and a further 50% are in decline (Wilkinson, 2004). The loss of coral cover has caused significant changes in the abundance and community structure of reef associated species, including coral reef fishes (Jones *et al.*, 2004; Graham *et al*., 2006; Pratchett *et al*., 2008). The greatest impact has been on those species with specialist habitat (Munday, 2004; Wilson *et al*., 2006, 2008) or dietary requirements (Pratchett *et al*., 2006; Graham, 2007), particularly those dependent on live branching corals. If these specialists also have restricted ranges and low abundance then this will greatly increase their intrinsic risk of extinction (Munday, 2004).

This study tests extinction risk theory in the marine environment by examining whether endemic reef fishes from isolated islands also have lower abundances and are more specialised than their widespread congeners. This study examines reef fishes at the remote Christmas and Cocos Islands in the northeastern Indian Ocean. The assemblage of angelfishes at these islands contains both endemic and geographically widespread species, which offers an ideal opportunity to compare patterns of abundance and specialisation among geographically restricted and widespread species. The specific aims of this study were to test whether:

1. Island endemics are less abundant than widespread relatives
2. Island endemics use a narrower range of resources than widespread relatives
3. Specialists are less abundant than generalists
4. Island endemics exploit different niches to widespread species
5. Island endemics face a triple jeopardy risk of extinction

5.3 METHODS

Study location and study species

This study focussed on pygmy angelfishes (genus *Centropyge*), which are found on coral reefs worldwide, typically inhabiting depths between 0-80 m (Allen *et al.*, 1998). There are 31 species of pygmy angelfishes, with a centre of diversity in the Indonesia-Philippines region (Allen *et al.*, 1998). The study locations, Christmas Island (10°30' S, 105°40' E) and the Cocos (Keeling) Islands (12°12' S, 96°54' E) are situated approximately 350 and 1000 km southwest of Indonesia. Nine species of pygmy angelfishes have been recorded at Christmas Island and seven at the Cocos Islands (Allen and Smith-Vaniz, 1994; Allen *et al.*, 2007; Hobbs *et al.*, 2007, 2010).

Geographic range

To examine the relationships among geographic range size, abundance, and specialisation, the extent of occurrence (*sensu* Gaston, 1994) was calculated as a proxy for range size using published distributions for all but one of the pygmy angelfish species at Christmas and Cocos Islands (Allen *et al.*, 1998). The estimated range sizes of study species were: *Centropyge bicolor* (32 000 km^2), *C. bispinosa* (48 000 km^2), *C. eibli* (27 000 km^2), *C. flavicauda* (43 000 km^2), *C. flavissima* (1000 km^2), *C. joculator* (1000 km^2), *C. tibicen* (24 000 km^2), and *C. vrolokii* (32 000 km^2). *C. colini* is only found deeper than 60 m at Christmas and Cocos Islands and was not included in this study because it is beyond the limits of safe SCUBA diving. *C. flavissima* (Indian Ocean population) and *C. joculator* are endemic to Christmas and Cocos Islands, whereas the other 6 study species are more widely distributed throughout the Indian and/or Pacific Oceans (Allen *et al*., 1998). The Indian Ocean population of *C. flavissima* is separated by more than 3000 km from the Pacific Ocean populations, and this distance combined with different facial markings and colouration suggests it is a separate species (Allen *et al*., 1998). Three of the widespread study species (*C. bicolor, C. tibicen* and *C. vrolokii*) are distributed throughout the west Pacific and the Indonesian-Philippines region with Christmas and Cocos Islands representing the western edge of their range. Two widespread species (*C. bispinosa* and *C. flavicauda*) are distributed throughout the Indian and Pacific Oceans and Christmas and Cocos Islands occur close to the centre of their range. The study islands also occur near the centre of the geographic range of *C. eibli*, which is distributed from Sri Lanka to the Western Australian coastline

Abundance

To determine if the abundance of endemic angelfishes is lower than widespread congeners, or if abundance is negatively correlated to specialisation, densities of each angelfish were estimated by underwater visual censuses on the outer reef slope at 12 sites at the Cocos Islands and 14 sites at Christmas Island in November and December 2002. At each site, densities of angelfish were attained using four replicate 50 x 6 m strip transects at 20 m depth. This depth was chosen because this is close to the mean depth range used by all study species (see results). Surveys were also conducted at 5 m depth, but only one species was observed (*C. flavissima*), and therefore these data were not analysed. Preliminary observations at 40 m depth only found 2 species, and only one species was common (*C. joculator*). The density of *C. flavissima* at 5 m and *C. joculator* at 40 m was similar to their density at 20 m. Due to unequal variances, a Mann-Whitney *U* test was used to compare the mean abundance of endemic and widespread pygmy angelfishes.

Resource use

Patterns of resource use were determined for endemic and widespread angelfishes at Christmas Island in May and June 2005. Three aspects of resource specialisation considered important to reef fishes were examined: depth range, microhabitat use and diet. Observations and collections were undertaken whilst SCUBA diving at survey sites on the outer reef slope on the eastern, northern and western sides of the island.

Depth range

To determine whether endemics use a narrower depth range than widespread congeners required examination of the depths inhabited by the study species at Christmas Island. The depth range of each study species was estimated at Christmas Island by recording the depth at which individuals were encountered whilst swimming up the reef slope from 40 to 0 m at north coast sites. Preliminary observations revealed that most individuals of the study species occur above 40 m, and the limitations of SCUBA diving also prevented detailed surveys below 40 m. Whilst swimming up the reef, care was taken to make sure equal time was spent surveying across all depths. Surveys were repeated at several sites until a minimum cumulative total of 20 individuals was achieved for each species. A total of 20 individuals were chosen because of the time required to locate 20 individuals of the rarer species. Observations on 84 individuals of a common species (*C. joculator*) indicated that estimates based on 20 individuals were a reliable representation of depth range. The number of individuals encountered per species varied from 20 to 84, and to allow for effective statistical comparison of depth ranges, 20 individuals were randomly subsampled from the more common species. Regression analysis was used to test for a relationship between geographic range size and depth range. For depth range, the mean deviation was used as a measure of niche breadth, and this was calculated by taking the average of the absolute deviations from the mean depth inhabited by a species (based on 20 individuals).

Microhabitat use

To determine whether endemics angelfishes were habitat specialists, underwater observations were conducted to compare the variety of microhabitats used by endemics and widespread congeners. To quantify microhabitat use, an individual or social group was identified and its home range determined by observing the behaviour and movements of the individual(s) for approximately 5 minutes. Once the home range was determined a 3 m line intercept transect was placed on the substrate through the centre of the territory and the amount of each microhabitat within the territory was recorded. Ten types of substrate microhabitat were identified (Table 5.1). Due to differences in abundance and spatial distribution the number of individuals or social groups surveyed varied among species: *C. joculator* (n=24), *C. flavissima* (n=19), *C. bicolor* (n=6), *C. eibli* (n=13), *C. bispinosa* (n=14), *C. tibicen* (n=5), *C. flavicauda* (n=14), and *C. vrolokii* (n=7). To determine if there was a relationship between geographic range size and the diversity of microhabitats geographic range size of each species was correlated with the diversity of habitats in their home ranges. The Shannon-Weiner index, $H' = -\sum p_j \log p_j$ (where p is the proportion of each habitat used) was to estimate habitat diversity within home ranges because it accounts for both the number and evenness of different habitats used.

Table 5.1 Ten substrate microhabitats used by angelfishes at Christmas Island. Descriptions are based on Veron, 1986, Eagle *et al*., 2001.

Microhabitat	**Characteristics**
Calcareous algae	Encrusts the substrate and is often pink in colour
Turfing algae	Epilithic algae growing on the surface of the substrate
Branching corals	Arborescent, corymbose, columnar and digitate scleractinian corals
Massive corals	Mound shape, spherical and hemispherical scleractinian corals
Tabular corals	Plating or laminar scleractinian corals
Foliaceous corals	Thin leaf-like scleractinian corals that form whorls.
Encrusting corals	Scleractinian corals growing as a thin veneer over the substrate
Sand	Silicious or calcareous grains
Bare rubble	Parts of dead coral skeletons that are not covered in live algae of coral
Soft corals	Alcyonarian corals that lack a hard calcium carbonate skeleton

Diet

To determine the relationship between range size and dietary specialisation, the diet of endemic and widespread angelfishes was estimated by examination of gut contents. At Christmas Island, haphazardly selected individuals of the 8 study species were collected by spearfishing. Within 1-2 hrs of collection, the stomach of each fish was dissected out and placed in 10% buffered seawater-formalin solution. After fixation for 24 hours the stomach and contents were transferred to 80% ethanol for storage. Gut contents were later examined in the laboratory by cutting the stomach open and spreading the contents onto a gridded petri dish. Gut contents of each individual were examined under a stereo-dissecting microscope and quantified by recording the food type present at 10 randomly assigned point intercepts on the grid. The food types were allocated to one of 6 categories (Table 5.2). Gut contents were quantified for 19-21 individuals of each species. The Shannon-Weiner diversity index was used to estimate dietary specialisation of each species.

Table 5.2 Six diet categories used to classify food types consumed by angelfishes at Christmas Island. Descriptions based on Eagle and Jones (2004).

Diet	Characteristics
AOM	Amorphous organic matter that lacks form (detritus)
Chlorophyta	Filamentous or thallate green algae
Rhodophyata	Filamentous or thallate red algae
Sediment	Silicious or calcareous grains
Sponge	Honeycomb like structure with perforated walls, or loose spicules.
Miscellaneous	Rare items such as urchin spines, invertebrate exoskeletons, fish scales, cyanobacteria

Ecological differences between endemic and widespread species

Potentially, endemic and widespread species could exhibit similar levels of specialisation but may utilise a completely different suite of resources. To determine if endemics inhabit different depths than widespread species an ANOVA was used to compare the mean depth inhabited based on 20 individuals for each species (described above).

Canonical discriminant analysis (CDA) was used to determine if endemics utilise different microhabitats compared to widespread species. CDA focuses on the variation between known groups (in this case species) and can produce a two dimensional representation of multivariate data. The closer that species are grouped together in multivariate space (displayed on a biplot), the greater the similarity in the types and frequency of microhabitats used. To examine if species overlapped in the microhabitat they used, 95% confidence intervals were plotted as circles around the group centroids using the formula:

$$95\%\ \mathrm{CL} = \surd(\chi^2_2,\ 0.05/n)$$

where n represents the number of replicates (Seber, 1984). The structure coefficients were plotted as vectors to show the microhabitats that were important in distinguishing between species.

CDA was also used to compare the diets of endemic and widespread species. Vectors were plotted on the CDA biplot using the structure coefficients to illustrate the importance of particular food types in distinguishing between the diets of different species. The miscellaneous diet category was not included in the CDA analysis because it was present in less than 2% of the total number of individuals and was not informative in distinguishing among species.

Multiple threats of extinction

To determine the proportion of study species facing multiple threats of extinction required identification of species that exhibit different combinations of the three forms of rarity (small geographic range size, low abundance and specialisation). The following definitions were used to designate species as exhibiting one of the forms of rarity. The two endemic species were classified as having a small geographic range size (< 2000 km^2). Species were deemed to have low abundance if their mean density was below 3 individuals per 300 m^2. The thresholds for small geographic range size and low abundance were post hoc definitions that were determined by the distribution of these traits in the study species. Although the categories of small range size and low abundance were arbitrarily defined, they are representative of the way these terms are used to describe reef fish. To compare relative specialisation within the group of angelfishes we identified 1-2 species that were the most specialised for any of the three components of resource use. Using this method specialist species were defined as those species that had either a depth range mean deviation less than 3.5, or a microhabitat use diversity index less than 0.5 or a diet diversity index less than 0.35.

5.4 RESULTS

Range size–abundance

The mean abundance of endemic pygmy angelfishes was significantly higher than widespread species at both Christmas (Mann-Whitney U: $Z = 2.0$, $p < 0.05$) and Cocos Islands (Mann-Whitney U: $Z = 2.0$, $p < 0.05$). At Christmas Island the mean density of the two endemic pygmy angelfishes (8.61 per 300 m^2) was more than 50 times higher than the mean density of widespread relatives (0.16 per 300 m^2) (Figure 5.1a). Eight widespread angelfishes from other genera (*Apolomichthys*, *Genicanthus*, *Paracentropyge*, *Pomacanthus*, *Pygoplites*) also occur at Christmas Island, and these species had low abundances (< 1.02 individuals per 300 m^2), or were absent in the surveys. At the Cocos Islands, the mean density of the two endemic species (6.6 per 300 m^2) was more than 80 times greater than widespread congeners (0.01 per 300 m^2) and other angelfishes (0.08 per 300 m^2) (Figure 5.1b). Therefore, out of a total of 16 angelfish species recorded at Christmas and Cocos Islands, the endemic species were by far the most abundant.

