

This file is part of the following work:

**Wen, Colin Kuo-Chang (2012) *Recruitment hotspots in the ecology and management of large predatory fishes on coral reefs*. PhD Thesis, James Cook University.**

Access to this file is available from:

<https://doi.org/10.25903/stbr%2D5080>

Copyright © 2012 Colin Kuo-Chang Wen

The author has certified to JCU that they have made a reasonable effort to gain permission and acknowledge the owners of any third party copyright material included in this document. If you believe that this is not the case, please email

[researchonline@jcu.edu.au](mailto:researchonline@jcu.edu.au)

# ResearchOnline@JCU

This file is part of the following reference:

**Wen, Colin Kuo-Chang (2012) *Recruitment hotspots in the ecology and management of large predatory fishes on coral reefs*. PhD thesis, James Cook University.**

Access to this file is available from:

<http://eprints.jcu.edu.au/31083/>

*The author has certified to JCU that they have made a reasonable effort to gain permission and acknowledge the owner of any third party copyright material included in this document. If you believe that this is not the case, please contact [ResearchOnline@jcu.edu.au](mailto:ResearchOnline@jcu.edu.au) and quote <http://eprints.jcu.edu.au/31083/>*

# Recruitment hotspots in the ecology and management of large predatory fishes on coral reefs

Thesis submitted by  
Colin Kuo-Chang WEN MSc  
in August 2012

for the degree of Doctor of Philosophy  
in the School of Marine & Tropical Biology  
James Cook University

Statement on the contribution of others

Nature of Assistance	Contribution	Name, Titles and affiliations of Co-Contributors
Intellectual Support	<p>Manuscript revision</p> <p>Research and statistic consulting</p> <p>English editing</p> <p>Proof-reading</p>	<p>Dr. Geoff Jones Dr. Morgan Pratchett Dr. Glenn Almany Dr. Laura Castell</p> <p>Dr. David Williamson Dr. Mary Bonin</p> <p>Ms Rosemary Dunn Ms Kellie Johns</p> <p>Susannah Leahy Tine Carl Jennifer Donelson Ian McLeod Erika Woolsey Vera Horigue Florida Flores</p>
Financial Support	<p>Research grant Field research</p> <p>Stipend</p> <p>Scholarship (tuition fee)</p>	<p>Great Barrier Reefs Marine Park Authority ARC CoE James Cook University JCU Graduate Research Scheme</p> <p>JCU scholarship</p> <p>Scholarship for Postgraduate Study Abroad, Ministry of Education, Taiwan</p>
Data collection (field trip)	<p>Research assistance</p> <p>Diving gears and field organizing</p> <p>Sampling identification</p>	<p>Dr. M. Srinivasan Dr. R. Evans T. Mannerings J. Smith R. Brook S. Golderberg M. van der Meer T. Nielsen Brett. Burke A, Mechenin A. Wenger H. Harrison</p> <p>Peter Williams and Raewyn Ramage Robert and Kylie Eddie Lachin Turner, Louise Wilkins Philip Osmond</p> <p>A. González-Cabello J. Stella</p>

## **Acknowledgments**

Firstly, I would like to thank all my supervisors – Prof. Geoffrey P Jones, Prof. Morgan S Pratchett and Dr. Glenn R. Almany. I appreciated all their help and support through my PhD. I always felt lucky to have all these supervisors who are great academics and have different characters that inspire me. Geoff is always a knowledgeable advisor - he inspired me when I was confused and directed me when I was stuck. Morgan is always an energetic scientist - he advised me when I got idle and inspired me when I was sluggish. Glenn is an enthusiast - he encouraged me when I was diffident and motivated me when I was dispassionate. Even though I had only learned a small part of them, I would have them as my role models for my scientific career and journey. I also would like to thank Dr. Jeffrey Leis (Australian Museum) and Dr. Dennis Gordon (NIWA). I wouldn't have had a chance to contact Geoff without their introduction.

Secondly, it was my great pleasure to have worked with all the colleagues in Geoff's lab. Dr. D. Williamson and Dr. R. Evans gave me a great help on field trips and ideas of research. Dr. M. Srinivasan, Mrs. S. Francis and Mrs. D. Ford guided me through all the incredible complicated paperwork during PhD candidature. Several experienced scientists: Prof. S. Connolly, Prof. P. Munday and Dr. M. McCormick who gave me great advice on my research project. I also enjoyed all the field trips and research works I had experienced with other colleagues - Dr. M. Bonin, Dr. M. Srinivasan, Dr. N. Gardiner, Dr. V. Messmer, Dr. J. Donelson, Dr. D. Dixon, T. Mannering, I. Mcloed, Y. Sato, K. Chong-Seng, M. van der Meer, J. Smith, A. Mechenin, A. Wenger, H. Harrison, R. Brooker and S. Hasen.

I would also like to thank James Cook University, ARC Centre of Excellence for Coral Reef Studies and the Great Barrier Reef Marine Park Authority for funding my project. Many thanks for the scholarship from James Cook University and "Postgraduate Study Abroad" program from Ministry of Education, Taiwan. Besides Geoff's students mentioned above, I was grateful for the help of numerous other volunteers helping in my fieldwork: S. Golderberg, T. Nielsen

and B. Burke. I also would like to thank A. González-Cabello and J. Stella for their important suggestions on prey identification. This project would not have been possible without help from Keppel Lodge caretakers - P. Williams and R. Ramage. Thanks to staff from Orpheus Island Research Station: Condo, L. Turner, L. Wilkins, R. and K. Eddie for field work support.

This dissertation would not have been possible without the English revising support from Dr. L. Castell and English advisors: R. Dunn and K. Johns. Other great help to improve my English from advisors of English discussion group: Dr. A. Cairns, Dr. M. Srinivasan and Dr. F. Christidis. Also, thanks to friends who proof-read my draft: S. Leahy, T. Carl, E. Woolsey, V. Horigue, F. Flores, Dr. J. Donelson, J. Hopf, J. Kerry and I. McLeod. I am also highly appreciated for the great suggestions from examiner Dr. R. Taylor and Dr. S. Newman.

Finally, I was truly indebted and thankful for my family, especially my parents WEN, JIN-HU and YU, BAO-JHU who always stood by me, especially with some obstacles in my personal life during PhD. My siblings Jack and Yvonne Wen and my best high school friends also showed their love across the distance when I felt depressed. All the friends I made here really made my life delightful as in a foreign country. Thank you all!!

## Table of Contents

CHAPTER 1 : General Introduction.....	1:12
1.1 Overfishing: the fate of large predatory fish on coral reefs .....	1:12
1.2 Recruitment of coral reef fishes .....	1:13
1.3 Marine reserves and recruitment.....	1:14
1.4 Effects of marine reserves on recruitment.....	1:16
1.5 The prey and habitat preference of the recruits of predatory fishes.....	1:17
1.6 Experimental microhabitat and prey selection of coral trout recruits .....	1:18
1.7 Recruitment hotspots and reserves .....	1:19
1.8 Aims and outline of thesis .....	1:20
1.9 Study system .....	1:21
CHAPTER 2 : Evaluating the effects of marine reserves on diet, prey availability and prey selection by juvenile predatory fishes .....	2:24
2.1 ABSTRACT .....	2:24
2.2 INTRODUCTION.....	2:24
2.3 MATERIALS AND METHODS .....	2:26
2.3.1 Study sites and species .....	2:26
2.3.2 Recruit abundance .....	2:27
2.3.3 Diet.....	2:28
2.3.4 Prey availability.....	2:31
2.3.5 Prey selection .....	2:32
2.4 RESULTS.....	2:32
2.4.1 Recruit abundance .....	2:32
2.4.2 Diet .....	2:33
2.4.3 Prey availability.....	2:34
2.4.4 Prey selection .....	2:34
2.5 DISCUSSION .....	2:35
2.5.1 Recruit abundance .....	2:35
2.5.2 Diet.....	2:36
2.5.3 Prey availability.....	2:37
2.5.4 Prey selection .....	2:38
2.6 CONCLUSIONS .....	2:39
CHAPTER 3 : Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia .....	3:48
3.1 ABSTRACT .....	3:48
3.2 INTRODUCTION.....	3:48

3.3 MATERIALS AND METHODS .....	3:51
3.3.1 Study species .....	3:51
3.3.2 Field sampling .....	3:52
3.3.3 Data analysis .....	3:53
3.4 RESULTS.....	3:54
3.4.1 Spatial variation in abundance of fishes.....	3:54
3.4.2 Microhabitat associations.....	3:55
3.5 DISCUSSION .....	3:57
CHAPTER 4 : Role of prey availability in microhabitat preferences of juvenile coral trout ( <i>Plectropomus</i> : Serranidae).....	4:70
4.1 ABSTRACT .....	4:70
4.2 INTRODUCTION.....	4:71
4.3 MATERIALS AND METHODS .....	4:73
4.3.1 Field sampling .....	4:73
4.3.2 Aquarium experiments .....	4:74
4.4 RESULTS.....	4:77
4.4.1 Prey availability among different habitats .....	4:77
4.4.2 Microhabitat preferences.....	4:78
4.4.3 Prey selection .....	4:79
4.5 DISCUSSION .....	4:79
CHAPTER 5 : Role of recruitment hotspots in the effectiveness of no-take marine reserves for large predatory fishes .....	5:87
5.1 ABSTRACT .....	5:87
5.2 INTRODUCTION.....	5:88
5.3 METHODS.....	5:90
5.3.1 Study location and species .....	5:90
5.3.2 Sampling design and survey methods .....	5:91
5.3.3 Data analysis .....	5:92
5.4 RESULTS.....	5:93
5.4.1 Adults: Effect of recruitment hotspots on magnitude of reserve-effect.....	5:93
5.4.2 Subadults: Effect of recruitment hotspots .....	5:93
5.4.3 Size frequency distributions, recruitment and the legal size limit .....	5:94
5.5 DISCUSSION .....	5:95
CHAPTER 6 : General Conclusions.....	6:107
6.1 Effects of marine reserve status on the diet of juvenile predatory fishes.....	6:107

6.2 Patterns of recruitment and microhabitat associations for three predatory coral reef fishes .....	6:109
6.3 Role of prey availability in microhabitat preferences of juvenile coral trout .....	6:109
6.4 The importance of recruitment hotspots in determining the efficacy of marine reserve .....	6:111
6.5 Future directions.....	6:112
REFERENCES .....	114
APPENDIX I Reviews on habitats and diets study of three predatory genera .....	132
APPENDIX II Journal articles published during PhD Candidature .....	139

## List of Tables

Table 2-1 Sample size of gut content .....	2:41
Table 2-2 Two-way ANOVA of zone and site(zone) on recruit abundance.....	2:42
Table 2-3 PERMANOVA of four factors of diet.....	2:42
Table 2-4 PERMANOVA results of three factors on prey availability .....	2:43
Table 2-5 PERMANOVA result of three factors on prey selection.....	2:43
Table 3-1 Results from independent Kruskal-Wallis tests.....	3:63
Table 3-2 Percentage cover and relative use of microhabitats by study fishes.....	3:64
Table 4-1 Two-way ANOVA of prey fishes and crustaceans among locations and microhabitat .....	4:84
Table 5-1 Two-way ANOVA of (a) adult and (b) subadult of three predatory fishes .....	5:99
Table 5-2 Paired K-S test results from reserves and recruitment hotspots .....	5:100

## List of Figures

Figure 1-1 Map of study system.....	1:23
Figure 2-1 Bar chart of abundance of three species inside and outside reserves.....	2:44
Figure 2-2 Ontogenetic diet shift of three species inside and outside reserves.....	2:45
Figure 2-3 PCO plot of prey availability inside and outside reserves.....	2:46
Figure 2-4 Ontogenetic shift of prey selection from three species .....	2:47
Figure 3-1 Map of Keppel Islands.....	3:65
Figure 3-2 Densities of recruit, subadult and adult fishes at six locations in the Keppel Islands .....	3:66
Figure 3-3 Densities of recruit, subadult and adult among physiognomic reef zones .....	3:67
Figure 3-4 Proportional use of contrasting microhabitats by recruit, subadult and adult fishes .....	3:68
Figure 3-5 Frequency of use of different compound microhabitats by recruits.....	3:69
Figure 4-1 Abundance of prey fishes and crustaceans on five compound microhabitats .....	4:85
Figure 4-2 Occupancy of five microhabitats by juvenile coral trout .....	4:86
Figure 4-3 Frequency of prey selection of juvenile coral trout.....	4:86
Figure 5-1 Map of sampling sites.....	5:101
Figure 5-2 Abundance of subadult and adult among two treatment .....	5:102
Figure 5-3 Length-frequency histogram of three species among two factors.....	5:104

## GENERAL ABSTRACT

Large predatory fishes make up the main catch in coral reef fisheries around the globe. However, primarily due to overfishing, populations of these predatory fishes have declined rapidly in the past century. No-take marine reserves have proven to be an effective way to protect reef predators and allow populations of exploited fishes to recover. However, the long-term benefits of reserves can only accrue through the maintenance of recruitment processes. In general, patterns of recruitment and the ecology of juveniles in key predator families such as the Epinephelidae, Serranidae and Lutjanidae are poorly documented. The overall aim of this study was to investigate spatial patterns in the recruitment of three exploited predatory fishes on the Great Barrier Reef in order to understand both the top-down and bottom-up role of recruitment in marine reserve dynamics. That is, to understand how reserves and increases in adult numbers impact on recruitment, and how patterns of recruitment influence the effectiveness of marine reserves. The thesis focuses on the juvenile ecology of coral trout (*Plectropomus maculatus*), the stripey snapper (*Lutjanus carponotatus*) and the long-finned rock cod (*Epinephelus quoyanus*) at the Keppel Island Group, southern Great Barrier Reef.

Chapter 2 examined the effects of reserves on the ecology of the juvenile stages of the three predators, including the direct effects of predation pressure from adults in reserves and non-consumptive effects on foraging behaviour, including diet and prey selection. I examined differences between reserves and fished areas in recruit abundance, diet, prey availability, and prey selection indices for recruits and juveniles of the 3 predatory fish species. After quantifying recruit abundance in nearshore reef habitats at each of four sites at the Keppel islands (2 reserves and 2 non-reserves), I sampled recruits and juveniles from these same sites and analysed their gut contents to quantify their diets, then quantified prey availability to assess prey selectivity. Recruit abundance was similar between reserves and open areas, indicating that large predators do not directly reduce recruitment. The diets of the three study species did not differ between reserves and open areas, with variation in diets largely explained by fish species

and body size. At small sizes, all species consumed high numbers of shrimp (Caridea), but diets diverged with growth: *P. maculatus* selectively consumed damselfishes (Pomacentridae) and wrasses (Labridae), *L. carponotatus* focused on gobies (Gobiidae) and crabs (Brachyura), and *E. quoyanus* primarily targeted crabs (Brachyura). Prey availability and prey selection differed between reserves and open areas, but only for a few categories of cryptic invertebrate prey. Overall, our results produced little evidence that more abundant predators inside reserves influence juvenile feeding ecology. However, recently recruited predators appeared to select a narrow range of invertebrate and small fish prey, and predator populations may therefore be susceptible to the loss of these resources.

Chapter 3 examined the role of the availability of suitable settlement habitat in determining patterns of recruitment and the likely consequences of habitat degradation. Juveniles of all 3 predators exhibited significant habitat selectivity, using specific microhabitats (mostly *Acropora* corals) disproportionately to their availability, but habitat selectivity was highest for recruits and lowest for adults. There was also, an apparent ontogenetic shift in microhabitat associations for all 3 species, with recruits associated mostly with corymbose *Acropora*, but adults were more commonly found associated with tabular *Acropora*. The proportion of *P. maculatus* (72%) that associated with live corals was higher than for *L. carponotatus* (68%) and *E. quoyanus* (44%), but recruits from all three species were found predominantly in structural habitats comprised of live branching corals. Moreover, recruits of all 3 species were found predominantly on patches of live-coral habitat located over loose substrates (sand) rather than consolidated substrata. Densities of recruits were highly variable among locations and among reef zones, but these differences were only partly attributable to availability of microhabitats. Specific reliance on live coral microhabitats has yet to be tested, but these findings show that at least some carnivorous reef fishes strongly associate with live corals (especially during early life-history stages), and may therefore be highly sensitive to increasing coral loss and degradation of reef habitats.

The ecological basis for microhabitat selection was investigated in chapter 4. Here I used a combination of field-based sampling and aquarium-based experiments to establish trade-offs between shelter requirements versus prey selection in microhabitat selection by larval coral trout (mostly, *Plectropomus maculatus*). Coral trout show strong affinity for structural microhabitats (e.g. live or dead colonies of *Acropora*), but the underlying habitat (sand versus consolidated reef substratum) further influences patterns of microhabitat use. Field-based surveys revealed that live coral habitats support higher densities of potential prey species compared to dead corals. Furthermore structural microhabitats on sand have higher densities of prey (especially crustaceans) compared to comparable microhabitats on consolidated carbonate substrata. In the absence of prey, juvenile coral trout did not distinguish between live versus dead corals, but both these microhabitat were preferred over rubble, macroalgae and sand. In aquarium-based studies of prey use, juvenile coral trout consumed prey fishes that associate with non-coral habitats (e.g. *Eviota zebrina*) and mid water species (e.g. *Aioliops tetraphthalmus*), but did not consume those fishes with an obligate association with live corals. Our results suggest that studies of microhabitat preferences should consider both the structure and location of specific microhabitats. It is presumed the structural microhabitats are essential for evading predators, while occupation of live corals positioned over sandy substrata maximises accessibility to a diverse array of potential prey fishes and crustaceans.

Chapter 5 examined the role of recruitment in explaining the magnitude of reserve-effects for adults of the 3 predators. The rationale was that long-term increases in reserves can only be sustained if there is adequate juvenile recruitment, but patterns of recruitment inside and outside reserves have seldom been quantified. I hypothesised that the effectiveness of reserves depends on whether or not they contain “recruitment hotspots” (or sites that contain a disproportionate abundance of juveniles). To test this, I used an orthogonal sampling design to compare the abundance of sub-adults and adults of three predatory fishes at both reserve and fished reefs, with and without recruitment hotspots. For *P. maculatus* and *L. carponotatus*, adult densities were 2-3 times greater in reserves with recruitment hotspots, compared with reserves without

hotspots or fished areas, which were all similar. The abundance of sub-adults was primarily explained by the presence of recruitment hotspots, not reserve status. Compared with reserves, the size-distributions of *P. maculatus* and *L. carponotatus* were truncated at the minimum size limit (MSL) for all fished populations, regardless of recruitment patterns. My results suggest that identifying recruitment hotspots could be a valuable addition to reserve selection criteria, particularly for reserves targeting large exploited species using common recruitment areas.

This thesis has provided valuable new information on the ecology of the juvenile stages of important predators on the Great Barrier Reef, highlighting the critical importance of juvenile diet and habitat, and recruitment hotspots. While adult stages of these predators appear to have relatively little impact on juveniles, the juvenile ecology may be a key determinant of patterns in adult abundance and the effectiveness of marine reserves. I conclude that a greater focus on recruitment would greatly benefit conservation and fisheries management for those species examined in this study and thus contribute to improving the design and implementation of marine reserves.

## **CHAPTER 1: General Introduction**

### **1.1 Overfishing: the fate of large predatory fish on coral reefs**

Fishing pressure on marine resources has dramatically increased due to the exponential growth of the human population in the past half-century (Pauly et al. 2002). Recent fishery reports suggest that the majority of the world's exploited marine species are either fully exploited or overfished (Pauly et al. 1998; FAO 2010). The global fishery catch peaked in the 1980s, and despite increasing fishing effort, is currently in decline (FAO 2010). Many of the extreme examples of overfishing include the larger apex predatory fishes, which are usually targeted first before stocks are depleted (Myers and Worm 2003, 2005). Their naturally low abundance, long life span, slow growth and low recruitment rates increase their susceptibility to rapid stock depletion (Jennings et al. 1998; Musick 1999). Reproductive stocks of many larger exploited species have been reduced to such low levels that there is now insufficient recruitment for recovery – so-called “recruitment overfishing” (Myers et al. 1994; Roberts 1997). Recruitment - the demographic process by which juveniles join the adult population, is widely recognised as a critical bottleneck for population growth in marine populations (Werner and Gilliam 1984; Menge and Sutherland 1987). However, this life history stage is poorly understood for most marine predators and in many cases, the juvenile stage has rarely been observed.

Pressure on tropical marine fisheries has grown significantly with human population in recent decades (Sadovy 2005). Large predatory fishes associated with coral reefs are prime targets in commercial and subsistence fisheries around the globe (Myers and Worm 2005). There is increasing evidence that removing top predators is not only depleting target species (Beets 1997; Myers and Worm 2003), but resulting in trophic cascades that impact on prey species and alter the structure of coral reef ecosystems (Jackson et al. 2001; McClanahan and Arthur 2001; Hughes et al. 2003; Bellwood et al. 2004; Heithaus et al. 2008). In addition to their intrinsic susceptibility to overfishing, extrinsic factors, such as coral bleaching and habitat loss, are also

contributing to the long-term decline of large predators (Graham et al. 2007; Wilson et al. 2008). The threat to large predators has led to much recent conservation interest, with many large groupers and wrasses now listed by the IUCN as threatened species (IUCN 2011). Although large predators are increasingly subject to targeted research and management initiatives, this focus has almost always been on adult fishes (Appendix 1). Little is known about the juvenile stages of many large predators and the effects of management actions on recruitment have received little attention to date.

## **1.2 Recruitment of coral reef fishes**

Like most other marine organisms, coral reef fishes have two distinct phases of life, a pelagic larval stage and a relatively sedentary adult stage (Leis and McCormick 2002). Most coral reef fishes are either pelagic spawners that release gametes into open water, or demersal spawners that attach their eggs to the substratum. In both cases, newly developed embryos develop into a pelagic larval stage before they settle back onto the coral reefs. The dispersal from spawning and settling location is related to the duration of the pelagic larval stage (Cowen and Sponaugle 2009), which is also called pelagic larval duration (PLD). The PLD of coral reef fishes varies from 10-60 days, with an average duration of 28-35 days (Sale 2004). This mechanism of releasing offspring into the open ocean and then settling down back onto reefs results in widely spread reefs having high levels of connectivity (Cowen 2002). This connectivity between populations is also the main source of replenishment for coral reef fish populations (Cowen et al. 2007).

Recruitment in reef fishes is usually considered the process in which pelagic larval stages progress to successfully settle on reefs (Doherty 1981). Recruitment is the main source in the replenishment of local fish populations as for most species as there is relatively limited migration between reefs (Victor 1983; Mapstone and Fowler 1988; Booth and Brosnan 1995). Many reef fishes are considered to be “recruitment-limited” in the sense that insufficient

numbers of juveniles join the adult population to exceed the carrying capacity of the environment (Doherty 1981; Caley et al. 1996). Furthermore, patterns of recruitment may be modified to varying degrees by post-recruitment processes, such as predation or habitat availability (Connell and Jones 1991; Jones 1991; Beets 1997). Hence, monitoring the recruitment process is essential to understand the demographic dynamics of fish populations, which in turn is necessary for planning resource management strategies (Sale 2004).

Most studies on the recruitment of coral reef fishes have focussed on small taxa, such as damselfish and wrasses, where settlement can be readily observed (reviews in Sale 1979; Shulman 1984; Doherty 2002). A wide range of factors are known to affect recruitment (Jones 1991). These include predation pressure (Shulman 1985; Almany 2004a,b; Hixon and Jones 2005), competition (Shulman et al. 1983; Sweatman 1985), availability and location of suitable habitat (Jones 1986; Booth and Beretta 1994), habitat complexity (Connell and Jones 1991; Beukers and Jones 1998), habitat degradation from human disturbance (Feary et al. 2007) and oceanographic features (Victor 1986). These factors may operate together to create complex patterns of recruitment (e.g. Walters and Juanes 1993; Forrester 1995; Forrester and Steele 2004). It is likely that large predatory fishes (e.g. Epinephelidae, Serranidae and Lutjanidae) are subject to many of the same processes during recruitment, however, information on factors affecting recruitment for these fishes is scarce.

### **1.3 Marine reserves and recruitment**

No-take marine protected areas (MPAs) or marine reserves have been widely advocated and implemented for coral reefs, both for conservation and fisheries management (Roberts and Polunin 1991; Rowley 1994; Halpern and Warner 2002; Hughes et al. 2007). Marine reserves are designed to exclude human predation from the marine environment to preserve the natural biodiversity of marine organisms (Bohnsack 1993). Reserves appear to be effective in protecting large predatory species whose range of movement is often restricted to individual

reefs (Zeller and Russ 1998). Reserves can be effective in the recovery and protection of reproductively viable stocks, ensuring that recruitment overfishing does not occur (Bohnsack 1998). The supply of offspring to adjacent areas open to fishing has the potential to sustain or enhance fishery production (Rowley 1994; Holland and Brazee 1996; Bohnsack 1998). In terms of conservation, marine reserves may not only protect target species, but could also protect coral reefs from indirect effects of fishing and improve the resistance of the ecosystem to other anthropogenic impacts such as sedimentation, pollution and global warming indirectly (Hughes et al. 2003; Mumby et al. 2006). However, while many of the benefits of reserves have been established, the processes by which reserves protect species and contribute to sustainable fishing have not been fully explored.

An understanding of recruitment is essential to gauge how populations of predatory fishes will change, both inside reserves and in fished areas. Theoretically, the abundance and size of target species in marine reserves will increase due to low or zero levels of fishery mortality (Halpern and Warner 2002; Russ 2002; Evans and Russ 2004). However, demographic change in protected areas will be a function of all vital demographic rates, including recruitment and movement. The role of recruitment in determining patterns of change in abundance of adult fishes in reserves has not been investigated. Reserves established in places that consistently receive high levels of recruitment may have faster recovery than reserves with low recruitment. On the other hand, the increase of adults in reserves may impact on recruitment due to the top down effects of predation. Hence the relationships between adult numbers and recruitment inside reserve boundaries are complex, including both bottom-up and top-down processes.

Fishes in marine reserves also appear to grow to larger sizes as a consequence of protection (Russ and Alcala 1996b; Roberts et al. 2001). The combination of greater numbers of larger fish in reserves means that reserves may provide a differential supply of juveniles to fisheries outside reserves (Rowley 1994; Evans et al. 2008). Harrison et al. (2012) provides encouraging

evidence that marine reserves are having an important effect in this regard. This is particularly true for large predatory reef fish species where there is a paucity of knowledge on recruitment.

#### **1.4 Effects of marine reserves on recruitment**

In theory, the basic effect of marine reserves on recruit (young-of-year) fishes is increased predation pressure inside the reserves. Since the most sought after fishes on coral reefs are predatory fishes i.e. carnivores or piscivores (Pauly 2008), a higher abundance of predatory fish in marine reserves is expected when fishing ceases (Roberts and Polunin 1991). This effect has been demonstrated in many studies (e.g. Russ and Alcala 1996a; Halpern and Warner 2002; Evans and Russ 2004; Williamson et al. 2004; Lester et al. 2009). This higher abundance of predators may also increase the mortality of the prey communities in reserves (Planes et al. 2000). For example, Graham et al. (2003) found a four-fold increase in the number of piscivorous coral trout (*Plectropomus leopardus* & *P. maculatus*) in marine reserves and a 3-4 times decrease in the prey fish *Acanthochromis polyacanthus*, which are commonly found in the gut contents of coral trout (Kingsford 1992; St John et al. 2001). Another top-down control mechanism, the so-called trophic cascade arising from increased predatory fishes impacting on prey composition in marine reserves have also been suggested (Sonnenholzner et al. 2007; Harborne et al. 2008; Heithaus et al. 2008). The increased number of fished species in marine reserves might also influence patterns of recruitment through an effect on habitat structure. Fishing of herbivorous fishes has been implicated in phase-shifts from coral to macro-algal dominated habitats (McClanahan et al. 2001). This may in turn reduce the recruitment of predator species and other small fishes associated with coral substrata. (McClanahan et al. 2000; O’Leary et al. 2012). To date, no study has examined the influence from increases in predatory fish populations on the ecology of juvenile stages of predators. The direct and indirect effects from increased predatory fishes on recruitment processes in marine reserves also remain to be investigated.

The increase in abundance of predatory fishes may have a direct impact on prey by increasing mortality through consumption (e.g. Graham et al. 2003). However, it is also possible that predation pressure alters the behaviour of prey – which may result in a number of “non-consumptive” effects. Non-consumptive effects have been found broadly in all environments (reviews in Preisser et al. 2009; Fill et al. 2012). This alternative behaviour can vary from increasing hiding (Lima 1998), less feeding (Madin et al. 2010) or decreasing the size of the home range (Duffus and Dearden 1990). Changes in behaviour may be facilitated by chemical alarm signals induced by the presence of predators (Holmes and McCormick 2011; Leahy et al. 2011; Mitchell et al. 2011). This altered behaviour is associated with a less preferred habitat or food, which may induce slow growth or late maturity (Almany 2004c). In theory, the increased abundance of predatory fishes in marine reserves may induce a range of non-consumptive effects on juvenile stages of predators, but so far these have not been studied.

### **1.5 The prey and habitat preference of the recruits of predatory fishes**

Food and habitat resources are important factors that may affect the recruitment of predatory coral reef fishes. A large proportion of coral reef fishes have strong associations with coral reefs as shelter and as a food resource in part or all of their lifespan (Sale 1977). Clear relationships have been shown between the coral coverage and fish abundance/diversity (Bell and Galzin 1984; Jennings et al. 1996; Findley and Findley 2001). Coral degradation in Papua New Guinea has been followed by significant decline in the abundance of a wide range of coral reef fishes as a result of the loss of recruitment habitat (Jones et al. 2004). However, different coral reef fishes show a varied level of dependence on coral reefs. Corallivores, including many fishes of the family Chaetodontidae (butterflyfishes), are directly affected by coral loss due to declining availability this resource (Pratchett et al. 2004; Pratchett et al. 2006). Coral gobies and other coral dwelling fishes that live in specific coral related microhabitats might be exposed to predators due to coral degradation (Munday 2004; Wilson et al. 2008; Coker et al. 2009). However, the specific microhabitat or prey preferences of recruits of predatory fishes are not

well known (but see Light and Jones 1997; Connell and Kingsford 1998; Kingsford 2009). Understanding the habitat or food preference of recruits of predatory fishes would be important to preserve these resources from decline within marine reserves.

Coral reef fishes typically change their diet and habitat utilisation at different ontogenetic stages. The ontogenetic diet/habitat shifts occur as a consequence of changing dependence on shelter and access to food in relation to body size (Werner and Hall 1988). The habitat and prey preferences of large adult predatory fishes are well documented due to their importance in coral reef fisheries, especially the Epinephelidae, Serranidae and Lutjanidae (Appendix 1). Some lutjanids use mangroves and seagrass beds as nursery areas and show an ontogenetic habitat shift to coral reefs. Some serranids exhibit ontogenetic shifts from shallow rubble areas to deeper reefs. However, the habitat and prey preference of juvenile coral trout (*Plectropomus* spp.), one of the most important fishery species in coral reefs, is poorly known. The lack of ecological information of early juvenile coral trout makes it difficult to assess the critical environment for their whole life cycle. Therefore, identification of the complete spectra of habitat and prey preference of fishery reef species is important for conservation of target species in marine reserves.

## **1.6 Experimental microhabitat and prey selection of coral trout recruits**

Patterns of recruitment in reef fishes may be strongly influenced by habitat and prey preferences at the time of settlement (Shulman 1985). Choice of microhabitats may be a trade-off between the need for adequate shelter and food availability (Werner et al. 1983). For juvenile fishes, habitat choice is thought to relate more to predator avoidance, due to the vulnerability to predators at small sizes (Beukers and Jones 1998). In addition, because of the small gape, small fishes may be more restricted in diet and have less opportunity to select prey (Hixon and Beets 1993). It can be difficult to distinguish the roles of microhabitat and prey selection from field observations as different microhabitats may support different prey. However, detailed

descriptions of habitat use and diet can be used to generate hypotheses about the resources that are critical during the juvenile stages. Most of the advances in our understanding of habitat and prey selection have come from experiments designed to directly measure habitat and prey preferences (i.e. Sale 1976; Shulman 1984; Jones 1987). As for other questions i.e. competition and predation, most of this work has been conducted on small sedentary fishes (Munday 2001; Almany 2003). There have been few investigations into microhabitat and prey preferences of the juvenile stages of large predators (Appendix 1), and there are especially limited in coral trouts (*Plectropomus* spp.). Therefore, further experimental manipulations of habitat and microhabitat choice by coral trouts are needed to validate the data from field observations.

### **1.7 Recruitment hotspots and reserves**

Recruitment of most coral reef fishes appears to be extremely patchy and particular sites where a large proportion of juveniles enter reef populations can be identified. Specific locations that consistently receive higher than average recruitment are termed “recruitment hotspots” (Booth et al. 2000; Eagle et al. 2012). Hotspots may arise through larval accumulation as a result of consistent hydrodynamic processes and/or specific habitat preferences for newly settled fishes (Kingsford et al. 1991; Wolanski et al. 1997), whether due to shelter and/or food. This phenomenon of animals concentrating in patches of favourable resource has been termed the “resource concentration hypothesis” (Ritchie and Olff 1999; Hambäck and Englund 2005). There is increasing evidence that recruitment hotspots are particularly important for large predatory fishes (Light and Jones 1997; Dahlgren and Eggleston 2001), but the underlying factors that explain hotspots are not always known.

The role of recruitment hotspots in the effectiveness of marine reserve protection has not been well-studied yet. Since only successful recruitment can contribute to the local adult population (Doherty et al. 2004), recruitment hotspots determine the major demographic replenishment for populations. Hypothetically, preservation of recruitment hotspots would be expected to increase

the replenishment to local populations. This represents one of the goals of marine reserves - to enhance the adult population for sustainable fisheries. However, the optimal design of marine reserves to achieve this goal is still unclear (Halpern and Warner 2003). Understanding the ecological processes for the population regulation of target species is a critical component of the design of marine reserves (Sala et al. 2002). The supply of larval fishes and the existence of suitable habitats are both essential for marine reserves (Warner et al. 2000). Therefore, investigating and positioning the recruitment hotspots should be an important component of the design of marine reserves. Despite this, the location of recruitment hotspots and how they contribute to the replenishment of adjacent populations is a nascent area of coral reef research. Such hotspots may or may not be associated with MPAs and their contribution to population growth in protected areas remains largely unknown. A full understanding of the role of marine reserves in the management of predators requires not only an understanding of adult migration from protected areas, but also of the contribution of recruitment hotspots to population growth within marine reserves.

## **1.8 Aims and outline of thesis**

The overall aim of this thesis is to examine the role of the recruitment in the dynamics of predatory fish populations and their response to marine reserve protection. This included the potential for both top-down effects of adult fishes on juveniles and bottom-up effects of recruitment processes on the effectiveness of marine reserves. Within this brief, the following specific objectives were addressed: (1) to examine the top-down effects of increased predatory fish abundance in marine reserves on the ecology, behaviour and diet of the juvenile stages of predatory fishes; (2) to examine patterns of microhabitat use and ontogenetic changes in habitat associations in juvenile predators; (3) to experimentally examine the extent of prey and microhabitat preferences in juveniles of a focal predator; (4) to study the influence of recruitment hotspots on the efficacy of marine reserves and the population structures on fished and unfished reefs.

These 4 objectives were addressed in each of the following chapters:

Chapter 2. *Evaluation of the effects of marine reserve status on diet, prey availability and prey selection of juvenile predatory fishes (in press, Marine Ecology Progress Series).*

Chapter 3. *Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia (in press, Coral Reefs).*

Chapter 4. *Role of prey availability in microhabitat preferences of juvenile coral trout (Plectropomus: Serranidae) (in review, Journal of Experimental Marine Biology and Ecology).*

Chapter 5. *Role of recruitment hotspots in the effectiveness of no-take marine reserves for large predatory fishes (in prep).*

## 1.9 Study system

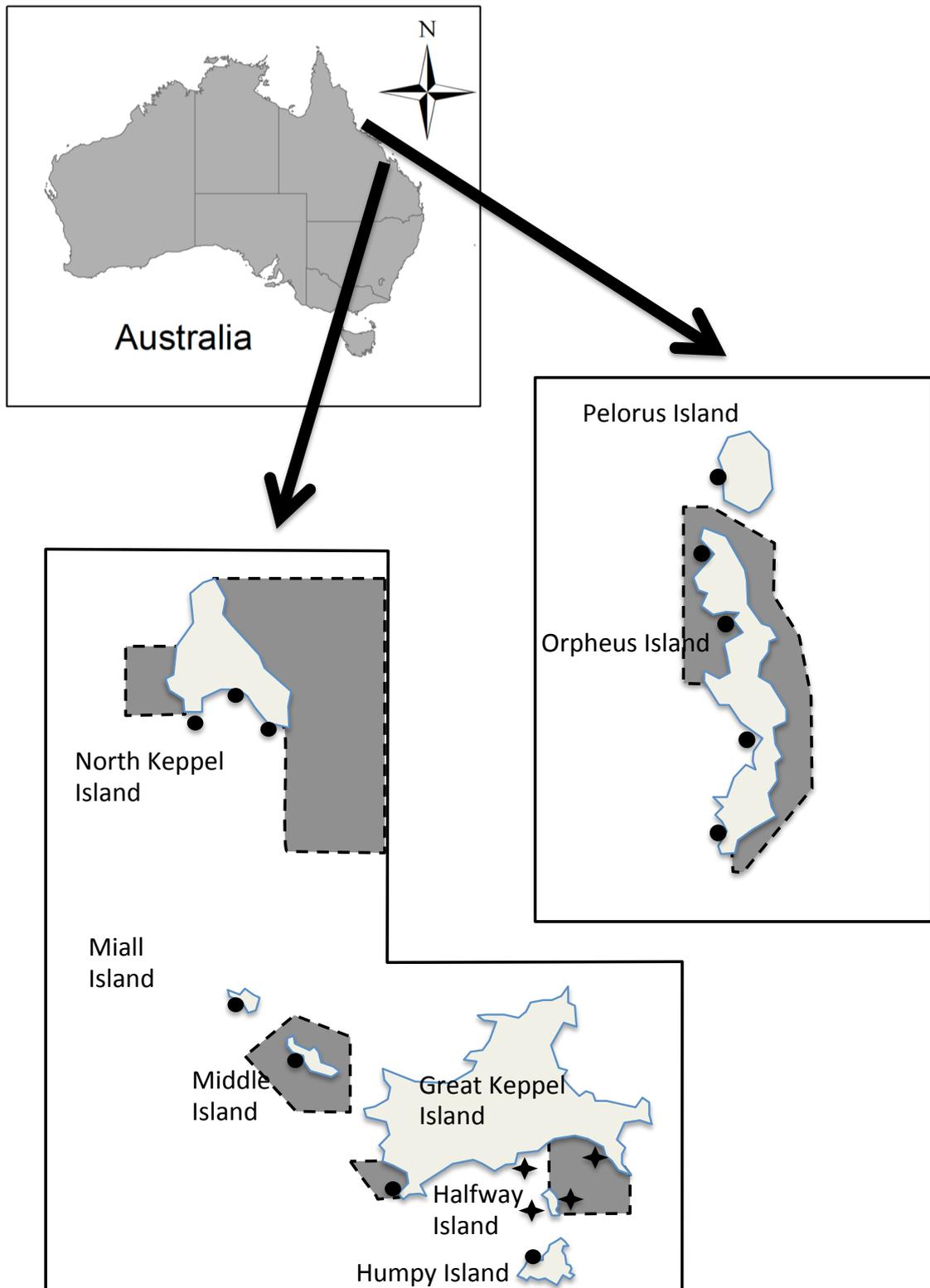
This study focused on three large species of carnivorous fishes, i) the inshore coral trout, *Plectropomus maculatus* (Bloch, 1790), ii) the stripey snapper, *Lutjanus carponotatus* (Richardson, 1842), and iii) the long-finned rock cod, *Epinephelus quoyanus* (Valenciennes, 1830). *Plectropomus maculatus* (family Serranidae) is one of 7 species of coral trout and the largest of the three study species, which is up to 60 cm TL (Ferreira and Russ 1992). It is a relatively long-lived (>12 years) and slow-growing species, restricted to the Indo-Australia archipelago and found predominantly in nearshore, often turbid waters (Ferreira and Russ 1992). *P. maculatus* is not a major component of commercial catches, which target mainly mid-shelf and outer-shelf reefs. However, because of its near-shore abundance *P. maculatus* is an important component of recreational catches (Williams and Russ 1994). *Lutjanus carponotatus* (family Lutjanidae) is a medium sized snapper (up to 34 cm TL) that can live up to 20 years (Newman et al. 2000). It is distributed widely in the Indo-west Pacific and commonly associated with coral reefs (Newman et al. 2000). *L. carponotatus* is caught commercially on the Great Barrier Reef (GBR), but is mainly taken by recreational fishers (Williams and Russ 1994). *Epinephelus quoyanus* (family Epinephelidae) is a relatively small grouper (up to 36 cm TL;

Connell and Kingsford 1998). It is widespread through the western Pacific, but like *P. maculatus*, is predominantly found in inshore and turbid reefs. *E. quoyanus* is often caught, but generally released by recreational fishers on the GBR (Diggles and Ernst 1997). In this study, fishes were then categorised as either recruits (young of the year), subadults, or adults (sexually mature individuals) based on size (Appendix 1) using data from independent studies on size at age, and size at first maturation (Evans et al. 2008; Mannering 2008).

Data were collected from 2008 to 2010 at Great Keppel Islands (Chapter 2, 3, 5) and Orpheus Island (Chapter 4) in the Great Barrier Reef, Australia (Fig 1-1). Underwater visual surveys were conducted and samples collected from the Great Keppel Island group (North Keppel Island, Great Keppel Island, Middle Island, Miall Island, Halfway Island and Humpy Island). The Great Keppel Islands region (23°10'S, 151°00'E) is located in the southern Great Barrier Reef. Sea surface temperature (SST) ranges between 18-30°C on a daily average (AIMS 2012). This island group is close to the southern edge of GBR and mainland coast (~10 km), and popular for recreational fisheries. Orpheus Island is located within the Palm Island group on central Great Barrier Reefs, and is also composed of inshore reefs as Great Keppel Island (~15km from mainland). The ecological and biological attributes of coral trout (*Plectropomus* spp.) around Orpheus Island are well studied (Ferreira and Russ 1992; Frisch and Van Herwerden 2006) and marine reserves have been shown to improve the predatory fish populations in the Great Keppels (Williamson et al. 2004). The other important reason that Orpheus Island was chosen for our manipulative study is because the Orpheus Island Research Station is equipped with a well-built aquaria facility with a constant seawater supply, which is important for handling coral trout recruits and prey fishes (Chapter 4).

**Figure 1-1 Map of study system**

Location of study sites in this thesis Orpheus Island group and Great Keppel Island group. Circle symbols represent the normal survey and collection sites. Star symbols represent the recruitment hotspots sites. Reserves areas were shown as dashed grey area.



## **CHAPTER 2 : Evaluating the effects of marine reserves on diet, prey availability and prey selection by juvenile predatory fishes**

Marine Ecology Progress Series (*in press*, DOI: 10.3354/meps09949)

### **2.1 ABSTRACT**

Implementation of effective no-take marine reserves almost universally results in an increase in the abundance of adult stages of exploited predatory fishes. However, the effects of reserves on the ecology of the juvenile stages of predators are unknown. Increased predation pressure from predatory adults in reserves may not only reduce juvenile recruitment directly, but as a result of non-consumptive effects, may impact on critical aspects of their foraging behaviour, including diet and prey selection. In general, the feeding ecology of juvenile stages of large predators is poorly understood due to their relatively low abundance and cryptic behaviour. Here, we examined differences between reserves and fished areas in recruit abundance, diet, prey availability, and prey selection indices for recruits and juveniles of three predatory fishes: *Plectropomus maculatus*, *Lutjanus carponotatus* and *Epinephelus quoyanus*. Recruit abundance was similar between reserves and open areas. The diets of the three study species did not differ between reserves and open areas, with variation in diets largely explained by fish species and body size. At small sizes, all species consumed high numbers of shrimp, but diets diverged with growth. Overall, our results provide little evidence that more abundant predators inside reserves influence juvenile feeding ecology.

### **2.2 INTRODUCTION**

No-take marine reserves, or areas protected from all fishing and collecting, are widely advocated and increasingly established with the goal of protecting or restoring biodiversity (Wood et al. 2008), or enhancing fishery sustainability and yields (Russ and Alcala 1996b; Russ et al. 1998; Pauly et al. 2002; Lubchenco et al. 2003; Mora et al. 2006). Most studies have

demonstrated that effectively enforced reserves result in greater biomass of adults of exploited species inside reserves compared to similar areas open to fishing (e.g. Halpern and Warner 2002; Watson and Munro 2004; Williamson et al. 2004; Russ et al. 2008). Commonly, the fishery target species increasing in reserves are carnivorous and piscivorous fishes (Roberts and Polunin 1991; Roberts and Polunin 1993). Their increased abundance and biomass inside reserves has been shown to have cascading effects on the abundance, demography and behaviour of their prey (Connell 1998a; Graham et al. 2003; Ruttenberg et al. 2011), and some evidence has been presented that predator recruitment inside reserves may be lower (Ayling et al. 1992). However, few studies have focused on the ecology of juvenile stages of these predators (but see Sweatman 1993; Light and Jones 1997; Kingsford 2009) and the impact of no-take reserves on the abundance and feeding ecology of juveniles is poorly known.

While contact between adults and juveniles may be reduced by ontogenetic shifts in habitat use that are common in predatory fishes (Ferreira and Russ 1992; Dahlgren and Eggleston 2000), adults often range across habitats and thus may still interact with juveniles. Greater predator abundance inside no-take reserves may influence the ecology of juvenile predators in a variety of ways. First, large predators may decrease juvenile abundance via direct consumption. Second, juveniles may be indirectly influenced via non-consumptive effects (*sensu* Blaustein 1997; Lima 1998) as a result of the influence of large predators on juvenile foraging behaviour or top-down effects that ultimately affect prey availability for juvenile predators. Increased pressure from large predators has been shown to influence the foraging behavior of small predatory fishes (Milinski and Heller 1978; Madin et al. 2010; McCauley et al. 2010). Indirect effects may also arise as increases in herbivorous fishes alter the structure of the benthic habitat, and therefore, habitat availability for small fishes and invertebrates that are the prey of juvenile predators (McClanahan et al. 2000; McClanahan and Arthur 2001; O'Leary et al. 2012). In addition, the presence of large predators may influence the diets of juvenile predators and alter the timing of ontogenetic changes in diet and behaviour (e.g. Preisser et al. 2005; Schellekens et al. 2010). As a consequence of these factors, an increase in the abundance of large predators

inside reserves could produce a range of differences in prey availability and juvenile diets compared to areas outside reserves. Most studies examining the diets of exploited coral reef fishes have focused on the adult stage (St John et al. 2001; Kulbicki et al. 2005), and the foraging ecology and prey consumption patterns of juveniles have received little attention (but see Kingsford 1992; Connell 1998b; St John 1999).