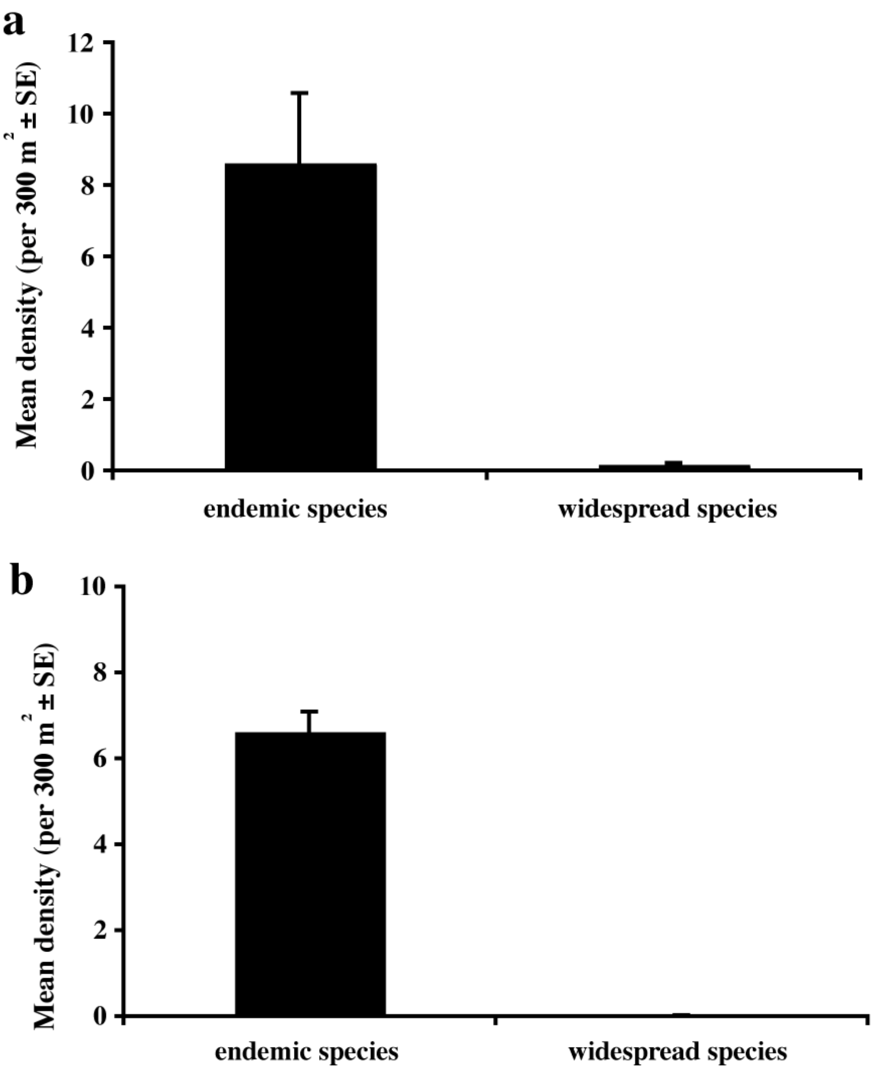

Figure 5.1 The mean density (per 300m^2 ± SE) of endemic and widespread pygmy angelfishes (genus: *Centropyge*) at a) Christmas Island and b) the Cocos Islands.

Range size–specialisation

There was no relationship between the breadth of the depth range inhabited by pygmy angelfish at Christmas Island and geographic range size ($F = 1.31$, $R^2 = 0.18$, $p = 0.30$, Figure 5.2a). The endemic *C. flavissima* had the broadest depth range (5–40 m), whilst the endemic *C. joculator* had the third broadest depth range (12–40 m).

No relationship was found between microhabitat specialisation and geographic range size ($F = 0.21$, $R^2 = 0.\ 034$, $p = 0.66$, Figure 5.2b). Endemic angelfishes used a similar diversity of microhabitats as most of the widespread species. Seven of the eight study species exhibited habitat use diversity indices (H’) between 0.76 and 0.89. The notable exception was *C. flavicauda*, which is the second most widely distributed study species yet utilised a considerably narrower range of microhabitats compared to the other species (H’ = 0.45).

No relationship was found between dietary specialisation and geographic range size ($F < 0.001$, $R^2 < 0.001$, $p = 0.997$, Figure 5.2c). The diversity of food types consumed by the endemics (H’= 0.38 and 0.45) was within the range exhibited by widespread congeners (H’= 0.28–0.51).

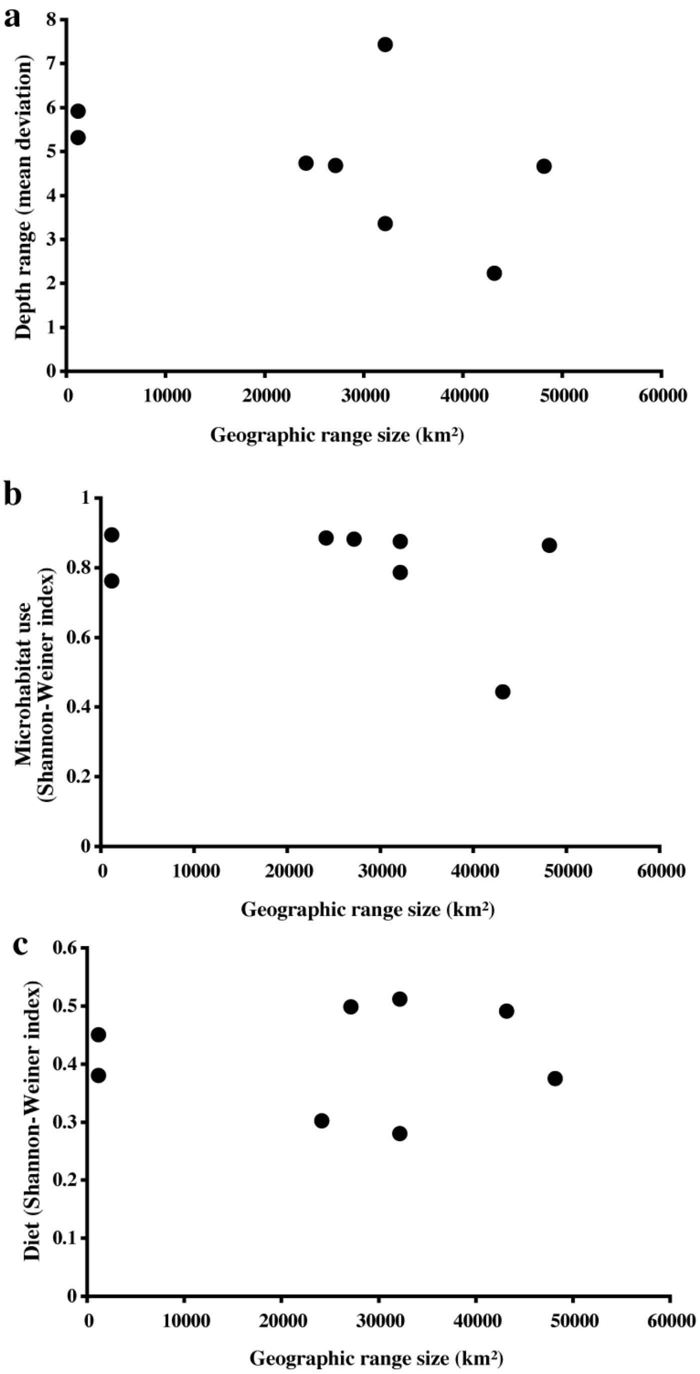

Figure 5.2 The relationship between geographic range size (km^2) and resource use for pygmy angelfishes at Christmas Island. Resource use includes: a) depth range (mean deviation), b) microhabitat use (Shannon-Weiner index), and c) diet (Shannon-Weiner index).

Specialisation–abundance

There was no relationship between abundance and any of the resource specialisation measures: depth range ($F = 0.75$, $R^2 = 0.\ 11$, $p = 0.42$, Figure 5.3a), habitat use ($F = 0.02$, $R^2 = 0.\ 004$, $p = 0.88$, Figure 5.3b) and diet ($F = 0.001$, $R^2 = 0.\ 0002$, $p = 0.97$, Figure 5.3c). Rerunning the analyses with the two highly abundant endemic species excluded did not substantially change any of the relationships ($p > 0.2$ for all comparisons).

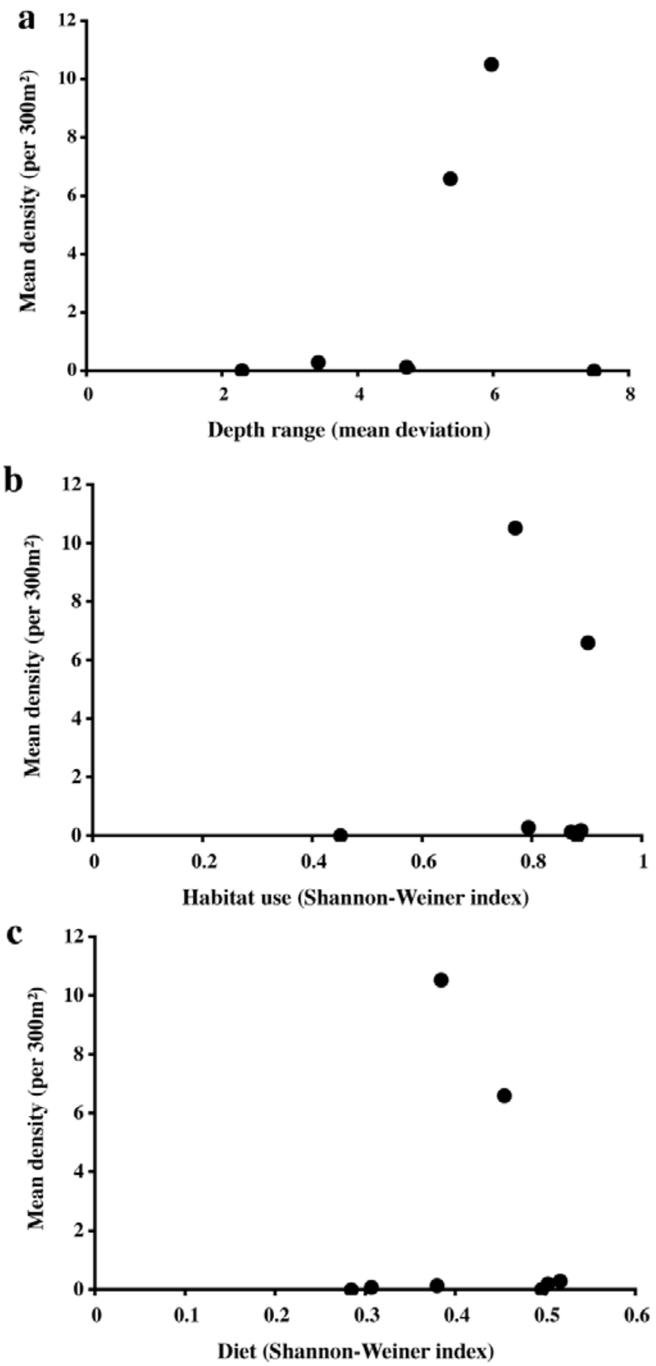

Figure 5.3 The relationship between mean density (per 300m^2 ± SE) and resource use for pygmy angelfishes at Christmas Island. Resource use includes: a) depth range (mean deviation), b) microhabitat use (Shannon-Weiner index), and c) diet (Shannon-Weiner index).

Ecological differences between endemics and widespread species

Not only was niche breadth similar between endemic and widespread pygmy angelfishes, but endemics also occupied the same niches as some of the widespread species. Endemic angelfishes did not occupy unique depth zones, but rather the position of their depth range overlapped considerably with most of the widespread congeners (Figure 5.4). The endemic *C. flavissima* was found between depths of 5 and 40 m (mean = 21.5 ± 1.6 SE), which was similar to four widespread species, but was significantly shallower than the mean depths inhabited by *C. tibicen* and *C. flavicauda*. The endemic *C. joculator* inhabited depths between 12 and 40 m (mean = 28.0 ± 1.8 SE) and this was similar to all species, except *C. vrolokii*, which occupied shallower water. Although there was variation among species in the mean depth inhabited (One-way ANOVA: $F = 10.1$, d.f. = 7, $p < 0.001$, Figure 5.4), Tukey's test revealed most of the significant differences ($p < 0.05$) were due to two widespread species, *C. vrolokii* and *C. tibicen*, that occupied depths that were shallower and deeper (respectively) than the rest of the species.