The goal of this study was to examine the effects of effective reserves on the foraging ecology of juvenile predators, including prey availability, diets and prey selection. We focused on three predatory fish species (*Plectropomus maculatus*, *Lutjanus carponotatus* and *Epinephelus quoyanus*) that have exhibited dramatic increases in adult numbers and biomass inside no-take reserves on the inner Great Barrier Reef (Williamson et al. 2004). We tested three hypotheses: (1) recruit abundance is lower inside reserves due to greater predation pressure inside reserves; (2) juveniles of the three species consume less prey (in terms of gut fullness) and a greater proportion of cryptic prey inside reserves as a result of juveniles limiting their exposure to more abundant predators; and (3) ontogenetic diet shifts from cryptic prey to mobile prey occur at larger sizes in reserves as a result of juveniles limiting their exposure to more abundant predators. To test these hypotheses, we quantified and compared recruit abundance, diet, prey availability and prey selection at two no-take reserves and two nearby areas that were open to fishing.

## **2.3 MATERIALS AND METHODS**

### **2.3.1 Study sites and species**

Sampling was conducted during the peak recruitment season (February-April) in 2008 and 2009 at six sites with similar reef condition in the Keppel Islands region (23°10' S, 150°57' E) of the Great Barrier Reef Marine Park. Two sites were located in no-take reserves, Clam Bay (protected since 2004, 122.5 ha) and Middle Island (protected since 1988, 165.5 ha), and four sites were open to fishing (North Keppel Island, Miall Island, Humpy Island and Halfway

Island). No-take reserves in the Keppel Islands region support approximately twice the density of large predatory fishes as adjacent fished areas, and the three study species are the most abundant predators in this area (Chapter 5). On the Great Barrier Reef, *P. maculatus* and *L. carponotatus* are primary targets of both recreational and commercial fisheries, whereas *E. quoyanus* is an incidental catch (Williamson et al. 2004). All three species are targeted in other parts of the Indo-West Pacific by recreational, commercial, artisanal and subsistence fishers (Sadovy 2000, 2001; Evans and Russ 2004).

The six sites were selected for this study based on the abundance of suitable habitat in nearshore, backreef areas where pilot study surveys had revealed that recruits (young-of-the-year) and older juveniles of the three study species were most abundant. Recruits (young-of-the-year) in each species were identified based on size (mm total length, TL) with reference to previous studies examining length-age relationships based on otolith analysis (Ferreira and Russ 1992; Newman et al. 2000; Kritzer 2004; Evans et al. 2008; Mannering 2008). For *P. maculatus* and *L. carponotatus*, recruits were <150 mm TL, whereas for *E. quoyanus*, recruits were <120 mm TL.

### **2.3.2 Recruit abundance**

Recruit abundance for each species was quantified using eight replicate 50m x 5m transects in the nearshore recruitment habitat at each of the six sites in 2009 before collecting recruits and juveniles for gut content analyses. An unbalanced sampling design was used due to a limited number of no-take reserves with suitable recruitment habitat. A single observer (CW) surveyed each transect to minimise observer bias, and all individuals classified as recruits in surveys were much smaller than the size cut-offs reported above. We also note that adults of all three species were frequently observed in nearshore recruitment areas during surveys, which confirms that adults are capable of influencing juveniles. We compared only recruit abundance among reserves and open areas as we considered these individuals to be those most likely to be directly

consumed by large predators. Data were Box-Cox transformed to meet the assumptions of parametric statistical tests due to the presence of zero data on some transects (Akritas 1990). A two-way nested ANOVA was used to test for differences in abundance between zones (reserve and non-reserve, fixed factor) and site (nested within zone, random factor).

### 2.3.3 Diet

Recruits and juveniles of the three study species were collected from the two reserve sites and two non-reserve sites (North Keppel Island and Halfway Island) in 2008 and 2009. The two other non-reserve sites (Miall Island and Humpy Island) were excluded from further analyses on prey availability, diet and prey selection as sample sizes from these locations were small due to the smaller areas of suitable recruitment habitat. Juveniles were collected by divers using SCUBA, spear guns, barrier nets, hand nets and a 10:1 solution of ethanol and clove oil used as an anaesthetic. The length of each individual was measured to the nearest millimetre. Sampled fishes were stored on ice for transport to the lab to minimise decomposition of gut contents and were dissected on the day of collection. The entire stomach was removed and stored in individual 10 ml containers filled with 10% seawater-buffered formalin solution to fix and preserve gut contents. Gut contents from a total of 527 *P. maculatus*, 483 *L. carponotatus* and 676 *E. quoyanus* were examined. Many of these individuals had empty guts and some had guts that contained unidentifiable prey items. Those individuals that contained identifiable prey items, and that were therefore included in the analysis, are tabulated in Table 2-1.

Prey items from gut contents were identified visually using a dissecting microscope (10X magnification) when from a small individual (< 50 mm TL) and with the unaided eye for larger individuals. Taxonomic identifications of prey were made using two standard field guides (Gosliner et al. 1996; Allen et al. 2003). Fish prey were identified to the Family level and included the following categories: Gobiidae (gobies), Blenniidae (blennies), Pomacentridae (damsel-fishes), Tripterygiidae (triplefins), Serranidae (sea basses), Labridae (wrasses),

Pseudochromidae (dottybacks), Labridae - subfamily Scarinae (parrotfishes), Chaetodontidae (butterflyfishes) and Unidentified Fish Larvae. Invertebrates were identified to the Family or Order level and included the following categories: Caridea (shrimp), Brachyura (crabs), Galatheidae (squat lobsters), Alpheidae (snapping shrimp), Stomatopoda (mantis shrimp), Other Small Crustaceans (includes Isopoda, Copepoda and Amphipoda), Cephalopoda (squid and relatives), Palaemonoidea (prawns), and Other Invertebrates (unidentified). The numbers of each prey category were recorded from each gut content sample. Where possible, partial or half-digested prey items were identified using key morphological features (i.e. head or claw). Other fragments that could not be identified were recorded as unidentified prey. We used the number of prey items rather than other metrics (e.g. proportion, volume, etc.) to facilitate direct comparisons with prey availability surveys.

We compared the proportion of samples from each site with empty guts as a measure of “hunger,” which has been used to estimate levels of stress and non-consumptive effects on fishes (Arrington et al. 2002). For each study species at each site, we calculated this metric (gut fullness index) as:

$$1 - \frac{\textit{number of individuals with empty stomachs}}{\textit{total number of individuals collected}}$$

and compared between reserves and non-reserves using one-way ANOVA.

We analysed the effects of five factors on the diet of the three species: (1) Year (2008 and 2009), (2) Zone (reserve and non-reserve), (3) Site (nested within Zone; 6 sites: 2 reserve and 4 open to fishing), (4) Species (the three study species) and (5) Size (TL of each individual). The estimate of variance between years was non-significant ( $p=0.34$ ), so data were pooled across years to increase sample size and statistical power, and Year was excluded from the model (Fletcher and Underwood 2002). Each gut content sample was considered as an independent

replicate. For each species, individuals were grouped into three arbitrary size classes based on the availability of sufficient samples for analysis: *P. maculatus* (0-99 mm TL; 100-199 mm TL; 200-300 mm TL), *L. carponotatus* (0-99 mm TL; 100-149 mm TL; 150-250 mm TL), *E. quoyanus* (0-99 mm TL; 100-199 mm TL; 200-300 mm TL).

In the four-factor model, TL (in millimetres) of each individual was used as a covariate following Anderson et al. (2008). We used permutational multivariate analysis of variance (PERMANOVA) to test for differences in the timing of ontogenetic diet shifts in the three study species. Homogeneity of multivariate variance was verified for all four model-terms using PERMDISP ( $p > 0.05$ ). The Bray-Curtis coefficient was selected to construct the similarity matrix after data were fourth root transformed to normalize the data for statistic analysis (Anderson et al. 2008). Type I (sequential) sums of squares and Monte Carlo randomization were used to meet the assumptions of PERMANOVA due to the unbalanced sampling design and small sample sizes in certain size classes.

To simplify the analysis and provide insights into how the types and foraging modes of consumed prey varied with predator size, we reclassified each of the prey categories enumerated above into one of four categories: (1) mobile vertebrate, (2) cryptic vertebrate, (3) mobile invertebrate, and (4) cryptic invertebrate. Assignment into each category was based on prey behaviour and habitat use. For example, small fishes in the Families Gobiidae, Blenniidae and Tripterygiidae typically remain motionless and in close contact with benthic substrates, and were therefore classified as cryptic vertebrates, whereas fishes in the Families Pomacentridae, Labridae and Scaridae are relatively mobile, and were thus classified as mobile vertebrates. We used PERMANOVA as above to test whether the three study species selected prey based on prey behaviour, and whether such patterns differed among zones, as a test of the influence of large predators on foraging by juvenile predators.

### 2.3.4 Prey availability

Prey availability was quantified at each of the four sites in April 2009. Based on the gut contents of the three study species, we surveyed the abundance of all prey taxa and defined prey as any organisms smaller than 30 mm TL. To quantify the abundance of non-cryptic prey, we conducted underwater visual census (UVC) surveys along four replicate 50m x 1m transects at each of the four sites. A single observer (CW) recorded prey abundance along each transect to reduce observer bias. The prey observed and quantified during UVC were primarily non-cryptic fishes and crustaceans, identified to the Family and Order level, respectively. To quantify the abundance of cryptic prey, we used a dilute solution of ethanol and clove oil (10:1) as an anaesthetics to sample five replicate 50cm x 50cm quadrats at each site at randomly selected points along the same transects established for UVC surveys. Two divers applied the clove oil solution to benthic substrates, waited approximately three minutes, and collected all anesthetised individuals for identification to the same taxonomic level used in visual surveys. Visual transects and clove oil surveys were conducted in the same locations before collecting recruit and juvenile predators for gut content analysis.

We tested for effects of two factors on prey availability: (1) Zone (fixed effect: reserve and non-reserve) and (2) Sampling Method (fixed effect: UVC transect and clove oil quadrat). Preliminary analysis revealed that variation among sites was non-significant ( $p > 0.05$ ), and data from visual transects (mobile prey) and clove oil quadrats (cryptic prey) were standardised and pooled within each site to represent the total prey community following Fletcher and Underwood (2002). We used PERMANOVA to test for effects of Zone and Survey Method on prey availability. Homogeneity of multivariate variance was confirmed for both factors using PERMDISP ( $p > 0.05$ ). Data were  $\log(x+1)$  transformed before constructing the similarity matrix due the occurrence of 0 values for some prey items. Bray-Curtis dissimilarity was used as the metric of comparison. Type I (sequential) sums of squares was used to meet the assumptions of PERMANOVA. Monte Carlo randomization was used to randomly sample data repeatedly and generate a probability distribution to calculate a p-value ( $p(\text{MC})$ ) for each factor.

Similarity percentage (SIMPER) analysis was used to evaluate the contribution of prey categories to variation between zones. The pattern of variation in prey availability between zones and survey methods was visualised using Principal Coordinates Analysis, termed PCO (Anderson and Willis 2003).

### **2.3.5 Prey selection**

Strauss's linear index of selectivity (L) was calculated using data from prey availability surveys and gut content analyses to quantify food preferences for each of the three predator size classes outlined in the diet analysis (Ivlev 1961; Manly et al. 2002). Values of L range between +1 and - 1. Positive values indicate selection for that prey category greater than expected based on its availability (selection), a value near 0 indicates that prey was selected as expected based on availability (neither selection or avoidance), and negative values indicates that prey category was selected less often than expected based on its availability (avoidance).

Multifactorial PERMANOVA was used to test for differences in prey selectivity using three explanatory variables: (1) Zone (reserve and non-reserve), (2) Species (the three study species) and (3) Size (three levels; the three size categories reported above for each species). Strauss's linear selection index for each prey category and predator size category were used as the response variables. Because Strauss' selection index can take values between -1 and 1, we used the Euclidean distance similarity index to construct the matrix, and Type I (sequential) sums of squares and Monte Carlo randomization was used to meet the assumptions of PERMANOVA due to the unbalanced sample sizes.

## **2.4 RESULTS**

### **2.4.1 Recruit abundance**

For all three study species, there was no significant difference in recruit abundance between reserves and non-reserves (Fig. 2-1, Table 2-2). Abundance of *P. maculatus* recruits was greater

at sites open to fishing, and this effect was nearly significant. With the exception of *L. carponotatus*, there was also no difference in recruit abundance among sampling sites (Table 2-1). However, we note that variability in recruit abundance among zones and sites was high, and thus our power to detect differences was low.

#### 2.4.2 Diet

For each study species, nearly half of all individuals collected had empty guts. The mean ( $\pm$ SD) percentages of samples across the 4 sampling sites in two years with empty stomachs were as follows: *P. maculatus* ( $58.5\pm 16.7\%$ ), *L. carponotatus* ( $57.2\pm 16.3\%$ ) and *E. quoyanus* ( $44.5\pm 15.6\%$ ). There was no significant difference in the proportion of empty stomachs between reserves and open areas ( $F=4.068$ ,  $p=0.1308$ ) suggesting that hunger level between zones was similar.

There was no evidence that the diet of recruits or juveniles differed between reserves and non-reserves. PERMANOVA analyses (Table 2-3) showed significant differences in diet between species and between predator size categories within a species, but there were no differences between zones (reserves and non-reserves) or sites within zones (Fig. 2-2). Recruits of both *P. maculatus* and *L. carponotatus* consumed a high proportion of cryptic invertebrates (shrimps and crabs), and the proportion of vertebrate prey in their diet increased in both species with size. Vertebrate prey items made up a greater proportion of the diet in *P. maculatus* than in *L. carponotatus* (Fig. 2-2); however, vertebrate prey species composition differed between the two predators: *P. maculatus* consumed cryptic gobies at smaller sizes and shifted to mobile damselfishes and wrasse at larger sizes, whereas *L. carponotatus* consumed small cryptic gobies (primarily *Eviota* spp.) when small and shifted to larger gobies (e.g. *Asterropteryx* spp. and *Istigobius* spp.) and crabs as they increased in size. In contrast, *E. quoyanus* predominantly consumed cryptic invertebrates, exclusively at larger sizes, but with occasional mobile and cryptic invertebrates included in the diet of smaller individuals. Each of the three study species

exhibited ontogenetic diet shifts, but the size at which these shifts occurred were similar between reserves and non-reserves (Fig. 2-2).

#### 2.4.3 Prey availability

As expected, prey availability data from visual transects and clove oil quadrats differed significantly (Table 2-4) as they sampled different types of prey (i.e. mobile versus cryptic). Principal Coordinates Analysis illustrated clear separation between the two sampling methods (Fig. 2-3). The composition of mobile prey (visual transects) was similar between reserves and non-reserves; however, the composition of cryptic prey (clove oil transects) differed between reserves and non-reserves. This resulted in a significant interaction between zone and survey method (Table 2-4).

SIMPER analysis revealed that reserves had a greater abundance of Galatheidae (contribution: 19.1%), Palaemonoidea (contribution: 14.1%), and Gobiidae (contribution: 7.9%) than non-reserves, but had less Caridea (shrimp) (contribution: 11.0%). These four prey categories explained 81% of the difference in prey availability between reserves and non-reserves.

#### 2.4.4 Prey selection

Prey selection indices calculated from diet analysis and prey availability confirmed that prey selectivity shifted as predators grew larger (Fig. 2-4). PERMANOVA analysis revealed that all three factors – Species, Zone and Size – had a significant influence on prey selection (Table 2-5). As expected based on diet analysis, the three species differed in the prey selected. The significant effect of Zone (reserve versus non-reserve) on prey selection reflects the differences in prey availability observed between zones rather than actual differences in prey consumed by a given species in different zones. The significant effect of predator size on prey selection is reflected in clear ontogenetic shifts for all three species (Fig. 2-4). Small *P. maculatus* (< 99 mm TL) preferentially selected shrimp (Caridea) in reserves and non-reserves whereas large

*P. maculatus* (> 200 mm TL) avoided shrimp and predominantly consumed damselfishes in both reserves and non-reserves. As *L. carponotatus* increased in size, their preference for gobies increased while consumption of Galatheidae and shrimps decreased in both reserves and non-reserves. Similarly, *E. quoyanus* showed a preference for crabs (Brachyura) that increased as their size increased, and a consistent avoidance of Galatheidae across all sizes classes.

## 2.5 DISCUSSION

Overall, we found little evidence that increases in the abundance of large predatory fishes inside no-take reserves on the Great Barrier Reef influence the abundance or feeding behaviour of recruits and juveniles. We found no support for the hypotheses that no-take reserves with a greater abundance of large predators influence recruitment, diet, or the timing of ontogenetic diet shift in juvenile predators. There were some unexplained differences in prey availability between reserves and areas open to fishing, which resulted in slight differences in the magnitude of prey selection indices for some taxa. However, overall the key trends in diet and prey selection were explained by body size. Recruits and juveniles of each of the three study species are found in the same nearshore habitat and have similar diets at small size classes, but their diets and prey preferences diverged as they increased in size.

### 2.5.1 Recruit abundance

Greater predator abundance inside reserves has been associated with decreased prey abundance and shifts in prey composition (Beets 1997; Stewart and Jones 2001; Graham et al. 2003), and we therefore hypothesized that recruit abundance of predatory fishes would be lower inside reserves. We found no evidence to support this hypothesis, although our power to detect differences was low due to high variability. Nevertheless, one likely explanation for this result is that in our study system recruits and juveniles of the three study species are most abundant in shallow nearshore reef habitats, whereas adults are most abundant on reef flats and slopes. As a result, encounter rates between adults and recruits/juveniles may be reduced, although we did

frequently observe adults in nearshore habitats. Quantifying encounter rates between adults and juveniles in different habitats (e.g. nearshore areas where juveniles are more abundant and reef slope habitats where adults are more abundant) would be useful to understand how juvenile predation risk varies across habitats. Predation risk for recruits and juveniles may also be lower for the three study species because at small sizes they are relatively cryptic and less abundant compared to other potential prey species, and may therefore only be opportunistic targets of large predators.

### 2.5.2 Diet

There was no evidence of a difference in the proportion of empty guts or in the diets of the recruits and juveniles of the three species between reserves and non-reserves. This finding was consistent across all sizes of recruits and juveniles, and suggests that their foraging behaviour was not influenced by the greater abundance of large predators inside reserves. The proportion of empty guts has been used as a basic metric of feeding rate in animals (Huey et al. 2001). Previous work demonstrates that fishes in higher trophic levels feeding on energy-rich food resources often have a higher proportion of empty guts (Arrington et al. 2002), but the relationship between frequency of empty guts and feeding ecology is still unclear (e.g. Gill and Hart 1994; Vinson and Angradi 2010). The proportions of empty guts in our samples were similar for the recruits and juveniles of all three species across all sampling sites (*P. maculatus*:  $58.5 \pm 16.7\%$ ; *L. carponotatus*:  $57.2 \pm 16.3\%$ ; *E. quoyanus*:  $44.5 \pm 15.6\%$ ), and greater than has been described for *P. leopardus* (30-40%; St John et al. 1999, St John et al. 2001). However, the size range of sampled *P. maculatus* in the present study (23-329 mm TL) was considerably smaller than that of *P. leopardus* (47-573 mm fork length: St John et al. 1999; 130-585 mm fork length: St John et al. 2001), which could account for differences between the two studies. Furthermore, the higher proportion of empty guts in the present study may in part be an artefact of our sampling design; samples were collected throughout the day rather than focusing on the peak crepuscular feeding periods of predatory fishes (e.g. dawn and dusk; St John 1999).

Although there was no effect of zone on the diets of recruits and juveniles, we found clear evidence of diet differences among species and ontogenetic diet shifts within species. At small sizes, *P. maculatus* and *L. carponotatus* consumed a higher proportion of fish prey than *E. quoyanus*. As they increased in size, juvenile *P. maculatus* and *L. carponotatus* diets diverged: *P. maculatus* switched to a diet dominated by fish prey, whereas *L. carponotatus* consumed a mix of fish and crustaceans. In contrast, *E. quoyanus* consumed mostly crustaceans and this remained relatively stable throughout their ontogeny. These patterns suggest that food competition between the three species, all of which occur in the same habitat, is relatively low (Root 1967).

Previous studies have documented similar ontogenetic diet shifts in predatory fishes. For example, *P. leopardus* on the Great Barrier Reef exhibit a similar shift in diet with growth as we observed in *P. maculatus*, from crustaceans at small sizes to mobile fishes at larger sizes, including pomacentrids (damselfish) and labrids (wrasse) (St John 1999). However, large *P. leopardus* in New Caledonia include invertebrates (crustaceans and molluscs) in their diet (Kulbicki et al. 2005), suggesting that diet varies regionally. Further evidence of a regional effect on diet comes from a comparison of the only published study we know of on diets of *L. carponotatus* and *E. quoyanus* and the results of the present study. We found that *L. carponotatus* fed on large numbers of blennies and *E. quoyanus* consumed a high proportion of crustaceans at the inshore Keppel Islands, whereas Connell (1998b) found that *L. carponotatus* consumed gobies and *E. quoyanus* consumed relatively more fishes at the offshore Capricorn-Bunker reefs, which are approximately 70 km from our study site.

### 2.5.3 Prey availability

Why abundances of Palaemonoidea, Galatheidae, Gobiidae and Caridea would differ between reserves and non-reserves is unclear, but several possible explanations exist. For example, most

Palemonoids we surveyed were from the genus *Coralliocaris*, which are strongly associated with live *Acropora* corals (Stella et al. 2011). Similarly, most gobies were from the genus *Gobiodon*, which are strongly associated with live *Acropora* corals (Munday et al. 1997). In a related study, we documented higher cover of live *Acropora* inside reserves in the Keppel Islands (Chapter 3; Wen et al. 2012b), which likely explains the greater abundance of Palemonoids and Gobies inside reserves. Furthermore, although not explicitly tested in this study, the removal of large predators can have cascading effects on both the structure of microhabitats and abundance of organisms in lower trophic levels (e.g. McClanahan et al. 2000; Hughes et al. 2007; Mumby et al. 2007), which could explain differences in the abundance of Caridea and Galatheidae between reserves and open areas. However, the specific trophic relationships between large individuals of the three predatory species in this study – which were significantly more abundant inside Keppel Island reserves – and lower trophic levels remain unclear and warrant further study (e.g. Kramer et al. 2012).

#### 2.5.4 Prey selection

Prey selection indices were calculated for three size classes of each study species using prey availability surveys and gut content analysis. All three study species exhibited selection for particular prey categories, and patterns of prey selection changed as species grew larger. At the smallest size class, the three species selected similar prey, but diets diverged at larger size categories. Ontogenetic shifts in prey selection are common in fishes and likely reflect differences in mouth size, muscle development, swimming ability, and predation risk between size classes. For example, small size classes of *P. maculatus* are relatively cryptic and remain close to shelter, and we found they selected benthic crustaceans and small cryptic fishes. As they grew, juvenile *P. maculatus* exhibited greater selection for non-cryptic, mobile fishes, which generally have a higher protein and lipid composition compared to prey selected at small size classes (Guillaume 2001). This dietary shift likely reflects an increase in swimming ability with increasing size and a decrease in predation risk that allows juveniles to forage farther from

shelter and pursue mobile prey. In contrast, shifts in diet with size of the strongly benthic-associated *E. quoyanus* likely reflect the greater ability of larger individuals to handle large prey (e.g. larger gape and increased muscle development). At small size classes *E. quoyanus* selected small shrimp and crustaceans, which have relatively thin shells, whereas larger *E. quoyanus* switched to consuming large crabs that have harder shells and higher protein content.

Although we did detect some minor differences in prey selection among the three species in reserves and non-reserves, these were most likely due to the as yet unexplained differences in the abundance of a few categories of cryptic prey between reserves and open areas. The Galatheidae and Palaemonoidea, which differed in abundance between reserves and fished areas, were largely avoided by all size classes of the three study species. In contrast, shrimp (Caridea), which were positively selected as prey by the smaller size classes of all three study species, were less abundant inside reserves, despite a similar abundance of recruits of the three study species in reserve and non-reserve zones.

## 2.6 CONCLUSIONS

In the present study we examined prey availability inside and outside reserves and evaluated the diets and patterns of prey selection of recruits and juveniles of three predatory fish species that are important fishery targets on Indo-Pacific coral reefs. We hypothesized that the greater abundance of large predators inside no-take reserves might influence the abundance of recruits and the diets and patterns of prey selection in recruits and juveniles. We found little evidence to support these hypotheses. Recruit abundances between reserves and open areas was similar for all species, and each species exhibited similar diets, patterns of prey selection, and ontogenetic diet shifts in reserves and open areas. Apart from providing some of the first quantitative data on juvenile dietary patterns for fishery species, this study demonstrates that there is little effect of a greater abundance of large predators inside reserves on the juvenile stages of these same predators. However, we note that similar studies should be conducted on other predator species,

and in locations where differences in predator biomass between reserves and open areas are greater, to determine whether our conclusions are broadly applicable.

**Table 2-1 Sample size of gut content**

Number of gut content samples analysed from each of the three study species (*Plectropomus maculatus*, *Lutjanus carponotatus* and *Epinephelus quoyanus*) categorised by predator size class and sample location. No-take reserve sites delineated by “reserve” and sites open to fishing (non-reserves) by “open”.

<i>P. maculatus</i>	Clam Bay (reserve)	Middle (reserve)	Halfway (open)	N Keppel (open)
<49mmTL			2	
50-99mmTL	2	4	24	10
100-149mmTL	18	5	17	12
150-199mmTL	4		8	5
200-249mmTL	13	2	10	8
250-299mmTL	3		5	7
>300mmTL				
<i>L. carponotatus</i>	Clam Bay (reserve)	Middle (reserve)	Halfway (open)	N Keppel (open)
<49mmTL			2	
50-99mmTL	6	7	9	7
100-149mmTL	9	9	15	9
150-199mmTL	11	4		5
200-249mmTL	3			
250-299mmTL				
>300mmTL				
<i>E. quoyanus</i>	Clam Bay (reserve)	Middle (reserve)	Halfway (open)	N Keppel (open)
<49mmTL	4	2	9	4
50-99mmTL	19	13	7	6
100-149mmTL	83	19	10	19
150-199mmTL	12	6	4	5
200-249mmTL	3	2	2	
250-299mmTL	2	3		
>300mmTL	2	2		

**Table 2-2 Two-way ANOVA of zone and site(zone) on recruit abundance**

Results of a two-way nested ANOVA testing for effects of zone (reserve & non-reserves) and sampling site (nested in zone) on recruit abundance of the three study species.

	zone		site(zone)	
	F	<i>p</i>	F	<i>p</i>
<i>P. maculatus</i>	3.253	0.078	2.074	0.101
<i>L. carponotatus</i>	0.255	0.608	3.109	0.025*
<i>E. quoyanus</i>	1.9	0.171	1.6	0.204

**Table 2-3 PERMANOVA of four factors of diet.**

Results of a multifactorial PERMANOVA testing effects of four factors on the composition of gut contents of the three study species: Zone (reserve & non-reserve), Species (three predator species: *Plectropomus maculatus*, *Lutjanus carponotatus*, and *Epinephelus quoyanus*), Site (nested within zone; four sites per zone), and Size (mm TL). \* indicates a statistically significant difference at  $\alpha = 0.05$ .

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Size (TL)	1	98555	98555	27.02	0.0001	9935	0.0001*
Zone	1	5115.7	5115.7	1.1706	0.3159	719	0.3561
Species	2	2.03E+05	1.02E+05	27.792	0.0001	9922	0.0001*
Site(Zone)	4	15467	3866.7	1.062	0.3714	9911	0.3633
Residual	599	2.18E+06	3640.9				
Total	607	2.50E+06					

**Table 2-4 PERMANOVA results of three factors on prey availability**

Results of a multifactorial PERMANOVA testing for effects of three factors on prey availability: Zone (reserve & non-reserves), survey Method (UVC & clove oil), and interaction between Zone and Method. P(MC) is the *p*-value calculated using Monte Carlo randomization. \* indicates a statistically significant difference at  $\alpha = 0.05$ .

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Zone	1	7799.4	7799	8.5175	0.0001	9956	0.0001*
Method	1	57712	57712	63.025	0.0001	9951	0.0001*
ZonexMethod	1	3289.6	3290	3.5924	0.0059	9953	0.0081*
Residual	43	39375	915.7				
Total	46	1.08E+05					

**Table 2-5 PERMANOVA result of three factors on prey selection**

Results of a multifactorial PERMANOVA testing effects of three factors on prey selection in the three study species: Zone (reserve & non-reserve), Species (three predator species: *Plectropomus maculatus*, *Lutjanus carponotatus*, and *Epinephelus quoyanus*), and Size (mm TL). \* indicates a statistically significant difference at  $\alpha = 0.05$ .

Source	df	SS	MS	Pseudo-F	P(perm)
Species	2	6.161	3.08	20.697	0.0001*
Zone	1	5.177	5.177	34.782	0.0001*
Size	5	11.26	2.252	15.134	0.0001*
Residual	216	32.15	0.149		
Total	233	71.21			

Figure 2-1 Bar chart of abundance of three species inside and outside reserves.

Density of three recruits species between zones. Open bars indicate areas open to fishing; closed bars represent no-take reserves.

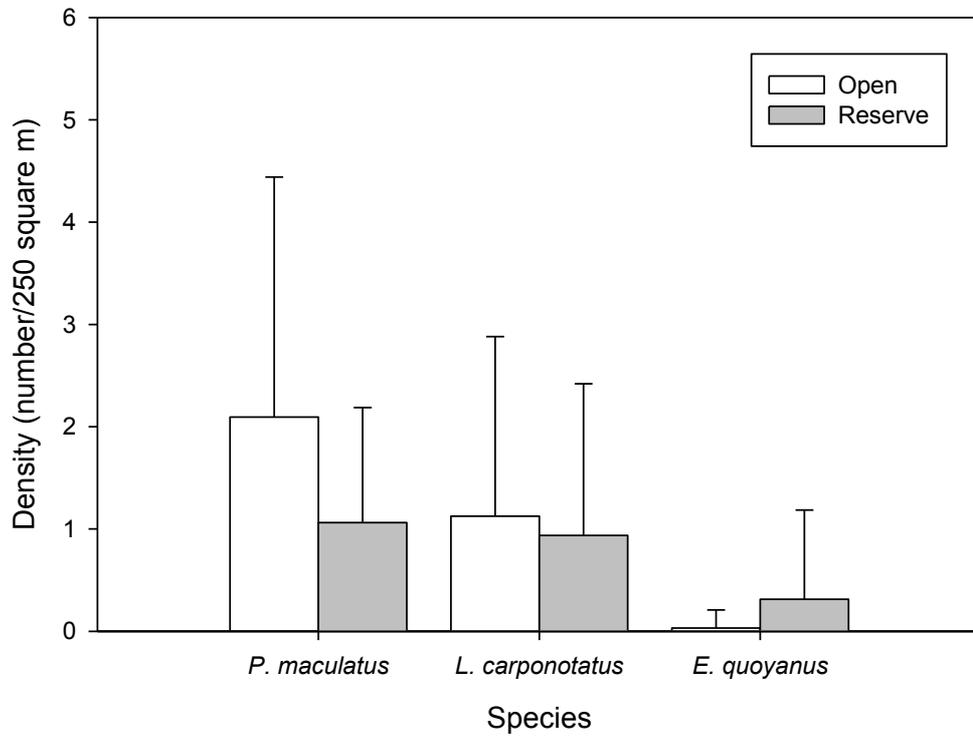
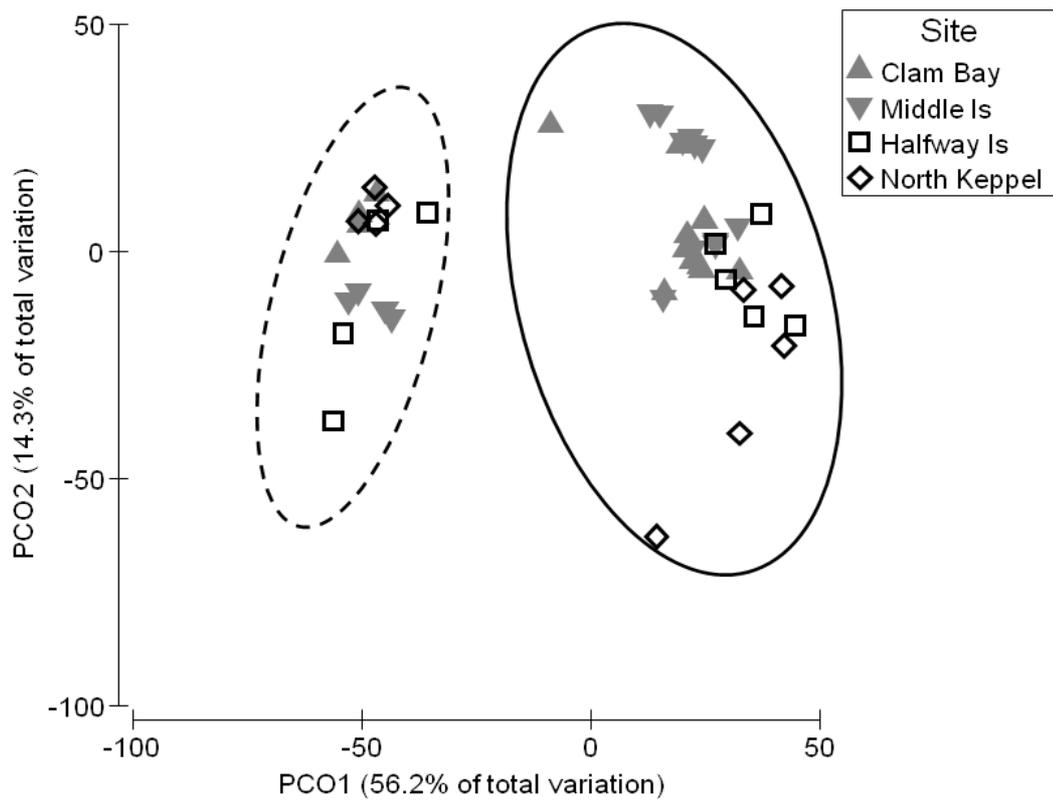




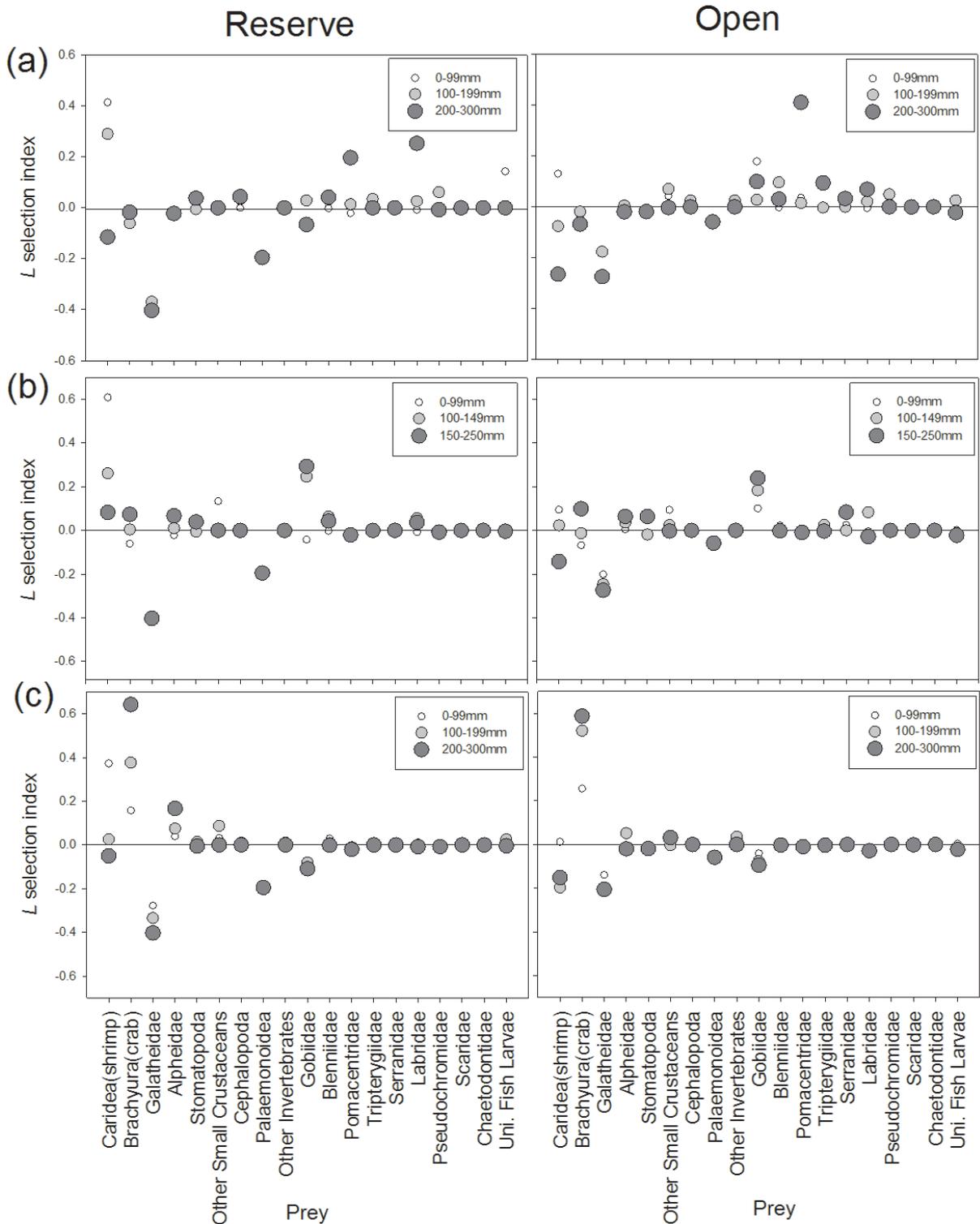
Figure 2-3 PCO plot of prey availability inside and outside reserves

Principal Coordinates Analysis (PCO) plot of prey availability at two no-take reserves (grey solid symbols) and two nearby areas open to fishing (open symbols). Each data point represents a single underwater visual census (UVC) transect or a clove oil quadrat. UVC transects are grouped together by the dashed line, clove oil quadrats by the solid line.



**Figure 2-4 Ontogenetic shift of prey selection from three species**

Ontogenetic changes in prey selectivity of the three study species inside no-take reserves (left panels) and open to fishing (right panels). Data are presented for (a) *Plectropomus maculatus*, (b) *Lutjanus carponotatus* and (c) *Epinephelus quoyanus*.



## **CHAPTER 3: Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia**

Coral Reefs (in press) DOI: 10.1007/s00338-012-0985-x

### **3.1 ABSTRACT**

Ongoing larval recruitment is fundamental in sustaining marine populations, especially those species subject to fisheries exploitation. Recruitment is conditional upon the availability of suitable settlement habitat, and widespread degradation of shallow marine habitats may pose a major threat to the sustainability of coastal fisheries. This study examined recruitment patterns and microhabitat associations for three carnivorous fishes, *P. maculatus*, *L. carponotatus* and *E. quoyanus* at the Keppel Islands, southern Great Barrier Reef, Australia. Habitat selectivity was highest for recruits and there was an apparent ontogenetic shift in microhabitat associations, with recruits associated mostly with corymbose *Acropora* while adults were more commonly associated with tabular *Acropora*. The proportion of *P. maculatus* (72%) that associated with live corals was higher than for *L. carponotatus* (68%) and *E. quoyanus* (44%), but recruits from all three species were found predominantly in structural habitats comprised of live branching corals. Moreover, recruits of all three species were found predominantly on patches of live-coral habitat located over loose substrates (sand) rather than consolidated substrates. Densities of recruits were highly variable among locations and among reef zones, but these differences were only partly attributable to availability of preferred microhabitats. Specific reliance on live coral microhabitats is yet to be tested, but these findings demonstrate that at least some carnivorous reef fishes strongly associate with live corals (especially during early life-history stages), and may therefore be highly sensitive to increasing coral loss and degradation of reef habitats.

### **3.2 INTRODUCTION**

Coral reef ecosystems provide habitat for thousands of fish species, many of which settle in very specific microhabitats, such as live coral heads. Jones et al. (2004) suggested that up to

75% of coral reef fishes rely on live corals at the juvenile stage for food, shelter or recruitment substrata. Accordingly, there is often a strong positive relationship between coral cover and both abundance (Carpenter 1981; Jennings et al. 1996; Findley and Findley 2001) and diversity (Bell and Galzin 1984; Sano et al. 1984; Bouchon-Navaro and Bouchon 1989; Chabanet et al. 1997; Munday 2004) of coral reef fishes. Global degradation of coral-dominated habitats (Gardner et al. 2003; Bellwood et al. 2004; Bruno and Selig 2007; Pratchett et al. 2011) thus poses a significant threat to ongoing recruitment and viability of reef fish populations (Sano et al. 1987; Jones et al. 2004; Pratchett et al. 2008a). However, coral reef fishes vary in their level of reliance on corals, ranging from highly specialised fishes that are critically dependent on a single coral species for food or habitat (Munday 2004; Pratchett 2005), to fishes that only very loosely associate with live corals (Wilson et al. 2008). Thus far, effects of coral bleaching or coral loss on fishes have been most apparent among highly specialised coral-dependent species, including butterflyfishes, damselfishes and gobies (Munday et al. 1997; Syms and Jones 2000; Booth and Beretta 2002; Pratchett et al. 2006). There is anecdotal information suggesting that some larger, carnivorous species such as coral trout (*Plectropomus* spp.) may also be adversely affected by significant declines in live coral cover (Graham et al. 2007; Russ et al. 2008). However, mechanisms underlying such effects are unclear because little is known about the specific habitat requirements of large predatory fishes.

Many coral reef fishes that do not typically feed on or live within live coral are nonetheless dependent on live coral, and may be negatively affected by loss of coral and associated declines in structural complexity (e.g. Jones et al. 2004; Wilson et al. 2006). These include fishes that rely on corals only during a specific period in their life histories (Graham et al. 2007). They may indirectly depend on coral-dominated habitats because such habitats provide increased access to prey (Westmacott et al. 2000) and moderate the effects of key biological processes such as competition and predation (Coker et al. 2009). On the Great Barrier Reef (GBR), densities of coral trout (*Plectropomus* spp.) declined >20% following extreme coral bleaching and marked changes in habitat structure at the Keppel Islands in 2006, whereas trout densities were stable or

increased at all other study locations where there was no change in coral cover (Russ et al. 2008). At One Tree Island, GBR, Kingsford (2009) found that coral trout (specifically, *P. leopardus*) were generally most abundant in areas with high coral cover and that recruitment was mostly to coral-rich habitats. Key habitat requirements of newly settled and juvenile life stages of coral trout and many other fisheries species have not been explicitly tested, but declines in abundance following severe coral loss suggest that live coral may be critical during recruitment. Following the catastrophic 1998 coral bleaching event in the Indian Ocean, Graham et al. (2007) used fisheries independent survey data to test for effects on fishery target species. While overall biomass of fishes was unchanged, Graham et al. (2008) found a marked decline in the abundance of juvenile fishes (<30 cm), reflecting recent recruitment failure across many different fish species (including piscivorous species), which was attributed to the loss of biological and physical habitat structure provided by live scleractinian corals.

In open marine populations, ongoing recruitment is fundamental to the persistence of local populations (Roughgarden et al. 1988; Caley et al. 1996). This is especially true for species subject to fishing and harvesting, whereby rates of recruitment must exceed fisheries catches in order to sustain local populations. Few fisheries management approaches explicitly consider differential (temporal or spatial) inputs from larval settlement (but see Mangel 2000). This is because larval supply and the resulting patterns of recruitment are generally considered to be highly stochastic in time and space, due to the large number of different processes (e.g. the size and reproductive fitness of source populations, planktonic dispersal and survival of larval fishes) that determine successful settlement (Doherty and Williams 1988; Jones 1991; Doherty 2002). If however, recruitment is limited by availability of specific settlement habitats (Tolimieri 1995; Schmitt and Holbrook 2000; Wilson et al. 2010b), then it may be possible to not only predict, but also identify and potentially manage disturbances that are likely to influence local recruitment rates for key fisheries species.

The purpose of this study was to explore microhabitat associations for three species of predatory reef fishes at the Keppel Islands (23°10'S, 151°00'E), on the inshore, southern Great Barrier Reef (GBR), Australia. We examine whether these species have a specific reliance on live coral habitats, and if so, what growth forms are most important. It was predicted *a priori* that these fishes would have a high reliance on structurally complex microhabitats, such as those provided by branching corals, especially during their early life-history when they are most vulnerable to predation (Almany 2004a). Relative use of specific microhabitats was compared to habitat availability, whereby disproportionate use of microhabitats was used to infer habitat preferences. Moreover, microhabitat use was compared across three distinct life-stages of each study species, testing for ontogenetic changes in the relative use of specific habitat types.

### 3.3 MATERIALS AND METHODS

#### 3.3.1 Study species

The study focussed on three species of carnivorous fishes, i) the inshore coral trout, *P. maculatus*, ii) the stripey snapper, *L. carponotatus*, and iii) the long-finned rock cod, *E. quoyanus*. *P. maculatus* (Serranidae) is the largest of the three study species ( $L_{\infty}$ = 60cm; Ferreira and Russ 1992). It is a relatively long-lived (>12 years) and slow-growing species, restricted to the Indo-Australia archipelago and found predominantly in nearshore, often turbid waters (Ferreira and Russ 1992). Although this species is not a major component of commercial fisheries, which mainly target midshelf and outer-shelf reefs, its nearshore abundance makes *P. maculatus* an important component of recreational catches (Williams and Russ 1994). *L. carponotatus* (Lutjanidae) is a moderate sized snapper (up to 34 cm TL) that can live up to 20 years of age (Newman et al. 2000). It is distributed mainly on inshore reefs of Great Barrier Reef (Newman and Williams 1996). *L. carponotatus* is caught commercially on the GBR, but is mainly taken by recreational fishers (Williams and Russ 1994). *E. quoyanus* (Epinephelidae) is a relatively small grouper (up to 36 cm TL; Connell and Kingsford 1998). *E. quoyanus* is often caught incidentally by recreational fishers on the GBR targeting other species (Diggles and

Ernst 1997). In this study, fishes were categorised as either recruits (young of the year), subadults, or adults (sexually mature individuals) based on size (Table 3-1) using data from independent studies on size at age, and size at sexual maturation (Mannering 2008).