Patterns of microhabitat use were compared using a CDA that explained 85.4 % in the first two canonical axes (CV1 = 69.7% and CV2 = 15.7%). The types of microhabitats utilised by endemics were broadly similar to those used by most of the widespread species (Figure 5.5). The endemic *C. joculator* used the same microhabitats as the widespread species *C. bicolor*, and the endemic *C. flavissima* inhabited similar microhabitats as the widespread species *C. eibli* and *C. bispinosa*. Neither of the endemics was associated with live branching corals. Three of the widespread species, *C. flavicauda*, *C. tibicen* and *C. vrolokii*, utilised microhabitats that were distinct from the other species. *C. flavicauda* was found in microhabitats dominated by calcareous and turfing algae, *C. tibicen* inhabited areas rich in sand, while *C. vrolokii* occupied areas containing relatively high amounts of tabular and branching corals.

Similarities in the diet of the study species were examined using CDA and the resulting biplot explained 87.3% of the variance (CV1 = 66.2% and CV2 = 21.1%). Endemic species did not feed on unique resources, but rather their diet overlapped with some of the widespread species (Figure 5.6). The diet of the endemic *C. joculator* overlapped with that of the widespread *C. bispinosa* and was characterised by a relatively high proportion of amorphous organic matter and a low proportion of sponge. The endemic *C. flavissima* consumed food types similar to the widespread species *C. bicolor* and *C. eibli* and their diets typically contained a relatively high proportion of Chlorophyta and a low proportion of sediment. The widespread species *C. tibicen, C. flavicauda* and *C. vrolokii* each had diets that were distinct from the rest of the study species.

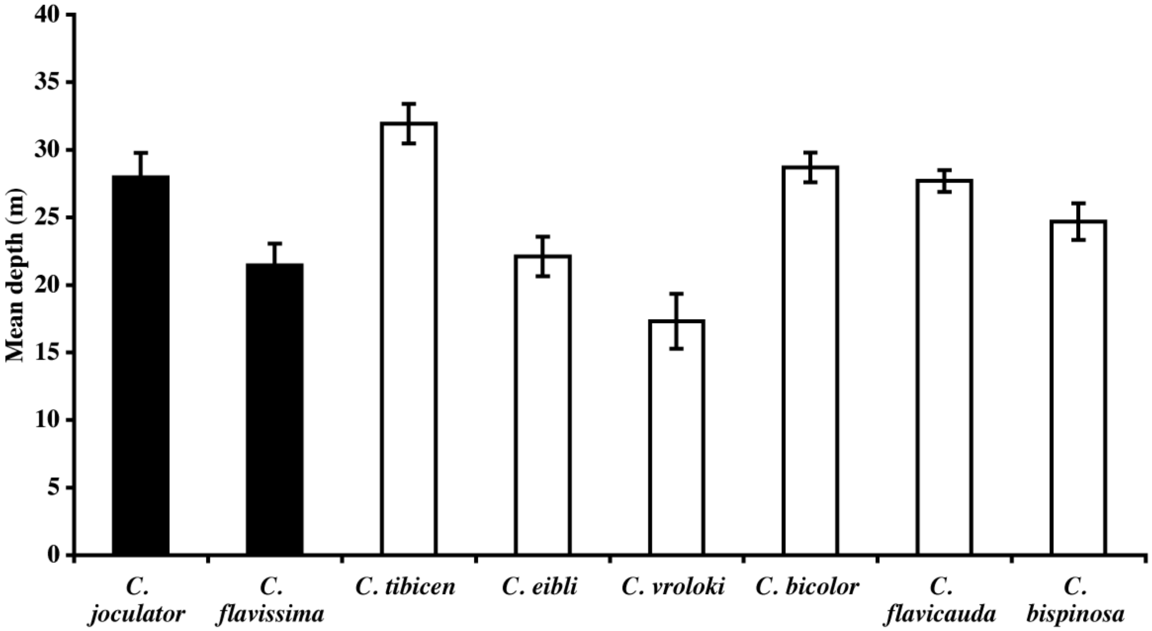

Figure 5.4 The mean depth (m ± SE) of water inhabited by endemic (black bars) and widespread (white bars) pygmy angelfishes at Christmas Island.

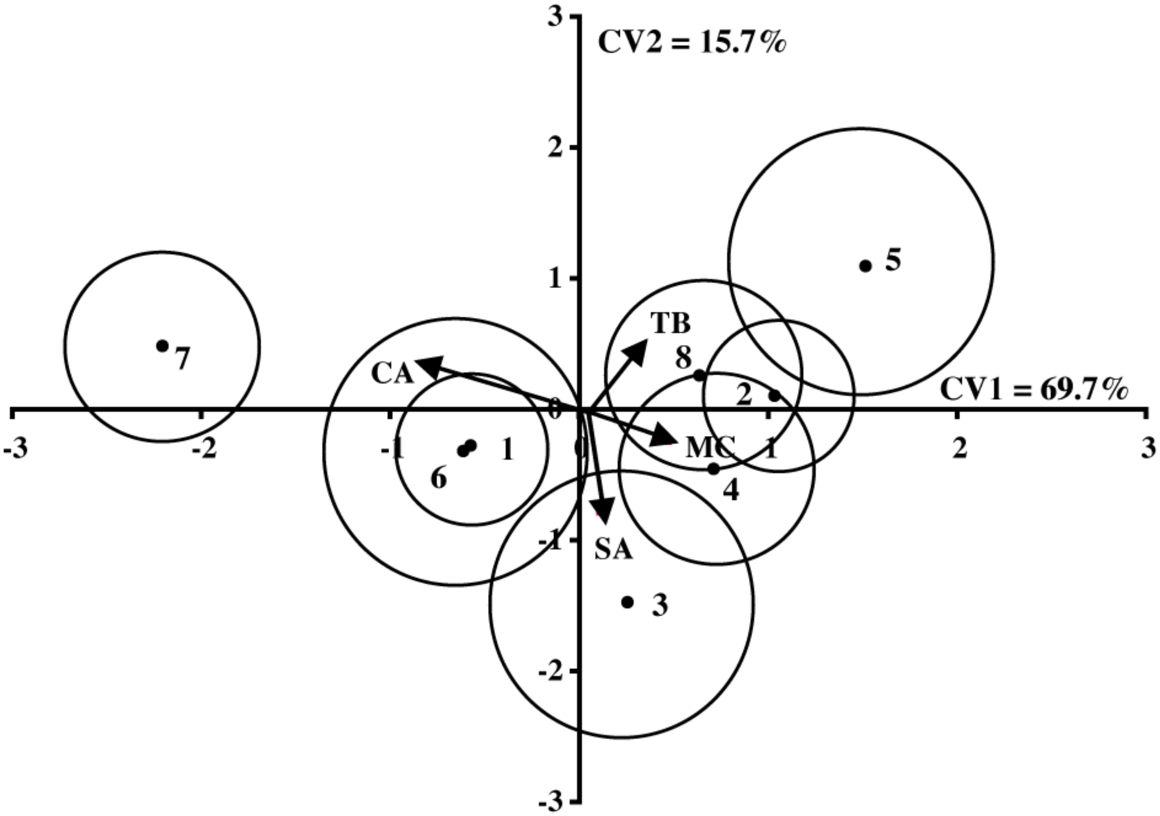

Figure 5.5 A canonical discriminant analysis (CDA) of microhabitat use of pygmy angelfishes at Christmas Island. The first two canonical variates explained 69.7 % (CV1) and 15.7 % (CV2) of the variation, respectively. Mean group centroids are plotted for each species with circles representing 95% confidence limits. Habitat types important to distinguishing between diets of the study species are shown as vectors (CA = calcareous algae, MC = massive corals, SA = sand, TB = tabular corals). Species labelled 1 and 2 are the endemic *Centropyge joculator* and *C. flavissima*, respectively. Widespread species are numbered in order from 3 to 8: *C. tibicen, C. eibli*, *C. vrolokii*, *C. bicolor*, *C. flavicauda*, and *C. bispinosa*.

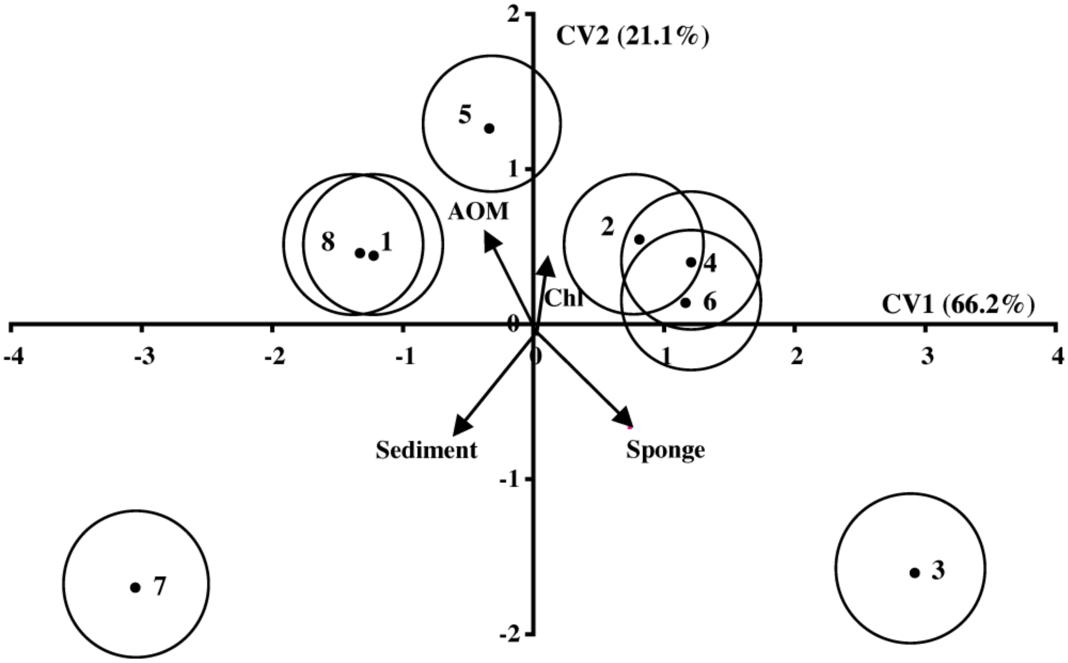

Figure 5.6 A canonical discriminant analysis (CDA) of the diets of pygmy angelfishes at Christmas Island. The first canonical variates explained 62.2 %(CV1) and 21.1 % (CV2) of the variation. Mean group centroids are plotted for each species with circles representing 95% confidence limits. Food types important to distinguishing between diets of the study species are shown as vectors (AOM = amorphous organic matter, Chl = chlorophyta). Species labelled 1 and 2 are the endemic *Centropyge joculator* and *C. flavissima*, respectively. Widespread species are numbered in order from 3 to 8: *C. tibicen*, *C. eibli*, *C. vrolokii*, *C. bicolor*, *C. flavicauda*, and *C. bispinosa*.

Multiple extinction threats

Examining the interrelationships among range size, abundance and specialisation revealed that none of the angelfish species at Christmas and Cocos Islands faced a triple jeopardy (i.e., no species had the combination of small range size, low abundance and was a resource specialist) (Figure 5.7). Three of the widespread species (*C. flavicauda*, *C. tibicen*, and *C. vrolokii*) had dual threats of extinction associated with low local abundance at Christmas and Cocos Islands and a relatively high degree of specialisation. Endemic species, however, did not have low abundance or specialised patterns of resource use, and therefore, their greatest risk comes from having a small range size. The remaining three widespread species had a single threat of extinction associated with low abundance at Christmas and Cocos Islands.