### 3.3.2 Field sampling

This study was carried out in the Keppel Island group (23°100 S, 150°570 E), which is an inshore group of islands in the southern Great Barrier Reef, Australia (Fig. 3-1). We surveyed fishes at six different locations, North Keppel, Clam Bay, Halfway Island, Middle Island, Miall Island and Humpy Island, which had generally similar exposure, but differ in their marine park status (Fig. 3-1). Eight replicate 50 x 6m belt transects (300m<sup>2</sup>) were surveyed at each location, with approximately equal sampling in shallow (1-3 m depth) and deep (4-6 m depth) habitats, but no explicit distinction was made between depth zones. Differences in abundance of fishes among reef zones were considered, but only at Clam Bay, where we ran eight replicate 50 x 6m belt transects (300m<sup>2</sup>) in each of six different zones (lagoon, back reef, reef flat, reef crest, reef slope and reef base). These transect-based surveys were used to establish the relative abundance of fishes among locations, and among zones, but we used additional surveys to obtain sufficient data on the specific microhabitat associations of recruit, subadult and adult fishes.

Specific microhabitat preferences for each of the three predatory fishes were recorded during timed swims in January 2010. Four replicate 30-minute swims were conducted at each location, with approximately equal sampling across different reef habitats (lagoon, back reef, reef flat, reef crest, reef slope and reef base), recording the specific microhabitat in which individual fish was initially sighted. In most coral reef studies (e.g. Wilson 2010b), microhabitat is used to describe principal structural habitats (e.g. certain species or types of corals) that are used by fishes, mostly at settlement. This is appropriate for fishes with very strong microhabitat preferences, such as coral dwelling gobies or damselfishes (Wilson 2010b), but for larger more mobile fishes, which may have only a very loose affinity with specific habitat features, there is a

need to carefully consider the appropriate scale and assignment of microhabitat types. During this study, we distinguished both the main structural habitat (e.g. branching coral, soft coral or macroalgae), as well as the underlying and surrounding substrate type. It was considered, for example, that corymbose corals on consolidated reef pavement would provide a fundamentally different habitat to the same coral positioned on sandy substrates. The structural habitats considered were; i) arborescent (or staghorn) *Acropora*, ii) tabular *Acropora*, iii) corymbose *Acropora*, iv) other branching corals (e.g. *Pocillopora*), v) massive corals (mostly massive *Porites*), vi) soft coral, vii) macroalgae, and viii) dead branching corals. The distinction among different growth forms of *Acropora* was considered important, partly due to the prevalence of *Acropora* at all study locations, but also based on readily apparent differences in the use of these habitats. The underlying habitats were divided into i) consolidated substrates, where the underlying habitat was carbonate pavement or terrigenous rock, versus ii) loose substrates, which included both sandy substrates and rubble banks. To relate spatial variation in recruitment of fishes to spatial variation in the availability of specific microhabitats, further sampling of benthic composition was conducted at each of the six study locations in March 2010. A total of 4 replicate transects was sampled in each of two different habitats (reef crest and reef slope) at each site. The relative abundance of different microhabitats was estimated using point-intercept transects following Pratchett et al. (2011) recording the microhabitat category underlying each of 100 evenly spaced points along every transect.

### 3.3.3 Data analysis

Variation in the abundance of fishes, both among locations and among reef zones, was analysed using non-parametric Kruskal-Wallis (KW) tests because data failed to meet assumptions of normality. These tests are comparable to 1-way ANOVA, but do not require that data are normally distributed (Zar 1999). We also used corrected values of H ( $H_c$ , rather than H) to take account of tied ranks (Zar 1999). Independent KW tests were run for each species and life-stage

(Table 3-1) and Bonferroni corrections were applied to minimise overall error rates following Sokal and Rohlf (1995).

Habitat selectivity by each of the three life stages (recruits, subadults and adults) for each of the fishes (*P. maculatus*, *L. carponotatus* and *E. quoyanus*) was analysed using log-likelihood statistics (Manly et al. 2002), which test whether available resources are used in proportion to their availability. If the proportional use of a particular microhabitat is significantly greater than its proportional availability, this indicates a microhabitat preference (Manly et al. 2002). Resource selection functions were then used to determine which microhabitat types were selected more or less frequently than expected based on their availability (Manly et al. 2002). Selection functions were calculated separately for each location, but then pooled to test for overall microhabitat preferences, and a Bonferroni-corrected 95% CI was calculated around each selection function. Use of specific microhabitats was deemed significantly disproportionate (either positively or negatively) to availability if the 95% CI did not encompass 1 (Manly et al. 2002).

## **3.4 RESULTS**

### **3.4.1 Spatial variation in abundance of fishes**

The most abundant of three carnivorous fishes surveyed in the Keppel Islands was *P. maculatus* (mean = 3.73 fish per transect  $\pm$  0.56 SE), and a very high proportion of the individuals (45.2%) were recruits (young of the year). By comparison, overall densities for *E. quoyanus* (mean = 2.27 fish per transect  $\pm$  0.37SE) were lower than for *P. maculatus*, but nearly half of all individuals recorded (54/109) were larger than the mean size at maturation, and only 6 recruits of this species were recorded on belt transects. Overall densities of all three fishes varied greatly among the 6 study locations (Fig. 3-2), especially among recruits for both *P. maculatus* and *L. carponotatus* (Table 3-1, Fig. 3-2). Most notably, there were three locations (North Keppel, Halfway Island and Clam Bay) that received high levels of recruitment (mean  $>3.7$  recruits per

transect), whereas densities of recruits at the three remaining locations (Miall Island, Humpy Island and Middle Island) were < 1.6 recruits per transect. These patterns were largely driven by variation in recruitment of *L. carponotatus* (Fig. 3-2), though the three sites with highest densities of *L. carponotatus* recruits (North Keppel, Halfway Island and Clam Bay) also had the highest densities of *P. maculatus* recruits. Spatial patterns in abundance of recruits did not correspond with patterns in abundance of subadult or adult fishes (Fig. 3-2). Similarly, variation in the abundance of subadults did not reflect variation in adult abundance across the six locations for the three fish species. In *L. carponotatus*, for example, the location with highest densities of adult fish (Middle Island; mean = 1.87 fish per transect  $\pm$  1.05SE) had the lowest densities of recruits and no subadults (Fig. 3-2).

The relative abundance of species and life stages varied greatly among zones (Fig. 3-3). The highest total abundance of *E. quoyanus* (across all life-stages) was in the shallow back reef (mean = 10.6 fish per transect  $\pm$  2.1SE), in habitats dominated by rubble, but densities of recruits, subadults or adults were not significantly different among habitats (Table 3-1). In contrast, densities of *L. carponotatus* were significantly different among zones, but mostly among early life history stages (Table 3-1); *L. carponotatus* was observed mostly on reef flats (mean = 7.0 fish per transect  $\pm$  2.1SE), while *P. maculatus* was most abundant on the reef base (mean = 15.9 fish per transect  $\pm$  1.6SE). Recruits of both *L. carponotatus* and *E. quoyanus* were mainly found in shallow reef zones and rarely found beyond the reef crest. Recruits of *P. maculatus* were most abundant on the reef base, but were also common on the reef slope, in the back reef and on the reef edge (Fig. 3-3).

#### **3.4.2 Microhabitat associations**

Patterns of microhabitat-use were documented for a total of 2,371 individual fishes, including recruits, subadult and adult fishes of all three species. All fishes were found associated with a wide range of different microhabitats, ranging from small distinct colonies of corymbose

*Acropora* (mostly, *Acropora millepora*) to macroalgae and open expanses of sand and rubble with no obvious structural habitat (Fig. 3-4). There was however, an apparent ontogenetic shift in microhabitat associations, which was similar for all three species. The proportion of individuals associated with corymbose *Acropora* declined with increasing size (and age), with a corresponding increase in the proportion of individuals found associated with tabular *Acropora*, massive *Porites* and other massive corals. This pattern was most apparent for *P. maculatus*, where 37% (78/212) of recruits were associated with corymbose *Acropora*, compared to only 3% (4/149) of adult fishes. In contrast, 24% (35/149) of adult *P. maculatus* were associated with tabular *Acropora*, compared to <5% (10/212) of recruits of the same species. Overall (across all life stages), 72% (574/798) of *P. maculatus* were associated with live coral habitats, compared to 68% (480/708) for *L. carponotatus*, and only 44% (382/865) for *E. quoyanus*.

All fishes exhibited significant selectivity in their association with different microhabitats (Table 3-2). Recruits of *L. carponotatus* exhibited the highest levels of selectivity ( $X_{LI}^2 = 682.3$ ,  $df = 35$ ,  $p < 0.001$ ), using corymbose *Acropora* disproportionately more than expected whilst the use of tabular *Acropora*, massive *Porites*, soft coral, macroalgae, and sand/rubble was much less than expected. For all three species, selectivity was highest among recruits and lowest for adults. Recruits of all three species used corymbose *Acropora* in significantly higher proportions than expected based on availability (Table 3-2). In contrast, most adult fishes used a wide range of microhabitats in approximate accordance with their availability, though adult *P. maculatus* used tabular *Acropora* disproportionately more than expected.

Availability of specific microhabitats was highly variable among the six study locations. Total live coral cover was significantly different among locations (ANOVA,  $F = 9.08$ ,  $df = 5/35$ ,  $p < 0.001$ ), ranging from 10.6% at Miall to 44.7% at Halfway. Miall Island had the lowest coral cover, but was also unusual because *Acropora* corals were underrepresented in coral communities at this location. At Miall Island *Acropora* accounted for only 72% of live coral cover, whereas *Acropora* (and mostly arborescent *Acropora*) accounted for > 81% of live coral

at all other locations. Cover of Pocilloporidae was also much higher at Miall Island compared to all other locations, but the most abundant taxa (after *Acropora*) were “other massive corals”, comprising mostly faviids. Other massive corals were also very abundant at Middle Island and Humpy, but much less abundant at Clam Bay, Halfway and North Keppel.

While previous studies tend to focus solely on the main structural habitat with which fishes are associated (e.g. corymbose *Acropora*), this study also considered underlying habitats, which were divided into consolidated substrata versus loose substrata. All fishes, especially *P. maculatus*, tended to use structural habitats located over loose substrates in preference to the same structural habitat located on consolidated substrates (Fig. 3-5). For *P. maculatus*, <20% of recruits were associated with structural habitats on consolidated substrates, and the single most frequently utilised compound habitat was corymbose *Acropora* on sand. Recruits of *L. carponotatus* and *E. quoyanus* also frequently associated with corymbose *Acropora* colonies located on sand (Fig. 3-5). All microhabitat associations of fishes were recorded by taking account of the compound habitat (the main structural habitat and the underlying habitat) but only structural habitats were surveyed during point-intercept transects, preventing selectivity analyses of compound habitats.

### 3.5 DISCUSSION

This study revealed strong associations with specific microhabitats for each of three species of predatory reef fishes (*P. maculatus*, *L. carponotatus* and *E. quoyanus*). Large predatory fishes form a significant part of the global catch in commercial, recreational and subsistence reef fisheries (Worm et al. 2005; Pauly 2008), and a large proportion of such species are overexploited (Myers and Worm 2003, 2005). The ecological and life history characteristics of predatory fishes, including low natural abundance, long lifespan; slow growth and low recruitment rates are clearly factors that contribute to their susceptibility to overfishing (Jennings and Kaiser 1998; Musick 1999). However, degradation of reef habitats and declines in

the availability of specific microhabitats are increasingly putting added pressure on large predatory reef fishes (Graham et al. 2007b; Wilson et al. 2010a; Pratchett et al. 2011). Among reef fishes, recruitment is widely acknowledged as a major factor that limits the size of adult populations and is central to population growth (Roughgarden et al. 1988; Caley et al. 1996). Recruitment is known to have a major influence on the natural population structure and dynamics for many reef fishes (e.g. Doherty and Williams 1988; Jones 1990; Doherty and Fowler 1994) and loss of recruitment habitat can have profound effects on the abundance of individual species and the structure of reef fish communities (e.g. Schmitt and Holbrook 2000; Jones et al. 2004). Typically, it is small strongly site-attached reef fish species (e.g. damselfishes) that are considered to be most dependent on specific habitat types (Sweatman 1988; Syms and Jones 2000; Wilson et al. 2010a). In contrast, many large and predatory fishes exhibit large home ranges (Samoilys 1997), and are thus assumed to respond to large-scale habitat features, such as depth profiles (Purkis et al. 2008), rather than the availability of specific microhabitats. However, this study demonstrates that even large predatory reef fishes may have very specific microhabitat requirements, especially in the first year after settlement (see also Light and Jones 1997; Kingsford 2009; Tupper 2007).

Strong associations with specific microhabitats were recorded for *P. maculatus*, *L. carponotatus* and *E. quoyanus*, with clear ontogenetic shifts in the use of microhabitats. For all three species, recruits were found predominantly in close association with live branching corals, and especially corymbose corals, such as *Acropora millepora*. Utilization of these specific coral habitats as recruits, but not as subadults or adults, may be related to the tight branching and low growth profile, which maximises opportunities for small fishes to evade predators. It is unclear however, why these fishes would associate strongly with live coral colonies situated over sand, while many other structural habitats (even extensive rubble beds) may provide similar opportunities to evade predators (Hixon and Beets 1993). Previous studies on the common coral trout, *P. leopardus*, suggested that the preferred habitat for new recruits were level patches of rubble substrata, whereas larger and older fishes utilised higher relief habitats (Light and Jones

1997). At One Tree Island however, Kingsford (2009) showed that recruitment by *P. leopardus* was highest in areas with high (> 20%) coral cover, and recruitment at these same sites stopped when cyclones reduced coral habitats to rubble. Direct observations of *P. leopardus* (Leis and Carson-Ewart 1999) and *L. carponotatus* (Quére and Leis 2010) during settlement reveal that these fishes are at high risk of predation and settle directly onto structural habitats (live or dead coral) to evade predators. High complexity of microhabitat, largely provided by branching corals, is therefore critical to survivorship of many small reef fishes (Coker et al. 2009) including juvenile stages of larger predatory species. As these fishes grow, the types of corals that act as effective refuges from predators also change, as reflected in a greater association with tabular *Acropora*. Kerry and Bellwood (2012) compared the relative use of corals with different growth morphologies by large reef fishes (across 11 different families, including Serranidae, Epinephelidae and Lutjanidae) and found that tabular *Acropora* are much more important than branching or massive corals for large reef fishes in providing effective concealment from roving predators, but also allowing increased manoeuvrability and rapid escape.

Aside from providing refuges from predators, microhabitat associations of predatory fishes may be driven by availability of, and accessibility to, preferred prey (Stewart and Jones 2001), which are also likely to change with ontogeny (Ferreira and Russ 1992; Dahlgren and Eggleston 2000). The distribution and abundance of many reef fishes are influenced by prey availability (Levin 1994; McIlwain and Jones 1997) and also food supply, which has a strong influence on juvenile growth and survival (Jones 1986; Forrester 1990). Microhabitats used by fishes must therefore serve the dual purpose of providing refuge from predators and access to prey. For *P. maculatus* and *L. carponotatus*, small fishes tend to feed mainly on cryptic invertebrates (predominantly, Crustacea), increasing the intake of fish as they transition into adults, whereas *E. quoyanus* feeds mostly on crustaceans throughout its life (Chapter 2, Wen et al. 2012a). These feeding habits may explain the preference for structural habitats positioned over loose substrates rather than consolidated substrates; loose substrates (sand and rubble) are likely to support higher

densities of cryptic invertebrates, due to both increased complexity and greater surface area of habitat within close proximity of the main top structural habitat (i.e. live or dead coral).

While strong associations with specific coral habitat do not necessarily imply that these fishes have an obligate association with live coral, fishes tend to preferentially use microhabitats that maximise individual survivorship (e.g. Tolimieri 1995). It appears therefore, that the fishes considered in this study (especially *P. maculatus* and *L. carponotatus*) would be adversely affected by coral loss, which is occurring at a significant and increasing rate throughout the world (Gardner et al. 2003; Bellwood et al. 2004; Hughes et al. 2011). Abundance and diversity of coral reef fishes often declines following extensive coral loss caused by climate-induced coral bleaching (e.g. Garpe et al. 2006; Graham et al. 2006) or other large-scale disturbances (reviewed by Wilson et al. 2006; Pratchett et al. 2008b). Many of these studies attribute changes in reef fish assemblages to the structural collapse of dead corals, which reduces overall topographic complexity of coral-reef habitats (e.g. Sano et al. 1987). Effects of coral depletion may, however, be exacerbated by declining topographic complexity and increased abundance of macroalgae (Pratchett et al. 2008b). Few studies have attempted to separate effects of changing biological versus physical habitat structure, although there is substantial correlative and indirect evidence that both live coral and topographic complexity are important attributes of coral-reef habitats that affect communities of coral reef fishes (Carpenter 1981; Holbrook et al. 2000; Munday 2000; Garpe and Ohman 2003; Graham et al. 2006). For *P. maculatus* and *L. carponotatus*, most fishes were found in close association with live corals and avoided habitats dominated by macroalgae. The specific types of coral preferred by these predatory fishes are highly susceptible to both coral bleaching (McClanahan et al. 2004) and predation by crown-of-thorns starfish (Pratchett et al. 2011).

The extent to which species can adapt to changes in resource availability and habitat structure depends on their ecological versatility. Highly specialised species, such as coral feeding butterflyfish, are obligately dependent on specific types of corals, and the loss of these corals

will inevitably lead to localised extinctions (Pratchett et al. 2008a). However, fishes that use a wide range of different resources or are capable of switching their patterns of resource use can withstand extensive coral loss (Pratchett et al. 2004). While all predatory fishes considered in this study used specific microhabitats disproportionately to their availability, the range of microhabitats used by each species of fish was extensive. There were, for example, a small number of fishes from all life stages across all three species that were found living among macroalgae or in open areas of loose substrates with no major structural habitat (Fig. 3-4). Variation in growth and survivorship of fishes associated with preferred versus non-preferred habitats should be quantified in order to assess the long-term consequences of coral loss and habitat degradation. However, it is likely that declines in availability of specific microhabitats (especially those used by recruits) may underlie declines in the abundance of predatory fishes following extensive coral loss (Graham et al. 2007b; Russ et al. 2008).

Declines in availability of microhabitats within a specific location are likely to lead to lower recruitment and abundance of fishes (Graham et al. 2007b), although spatial variation in fish abundance does not always correspond with abundance of preferred microhabitats (Tolimieri 1995). Patterns of recruitment of coral reef fishes are not random and there is increasing evidence that specific locations (termed recruitment hotspots, Booth et al. 2000; Eagle et al. 2012) consistently receive higher numbers of recruits compared to nearby comparable locations or habitat. Hotspots may arise through either consistently high levels of larval supply as a result of specific hydrodynamic processes, strong preferences for particular habitats or conspecifics that lead to increased rates of settlement at specific locations, and increased survivorship of newly settled fishes (Kingsford et al. 1991; Wolanski et al. 1997). In this study, North Keppel, Halfway Island and Clam Bay had greater recruit abundance (across all study species) compared to Miall Island, Humpy Island and Middle Island. The three locations with highest densities of new recruits were characterised by a high abundance of branching *Acropora* and a low cover of massive corals. However, large-scale variation in the recruitment of *P. maculatus*, *L. carponotatus* and *E. quoyanus* (among locations and reef zones) was poorly correlated with

live coral cover or the specific abundance of preferred microhabitats. Moreover, spatial variation in abundance of these fishes was not related to localised differences in levels of protection from fishing; Clam Bay is a strict no-take area, but the two other locations with high recruit abundance are open to fishing (Fig. 3-1).

In conclusion, field surveys revealed strong microhabitat associations for three species of predatory reef fishes at the Keppel Islands on the inshore GBR. However, microhabitat associations alone did not account for marked variation in recruitment and abundance of these species among locations or physiognomic reef zones. Further research is required to understand the establishment of, and benefits accrued from, strong microhabitat associations. However, these data suggest that ongoing degradation of coral reef ecosystems and loss of live coral may have significant consequences for coral reef fishes, affecting not only small site-attached fishes (Munday 2004; Pratchett et al. 2006), but also larger predatory species.

**Table 3-1 Results from independent Kruskal-Wallis tests**

Variation in abundance of recruit, subadult and adult fishes of three carnivorous species among A) locations and B) habitats. Variation in abundance was analysed using independent Kruskal-Wallis tests that were corrected for tied ranks. “\*” indicates significant differences (alpha = 0.05) after accounting for Bonferroni correction.

A) Locations

Species	Life Stage	Hc (corrected)	<i>p</i>
<i>Plectropomus maculatus</i>	Recruits	14.99	0.01*
	Subadults	7.09	0.22
	Adults	11.19	0.04*
<i>Lutjanus carponotatus</i>	Recruits	11.07	0.04*
	Subadults	27.16	0.00*
	Adults	8.79	0.32
<i>Epinephulus quoyanus</i>	Recruits	7.48	0.93
	Subadults	13.58	0.02*
	Adults	3.19	0.73

B) Habitats

Species	Life Stage	Hc (corrected)	<i>p</i>
<i>Plectropomus maculatus</i>	Recruits	25.20	0.00*
	Subadults	31.10	0.00*
	Adults	10.34	0.27
<i>Lutjanus carponotatus</i>	Recruits	27.88	0.00*
	Subadults	10.35	0.17
	Adults	17.93	0.06
<i>Epinephulus quoyanus</i>	Recruits	20.78	0.02
	Subadults	11.29	0.05
	Adults	6.72	0.29

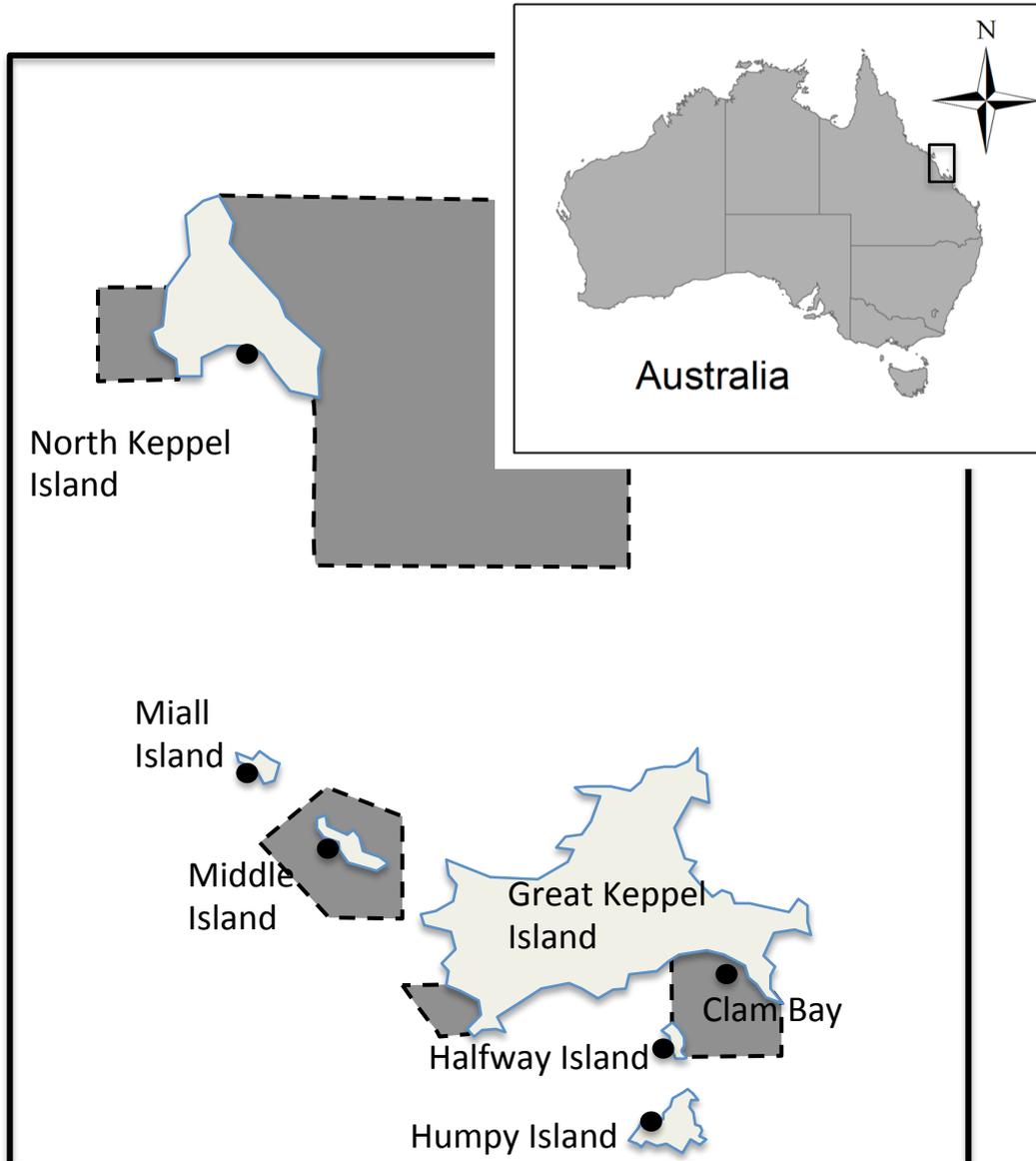
**Table 3-2 Percentage cover and relative use of microhabitats by study fishes**

Microhabitat selection by carnivorous fishes at Keppel Islands. Significance of habitat selectivity was ascertained using the log-likelihood statistic ( $X_{LI}^2$ ), and in all cases  $p < 0.01$ . Selection for microhabitats was determined using Bonferroni-corrected 95% CI (alpha = 0.05) around selection functions. “U” = microhabitats not used, “+” = microhabitats used significantly more than expected, “-” = microhabitats used significantly less than expected, and blank cells refer to microhabitats used in approximate proportion to their availability.

Species	Life stage	Size (cm)	$X_{LI}^2$	Corymbose <i>Acropora</i>	Arborescent <i>Acropora</i>	Tabular <i>Acropora</i>	Other branching coral	Massive <i>Porites</i>	Other massive coral	Soft coral	Macroalgae	Dead branching coral	Carbonate pavement	Sand/ Rubble
<i>Plectropomus maculatus</i>	Recruit	<15	549.0	+			U		-		-		U	
	Subadult	15-35	375.7	+	+						-		U	
	Adult	>35	309.6			+			-	-	-		U	
<i>Lutjanus carponotatus</i>	Recruit	<15	682.3	+		-	U	-		-	-		U	-
	Subadult	15-30	342.4				U				-			
	Adult	>30	316.1				U	U	U	U				
<i>Epinephelus quoyanus</i>	Recruit	<12	316.7	+	-		U			U	-		U	
	Subadult	12-30	298.2				U				-		U	
	Adult	>30	244.8								-		U	
				6.3%	13.9%	1.9%	0.5%	0.3%	1.2%	1.6%	28.5%	14.6%	4.5%	26.5%

**Figure 3-1 Map of Keppel Islands**

Map of Keppel Islands showing study locations (black circles) and Great Barrier Reef Marine Park zoning; grey shade with dashed areas are the national park zones where all fishing and harvesting is prohibited. The rest areas were fishing is permitted.



**Figure 3-2 Densities of recruit, subadult and adult fishes at six locations in the Keppel Islands**

Mean ( $\pm$  SE) densities of recruit, subadult and adult fishes of three carnivorous species at six locations in the Keppel Islands. Densities of fishes were recorded on replicate (n = 8) 50 x 6m belt transects (300m<sup>2</sup>) at each location. Fishes were categorised as recruits (young of the year), subadults, or adults (sexually mature individuals) based on size.

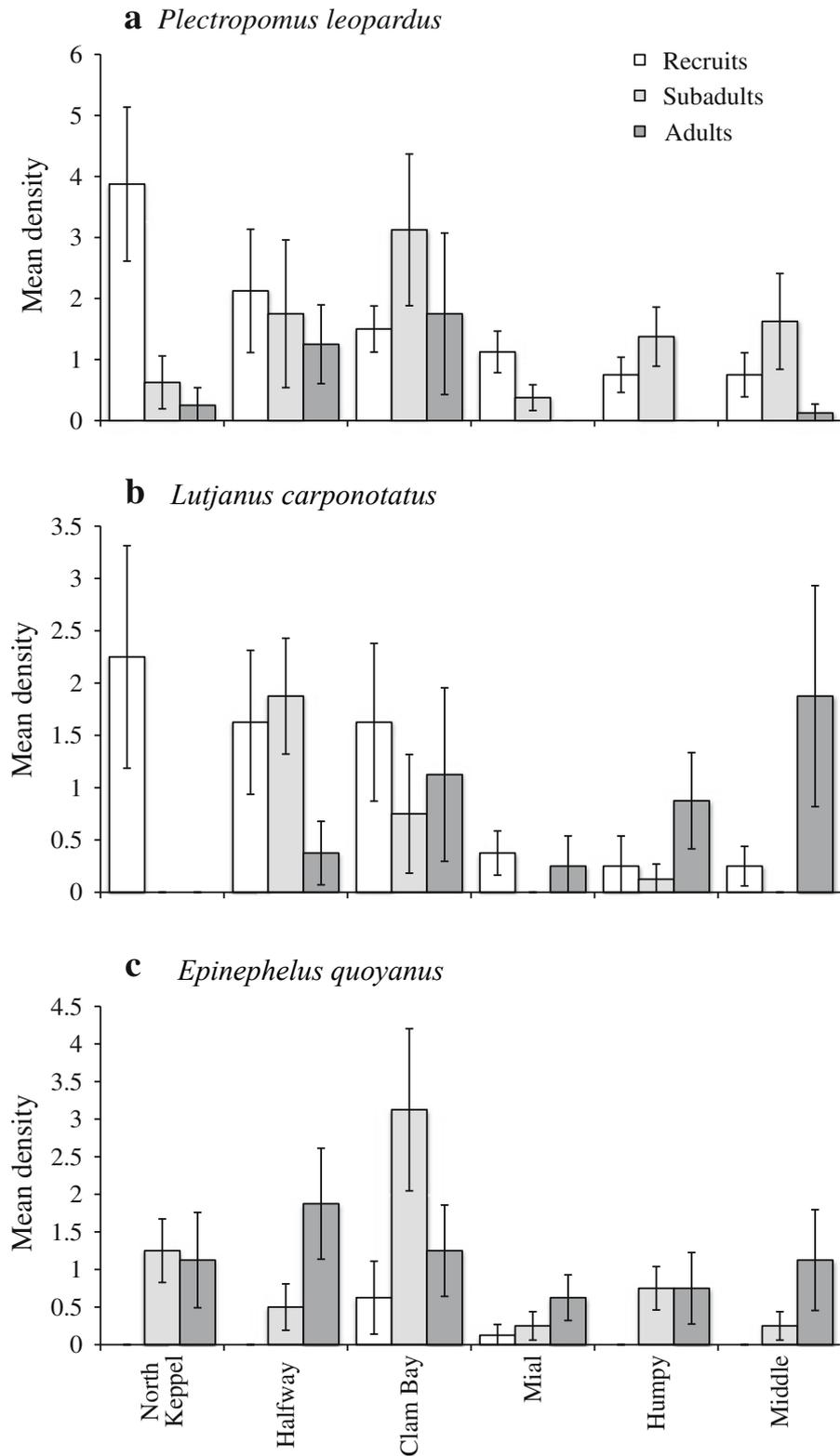
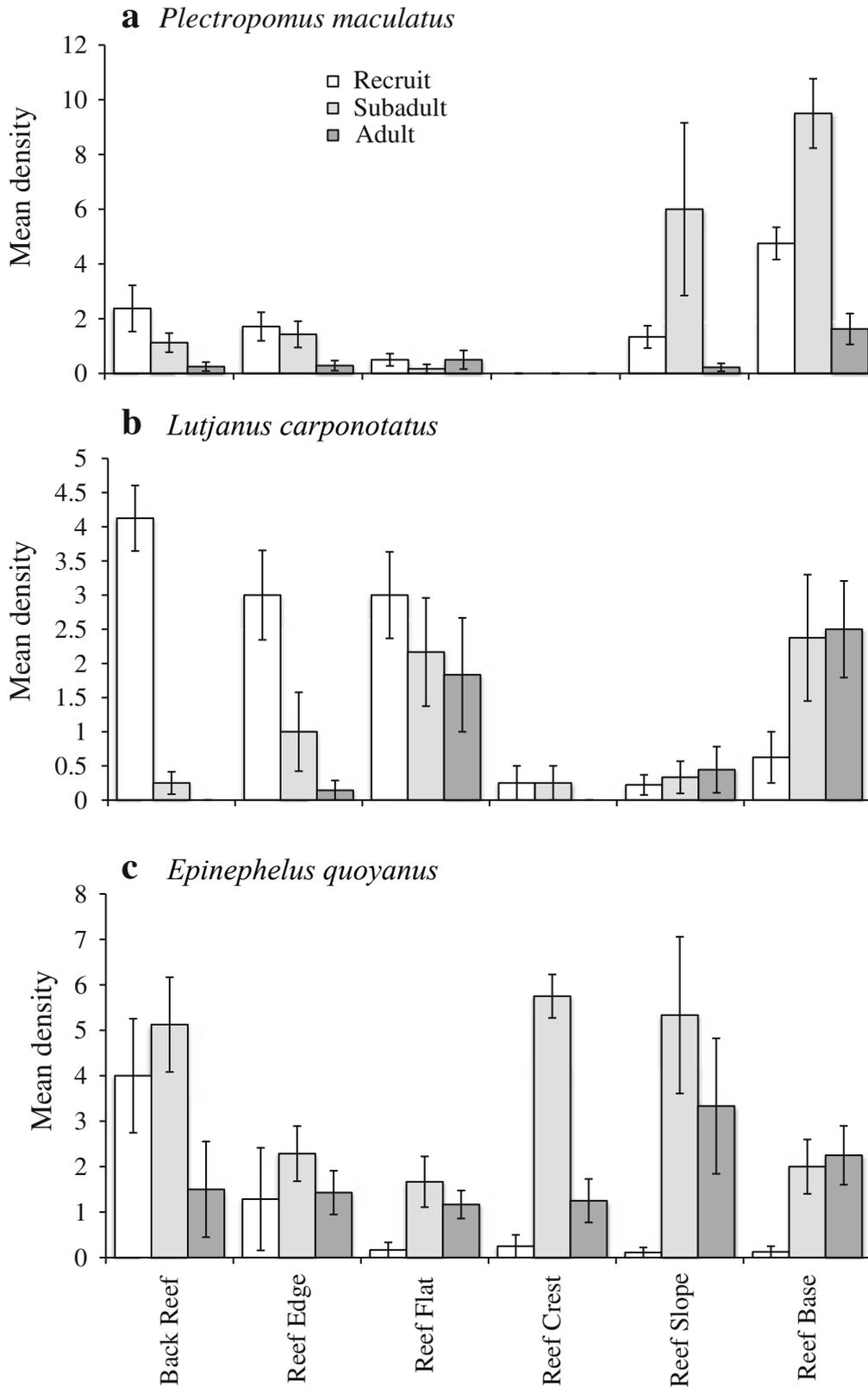


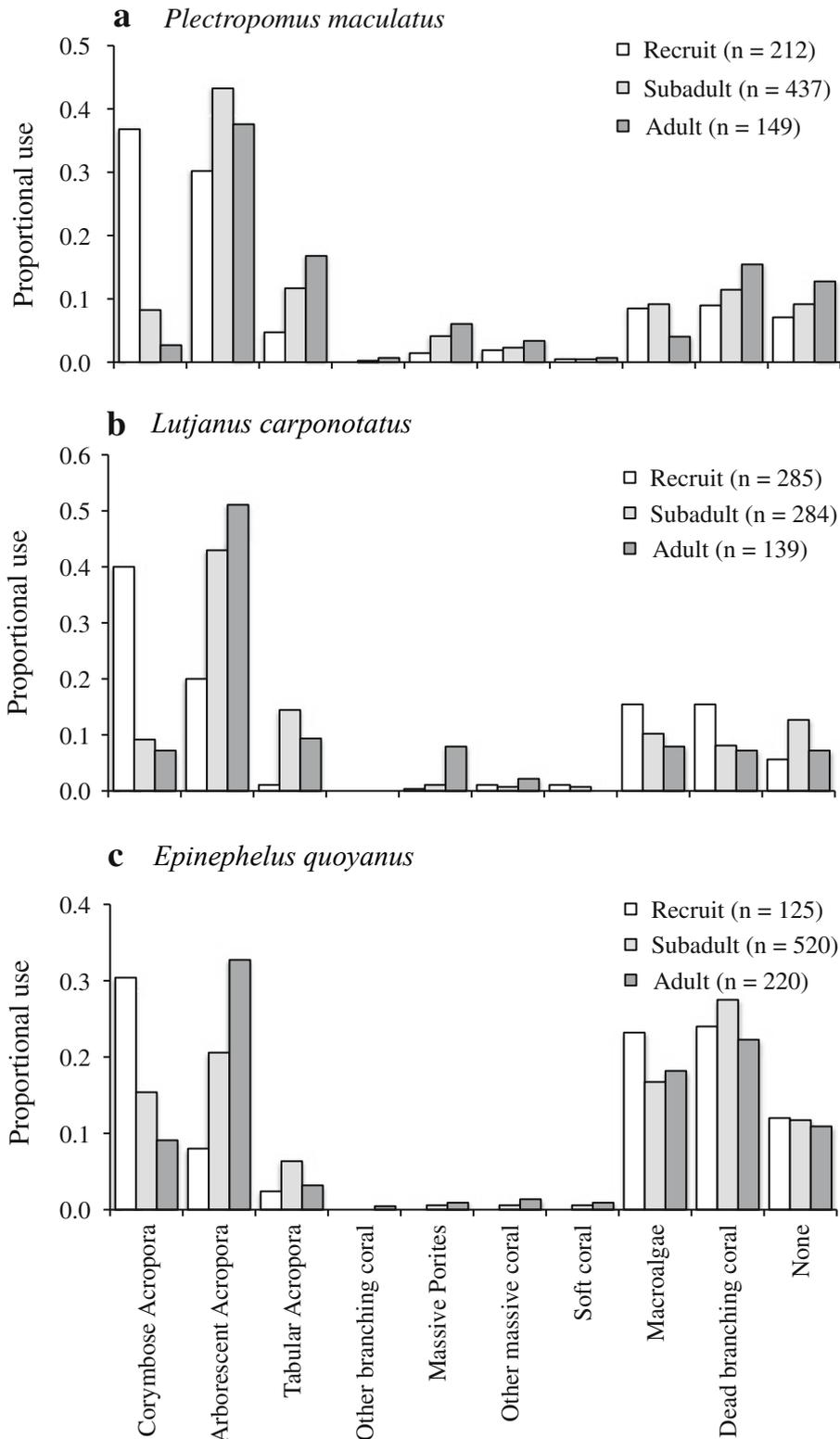
Figure 3-3 Densities of recruit, subadult and adult among physiognomic reef zones

Mean ( $\pm$  SE) densities of recruit, subadult and adult fishes of three carnivorous species among physiognomic reef zones at one location (Clam Bay, Keppel Island). Fishes were categorised as recruits (young of the year), subadults, or adults (sexually mature individuals) based on size.



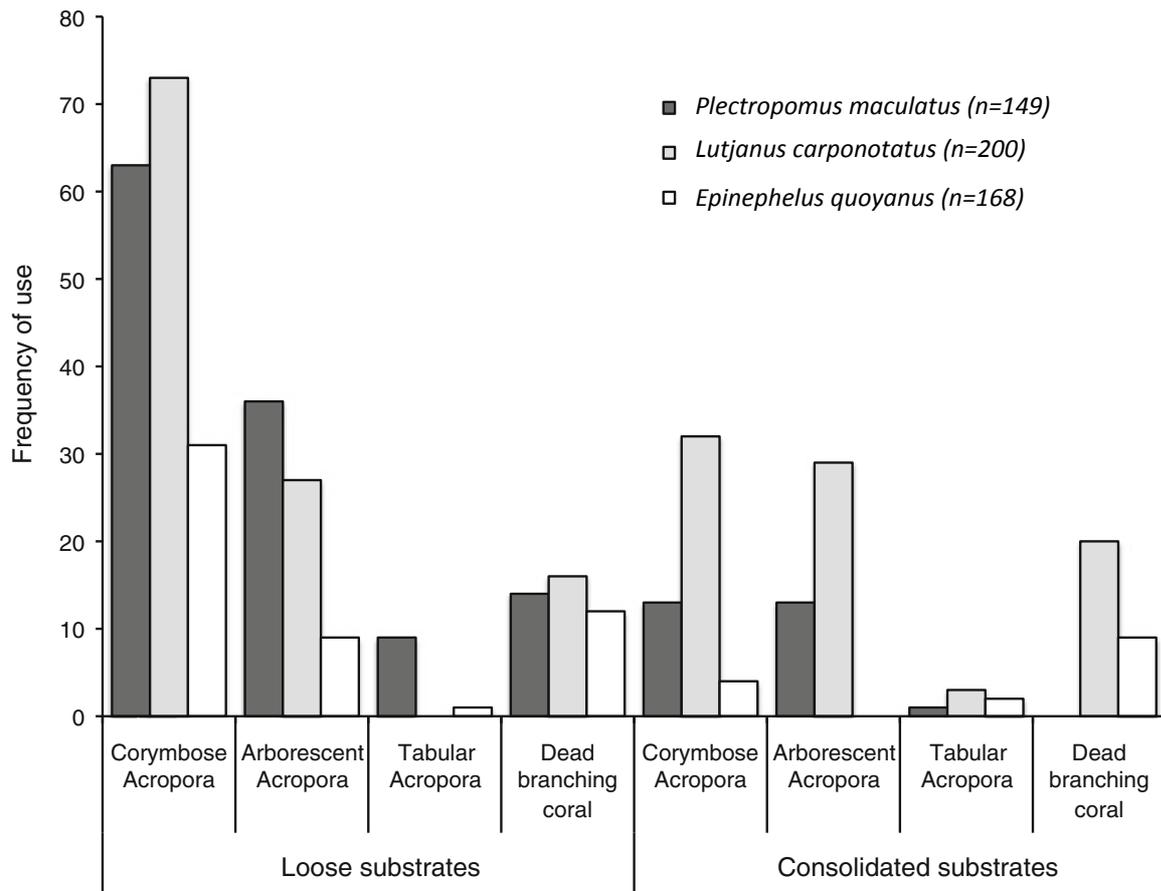
**Figure 3-4 Proportional use of contrasting microhabitats by recruit, subadult and adult fishes**

Proportional use of contrasting microhabitats by recruit, subadult and adult fishes of three carnivorous species in the Keppel Islands. Data were pooled across all locations and reef zones. Fishes were categorised as recruits (young of the year), subadults, or adults (sexually mature individuals) based on size.



**Figure 3-5 Frequency of use of different compound microhabitats by recruits**

Frequency of use of different compound microhabitats by recruits (young of the year) of three carnivorous fishes in the Keppel Islands. Compound habitats comprise the major structural habitat (e.g. live corals) and explicit consideration of the underlying habitat, which were divided into loose substrates (sandy substrates and rubble) and consolidated substrates (carbonate pavement or terrigenous rock).



## CHAPTER 4: Role of prey availability in microhabitat preferences of juvenile coral trout (*Plectropomus*: Serranidae)

Submitted to Journal of Experimental Marine Biology and Ecology (in revision)

### 4.1 ABSTRACT

Availability of specific microhabitats can exert a strong influence on the recruitment and abundance of coral reef fishes, but the ecological basis for microhabitat selection is not always clear. This study used a combination of field-based sampling and aquarium-based experiments to establish trade-offs between shelter requirements versus prey selection in microhabitat selection by larval coral trout (mostly, *P. maculatus*). Coral trout show a strong affinity for structural microhabitats (e.g. live or dead colonies of *Acropora*), but the underlying habitat (sand versus consolidated reef substratum) further influences patterns of microhabitat use. Field-based surveys revealed that live coral habitats support higher densities of potential prey species compared to dead corals. Furthermore structural microhabitats on sand have higher densities of prey (especially crustaceans) compared to comparable microhabitats on consolidated carbonate substrates. In the absence of prey, juvenile coral trout did not distinguish between live versus dead corals, but both these microhabitats were preferred over rubble, macroalgae and sand. In aquarium-based studies of prey use, juvenile coral trout consumed prey fishes that associate with non-coral habitats (e.g. *Eviota zebrine*; Lachner and Karnella, 1978) and mid water species (e.g. *Aioliops tetrophthalmus*; Rennis and Hoese, 1987), but did not consume those fishes with an obligate association with live corals. Our results suggest that studies of microhabitat preferences should consider both the structure and location of specific microhabitats. It is presumed the structural microhabitats are essential for evading predators, while occupation of live corals positioned over sandy substrates maximises accessibility to a diverse array of potential prey fishes and crustaceans.

## 4.2 INTRODUCTION

Patterns in the distribution and abundance of organisms in time and space are often related to the availability of particular microhabitats (e.g. Bell et al. 1985b; Pulliam 1989; Orians and Wittenberger 1991; Rosenzweig 1991). Optimal microhabitats are those, which provide both food and shelter, thereby maximizing growth while also reducing the risk of predation (Werner et al. 1983). However, few habitats are optimal for food and shelter (Myserud and Ims 1998), leading to trade-offs that may be reflected in complex patterns of associations between organisms and alternative microhabitats throughout their life cycle (Holt 1985). However, the relative importance of the different functions of microhabitats at specific life stages is not always known.

On coral reefs, the distributions and abundances of many reef fishes are strongly associated with variation in the availability of scleractinian coral habitats. This is particularly true for species that rely heavily on hard corals for food and/or shelter (e.g. Bell and Galzin 1984; Bouchon-Navaro et al. 1985; Kuwamura et al. 1994; Jennings et al. 1996; Munday et al. 1997; Holbrook et al. 2000; Pratchett and Berumen 2008). A recent study estimated that 8-10% of coral reef fishes live or shelter within live scleractinian corals throughout their life cycle (e.g. Munday et al. 2008), but many more species depend on live corals during particular phases of their life history. Most notably, it has been shown that up to 65% of coral reef fish species are adversely affected by extensive depletion of scleractinian corals (Pratchett et al. 2008b).

Close associations between reef fishes and their preferred microhabitats may be determined by strong habitat selection at settlement, or movement among habitats soon thereafter (Jones 1991; Ault and Johnson 1998; Beukers and Jones 1998). Additionally, these patterns may be established or further reinforced by differential survivorship within specific microhabitats (e.g. Connell 1996; Jones 1997). Susceptibility to predation is generally highest among newly settled fishes, and decreases with increasing size and age (Shulman 1985; Almany 2004a; Almany and Webster 2006). Consequently, initial microhabitat choices are probably dictated primarily by

the need of newly settled fishes to evade predators (Hixon and Beets 1993). As fishes grow, the suitability of specific microhabitats may then change, either due to changes in habitat and prey requirements (Kerry and Bellwood 2012) or because access to prey becomes more important than evading predators (Malcolm 1992; Martin and Hammerschlag 2012). This often leads to ontogenetic shifts in habitat-use (Lecchini and Galzin 2005; Pratchett et al. 2008a).