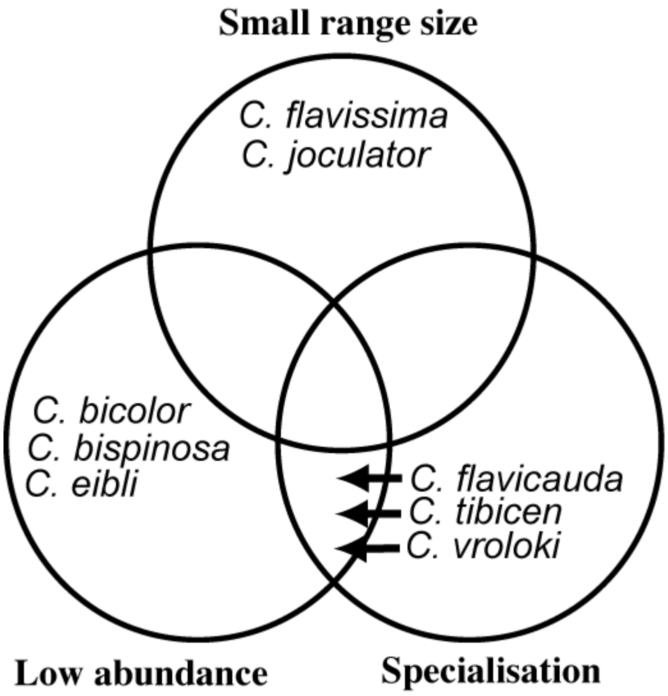

Figure 5.7 A Venn diagram illustrating the number of pygmy angelfishes that have multiple threats of extinction associated with small range size (< 2000 km^2), low abundance (< 3 individuals per 300 m^2) and specialisation (depth range mean deviation < 3.5, or microhabitat use index < 0.5, or diet index < 0.35).

5.5 DISCUSSION

This study of coral reef angelfishes at two isolated islands did not find support for positive associations among small geographic range, low abundance or ecological specialisation evident for many terrestrial organisms. In fact, some opposite patterns appeared to hold, with endemics being 50–80 times more abundant than widespread species, and being among the more generalist species in terms of depth range, diet and habitat use. These factors are expected to partially compensate for any global extinction risk posed by their small range and geographic isolation. In contrast, some widespread species exhibited a combination of specialisation and low abundance and this may expose them to a local extinction risk at these isolated islands, although they are unlikely to be at risk of global extinction due to their large geographic ranges.

The positive relationship between range size and abundance is regarded as “one of the most general and robust patterns in nature” (Gaston *et al.*, 1997), yet the inverse relationship was found in this study. Endemic reef fishes have also been found to have relatively high abundances in other locations (Fishelson, 1977; Hourigan and Reese, 1987; Randall, 1998; Allen *et al.*, 1998; Jones *et al.*, 2002; DeMartini, 2004; DeMartini and Freidlander, 2004). A large proportion of endemic reef fishes are found on remote islands (Jones *et al.*, 2002), and in the terrestrial environment the few cases where endemic species are abundant also occurs in isolated habitats or locations (Blackburn *et al.*, 1997; Päivinen *et al.*, 2005; Reif *et al.*, 2006). Isolation may allow endemics to become better adapted to local conditions, thereby enabling them to exploit unoccupied niches, or out-compete other species (Hourigan and Reese, 1987; Thiollay, 1997; Reif *et al.*, 2006). However, in this study the highly abundant endemic angelfishes used the same resources as widespread relatives, and often coexisted with congeners in overlapping territories with no signs of competitive interactions (cohabitation between congeneric angelfish has also been reported elsewhere: Eagle *et al.*, 2001). Potentially, endemic species may be more efficient at exploiting the same resources used by widespread congeners. Alternatively, other ecological or life history traits, not associated with resource use, may be responsible for high abundances. Given that highly variable recruitment is characteristic of most reef fishes (Doherty and Williams, 1988; Doherty, 1991), possessing an ability to maintain high abundances would be critical to increasing persistence time (McKinney, 1997). Endemic reef fishes without such adaptive traits will have low abundances and therefore are unlikely to be present in a community because they have already gone extinct ("extinction filtering" see Gaston, 1998; Johnson, 1998).

Range size is expected to be negatively associated with specialisation because the geographic distribution of a specialist is constrained by the distribution of a limited number of resources (Brown, 1984). While some studies of reef fishes have found support for such a relationship (Hawkins *et al.*, 2000), others studies have not (Jones *et al.*, 2002; this study). A lack of supporting evidence could occur because the appropriate resources have not been examined. However, this study found endemic fishes were not more specialised than widespread congeners in both habitat and dietary resources, including those resources that have been found to correlate with range size in other reef fish studies (Hawkins *et al.*, 2000). In addition, specialisation is predicted to covary across a number of resources (Brown, 1995, McKinney, 1997), and in this study endemic species were generalists in all measures of resource use (depth range, microhabitat use and diet).

Abundance is predicted to be positively correlated with niche breadth (Brown, 1984). Whilst several reef fish studies have found evidence of such a relationship (Meekan *et al*., 1995; Bean *et al*., 2002; Jones *et al*., 2002; Munday, 2004; Pratchett *et al*., 2008), no such support was found in this study. Abundance was not related to depth range, microhabitat use or diet. Support for this relationship is also generally lacking in the terrestrial environment and the reasons for the hypothesised relationship are not obvious (Gaston *et al*., 1997). If the abundance–specialisation relationship is dependent on a positive range-size abundance relationship and a positive range size–niche breadth relationship, then the predicted abundance–specialisation relationship would not be expected in this study because the other two relationships were not found.

When range size is associated with low abundances and specialisation, endemic species face an extreme risk of extinction (Angermeier, 1995; Munday, 2004). At least one example of such a triple jeopardy has been documented for reef fishes (Munday, 2004) and instances of double jeopardy have also been reported (Jones *et al*., 2002). However, it is fortunate that such relationships are not universal (Hourigan and Reese, 1987; Randall, 1998; Allen *et al*., 1998; DeMartini, 2004; Pratchett *et al*., 2008). In this study, extinction risk in endemic species due to small range size is buffered by a high abundance and a generalist pattern of resource use. Because of their high abundance and lack of specialisation, the greatest threats to endemic angelfishes are likely to be disturbances that impact on a scale that encompasses all of their geographic range.

The greatest broadscale threats to coral reef fishes are overfishing and a loss of live coral habitat due to increasing sea temperatures (Jennings *et al.*, 1999; Dulvy *et al.*, 2003; Pratchett *et al.*, 2008; Munday *et al.*, 2008). Although the endemic *C. joculator* is collected for the aquarium fish trade, overfishing is unlikely because there is only one collector who visits a small number of sites at the Cocos Islands and the annual catch represents less than 1% of the population (J. Cluniess-Ross pers. comm.). Widespread loss of live coral has caused local extinctions of small reef fishes on Indian Ocean reefs (Graham *et al.*, 2006), and further decreases in live coral habitat are predicted, particularly for the region including Christmas and Cocos Islands (Sheppard, 2003). While pygmy angelfishes do not feed on live coral, they do rely on coral reef habitat for shelter sites (Allen *et al.*, 1998), so much so, that they do not persist on reefs when habitat complexity collapses (Sano *et al.*, 1987). Therefore, the immediate death of corals is likely to have little impact on pygmy angelfishes, however the long-term impact (reduced habitat complexity) is likely to pose a significant threat to these small bodied reef fishes (Sano *et al.*, 1987; Wilson *et al.*, 2006).

Due to the enormous diversity of marine fishes currently threatened by a multitude of impacts, there is an urgent need to identify the type of species most at risk, and therefore of greatest priority to conservation efforts (Dulvy *et al.*, 2003). Although there has been considerable research on extinction risk in terrestrial species and large marine species (e.g. cetaceans), differences in life histories and environmental conditions make it difficult to predict extinction risk in marine fishes based on these groups. For example, marine fishes were thought to be resistant to extinction due to their large geographic ranges and high fecundities, however, it appears that their risk of extinction may be just as high as that facing terrestrial species (Dulvy *et al.*, 2003). In the terrestrial environment, small-bodied species are often short-lived and prone to extinction, while large, long-lived species are least likely to go extinct (Diamond, 1984). In marine fishes, large bodied species have the greatest vulnerability to fishing (Dulvy and Reynolds, 2002; Reynolds *et al.*, 2005), while small-bodied fishes appear most vulnerable to the loss of habitat complexity and shelter holes (Wilson *et al.*, 2006). Given that endemic reef fishes tend to have smaller body sizes (Hawkins *et al.*, 2000), we may expect endemic species to be most vulnerable to impacts that reduce habitat complexity. Determining which traits predispose marine fishes to a high risk of extinction will depend on the type of impact being considered.

Overall, this study has found that terrestrial macroecological patterns associated with extinction risk do not necessarily apply to reef fishes. Endemic angelfishes at the remote Christmas and Cocos Islands were not specialists and did not have low abundance and therefore do not face an extreme risk of extinction. The reason why endemics can reach such extraordinary abundance on isolated islands requires further investigation. Exploration of macroecological patterns in other marine taxa will be necessary to identify whether ecological factors combine to increase extinction risk. While the risk of extinction for the endemic species in this study appears to be relatively low, conservation of endemic species should remain a priority given that that the greatest extinction rates in the terrestrial environment have been reported for endemics on offshore islands (Frankham, 1998; Whittaker, 1998) and the only known extinctions of coral reef fishes have been endemics on isolated islands (Dulvy *et al*., 2003). Although high abundance and generalist patterns of resource use may compensate for the risks of being restricted to a small area, it may not be sufficient to buffer endemics from the impacts of broadscale disturbance events that have been predicted to increase in ocean environments.

CHAPTER 6: **High genetic diversity in isolated populations of endemic and widespread coral reef angelfishes (genus: *Centropyge*)**

6.1 ABSTRACT

In the terrestrial environment, endemic species and isolated populations of widespread species often have low genetic diversity, due to small population size and reduced gene flow. Since low genetic diversity increases the risk of extinction, it is important to test these predictions for other environments. This study tested the prediction that populations of coral reef angelfishes (genus: *Centropyge*) at Christmas and Cocos (Keeling) Islands in the northeast Indian Ocean would have low genetic diversity. Analyses of the 436 base-pair control region of the mtDNA revealed that the endemic *C. joculator* exhibited high haplotype ($h > 0.98$ at both locations) and nucleotide diversity (Christmas $\pi\% = 3.63$, Cocos $\pi\% = 9.99$). Similarly, the isolated populations of widespread angelfishes (*C. bispinosa* and *C. flavicauda*) at Christmas Island also had high haplotype ($h > 0.98$) and nucleotide diversity ($\pi\% = 2.81$ and $\pi\% = 5.78\%$, respectively). The genetic diversity of all three species was higher than expected with haplotype and nucleotide diversities among the highest reported for marine fishes. Likely causes for the high genetic diversity in the endemic *C. joculator* include extremely high abundance, refuge and or relict populations, multiple clades and rapid mutation rate of the mtDNA control region. For the widespread *C. bispinosa* and *C. flavicauda*, possible causes for high genetic diversity are a rapid mutation rate and sufficient gene flow from distant populations. High genetic diversity should reduce extinction risk in these species as it could provide the

evolutionary potential to adapt to the rapidly changing environmental conditions that have been forecast for coral reefs. However, given that isolated islands may represent hotspots for genetic diversity in reef fishes, their conservation should be a priority.

6.2 INTRODUCTION

The highest rates of extinction have been recorded for endemic species and populations of widespread species inhabiting islands (Frankham, 1997, 1998; Whittaker, 1998). The high risk of extinction in this group has been attributed to a range of demographic, environmental and genetic factors (Pimm, 1991; Frankham, 1997, 1998). The genetic characteristics that increase extinction risk in this group are low genetic diversity and inbreeding depression (Frankham, 1997, 1998). Low genetic diversity increases extinction risk because it reduces the potential for species to adapt to rapid environmental change. In endemics, and isolated populations of widespread species, inbreeding depression is thought to occur because of the low number of individuals forming the founder population and the small size of the extant population (Frankham *et al.*, 2002). The importance of maintaining genetic diversity to reduce extinction risk is recognised by the IUCN and is considered to be a conservation priority (McNeely *et al.*, 1990; Frankham *et al.*, 2002).