Previous work has shown that the juveniles of two common predatory fishes of the Great Barrier Reef, *Plectropomus maculatus* and *Lutjanus carponotatus*, have strong affinities with live branching corals located on sandy substrates (Wen et al. 2012b; Chapter 3). It was hypothesised that this habitat was preferred because it simultaneously provided a refuge from predators as well as greater access to preferred prey, in particular, small cryptic fishes and motile invertebrates (Wen et al. 2012b; Chapter 3). The literature indicates that other predatory fishes also use the same habitat, a mixture of corals and sand in back-reef and lagoon locations, as nursery areas (Adams and Ebersole 2002; Adams et al. 2006; Aguilar-Perera et al. 2006; Kingsford 2009). However, the relative importance of shelter versus prey in the selection of microhabitats by juvenile predatory reef fishes remains unknown.

The overall aim of this study was to distinguish the roles of shelter versus prey in determining microhabitat preferences in coral trout *Plectropomus* spp., which are important fishery species throughout their range. The specific objectives were to:

- (1) Quantify prey availability across a range of alternative microhabitats, to test the hypothesis that preferred microhabitats maximise access to potential prey items.
- (2) Determine the preferred microhabitats of *P. maculatus* in the absence of prey under controlled experimental conditions in aquaria to test whether microhabitat selection is related to specific attributes of the coral substratum.
- (3) Experimentally test whether prey fishes found associated with preferred microhabitats are preferentially consumed by juvenile *P. maculatus*.

## 4.3 MATERIALS AND METHODS

### 4.3.1 Field sampling

Field sampling to assess the relative abundance of alternative prey items associated with specific microhabitats was conducted at the Keppel Islands (23°10'S, 151°00'E), in the southern section of the Great Barrier Reef (GBR). *In situ* prey surveys were conducted at two locations (Clam Bay and Middle Island) in February 2010. Systematic sampling was conducted to compare prey abundance among: (1) live coral on sand, (2) dead coral on sand, (3) live coral on carbonate reef matrix, (4) dead coral on carbonate reef matrix, and (5) sand without any structural habitat. All sampling was conducted on the shallow back-reef to reef flat with a depth range of 3-4m. The abundance of prey fish and crustaceans was quantified using (1) underwater visual census for mobile prey fish species, (2) clove oil collections to obtain cryptic coral-dwelling prey fishes and crustaceans from among structural microhabitats, following Munday and Wilson (1997), and (3) an airlift vacuum sampler to collect invertebrate infauna from substrates surrounding structural microhabitats (Vogele et al. 1971; Munro 2005).

Five replicate habitats of each of the 5 microhabitat types were sampled in each location (Clam Bay, Great Keppel Island and Middle Island). To standardise the habitat area sampled, structural microhabitats (live and dead corals) were selected based on size (30cm diameter), while 30 x 30 cm quadrats were used to delineate the sample area on sand. However, there was still some variation in that actual size of microhabitats, so estimates of prey abundance were adjusted to account for total projected (2-dimensional) area and presented as the number of individuals per m<sup>2</sup>. All coral habitats (live and dead) were of the same growth form – corymbose *Acropora* [mostly *Acropora millepora* (Ehrenberg, 1834) in this region].

To survey prey fishes and invertebrates in structural microhabitats, active/mobile species were first surveyed using underwater visual census, recording all fishes clearly associated with the specific habitat from a distance of 1-3 meters. Following visual surveys, clove oil was used to extract all cryptic prey species following Munday and Wilson (1997). To sample prey items

associated with sandy substratum, all sand was collected to a depth of 30cm and then passed through a series of filters to separate particles greater than 2mm. These larger particles were then sorted, to identify all macro-invertebrates. Smaller interstitial invertebrates were excluded, as they are unlikely to form a significant component of the prey for coral trout (Wen et al. 2012b, Chapter 3).

Analyses of prey abundance within each microhabitat were conducted separately for crustaceans and fishes using univariate ANOVAs. Abundance of each prey was  $\log(x+1)$  transformed to meet the normality assumption of parametric statistical tests. Initial analyses were conducted to test for differences among (1) microhabitats, 5 levels; and (2) location, 2 levels. Tukey's pairwise comparison was undertaken when a significant difference was evident ( $p < 0.05$ ). To establish the importance of underlying habitats a further set of analyses were conducted, excluding data from sand without any structural microhabitats. These 2-way ANOVAs distinguished (1) live or dead coral and (2) sandy or consolidated reef substratum.

#### 4.3.2 Aquarium experiments

Experimental tests of prey and microhabitat preferences of juvenile coral trout (mostly, *P. maculatus*) were conducted at Orpheus Island Research Station, which is the only field-based aquarium facility on the inshore Great Barrier Reef. All experiments were conducted in flow-through aquaria, using juvenile coral trout (50 to 70 mm total length) collected from reef habitats in Pioneer Bay, Orpheus Island in 2010. At a small size it was difficult to distinguish between *P. maculatus* and *P. leopardus* (Lacepède, 1802), however most coral trout observed at Orpheus Island are *P. maculatus* and any individual that could be unequivocally identified as *P. leopardus* was excluded from experiments. All coral trout were collected using clove oil and kept in aquaria for 48 h to acclimatise prior to experiments.

#### 4.3.2.1 Microhabitat preferences

Microhabitat preferences were tested for a total of 30 juvenile coral trout using 5 independent experimental runs in each of 6 replicate aquaria (1.5 m diameter). The base of each aquarium was covered with clean coral sand (5 cm depth) and then alternative microhabitats, (1) live corymbose *Acropora millepora*, (2) dead corymbose *Acropora* sp., (3) macroalgae (*Sargassum* spp.), and (4) coral rubble, were arranged around the circumference of the aquaria, equidistant from one another. The relative position of each microhabitat was randomised between each experimental run to minimise possible bias associated with the absolute and relative position of microhabitats (e.g. variation in water flow or light regimes). Each of the alternative microhabitats was 30-cm in diameter. To test for microhabitat preference, individual fish was released into the centre of the aquaria. The location of fishes relative to alternative microhabitats was recorded immediately after release (day 0), then every 2-hours during daylight hours on days 1 and 2. Fishes were released back into their original sampling location after two days.

Patterns of microhabitat use were analysed by comparing proportional use of different microhabitats (live *Acropora millepora*, dead corymbose *Acropora* sp., the macroalgae (*Sargassum* spp.), coral rubble, and sand) to their proportional availability. Due to difficulties in finding individual coral trout during some observation periods, the experimental design was analysed as unbalanced to account for missing data. A non-parametric Kruskal-Wallis test using the freeware PAST (Hammer et al. 2001) was used to compare the relative occupancy in each habitat at each time period. The null hypothesis of the Kruskal-Wallis test is that the tested samples have equal medians instead of equal means in an ANOVA. Post-hoc pairwise tests were used to identify the difference between each microhabitat when the  $p$  value  $< 0.05$  was evident from the Kruskal-Wallis test.

#### 4.3.2.2 Prey selection

To further test the role of prey selection in microhabitat preferences of coral trout, experimental tests were conducted to quantify relative consumption of different prey fishes placed in aquaria

along with the preferred microhabitat (live *Acropora millepora*) which was identified from previous studies (Wen et al. 2012b, Chapter 3). Five different prey fish species were used in these experiments, Gobiidae: *Eviota zebrina* (Lachner and Karnella, 1978), Pomacentridae: *Pomacentrus moluccensis* (Bleeker, 1853), *Neopomacentrus bankieri* (Richardson, 1846), Labridae: *Halichoeres melanurus* (Bleeker, 1851), and Ptereleotridae: *Aioliops tetraphthalmus* (Rennis and Hoese, 1987). These species were selected to include those that are strongly associated with this live coral habitat (e.g. *P. moluccensis*), versus those that live in close proximity, but not actually within corals (e.g. *E. zebrina*), and also species that swim in mid-water, rather than associating closely with specific benthic habitats (e.g. *A. tetraphthalmus*). All prey fishes were approximately 25mm TL, and observations were conducted to quantify habitat associations (specifically, the proportion of prey fishes that were within the branches or underneath the corals, versus those that could be seen in the water column or sitting on the sand away from the coral) of prey fish within aquarium settings. No invertebrate prey types were used in these trials because it proved extremely difficult to record presence/absence (and thereby estimate mortality) of the crustaceans (Galathiedae and Caridea) within aquarium environments.

Patterns of prey use were documented by quantifying the proportional loss of each prey species through time. Feeding trials were conducted for a total of 25 juvenile coral trout placed in individual aquaria measuring 0.5 m (length) x 0.3 m (width) x 0.2 m (height). The bottom of each aquarium was covered with clean coral sand and a single live colony of corymbose *Acropora* (ca. 30cm diameter) was placed in the centre of the aquarium. Juvenile coral trout (mean total length = 56.9mm  $\pm$  1.5mm SE) were captured from reefs near Orpheus Island using clove oil and hand nets. A single juvenile trout was released into each aquarium to acclimate for 24 hours prior to the introduction of prey fishes. Three similar size individuals of each of 5 different prey fishes (*E. zebrina*, *P. moluccensis*, *N. bankieri*, *H. melanurus*, and *A. tetraphthalmus*) were released into each aquarium at the same time to avoid any possible effects arising from prey numbers and size on selection (Holmes and McCormick 2010;

Beukers-Stewart et al. 2011). Prey fishes were initially contained within a 10cm diameter clear vertical cylinder to allow for minimal acclimation prior to exposure to coral trout.

The frequency at which prey were attacked (chasing) and the identity of the prey captured were recorded. The relative consumption of each prey species was analysed by comparing the proportional loss of each species after 24-hours, using one-way ANOVA. To satisfy assumptions of normality, data were  $\log(x+1)$  transformed due to the presence of some zero value in the data set. Tukey's pairwise comparison was conducted when a significant difference was detected using ANOVA ( $p$  value  $<0.05$ ).

## 4.4 RESULTS

### 4.4.1 Prey availability among different habitats

The abundances of potential prey fishes and crustaceans varied greatly among different microhabitats but were consistent between locations (Clam Bay and Middle Island) at the Keppel Islands (Table 4-1). The highest densities of both small benthic fishes (92.76 individuals per  $m^2 \pm 9.6$  SE) and crustaceans (726.8 individuals per  $m^2 \pm 130$  SE) were found in live colonies of *Acropora millepora* located on sand (Fig. 4-1). Most fishes (70-80%) were gobies (family Gobiidae), including *Gobiodon* spp. which live among the branches of live corals and *Eviota* spp., which tended to occur underneath or in the crevices of the corals. Both of these genera were the most abundant fishes recorded on or near live colonies of *Acropora* located on sandy substrates, but densities were less on live corals on consolidated reef substrates (Fig. 4-1A). The average prey fish density on dead coral was similar on both sand and consolidated reef substratum, and was lower than that observed on live coral (Fig. 4-1A). The major difference between live and dead corals was the complete lack of *Gobiodon* and damselfishes (Pomacentridae) on or near dead corals. *Eviota* and blennies (Blennidae) were equally abundant beneath live or dead coral habitats. Very few prey fish were observed on rubble/sand patches located  $>1m$  from structural microhabitats (Fig. 4-1A).

For crustaceans, it appears that the underlying substratum (sand versus consolidated reef) is more important than the nature of structural microhabitats (live versus dead corals) as density was similar on live and dead coral microhabitats after accounting for underlying substratum type (Fig. 4-1B). Some crustaceans (mainly, *Coralliocaris* spp., snapping shrimps) were found exclusively within live coral microhabitats. However, the mean density of crustaceans found in dead corals over sand (351 individuals per m<sup>2</sup> ±55 SE) was more than twice that recorded for live corals on the consolidated reef substratum (120 individuals per m<sup>2</sup> ±10.2 SE). Differences in the abundance of crustaceans between sand versus consolidated reef substrates was largely due to the greater abundance of small squat lobsters (family Galatheidae) that were found almost exclusively (99.7%) on sandy substrates. However, crustaceans, and especially squat lobsters, were never collected in rubble/sand patches >1m from structural microhabitats (Fig. 4-1B).

#### 4.4.2 Microhabitat preferences

Aquarium-based microhabitat trials, conducted in the absence of prey, revealed that juvenile coral trout have a strong affinity with structural microhabitats that presumably provide suitable shelter from predation. However, juvenile coral trouts are fairly indiscriminate in their choice between structural microhabitats (live vs. dead coral). When first released into the test arena, approximately equal numbers of coral trout sought shelter in live coral, dead coral, and rubble habitats (Fig. 4-2). These initial habitat selections were not considered necessarily reflective of microhabitat preferences given that fishes were relatively unaware of the different microhabitats available at this time. However, initial patterns of microhabitat use were significantly different from random (Fig. 4-2,  $H=10.72$ ,  $p<0.05$ ), as few fishes used macroalgae or open sand. Over the two days of the microhabitat trials, juveniles increased their use of both live and dead coral microhabitats (Fig. 4.2). Across all observations in all trials, coral trout used live corals slightly

more than dead corals (35% versus 30%), but this difference was not significant (Fig. 4-2,  $H=20.11$ ,  $p<0.01$ ).

#### 4.4.3 Prey selection

Juvenile coral trout consumed mostly *A. tertrophthalmus* and *E. zebrina* (Fig. 4-3;  $F=15.8$ ,  $p<0.05$ ) in aquarium-based feeding experiments with preferred coral trout habitat. This preferred habitat (live corymbose *Acropora* microhabitat on sand) was also observed as habitat in the field for different prey fishes in our study, except *A. tertrophthalmus*. An average of 2.41 ( $\pm 0.19$  SE) individuals of *A. tertrophthalmus* (representing 48.3%) were consumed across the 25 feeding trials, compared to 1.67 ( $\pm 0.19$  SE) individuals, or 33.3% of *E. zebrina*. In contrast, very few individuals (<10%) of *P. moluccensis*, *N. bankeri* and *H. melanurus* were consumed across all trials. Differences in prey preferences were further reflected in the order of prey species consumption in each trial. *A. tertrophthalmus* were consumed first most of the time (9 of 22, 41%) within 15 minutes after release compared to the other prey fishes. The differential consumption of prey species was largely related to differences in capture success, as there was no significant difference in attack frequency ( $H=0.198$ ,  $p=0.88$ ).

## 4.5 DISCUSSION

This study shows that there are marked differences in the availability of potential prey items (small cryptic fishes and motile invertebrates) associated with contrasting microhabitats used by juvenile stages of *Plectropomus* spp. Juvenile coral trout are found predominantly in close association with live colonies of corymbose *Acropora* on unconsolidated sand substrata (Wen et al. 2012b; Chapter 3), and it is these habitats that provide greatest access to both small cryptic fishes and motile invertebrates. In the absence of prey, coral trout did not discriminate between the structural microhabitats provided by either live or dead coral skeletons. This might be due to both coral structures providing equally effective shelter from predators. In field settings,

however, coral trout demonstrated a clear preference for live (over dead) coral habitats, which may be attributed to differences in prey availability.

Live branching corals represent an important habitat for many small, site attached fishes (e.g. Jones 1988; Ault and Johnson 1998; Holbrook et al. 2000). They are also fundamental to the recruitment and/or survival of a wide range of fishes (Jones et al. 2004; Munday et al. 2008; Pratchett et al. 2008b), including some large, predatory fishes (Wen et al. 2012b; Chapter 3). Preferential use of branching corals is most often attributed to high levels of colony complexity, providing an increased number of refuges for small fishes to shelter from predators (Coker et al. 2009). However, this explanation alone does not explain why coral-associated fishes exhibit rapid and pronounced declines in abundance following the loss of tissue from host corals (e.g. due to bleaching; Pratchett et al. 2008b) and in some cases, long before the structural integrity of these microhabitats actually declines (Graham et al. 2007b). Given most studies assume that strong microhabitat associations are maintained due to the high risk of predation (Hixon 1991; Hixon and Carr 1997), it has been argued that fishes vacate dead but intact coral hosts either because they are pre-empting the ultimate loss of habitat structure, or that live corals are more effective predator refuges than dead coral colonies with equivalent structure (Coker et al. 2009). However, this study suggests that fishes may also vacate dead coral hosts because of reduced access to prey resources (see as Stewart and Jones 2001).

The preferential use of live corals due to prey availability is usually discussed in relation to obligate corallivores (Cole et al. 2008; Pratchett et al. 2008a). However, live corals harbour many species of small fishes and invertebrates (Stella et al. 2011), representing potential prey for carnivorous fishes associated with these microhabitats. The present study indicates microhabitat associations for juvenile coral trout were influenced by both the physical structure of the microhabitat (the specific coral) as well as the underlying substratum, suggesting that prey availability exerts a strong influence over microhabitat use. Field based surveys of potential prey items showed that small cryptic fishes were most abundant on and in live corals,

whereas crustaceans were most abundant on unconsolidated sandy substrata. In combination, these data show that prey availability will be highest for live *Acropora* colonies over sand.

Habitat preferences may be based not only on prey availability, but the behaviour of the prey that are present in different microhabitats. In our aquarium-based feeding trials, the relative consumption of the five prey fishes was inversely correlated with the strength of their microhabitat associations. The predominant prey fishes consumed by juvenile coral trout (*A. tertrophthalmus* and *E. zebrina*) had the least affinity with structural microhabitats and were presumably much more exposed to predation: *A. tertrophthalmus* aggregated approximately 1-3cm below the water surface and never entered coral branches whereas *E. zebrina* occupied the benthic surfaces away from or underneath corals. In contrast, most individuals (>60%) of *P. moluccensis*, *N. bankeri* and *H. melanurus* remained sheltered among the branches of the live coral, or rapidly sought shelter within these corals whenever approached by coral trout, but few of these prey fishes were actually consumed. The best microhabitats for juvenile predators may be those that maximise shelter for themselves, at the same time as maximizing the availability of susceptible prey.

Coral trout are ambush predators and probably rely on structural microhabitats mostly to limit visual exposure to prey (Frisch 2006). This foraging strategy has been shown for hawkfishes (family Cirrhitidae) that inhabit *Pocillopora* spp. (DeMartini 1996; Kane et al. 2009) and the brown dottyback (*Pseudochromis fuscus*) that hunts from within *Acropora* corals (Coker et al. 2009). The diet of juvenile coral trout collected from the field contained mostly small benthic prey fishes, such as gobies and blennies (Wen et al. 2012b; Chapter 3). It is unknown however, whether these fishes were consumed within the confines of preferred microhabitats, or by ambushing prey on the surrounding reef substrata. Laboratory choice clearly showed that juvenile coral trout target fishes in close vicinity of, but not necessarily sheltering within, coral microhabitats. Nonetheless, these data suggest that juvenile coral trout do benefit from the high diversity and abundance of small reef fishes that associate with live coral habitats (Messmer et

al. 2011). Small benthic fishes and crustaceans are increasingly seen as a major driver of the trophodynamics of coral reef ecosystems (Depczynski and Bellwood 2003; González-Cabello and Bellwood 2009), and our sampling shows that there is a concentration of potential prey within close proximity to coral microhabitats, especially when positioned over unconsolidated sandy substrata.

A critical question is whether or not coral trout have an obligate dependence on live coral microhabitats. A previous study suggested that juvenile *P. leopardus* preferentially settle in rubble habitats (Light and Jones 1997) but these conclusions were based on field observations rather than experimental tests. It is likely that there is some scope for flexibility in microhabitat use, but the use of sub-optimal microhabitats may have consequences for individual growth and survivorship. Like most reef fishes, coral trout recruits are highly vulnerable to predation (Leis and Carson-Ewart 1999) and may preferentially settle or survive better in marginal reef habitats (e.g. rubble banks) where there are fewer potential predators. This may explain the abundance of *P. leopardus* recruits observed on rubble banks (Light and Jones 1997). For example, St John (1999) showed that *P. leopardus* feed on both benthic prey (fishes and crustaceans) and small pelagic fishes (Clupeidae) occupying the water column. Further work is necessary to understand spatial variation in prey composition for coral trout occupying a range of different microhabitats, as well as assessing how the foraging strategy of juvenile coral trout influences whether prey are captured inside or outside of structural microhabitats

This study demonstrates that juvenile coral trout preferentially utilise coral microhabitats that serve the dual purpose of offering suitable shelter while also increasing access to potential prey. In the absence of potential prey, aquarium based experiments demonstrated that juvenile coral trout do not distinguish between live and dead corals, presumably because they provide equally effective refugia from potential predators (Almany 2004b). In the field however, juvenile coral trout are strongly associated with live corals on unconsolidated sandy substrates, which provide

greater access to potential prey. It is therefore likely that declines in the availability of the preferred microhabitat (live colonies of *Acropora millepora* positioned over sand) will have an adverse effect on the abundance, growth and survival of newly settled and juvenile coral trout, a conclusion supported by the observation of long-term declines in coral trout abundance following extensive coral loss (Graham et al. 2007b; Russ et al. 2008). Effective management of coral trout, an important food fish on Indo-Pacific coral reefs, must therefore not only protect adult breeding stocks, but also include protection of the key juvenile recruitment habitats identified in this study.

**Table 4-1 Two-way ANOVA of prey fishes and crustaceans among locations and microhabitat**

Results from a two-way ANOVA comparing densities of prey (a) fishes and (b) crustaceans among sampling locations and microhabitat type.