Genetic diversity can be influenced by a range of factors including population size, natural selection, mutation rates, gene flow between populations, introgression from hybridisation and historical effects on these factors (e.g. population bottlenecks) (Frankham *et al.*, 2002). In the terrestrial environment, island endemic species usually have small populations (Gaston, 1994; Gaston *et al.*, 1997), and consequently, genetic diversity is predicted to be low as genetic variation is increasingly lost through genetic drift (Frankham, 1996). Isolated island populations of widespread species are also expected to have low genetic diversity because of limited gene flow with other populations and lower localised effective population sizes (Diamond, 1984, Frankham *et al.*, 2002). Therefore, low genetic diversity is expected to be a feature of terrestrial communities on remote islands because they contain a high proportion of endemic species and isolated populations of widespread species (Frankham, 1997, 1998; Whittaker, 1998). However, while genetic diversity has been determined for many terrestrial species (Frankham, 1997), little is known about the genetic structure of endemic or isolated populations of marine species.

Coral reef fishes are the most diverse vertebrate communities in the world and are found throughout the tropics, including numerous remote islands. These isolated islands are hotspots of coral reef fish endemicity (Randall, 1998; Robertson, 2001; Hughes *et al.*, 2002; Jones *et al.*, 2002) and also support isolated populations of species with broad geographic ranges. Determining whether these endemics and isolated populations conform to terrestrial patterns of low genetic diversity is crucial to assessing their risk of extinction. Of the known neo-extinctions of reef fishes, all have been from isolated islands or island groups (Roberts and Hawkins, 1999; Dulvy *et al.*, 2003). An appreciation of the genetic diversity of endemic reef fishes is also of importance for ascertaining extinction risk of this group to changes in their environment caused by local and global anthropogenic disturbances (Bellwood *et al.*, 2004a; Munday *et al.*, 2009).

Previous studies have revealed a range of genetic diversity values for populations of marine fishes, including those inhabiting coral reefs. Haplotype diversity (h) in populations of marine fishes has been found to vary vastly from 0 to 1, while nucleotide diversity (π%) is known to vary from 0.07 to 31.8 (Grant and Bowen, 1998; Craig *et al*., 2007; Klanten *et al*., 2007; Horne *et al*., 2008; Gaither *et al*., 2010). For marine fishes, haplotype diversity is generally considered to be low where $h < 0.5$ and nucleotide diversity is regarded as low where $\pi < 0.5\%$ (Grant and Bowen, 1998). Therefore, if reef fishes conformed to predictions based on terrestrial fauna, we would expect endemic species, and isolated populations of widespread fishes, to have low haplotype ($h < 0.5$) and nucleotide diversity ($\pi < 0.5\%$).

This study examines whether the genetic diversities of three congeneric species of coral reef fishes conform to patterns established for terrestrial species. Specifically, this study determines whether endemic, and isolated populations of widespread angelfishes (genus: *Centropyge*), at Christmas and Cocos Islands have low genetic diversity ($h < 0.5$ and $\pi < 0.5\%$). These islands are among the most-isolated in the tropical Indian Ocean (Briggs, 1974). *Centropyge joculator* is endemic to these two locations and is not found anywhere else in the world (Allen *et al*., 1998). *C. bispinosa* and *C. flavicauda* are among the most widely distributed angelfishes, ranging from east Africa to the central Pacific Ocean (Allen *et al*., 1998), with Christmas Island supporting geographically-isolated populations of these species. Christmas and Cocos Islands are separated by approximately 1000 km, therefore, we also predicted that the two populations of the endemic species (*C. joculator*) might be genetically subdivided between these locations due to low genetic exchange (Eble *et al*., 2009).

6.3 METHODS

Field collections

Genetic material for this study was obtained by collecting angelfishes from both Christmas (10’29S, 107’37E) and Cocos (Keeling) Islands (12’04’13S, 96’48’56E). Individuals of *C. joculator* were collected from both locations (Christmas n = 44 and Cocos n = 41). Samples of the widespread study species were only collected from Christmas Island (n = 24 for *C. bispinosa* and n = 28 for *C. flavicauda*), as they are absent from the Cocos Islands. All angelfishes were collected by spearfishing whilst SCUBA diving in May-August 2005. Shortly after capture, a small fin clip (~1 cm^2) was taken from each fish and preserved separately in 80% ethanol.

Laboratory procedures

The control region (D-loop) of the mitochondrial (mt) DNA was used to determine genetic diversity of endemic and isolated populations of widespread angelfishes. Samples were washed in TE buffer and DNA was obtained by first digesting with Proteinase K followed by standard salt (NaCl) extraction (Sambrook *et al.*, 1989). Amplification of a 436 base pair section of the mtDNA control region was performed using universal primers LI5995 (5’-AATTCTCACCCCTAGCTCCCAAAG-3’) and HI6498 (5’-CCTGAAGTAGGAACCAGATG-3’)(Lee *et al.*, 1995). Amplification involving polymerase chain reaction (PCR) was conducted using a 20 µl volume containing the following reagents: 2.5 mM Tris pH 8.7, 5 mM KCl, 5 mM $(NH_4)_2SO_4$, 200 µM each dNTP, 2 mM $MgCl_2$, 0.5 µM forward primer LI595, 0.5 µM reverse primer HI6498, 1 U *Taq* polymerase (Qiagen), and at least 10 ng of DNA template. The PCR was conducted as follows: a denaturing step of 94°C for 30 seconds, followed by an annealing temperature of 51°C for 30 seconds, then 72°C for 90 seconds and a final extension of 72°C for 10 minutes. This cycle was repeated 34 times. The success of PCR reactions was verified after running 2 µl of PCR product through a 2% agarose gel. The gel also revealed a single band of PCR product and a ladder verified that the amplified DNA fragment was the correct size. The remaining PCR product was cleaned using isopropanol, dried and sent to Macrogen Inc. (Seoul, Korea) for standard Sanger sequencing. Both the forward and reverse sequences were obtained using primers LI5995 and HI6498, respectively.

Data analyses

To determine genetic diversity, sequences were first visually aligned using Sequencher 4.5 (Gene Code Corporation, MI, USA), and then manually adjusted in BioEdit (Version 7.0.9: Hall, 2007) in preparation for importing into molecular statistical programs. Arlequin (version 2.0, Schneider *et al.*, 2000) was used to calculate haplotype diversity index (h), nucleotide diversity index (π%) and the number of nucleotide changes as input for constructing a minimum spanning tree of the haplotype network (Rohlf, 1973) for each of the three study species. Haplotype diversity index followed Nei (1987) where $h = n\,(1-\sum x_i^2)/(n-1)$, and n is the total number of individuals and x_i is the frequency of a given haplotype in the population. For the endemic *C. joculator*, haplotype and nucleotide diversity were calculated for each of the two populations (Christmas and Cocos), as well as for the total (i.e. both populations combined). Genetic population structure was examined in *C. joculator* using analysis of molecular variance (AMOVA) conducted in Arlequin. For the widespread species (*C. bispinosa* and *C. flavicauda*), haplotype and nucleotide diversity values were calculated for Christmas Island populations.

Phylogenetic analyses were also undertaken to determine how evolutionary history affects genetic diversity in *C. joculator*. Neighbour joining (NJ, Tamura-Nei model, 1000 bootstrap replicates) and Maximum Parsimony (MP) approaches were used to construct a phylogram in MEGA (Molecular Evolutionary Genetics Analysis, Version 4.0, Tamura *et al*., 2007). Maximum Likelihood (ML) analyses were also performed in GARLI (Zwickl, 2006). Ten independent ML analyses were run, each comprised of 10,000 generations, with the best tree determined by the lowest log-likelihood score. Information from the best tree was imported into PAUP (version 4.0, Swofford 2003) to produce a 50% consensus tree with NJ and MP support values added to the tree nodes. The tree was rooted using *C. bispinosa* and *C. flavicauda* as the outgroups.

6.4 RESULTS

Endemic *C. joculator*

Examination of the 436 bp control region mtDNA sequenced from 85 *C. joculator* individuals (Christmas n = 44 and Cocos n = 41) revealed 161 polymorphic sites, 143 transitions, 42 transversions and 8 indels. The AT:CG ratio was biased 31:19. There were 54 unique haplotypes and 12 shared haplotypes (shared between 2 to 6 individuals)(Figure 6.1). Haplotype diversity was high ($h > 0.98$) in both the Christmas and Cocos populations (Table 6.1). Nucleotide diversity was also high for both populations (π% = 3.63 for Christmas, π% = 9.99 for Cocos) due to the high number of pairwise differences between individuals arising from the large number of base pair substitutions (Table 6.1).

Phylogenetic analyses revealed two distinct clades within the endemic species (Figure 6.1), with an ancestral clade comprised of 10 individuals found only at the Cocos Islands. The second clade (the more recently diverged clade) contained fish from both Christmas and Cocos, and included the majority of the sampled individuals (75 of 85). The 10 individuals in the ancestral clade all had unique haplotypes, and haplotype diversity was also high in the more recently derived clade ($h > 0.98$), although there were 12 shared haplotypes. Nucleotide diversity was high for both clades (π% = 3.34 – 3.66, Table 6.1).

There was a significant difference in the haplotype frequency of the Christmas and Cocos populations of *C. joculator* (F_{st} = 0.011, p = 0.0007). This difference may have been driven by the presence of the localised ancestral clade at the Cocos Islands. However, re-analysing the data without the ancestral clade (10 Cocos individuals removed) showed that the Christmas and Cocos populations remain genetically differentiated, indicating that there is little gene flow between the two populations ($F_{st} = 0.013$, $p = 0.001$).

Widespread species *C. bispinosa* and *C. flavicauda*

A 436 bp section of the mtDNA control was successfully sequenced from 24 *C. bispinosa* individuals collected from Christmas Island. The sequences revealed 81 polymorphic sites, with 78 transitions, 2 tranversions, 4 indels and an AT:CG ratio of 7:3. Haplotype diversity was very high ($h = 0.99$) as 23 of the 24 sequenced individuals had unique haplotypes (Figure 6.2, Table 6.1). Nucleotide diversity in this isolated population was also very high ($\pi\% = 5.78$) due to the large number of base pair differences between individuals (mean = 24, Table 6.1, Figure 6.2a).

The same section of mtDNA was sequenced in 28 *C. flavicauda* individuals from Christmas Island. These sequences comprised 74 polymorphic sites, with 65 transitions, 8 transversions, 7 indels, and an AT:CG ratio of 31:14. All 28 individuals had a unique haplotype ($h = 1$), and nucleotide diversity was also high ($\pi\% = 2.81$) (Table 6.1, Figure 6.2b).

Table 6.1 Genetic diversity measures for the endemic *Centropyge joculator* from Christmas and Cocos Islands, and for the widespread species *C. bispinosa* and *C. flavicauda* from Christmas Island. *n* = number of individuals, n_h = number of haplotypes, *h* = haplotype diversity index. Nucleotide diversity is given as a percentage (π%) and standard deviations (SD) are provided in parentheses.

Species	Location	*n*	n_h	*h* (±SD)	π%(±SD)	Mean pairwise differences (±SD)
C. flavicauda	Christmas Island	28	28	1 (0.010)	2.81 (0.39)	12.08 (5.63)
C. bispinosa	Christmas Island	24	23	0.989 (0.012)	5.78 (0.73)	24.04 (10.95)
C. joculator	Christmas Island	44	35	0.983 (0.011)	3.63 (1.83)	15.70 (7.14)
C. joculator	Cocos Islands	41	37	0.995 (0.007)	9.99 (4.91)	41.65 (18.45)
C. joculator	Christmas and Cocos Islands	85	66	0.991 (0.004)	6.92 (0.34)	30.16 (13.30)
C. joculator	Clade 1 (Cocos Islands)	10	10	1 (0.045)	3.34 (1.85)	14.49 (7.10)
C. joculator	Clade 2 (Christmas and Cocos Islands)	75	56	0.988 (0.005)	3.66 (1.83)	15.83 (7.14)

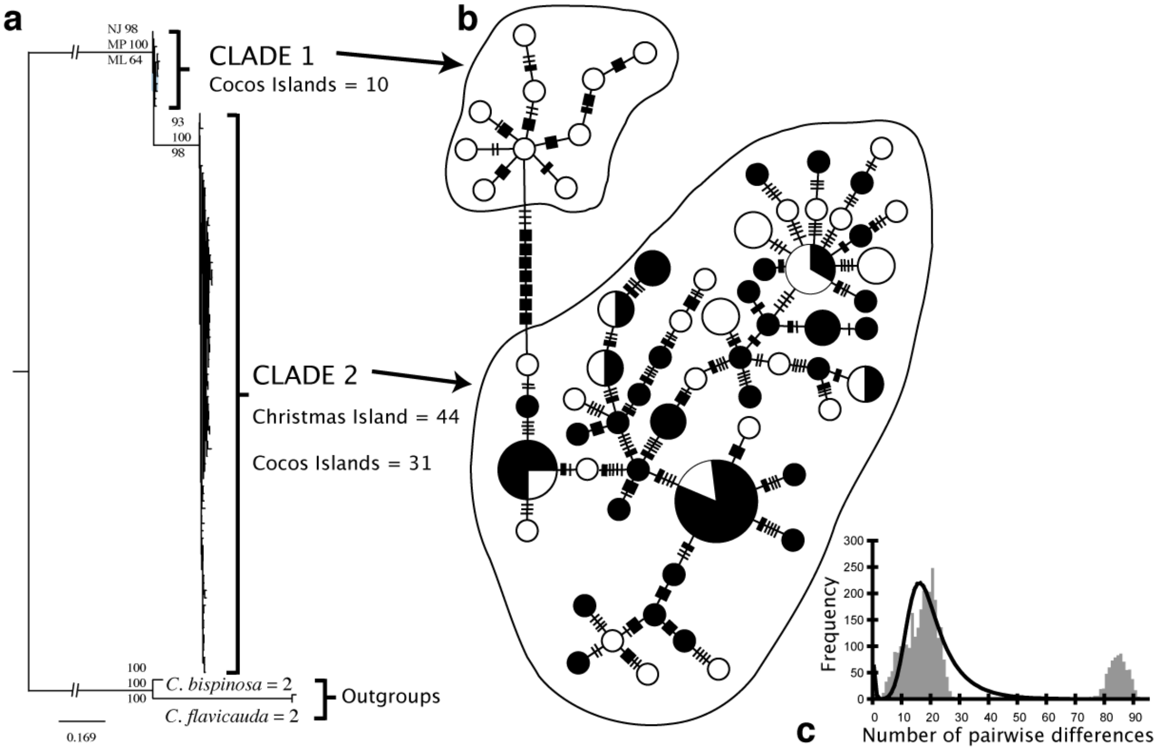

Figure 6.1 a) Outgroup rooted phylogram based on 436 bp control region mtDNA sequences from 85 *C. joculator* individuals (44 from Christmas Island and 41 from the Cocos Islands). The NJ, MP, ML support values are displayed at each node. b) Minimum spanning tree of *C. joculator* haplotypes. Black filled circles are Christmas Island individuals and unfilled circles are individuals from the Cocos Islands. The size of the circle indicates the relative frequency of each haplotype (smallest circle = 1 individual, largest circle = 6 individuals). Bars indicate the number of substitutions between haplotypes, with thin bars = 1 substitution, medium bars = 5 substitutions, and thick bars = 10 substitutions. c) Mismatch distribution of pairwise sequence differences for *C. joculator* and the expected distribution under an expansion model.

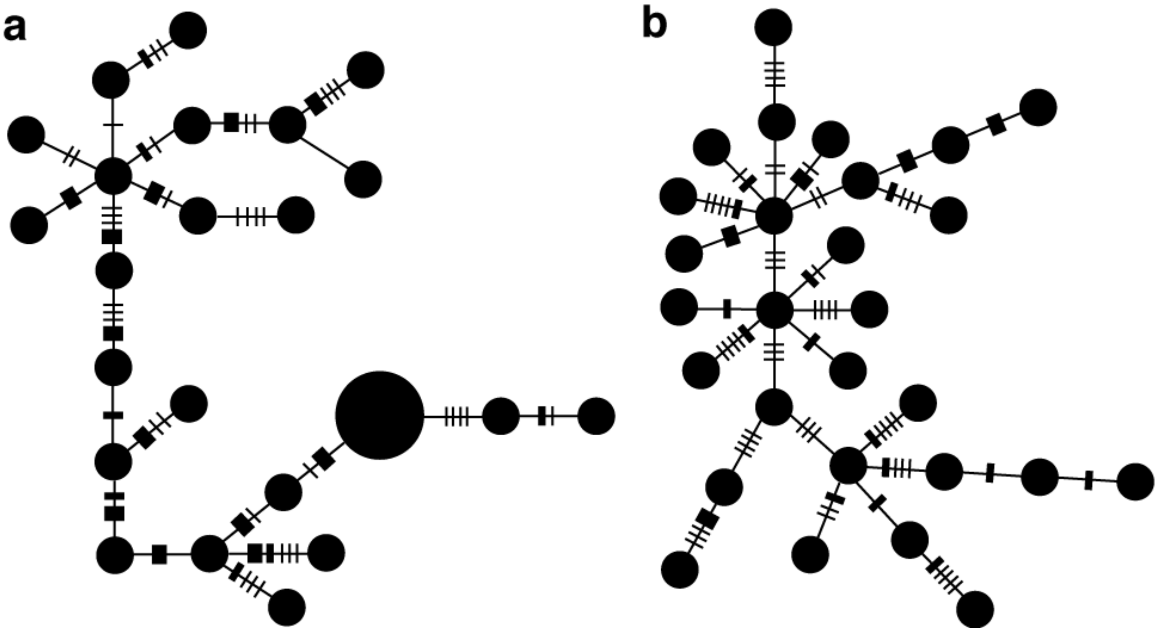

Figure 6.2 a) Minimum spanning tree for haplotypes of widespread species a) *Centropyge bispinosa* (n=24), and b) *C. flavicauda* (n=28) collected from Christmas Island. The size of the circle indicates the relative abundance of each haplotype (smallest circle = 1 individual, largest circle = 2 individuals). Bars indicate the number of substitutions between haplotypes, with thin bars = 1 substitution, medium bars = 5 substitutions, and thick bars = 10 substitutions.

6.5 DISCUSSION

In the terrestrial environment, genetic diversity of endemics and isolated populations of widespread species tends to be low and this may be an important factor contributing to their extinction risk (Frankham, 1996; 1997). Based on this, and the known range of genetic diversity for marine fishes (Grant and Bowen, 1998), this study predicted that island endemic reef fishes and isolated populations of species with broad geographic ranges would have low haplotype ($h < 0.5$) and nucleotide diversity ($\pi < 0.5\%$). However, in this study of coral reef angelfishes, the genetic diversity values of endemic and isolated populations ($h > 0.98$, $\pi > 2.8\%$) were among the highest recorded for marine fishes (Grant and Bowen, 1998; Bay *et al*., 2004; Bowen *et al*., 2006; Klanten *et al*., 2007; Horne *et al*., 2008; Hickey *et al*., 2009; Gaither *et al*. 2010; Winters *et al*., 2010). Hence, contrary to expectations based on terrestrial species, it appears that there are processes operating that are promoting, rather than reducing, genetic diversity in these endemic and isolated populations.

There are a number of factors that influence genetic diversity (Frankham *et al*., 2002). Endemic species usually have low abundance (Gaston, 1994; Gaston *et al*., 1997) and therefore are predicted to have low genetic diversity because of the increasingly deleterious effects of inbreeding and genetic drift on small populations (Hamrick and Godt, 1989; Frankham, 1996). However, if an endemic species was abundant then the effect of drift on genetic diversity may be minimal. Indeed, the abundance of the endemic study species *C. joculator* is more than 30 times greater than that of the 16 widespread species of angelfishes that are present at Christmas and Cocos Islands (Chapters 2 and 5). High genetic and nucleotide diversity is expected in fishes that maintain large populations through their evolutionary history (Grant and Bowen, 1998). If the current high abundance of *C. joculator* has been a feature of its evolutionary history then this will have contributed to its high haplotype and nucleotide diversity.

Irrespective of population size, genetic diversity can also be high if endemics occur in refugia (e.g. Pleistocene refugia: Lewis and Crawford, 1995) where environmental conditions have been relatively stable over evolutionary time scales allowing for the accumulation of genetic variation (see Aleksic and Geburek (2010) and references therein). Christmas and Cocos Islands are oceanic islands that have the Indonesian Archipelago as their nearest neighbour. Indonesia is an area where Pleistocene sea level fluctuations caused significant disruption to marine habitats and fauna (Voris, 2000). If Christmas and Cocos Islands were environmentally stable then they may have served as Pleistocene refugia. Also, *C. joculator* may have had high genetic diversity if it was once more widespread (as suggested by the occurrence of its closest relative *C. hotumatua* in peripheral islands of the south Pacific: Allen *et al.*, 1998) and as its range contracted this diversity may have been condensed and maintained in the relict populations at Christmas and Cocos Islands. These islands also support endemic relict populations of other reef fishes (e.g. *C. flavissima* and *Stegastes insularis*, Allen *et al.*, 1998; Froese and Pauly, 2010) whose disjunct geographic ranges are separated by the historically tumultuous

Indonesian Archipelago (Voris, 2000). Therefore, the high genetic diversity of *C. joculator* at Christmas and Cocos may also be because it is endemic to refugia and/or because it is a relict of a once widespread species.

Endemics can also have high genetic diversity if they represent a fusion of clades or have interbred with other species (i.e. introgression from hybridisation) (Torres-Diaz *et al.*, 2007; Fatemi and Gross, 2009; Zidana *et al.*, 2009). Christmas and Cocos Islands represents a suture zone where different clades or species come into secondary contact and interbreed (Hobbs and Salmond, 2008; Hobbs *et al.*, 2009). *C. joculator* has both high haplotype and nucleotide diversity, which is a signature of secondary contact between different clades or lineages (Grant and Bowen, 1998). Indeed, two distinct clades were detected in *C. joculator* and while the historical cause(s) for the origin of these clades is not known, it has clearly increased the genetic diversity of this species. Interestingly, genetic differences between the two clades are maintained despite their co-occurrence at the Cocos Islands. Individuals from these two clades could not be distinguished morphologically (colour and shape) or ecologically (water depth, reef zone and microhabitat use) (Hobbs personal observations) and therefore it is difficult to identify the pre or post zygotic barrier that is preventing introgression between these two clades. The occurrence of distinct clades despite cohabitation has also been reported for fishes on the Great Barrier Reef (Evans *et al.*, 2010) and throughout the Indo-Pacific (Horne *et al.*, 2008). However, because our study (and that by Evans *et al.*, 2010 and Horne *et al.*, 2008) used a mitochondrial marker, the distinct clades could represent maternal lineages, and further research using nuclear markers may reveal that introgression is occurring. While the two clades increase genetic diversity of the mtDNA in the endemic *C. joculator*, there was no evidence of this in the genetic structure of the widespread study species.

The limited gene flow between Christmas and Cocos populations of *C. joculator* supports the notion that endemic reef fishes have restricted dispersal (Eble *et al*., 2009). Limited gene flow may have also increased genetic diversity in *C. joculator*. If local adaptation occurs at each island location then this will lead to differences in the gene pools of the two populations. Rare dispersal events may allow for enough gene flow to increase genetic diversity in each population, but gene flow may be insufficient to homogenise the genetic composition of both populations.

Genetic diversity in isolated populations of widespread species is predicted to be low because population size is usually small and gene flow to other populations is low (Frankham, 1997). However, genetic diversity was high despite the very small population sizes observed for the two widespread study species at Christmas Island (0.05 - 0.18 individuals per 300 m^2: Chapter 5). It is possible these isolated populations still receive sufficient gene flow from other populations because these species are among the most widely distributed angelfishes in the world (Allen *et al*., 1998) and gene flow would be required to establish and maintain this broad distributional range. Isolated populations of other widespread *Centropyge* species have been found to have high haplotype diversity and high genetic connectivity (Bowen *et al*., 2006; Schultz *et al*., 2007). Furthermore, the recent arrival of *C. acanthops* at the Cocos Islands (Hobbs personal observation) demonstrates that larvae of widespread *Centropyge* species are capable of dispersing over 2500 km. Moderate to high genetic diversity (haplotype and/or nucleotide) has also been reported in several other widespread reef fishes present at Christmas and Cocos Islands (Klanten *et al*., 2007; Horne *et al*, 2008; Gaither *et al*., 2010; Winters *et al*., 2010). The gene flow received by populations of widespread species at Christmas and Cocos Islands (Klanten *et al*., 2007; Horne *et al*, 2008; Gaither *et al*., 2010) may be sufficient enough to counteract the loss of genetic diversity associated with genetic drift. For the widespread species examined in this study, additional sampling from other populations would be required to confirm that gene flow was the reason for their high genetic diversity at Christmas Island.

Genetic diversity can also be related to taxonomy with some groups having higher diversity due to faster mutation rates (Frankham *et al*., 2002). High haplotype diversity in an Atlantic *Centropyge* angelfish was partly attributed to the high mutation rate of the control region of mtDNA (Bowen *et al*., 2006). Similarly, a very high mutation rate has been detected in the mtDNA control region of butterflyfishes (McMillan and Palumbi, 1997), which are the sister group to angelfishes (Allen *et al*., 1998; Bellwood *et al*., 2004b). Therefore, the high genetic diversity observed in all three angelfishes in this study is probably influenced (at least partly) by the fast mutation rate of the mtDNA control region in this taxonomic group.

This study highlights that terrestrial patterns of genetic diversity do not always apply to marine fishes and it is possible that the findings of this study may be typical of many reef fishes. For example, endemic terrestrial species usually have low genetic diversity because they usually have low abundance (Frankham, 1996, 1997); however, endemic reef fishes frequently have high abundance (Fishelson, 1977; Hourigan and Reese 1987; Randall, 1998; Allen and Robertson, 1996; Allen *et al*., 1998; Jones *et al*., 2002; DeMartini 2004; DeMartini and Friedlander, 2004; Floeter *et al*., 2006; Travers *et al*., 2006; Hobbs *et al*., 2010) and therefore may not be expected to have low genetic diversity. In the terrestrial environment, isolated populations of widespread species usually have low genetic diversity because they have small populations and low gene flow. However, the dispersive larval phase of reef fishes increases the potential for genetic exchange over large areas and this gene flow may be sufficient to maintain high genetic diversity in isolated populations (Klanten *et al*., 2007; Horne *et al*., 2008; Gaither *et al*., 2010). Therefore, it not surprising that isolated populations of endemic and widespread reef fishes do not necessarily have low genetic diversity, given that their population sizes and life history traits do not conform to the explanations for low genetic diversity in terrestrial species.

The high genetic diversity of these endemic and isolated populations of widespread angelfishes suggests that they might be more resistant to extinction compared to terrestrial species on isolated islands. High genetic diversity will increase the evolutionary potential of these angelfishes to adapt to both local and global impacts that are escalating in coral reef environments (Bellwood *et al*., 2004a; Munday *et al*., 2009), thereby increasing their chance of being able to persist despite rapidly changing environmental conditions. On the other hand, populations on isolated islands should be a high conservation priority, not necessarily because of extinction risk, but because they are hotspots of genetic diversity and evolutionary novelty (Hobbs and van Herwerden, 2010).

CHAPTER 7: **General Discussion**

This study was the first to apply a multi-factorial and multi-scale approach to understanding patterns of local coral reef fish species richness, community composition and abundance on the remote Christmas and Cocos Islands in the eastern Indian Ocean. Their unique biogeographic location has been exploited as a model system to test a range of terrestrially-derived ecological generalisations in the marine environment. To test these generalisations I have conducted a range of field, laboratory and molecular studies and combined these results with data obtained from the literature to generate a comprehensive data set that was analysed using a variety of univariate, multivariate and modelling approaches. Using this comprehensive approach, this thesis has demonstrated that isolated reef fish communities at Christmas and Cocos Islands conform to some, but not all, of the tested ecological generalisations. The thesis eliminates some inappropriate generalisations and develops new hypotheses as to the key processes acting on and threatening biodiversity at these unique locations. Here, I draw together the main factors affecting local species richness, community composition, abundance, population maintenance, extinction risk and genetic diversity at these isolated islands.

Species richness

Island biogeography is one of the most widely accepted theories in ecology and explains how area and isolation determine species richness on islands (MacArthur and Wilson, 1963, 1967). According to this theory, the species richness of reef fishes at Christmas and

Cocos Islands would be predicted to be relatively low because these locations are among the most isolated and smallest island systems in the Indian Ocean. This was indeed the case, and the species-area relationship revealed that area was likely to be more important than isolation in determining species richness (**Chapter 2**); a pattern found for reef fishes in the Pacific Ocean (Bellwood and Hughes, 2001). The high dispersal ability of many reef fishes may mean that isolation is not as important as it is in terrestrial island communities. Area is theorised to be important in determining species richness because it affects speciation rates, colonisation rates, extinction rates and the diversity of habitats (Williams, 1964; MacArthur and Wilson, 1967; Gilpin and Diamond, 1976; Rosenzweig, 1995, 1999). Measuring the relative importance of these different factors was beyond the scope of this study, however it is clear that the absence of many taxa could be attributed (at least in part) to the low diversity of habitats associated with the small area of the study locations (e.g. at Christmas Island there are no estuaries, bays, mangrove coasts, seagrass meadows or lagoons) (Allen *et al*., 2007; Hobbs *et al*., 2010). Therefore, the overall low species richness of reef fishes at Christmas and Cocos Islands can be explained by Island Biogeography Theory.

At the local scale, patterns in species richness of butterflyfishes and angelfishes around Christmas and Cocos Islands were mostly influenced by depth and exposure, respectively (**Chapter 4**). Species richness of butterflyfishes was greatest on the protected north coast at both island locations, indicating that exposure to large oceanic swell limits species richness, possibly through direct effects on locomotion, or through in-direct effects on habitat complexity. Similarly, the importance of depth in determining patterns of species richness in angelfishes around Christmas and Cocos Islands appears to be related to habitat complexity and the availability of shelter sites. This indicates that while broadscale biogeographic effects determine the number of species present at Christmas and Cocos Islands, physical factors (related to exposure and depth) determine patterns of species richness around these islands.

Community composition

In the terrestrial environment, communities on isolated islands tend to contain a high proportion of endemics (Adler, 1992; Whittaker, 1998). In this study of reef fishes on isolated islands, Christmas Island had a high proportion of endemics but the Cocos Islands did not (**Chapter 2**). This pattern is also reflected in the terrestrial environment, with 253 endemic taxa recorded from Christmas Island and only 3 from the Cocos Islands (Woodroffe and Berry, 1994; James, 2007). Differences in endemism between the two locations are probably due to historical differences. Christmas Island is a high island that is approximately 37 million years old (Whittaker, 1998), whereas the Cocos Islands comprise a relatively recently formed coral atoll with the current ring of islands being less than 4000 years old (Woodroffe and McLean, 1994). The low level of endemism in reef fishes at the Cocos Islands is probably due its more recent origin (Briggs, 1974) and the effect of sea-level fluctuations on the lagoon, which currently represents about 90% of the islands’ shallow water habitats (Woodroffe and Berry, 1994). High variability in the amount and diversity of shallow water habitats, combined with its relatively recent origins, might have limited the evolution and persistence of endemic fishes at the Cocos Islands. While other studies of coral reef taxa support the terrestrial generalisation of high levels of endemicity on isolated islands (Roberts *et al.*, 2002), this study indicates the geological history of isolated islands can also influence patterns of endemicity.

In the terrestrial environment, the taxonomic composition of communities on isolated islands differs to mainland communities because they generally contain a greater representation of species with good dispersal abilities (Diamond *et al.*, 1975; Williamson, 1981; Whittaker, 1998; Burns, 2005; Donazar *et al.*, 2005). Because the taxonomic composition of isolated islands is not a proportion subset of mainland communities it is said to be “disharmonic” (Diamond *et al.*, 1975; Williamson, 1981; Whittaker, 1998). In this study, reef fish communities of Christmas and Cocos Islands were disharmonic compared to the Indonesian (“mainland”) region (**Chapter 2**). Bellwood and Hughes (2001) found a similar pattern for coral and reef fish communities at isolated locations in the Pacific and attributed this to taxonomic differences in tolerances to environmental conditions. However, this study has shown that the disharmony in reef fish communities at Christmas and Cocos Islands can be explained by an over-representation of good dispersers and an under-representation of poor dispersers (**Chapter 2**). Therefore, these findings conform to the terrestrial pattern that disharmonic communities form on isolated islands due to taxonomic differences in dispersal ability.

Given the importance of dispersal to colonising isolated locations, the biogeographic setting can have a significant affect on the taxonomic composition of island communities because the surrounding areas provide the source communities (Ricklefs and Schluter, 1993). For example, Wallace’s Line in southeast Asia represents the junction of the

Australian and Oriental biogeographic regions and the taxonomic composition of terrestrial communities on islands at this biogeographic border is influenced by the proximity of an island to the different biogeographic regions (Wallace, 1860; Carlquist 1965, 1974). Cocos and Christmas Island occur on the Indo-Pacific biogeographic border, which represents the junction of Indian and Pacific Ocean marine fauna (Hobbs and Salmond, 2008; Hobbs *et al.*, 2009). According to expectations from terrestrial studies, Christmas Island should have a greater proportion of Pacific Ocean species due to its closer proximity to this region, whereas the Cocos Islands should have a greater proportion of Indian Ocean species. However, this was not the case and both locations had a similar proportion of Indian and Pacific Ocean species (**Chapter 2**). This result contrasts with terrestrial studies and I propose that prevailing oceanographic currents play an important role in the dispersal of fish larvae that can override the affect that proximity to different biogeographic regions has on the taxonomic composition of reef fish communities.

Although the taxonomic composition of the reef fish communities at Christmas and Cocos Islands is not influenced by proximity to different biogeographic regions, the mixing of Indian and Pacific species has had an affect on the number of hybrids in the community. In the terrestrial environment, communities on biogeographic borders often contain a high proportion of hybridising species due to the interaction of species from different regional biotas, particularly if this represents secondary contact (termed "suture zone": Remington, 1968; Hewitt, 2000). In the tropical marine environment, hybridisation is considered to be rare and unimportant (Hubbs, 1955; Arnold, 1997) despite the existence of biogeographic borders. However, this study has shown that hybridisation is prevalent in reef fish communities at the Indo-Pacific biogeographic border and this is the first reported suture zone in the tropical marine environment (**Chapter 3**). Nineteen reef fishes were found to be hybridising at Christmas and/or Cocos Islands (**Chapter 3**) and more recent surveys have revealed a further 6 species are hybridising (Hobbs, unpublished data), bringing the total so far to 25 species across 7 families. This total represents not only the most hybridising reef fishes, but also the most hybridising marine species, reported for any location in the world (Gardner, 1987). Extensive hybridisation of reef fishes at Christmas and Cocos Islands appears to be due to the interaction between Indian and Pacific Ocean regional faunas that have come into secondary contact following allopatric speciation arising from Pleistocene sea level changes.

Although this study only examined reef fishes, hybridisation is likely in other taxonomic groups because the Indo-Pacific biogeographic border applies to most tropical marine species (Benzie, 1999; Hewitt, 2000), and other Indian and Pacific Ocean marine taxa co-occur at Christmas and Cocos Islands (Hobbs and Salmond, 2008). Hybridisation is not only restricted to the Indo-Pacific biogeographic border, but is also concentrated on biogeographic borders in the Pacific Ocean (Hobbs *et al.*, in press) and Atlantic Ocean (Avise, 2000). Therefore, hybridisation appears to be a common feature of marine communities on biogeographic borders, and the interaction of species in these communities can have important implications to the evolution and systematic classification of marine species. Statements that hybridisation is rare and unimportant in the marine environment appear to be premature (Arnold, 1997). The concentration of hybrid reef fishes at biogeographic borders (**Chapter 3**; Hobbs *et al.*, in press) conforms to the geographic patterns of, and the explanatory reason (secondary contact) for, hybridisation in the terrestrial environment.

While the biogeographic setting, in combination with dispersal abilities and oceanographic currents, can influence which species arrive at an island, successful colonisation may depend on other factors, such as suitable habitat. Taxonomic composition of terrestrial communities can be influenced by the variety of habitats present on an island (MacArthur and Wilson, 1967; reviewed by Whittaker and Fernandez-Palacios, 2007). Christmas and Cocos Islands are small islands (compared to other Indian Ocean island locations: Spalding *et al.*, 2001), and lack certain habitats (e.g. Christmas Island lacks estuaries, bays, mangrove coasts, seagrass meadows and lagoons). Therefore, species that rely on these habitats (either as juveniles or adults) are noticeably absent (Allen *et al.*, 2007; Hobbs *et al.*, 2010; **Chapter 2**). The absence of reef fish species from the Christmas and Cocos communities due to the lack of certain habitats is consistent with the predications of Island Biogeography Theory (MacArthur and Wilson, 1967).

The finding that the community composition of reef fishes at Christmas and Cocos is partly influenced by habitat availability was also evident in more detailed examination of the community structure of butterflyfishes (**Chapter 4**). For example, butterflyfishes that use lagoonal habitats as juveniles are absent or rare at Christmas Island, but are common at the Cocos Islands where there is a large lagoon. However, for angelfishes, depth was the most important of the six measured factors influencing patterns of community composition at the Islands (**Chapter 4**). Collectively, these results illustrate that the composition of reef fish communities at Christmas and Cocos Islands is a result of a combination of factors operating at biogeographic and local scales. While isolation may determine which species can disperse to the islands, habitat availability determines which species can colonise an island, and local factors associated with depth (e.g. habitat complexity, availability of shelter holes) can determine the distribution of species around the islands.

Abundance

Studies in the terrestrial environment have identified a variety of historical, physical, biological and ecological factors that influence a species' abundance across a range of spatial scales (Ricklefs and Schluter, 1993; Gaston, 1994; Begon *et al*., 2006). At broad spatial scales, a species' abundance is expected to decrease from the centre of its range to the edge (Brown, 1984; Gaston *et al*., 1997). However, this was not found to be the case for reef fishes examined in this study, including both Indian and Pacific Ocean species whose range edge occurs at Christmas and Cocos Islands (**Chapter 2**). Studies in other locations have also reported reef fishes at the edge of their range do not necessarily have low abundance (Jones *et al*., 2002; Tuya *et al*., 2008).

In addition to range edge effects, terrestrial studies have also identified a positive relationship between the size of a species' geographic range and its abundance (i.e.

endemics have low abundance). This pattern is so commonly observed across a broad suite of terrestrial communities that it is considered “one of the most general and robust patterns in nature” (Gaston *et al*., 1997). However, the opposite pattern was observed in this study with endemics damselfishes and angelfishes being much more abundant than widespread relatives (**Chapters 2 and 5**). These findings appear to represent a common phenomenon in reef fishes throughout the world. That is, endemic reef fishes are frequently reported to have high abundance, often being the most abundant within their taxonomic group or ecological guild (Fishelson, 1977; Hourigan and Reese, 1987; Allen and Robertson, 1996; Allen *et al*., 1998; Randall, 1998; Jones *et al*., 2002; DeMartini 2004; DeMartini and Friedlander, 2004; Choat *et al*., 2006; Floeter *et al*., 2006; Travers *et al*., 2006; Hobbs and Feary, 2007; Hobbs *et al*., 2008).

Based on terrestrial studies, species that exhibit ecological specialisation are expected to have low abundance because their abundance is constrained by the distribution and abundance of a limited number of resources (Brown, 1984; Hanski *et al*., 1993). However, no such pattern was observed in this study. A detailed examination of niche breadth in angelfishes at Christmas Island involving analyses of depth range, microhabitat use and diet failed to find any relationship between specialisation and abundance (**Chapter 5**). These findings are further supported by abundance patterns of butterflyfishes. For example, *Chaetodon trifascialis* is an extreme ecological specialist (Pratchett, 2005), yet it had the second highest abundance of any of the 32 butterflyfishes found at Christmas Island (**Chapter 4**).

Species on islands are also expected to attain higher local abundances due to reduced interspecific competition owing to the low species richness of island communities (density compensation: MacArthur *et al.*, 1972). However, in this study there was no evidence of density compensation in reef fishes on isolated islands (**Chapter 2**). That is, the butterflyfishes at Christmas and Cocos Islands did not have lower abundance than butterflyfishes in the adjacent species rich Indonesian ("mainland") community. There is also a lack of support for density compensation in butterflyfishes at other isolated locations (Findley and Findley, 2001).

In addition to ecological and broadscale geographic factors, abundance can also be influenced by local scale factors, such as the physical and biotic characteristics of the habitat. Multivariate analyses revealed that water depth and exposure to swell were the local variables that explained the most variation in the abundances of angelfishes and butterflyfishes (respectively) at Christmas and Cocos Islands (**Chapter 4**). In addition to the direct effect of swell on swimming abilities of butterflyfishes (Fulton and Bellwood, 2005), it is likely that swell and depth affect habitat complexity and the availability of shelter holes, which are known to strongly influence the abundance of small bodied fishes such as butterflyfishes and angelfishes (Sano *et al.*, 1987; Allen *et al.*, 1998; Pratchett *et al.*, 2008; Graham *et al.*, 2009).

Key processes maintaining island populations

Patterns of species' abundances in this study did not conform to many of the terrestrially-derived ecological generalisations, which indicates that population maintenance in reef fishes differs to most terrestrial species. Reef fishes typically have a bi-partite life cycle characterised by a highly dispersive larval stage combined with a sedentary adult stage, and both larval retention and dispersal play critical roles in population maintenance of reef fishes (Jones *et al.*, 2009). The dispersal larvae stage means offspring frequently recruit to non-natal populations (Mora and Sale, 2002), and the size of a local population does not necessarily determine how many recruits it will receive (Caley *et al.*, 1996). Reef fishes are also highly fecund, with many species capable of producing thousands of offspring during a single spawning. However, high mortality rates during the larval stage mean that recruitment of offspring to the adult population is very low and highly variable (Doherty and Williams, 1988; Doherty, 1991; Caley *et al.*, 1996). Therefore, reef fish populations are maintained by recruitment that is characteristically unpredictable (in relation to local population size) and highly variable.

Recruitment in reef fish populations contrasts with that of terrestrial animals. Terrestrial animals usually produce far fewer offspring, have greater offspring survivorship (due to greater parental care) and less dispersal of offspring. This should lead to recruitment that is more consistent and predictable (based on local population size). Given that high recruitment variability is linked with increased extinction risk (Diamond, 1984; Pimm, 1991; McKinney, 1997), terrestrial species should be able to maintain viable populations at lower densities than marine species. For example, endemic species are frequently reported to have low abundance in the terrestrial environment (Gaston *et al.*, 1997). However, given the unpredictable and highly variable recruitment of reef fish populations, it would be difficult for endemics to persist. For endemic reef fishes to persist over long time periods would require favourable traits such as high local abundance, reduced dispersal, and high and consistent recruitment. Indeed, this study (**Chapter 5**), and many others, have reported endemic species to be highly abundant (Fishelson, 1977; Hourigan and Reese 1987; Randall, 1998; Allen and Robertson, 1996; Allen *et al*., 1998; Jones *et al*., 2002; DeMartini, 2004; DeMartini and Friedlander 2004; Floeter *et al*., 2006; Travers *et al*., 2006; Choat *et al*., 2006; Hobbs and Feary, 2007; Hobbs *et al*., 2008). Furthermore, in Hawaii (which contains the world's highest number of endemic reef fishes), endemics appear to have restricted dispersal (Eble *et al*., 2009) and the highest and most consistent recruitment (DeMartini, 2004, DeMartini and Friedlander, 2004). Therefore, due to the way reef fish populations are maintained, endemic species that conform to the terrestrial pattern of low abundance do not persist and consequently are poorly represented in reef fish communities.

Because reef fishes exhibit the typical bi-partite life history of the majority of marine organisms it might be expected that the positive abundance-range size relationship does not hold for marine communities in general. Populations of invertebrate marine organisms are characterised by highly variable recruitment due to stochastic environmental factors (see Ripley and Caswell, 2006 and the references therein), and therefore only those endemic species that can maintain high abundance are likely to persist. Further work is required to test the abundance-range size relationship in other marine taxa, however it is clear from reef fishes that it should not be assumed that ecological relationships and theories established in terrestrial systems are always universal.

Extinction risk and genetic diversity

The ecology of isolated islands is of conservation significance because island communities contain a high proportion of endemics, which suffer the highest rates of extinction (Frankham, 1997, 1998; Whittaker, 1998). In the terrestrial environment, endemic species are particularly vulnerable to extinction because they usually have small populations (Gaston *et al*., 1997; Gaston, 1998) and this makes them susceptible to a range of demographic, environmental and genetic effects (Pimm, 1991; Frankham, 1996, 1997, 1998). Furthermore, endemicity may be associated with other vulnerable traits, such as ecological specialisation (Brown, 1984, 1995; Lawton and May 1995; Gaston *et al*., 1997; McKinney, 1997).

In the marine environment isolated islands also contain a high proportion of endemics (Bellwood and Hughes, 2001; Roberts *et al*., 2002; Jones *et al*., 2002). Although the fossil record indicates that marine species are less vulnerable to extinction than terrestrial species (McKinney, 1997), numerous marine species have gone extinct in recent years, including many endemics (Dulvy *et al*., 2003; Del Monte-Luna *et al*., 2007). However, endemic reef fishes may be less vulnerable to extinction (compared to their terrestrial counterparts) because they usually do not have small populations (see above). Therefore, endemic reef fishes are less at risk from demographic and environmental stochasticity. In addition, this study found that, unlike the terrestrial endemics, some reef fish endemics are not specialists (**Chapter 5**) and have high genetic diversity (**Chapter 6**) and therefore are less vulnerable to extinction. Overall, endemic reef fishes do not conform to terrestrial ecological generalisations relating to vulnerable traits and therefore their risk of extinction is less than that of terrestrial endemics. However, there have been two recent extinctions of reef fishes and both have been island endemics (Dulvy *et al*., 2003), which indicates that while endemic reef fishes are less vulnerable then terrestrial endemics, they are still more vulnerable then widely distributed reef fishes.

In the terrestrial environment, isolated populations of widespread species are vulnerable to local extinction due to having small populations and low gene flow (Frankham, 1997; 1998). However, this study showed that densities of reef fishes on isolated islands are not significantly different from mainland communities (**Chapter 2**). Furthermore, isolated reef fish populations do not necessarily have low gene flow or low genetic diversity (e.g. Craig *et al*., 2007; Horne, *et al*. 2008; Gaither *et al*., 2010; Winters, *et al*. 2010). Isolated populations of widespread reef fishes are less vulnerable to extinction than isolated terrestrial populations because they do not conform to the pattern of low abundance and little gene flow. While endemic reef fishes, and isolated populations of widespread species, appear less vulnerable to extinction than terrestrial equivalents, further studies are required on other marine taxa determine if this is a general pattern for marine species.

Future research

The results of this study at Christmas and Cocos Islands have highlighted that there are differences between isolated reef fish communities and isolated terrestrial communities. Further work is required at other remote locations to determine whether these differences are universal and if there are general ecological rules for marine communities on oceanic islands. It is already evident that endemic reef fishes in general do not conform to having low abundance. This result is surprising given that generality of endemics with low abundance in terrestrial communities (Gaston *et al.*, 1997), and testing the range size-abundance relationship in other marine taxa is required to determine if reef fishes are the only exception to the rule. Identifying the trait responsible for the high abundance of endemic reef fishes requires investigation.

Although endemic reef fishes generally have high abundance, further research is required to determine if endemism is correlated with other life history traits (e.g. specialisation) that increase extinction risk. Examination of genetic diversity should also be included in the assessment of extinction risk in endemic species to determine whether the unexpected high genetic diversity detected in the study species is typical of other endemics. High genetic diversity will be particularly important to determining extinction risk because it increases the chances of species being able to adapt to changing environmental conditions. Determining which factors combine to increase extinction risk in marine species is a pressing issue given the continuing worldwide degradation of marine systems (e.g. overfishing, increased disease, habitat loss, ocean warming and acidification) (Harvell *et al.*, 1999; Jackson *et al.*, 2001; Hughes *et al.*, 2003; Bellwood *et al.*, 2004; Orth *et al.*, 2006; Hoegh-Guldberg *et al.*, 2007).

Finally, the surprise discovery of numerous reef fish hybrids at Christmas and Cocos Islands warrants further investigation. Of greatest interest is determining the causes (i.e. how are barriers to reproductive isolation overcome?) and evolutionary consequences of this extensive hybridisation. Other areas for research include determining if hybridisation is widespread in other marine taxa that have co-occurring Indian and Pacific Ocean species at Christmas and Cocos Islands.

In conclusion, this study has tested the applicability of a range of terrestrial generalisations on isolated reef fish communities at Christmas and Cocos Islands. To do this I have integrated the fields of biogeography, macroecology, community ecology, conservation biology and conservation genetics to determine how broadscale and local processes structure reef fish communities on isolated islands and how ecological relationships influence extinction risk. This comprehensive study has demonstrated that ecological hypotheses derived from terrestrial ecosystems do not always hold for isolated reef fish communities, particularly in relation to patterns in abundance. I propose that variation in patterns of abundance between terrestrial species and reef fishes are due to differences in population maintenance. As a result of these differences, endemic reef fishes have a lower extinction risk compared to their terrestrial counterparts. However, while remote islands are far removed from many of the threats to marine environments, the small reef area and unique communities present at these islands suggest they should have a high conservation priority.

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