(a)

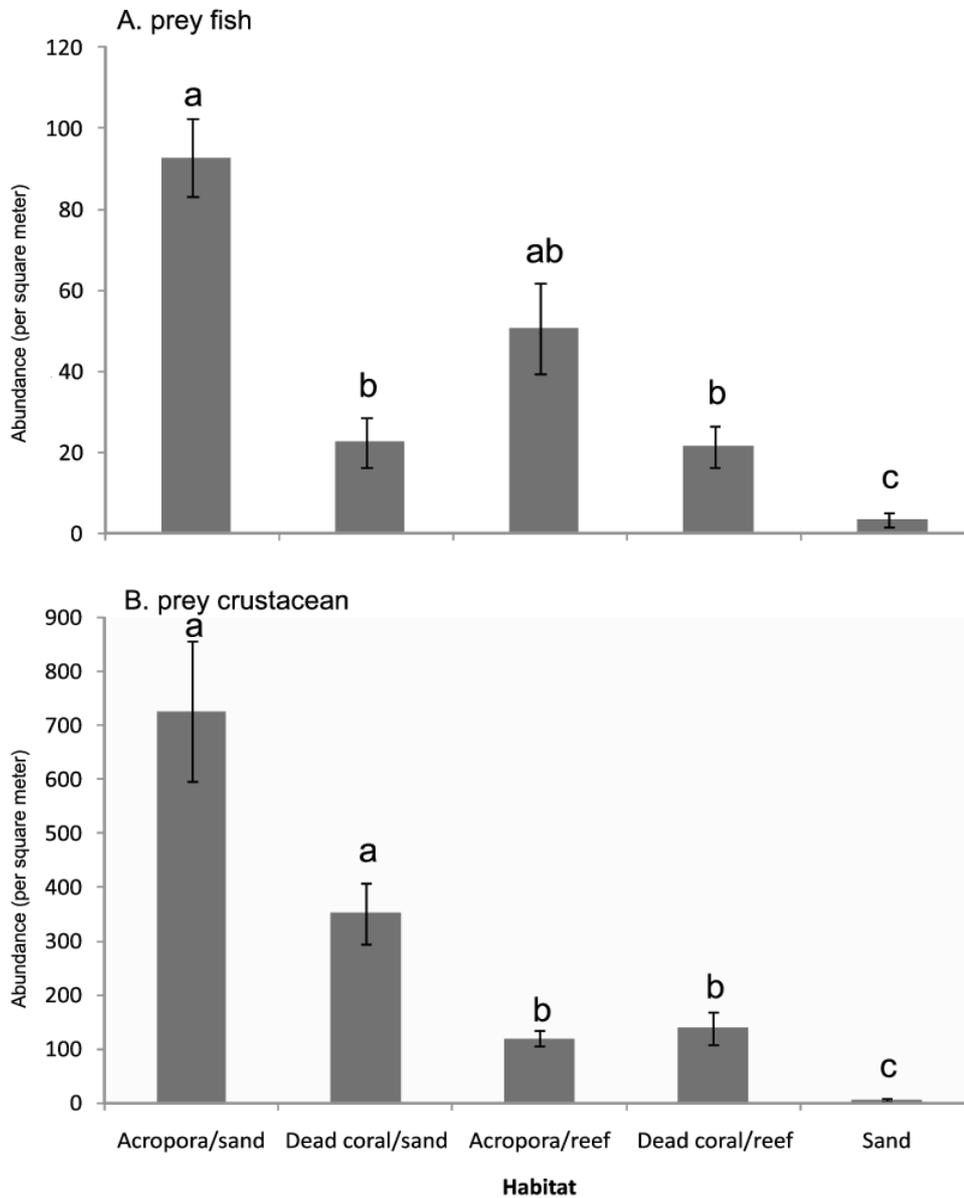
	SS	df	MS	F	p
Location	1542	1	1542	3.566	0.066
Habitat	48800	4	12200	28.210	<b>0.000</b>
Interaction	6847	4	1712	3.959	<b>0.008</b>
Error	17300	40	432		
Total	74480	49			

(b)

	SS	df	MS	F	p
Location	0.000	1	0.000	0.001	0.970
Habitat	29.420	4	7.355	61.630	<b>0.000</b>
Interaction	0.922	4	0.230	1.931	0.124
Error	4.774	40	0.119		
Total	35.110	49			

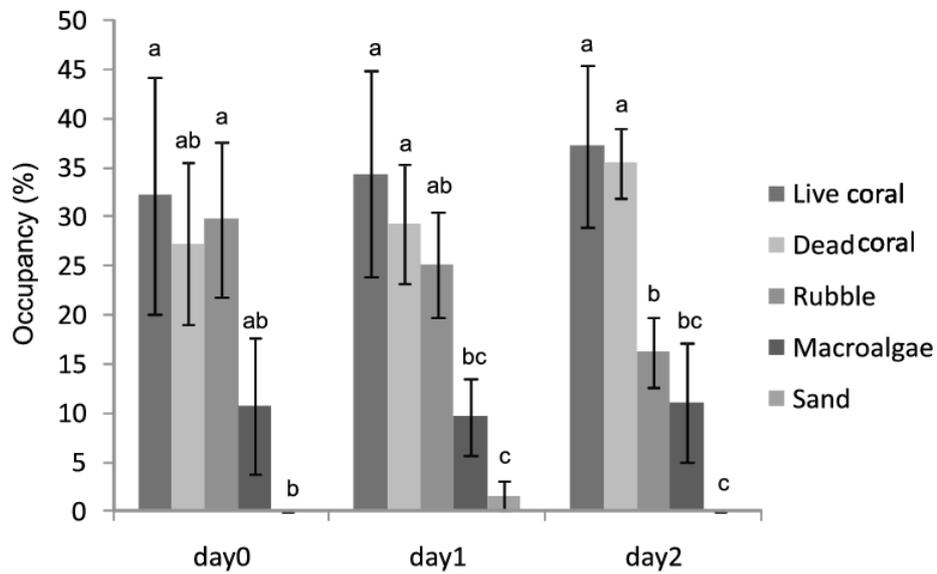
**Figure 4-1 Abundance of prey fishes and crustaceans on five compound microhabitats**

Mean ( $\pm$ SE) abundance of prey (A) fishes and (B) crustaceans on five compound microhabitats. Data were pooled across two different sampling locations (Clam Bay and Middle Island). All counts were standardised by the 2-dimensional area sampled and are presented as the density per square metre.



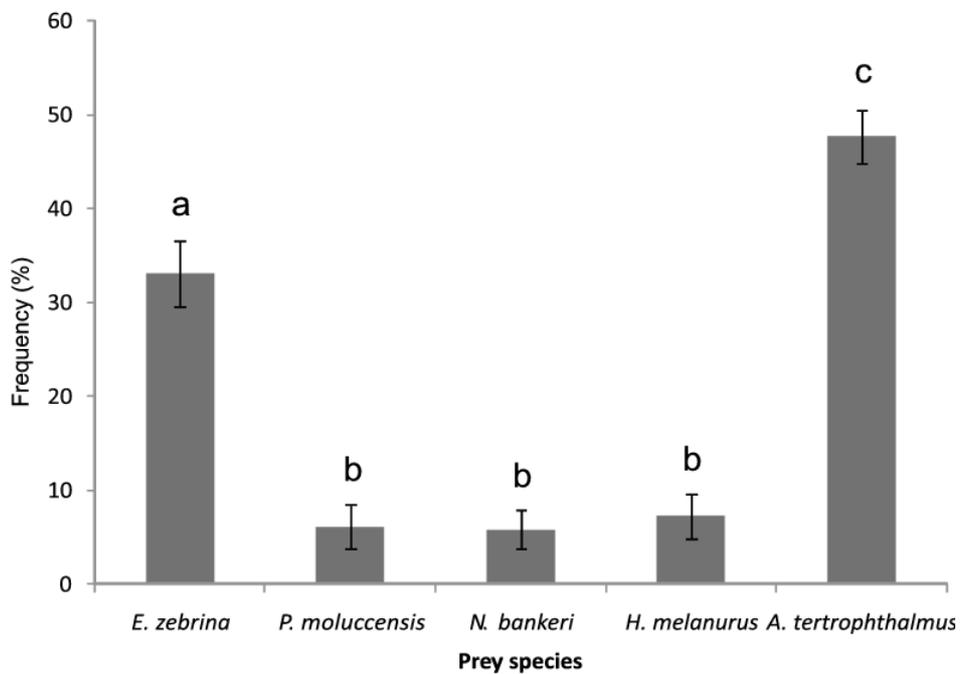
**Figure 4-2 Occupancy of five microhabitats by juvenile coral trout**

Mean ( $\pm$ SE) occupancy of five microhabitats by juvenile coral trout (N = 30).



**Figure 4-3 Frequency of prey selection of juvenile coral trout**

Mean ( $\pm$  SE) frequency of prey selection of juvenile coral trout in aquarium trials.



## CHAPTER 5: Role of recruitment hotspots in the effectiveness of no-take marine reserves for large predatory fishes

### 5.1 ABSTRACT

Marine reserves are widely advocated as a conservation tool promoting the recovery of relatively sedentary fishes that have been over-exploited. Where reserves have successfully been implemented, dramatic increases in fish densities and biomass have been observed within reserve boundaries. However, the magnitude of reserve-effects varies within and among studies, and the demographic processes that bring about more and larger fish in reserves are not always known. Long-term increases in reserves can only be sustained if there is adequate juvenile recruitment, but patterns of recruitment inside and outside reserves have seldom been quantified. I hypothesised that the effectiveness of reserves depends on whether or not they contain “recruitment-hotspots” (or sites that explain a disproportionate abundance of juveniles). To test this, I used an orthogonal sampling design to compare the abundance of sub-adults and adults of three predatory fishes (*P. maculatus*, *L. carponotatus* and *E. quoyanus*) at both reserve and fished reefs, with and without recruitment-hotspots (at the Keppel islands, Great Barrier Reef). For *P. maculatus* and *L. carponotatus*, adult densities were 2-3 times greater in reserves with recruitment hotspots, compared with reserves without hotspots or fished areas, which were all similar. The abundance of sub-adults was primarily explained by the presence of recruitment hotspots, not reserve status. Compared with reserves, the size-distributions of *P. maculatus* and *L. carponotatus* were truncated at the minimum size limit (MSL) for all fished populations, regardless of recruitment patterns. Our results suggest that identifying recruitment hotspots could be a valuable addition to reserve selection criteria, particularly for reserves targeting large exploited species using common recruitment areas.

## 5.2 INTRODUCTION

Marine reserves or no-take marine areas have been increasingly implemented for biodiversity conservation and fisheries management (Roberts and Polunin 1991; Beverton and Holt 1993; Dayton et al. 2000). Numerous studies have demonstrated that the number, size and biomass of adult fishes of exploited species can increase dramatically within reserve boundaries (Russ and Alcala 1996b; Halpern and Warner 2002; Williamson et al. 2004; McLean et al. 2011). For reef associated areas where levels of exploitation are impacting on fish stocks, and that reserves are an effective means of promoting recovery. However, the magnitude of the increases in adult abundance inside reserves varies, with documented increases ranging from ~20 to ~490% compared with fished areas (Paddack and Estes 2000; Williamson et al. 2004; Abesamis et al. 2006; Harmelin-Vivien et al. 2008), while some studies show little or no effect of reserves (Ayling and Ayling 1986; Samoily 1988; Mapstone et al. 1999).

A large number of factors may contribute to the success or failure of reserves, including historic fishing pressure (Claudet et al. 2010), levels of compliance (Guidetti et al. 2008; Claudet and Guidetti 2010; McCook et al. 2010; Pollnac et al. 2010) and the life history and behavioural characteristics of the species (Halpern and Warner 2003). However, apart from the reduction in fishing mortality in reserves, the demographic processes associated with the increased numbers or sizes of fish in reserves are poorly understood (Sale et al. 2005). While the long-term recovery and persistence of populations in reserves can only be sustained if they have adequate recruitment (Planes et al. 2000), the recruitment dynamics of populations in reserve and fished areas have seldom been investigated.

One factor that may contribute to the success of reserves is that they are located in places that consistently receive high levels of recruitment. Recruitment is defined broadly as “the process of adding new juveniles to a population or subpopulation” (Merriam-Webster 2005). While all reserves will benefit from the reduction in fishing mortality, it could be hypothesised that reserves that consistently receive a disproportionate supply of juveniles will perform better than

those with low recruitment. Many fishes recruit into “nursery areas” and subsequently migrate to adult feeding grounds, and these juvenile habitats have often been targeted in the selection of sites for reserves (e.g. endemic species in Lake Victoria; Witte et al. 1992; Dahlgren et al. 2006). For more sedentary species, recruitment may occur in habitats in close proximity to adults. However, the effects of protecting nursery sites or better recruitment areas on the efficacy of adjacent reserves that target adult stocks has not been investigated.

For coral reef fishes, recruitment occurs when fishes survive the pelagic larval stage and settle in a local reef-associated population (Holm 1990). It has been established that rates of recruitment can be important in determining adult population size and the structure of coral reef fish communities (Sale 1980; Doherty and Williams 1988; Jones 1990; Jones 1991). Increased recruitment success can be critical for maintaining adult populations of fishery species (Myers and Barrowman 1996). Coral reef fishes typically exhibit predictable spatial patterns in recruitment, both within and among reefs (Williams and Sale 1981; Sale et al. 1984; Valles et al. 2008). Places that consistently receive above average levels of recruitment can be referred to as “recruitment hotspots” (Booth et al. 2000; Eagle et al. 2012). The location of recruitment hotspots may be explained by a variety of processes including pre-recruitment larval supply (Meekan et al. 1993; Sponaugle and Cowen 1996) and juvenile habitat quality (Tolimieri 1995; Feary et al. 2007). The proximity of recruitment hotspots could potentially have a huge bearing on the long-term effectiveness of coral reef reserves. Selection of sites for reef marine reserves has typically been based on a range of factors, both ecological and social (Fernandes et al. 2005). Currently, recruitment hotspots can be found both inside and outside of marine reserves (chapter 3; also see Valles et al. 2001; Grorud-Colvert and Sponaugle 2009). While the benefits of reduced fishing pressure for exploited coral reef fishes have been well-documented, the additional benefits that could be gained by taking into account recruitment dynamics have not been investigated.

The aim of this chapter was to examine the relationship between the magnitude of increases in adult fish abundance in reserves relative to fished areas and the presence of recruitment hotspots in reserves. The study focuses on three exploited fishes (*P. maculatus*, *L. carponotatus* and *E. quoyanus*) that have exhibited positive responses to protection status at the Keppel islands, southern Great Barrier Reef (Williamson et al. 2004). These three species exhibit congruent hotspots that are currently located in both reserve and non-reserve areas. Consequently, it was possible to establish an orthogonal experimental design to compare numbers of adult fish in reserves with and without recruitment hotspots, and fished areas with and without recruitment hotspots. In a previous chapter (Chapter 2), I established that the increase in predators in marine reserves had little or no influence on recruitment of predatory reef fishes. The characteristics of recruitment hotspots and the microhabitat associations of sub-adults and adults were addressed in Chapters 3 and 4. Here, I address the hypothesis that the presence of recruitment hotspots increases the effectiveness of marine reserves through the supply of juvenile fishes. In addition to examining effects on the numbers of both adult and subadults of each species, I examine the effects each of the 4 factors on the size-frequency distribution of fishes, with specific reference to the legal size limit for each species.

## 5.3 METHODS

### 5.3.1 Study location and species

This study was conducted in February 2010 at eight sites around the Great Keppel region (23°10' S, 150°57' E), an inshore archipelago near the southern Great Barrier Reef. In this region there are 6 discrete marine reserves or “green zones.” It focuses on 3 large predatory fishes that form part of an important recreational fishery for coastal communities: *P. maculatus* (bar-cheeked coral trout), *L. carponotatus* (stripey snapper), and *E. quoyanus* (rocky cod). Both *P. maculatus* and *L. carponotatus* are key targets of recreational and commercial fisheries on the Great Barrier Reef, whereas *E. quoyanus* is part of the incidental catch. All species have

exhibited an increase in abundance and biomass since the rezoning of the Great Barrier Reef in 2004 (e.g. Russ et al. 2008).

### **5.3.2 Sampling design and survey methods**

Of the eight sites, 4 sites were located within no-take reserves [Clam Bay of Great Keppel Island (CB), Eastern shore of Halfway Island (EHW), Monkey Point of Great Keppel Island (MP) and south-eastern bay of Middle Island (MD)] and 4 sites were in areas open to fishing [Miall Island (ML), western shore of Halfway Island (WHW), Wyndham of southern Great Keppel Island (WD) and Humpy Island (HP)] (Fig 5-1). Two of the reserve sites and 2 of the sites open to fishing were chosen because previous work had established that these were recruitment hotspots, (i.e. areas defined as having higher than average recruit abundances). These were: Clam Bay (CB), Wyndham (WD), Eastern Halfway Island (EHW), and Western Halfway Island (WHW). The other 4 sites were areas of low recruitment defined as non-recruitment hotspots (Monkey Point, Middle Island, Miall Island and Humpy Island). All locations were generally similar in aspect, exposure, and zonation, although hotspots tended to have a greater development of reef flat/backreef areas (see Chapter 3).

Abundance and size of these three species at each location were recorded using standardised UVC (underwater visual census) timed-swims (McCormick 1995). Each timed-swim was conducted for 30-minutes carefully searching for all recruits, sub-adult and adult fish within 5 m of the transect path. Six transects were conducted from along shallow (reef flat edge) and deep (reef base) locations to cover most of the region, due to the depth distribution of these predatory fishes (see chapter 3). Six extra transects were applied at Clam Bay to get more accurate results due to the relatively large reef area.

Individuals of predatory fishes were divided into three groups; recruit (young of the year, YOY), subadult (between recruits and sexual mature) and adult fish (sexual maturity based on

references of gonad histology studies). The size ranges of each of the three species are as follows: *P. maculatus*, ~15cm: recruit, 15~35cm: subadult, 35cm~: adult; *L. carponotatus*, ~15cm: recruit, 15~30cm: subadult, 30cm~: adult; *E. quoyanus*, ~12cm: recruit, 12~30cm: subadult, 30cm~: adult (Ferreira and Russ 1992; Kritzer 2004; Mannering 2008).

### 5.3.3 Data analysis

A two-way crossed ANOVA was used to test for differences in the abundance of adults and subadults of each species between zones (reserve and non-reserve) and recruitment levels (hotspots and non-hotspots). Data were Box-Cox transformed to meet the assumptions of parametric statistical tests due to the presence of zero data on some transects (Box and Cox 1964; Akritas 1990). All statistic analyses were performed using PAST (Hammer et al. 2001).

The size frequency distributions of fishes in the 4 different treatments were visually compared in relation to the legal size limits for the three different fish species. The legal minimum size limit (MSL) in Queensland water for *P. maculatus* is 38cm, *L. carponotatus* is 25cm and *E. quoyanus* is 38cm (Fisheries Act 2003).

Length frequency distributions of each of the three species were compared between reserves and recruitment hotspots. The number of bins used in the characteristic of the length frequency distributions was optimised following Scott (1979) and Wand (1997). The optimal bin width formula can provide information on the true distribution between too much detail (under-smoothing) and too little detail (over-smoothing).

The difference of length – frequency histograms between the two treatments were examined using a Kolmogorov-Smirnov (K-S) test following Bell et al. (1985a). The Kolmogorov-Smirnov test is a non-parametric test for probability distribution of two univariate samples. The null hypothesis is  $H_0$ : The two samples are taken from populations with equal distribution.

Besides the significant value  $p$ , the statistic  $D$  is the maximum deviation between the two empirical cumulative distribution functions (Stephens 1970). Abbreviated terms were used to represent the combination of treatments marine reserves and recruitment hotspots. They are **Res**(reserves), **nRes**(non-reserves), + or – (with or without) **HS**(recruitment hotspots). All the length frequency histograms and K-S statistical analyses were performed using PAST (Hammer et al. 2001).

## 5.4 RESULTS

### 5.4.1 Adults: Effect of recruitment hotspots on magnitude of reserve-effect

The densities of adult *P. maculatus* exhibited significant differences, both between reserves and non-reserve areas, and between sites with recruitment hotspots and those with non-hotspots (Fig. 5-2a; Table 5-1a). The highest densities of adult *P. maculatus* were recorded in reserves with recruitment hotspots, where densities were nearly 3 times higher than for the other treatments. Reserves without hotspots exhibited density levels that were not significantly different from reefs open to fishing. Similar patterns were observed for *L. carponotatus*, although in this case only the reserve status was statistically significant and the recruitment hotspot factor bordered on significance (Fig. 5-2a, Table 5-1a). The reserves with hotspots recorded over double the densities of adults in the other treatments. In this study, the non-target species, *E. quoyanus*, exhibited no significant differences in the abundance of adults, either due to reserve status or recruitment levels (Fig. 5-2a, Table 5-1a).

### 5.4.2 Subadults: Effect of recruitment hotspots

In contrast to adults, densities of sub-adults of each species were more influenced by recruitment levels than by reserve status (Fig. 5-2b, Table 5-1b). The density of subadult *P. maculatus* only showed a difference between recruitment hotspots and non-hotspots, with densities at hotspots being 2~4 times higher than low recruitment sites (non-hotspots). A similar result was observed for *L. carponotatus*, although due to variation in the data, the difference

between the recruitment treatments was not statistically significant (Table 5-1b). Again, for *E. quoyanus*, there was no effect of any of the treatments on sub-adult densities.

#### 5.4.3 Size frequency distributions, recruitment and the legal size limit

The size frequency distributions confirm that recruitment hotspots contain higher densities of multiple cohorts of juveniles of all species (Fig. 5-3a-c). The length – frequency histogram of *P. maculatus* in the four treatments showed a higher abundance of recruits (<15cmTL) in the hotspot treatment than the non-hotspot treatments (Fig. 5-3a). The larger size of *P. maculatus* in non-reserves showed a dramatic drop in the numbers of fish at the MSL of 38cmTL, both at hotspot and non-hotspot sites. The K-S test result indicated the recruitment hotspots did not alter the size distribution in reserve treatments (Table 5-2a). Similarly, reserves and non-reserves without recruitment hotspots did not show any significant difference in size distribution (Table 5-2a).

The size-frequency distribution of *L. carponotatus* did not indicate the presence of multiple cohorts of juveniles at recruitment hotspots (Fig. 5-3b). The two treatments, reserves and recruitment hotspots, showed no effect on the length – frequency distribution (Table 5-2b), except between Res+HS and nRes-HS. However, the same truncation of the size distribution occurred at non-reserve sites. For *E. quoyanus*, there was a greater representation of the smaller size classes at hot-spot sites (Fig. 5-3c). The treatments also affected the distribution of *E. quoyanus* (Table 5-2c), except between non-reserves with and without recruitment hotspots. However, virtually none of the fish that were recorded in surveys were above the MSL in any of the treatments. Only a few larger than MSL individuals were observed in marine reserves without recruitment hotspots (Fig 5-3c).

## 5.5 DISCUSSION

Our study illustrates the potential importance of recruitment hotspots in contributing to the success of marine reserves for fishes targeted in coastal recreational fisheries (specifically *P. maculatus* and *L. carponotatus*). I show that reserves with recruitment hotspots exhibit 2-3 times the adult densities of reserves that do not encompass good recruitment areas. Recruitment hotspots substantially increase the number of subadults entering the fishable population. Hence, recruitment hotspots are likely to be critical avenues through which juveniles enter regional populations, and therefore, should be considered important focal points for protection.

Knowledge of recruitment has long been seen as critical information for marine reserve design (Dahlgren et al. 2006; Roberts and Polunin 1991; Sale et al. 2005). This follows from the fact that juvenile recruitment is the primary means by which coral reef populations are replenished (Victor 1983; Mapstone and Fowler 1988; Jones 1990). Despite this, very few studies of marine reserves have provided any information on recruitment (but see Lipcius et al. 2001). Clearly, a lot of information goes into selecting sites for marine reserves (Fernandes et al. 2009), and it may not be possible to include a lot of species-specific criteria. However, for the two fish species in this study, the chance inclusion or exclusion of recruitment hotspots could be a critical factor in their success. For example, the two marine reserves without recruitment hotspots in this study— Middle Island and Monkey Point (Great Keppel Island) were protected from 1999 and 2003 for their well-developed fringing reef and seagrass beds (GBRMPA 2005). Insufficient recruitment in these two reserves might be the main reason for the low abundance of target species after many years of protection.

The results of this study are preliminary and there are certainly factors other than recruitment, which may be important. Reserves that do less well may also be those placed in habitats that are less suitable for subadult and adult fish. Wen et al (2012b; Chapter 3) described the depth and habitat preferences of these three predatory fishes, which show a strong reliance on tabular

*Acropora* on sandy substrata along the reef base and lagoon (also see Kerry and Bellwood 2012). These deeper and tabular *Acropora* are relatively limited in Middle Island and Monkey Point, which are shallow (3-7 m) and covered with mainly branching *Acropora*. Other studies have suggested the weak enforcement and illegal fishing in the reserves might be the primary reason explained the decrease or no change in the abundance and density of target species in marine reserves (Ayling and Ayling 1986; Samoily 1988; Mapstone et al. 1999; McLean et al. 2011). The negative or neutral effect after protected in reserves like above case studies might due to insufficient recruitment as Middle Island and Monkey Point in this study. However, these negative or neutral reserves might be under reported due to the lack of interest by scientific publication system (Guidetti et al. 2008), then some important features for recovery of marine reserves in coral reefs could be overlooked i.e. recruitment hotspots in this study.

The relationship between numbers of adults and recruits in relation to reserve status may not be a simple cause-effect scenario. Ayling and Ayling (1986) found higher adult abundances of *P. leopardus* were associated with lower densities of juveniles and suggested that this may be due to cannibalism. However, in this study the greater predator abundance in reserves appears to have little or no effects on recruitment (Chapter 2) and sites of higher recruitment (recruitment hotspots) have been found inside and outside of marine reserves. Nevertheless, it is likely that recruitment levels are quantitatively linked to adult densities at some scales. Evidence that larvae may not disperse substantial distances from natal populations is accumulating (Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000; Jones et al. 2005; Almany et al. 2007). Harrison et al (2012) recently showed that a substantial number of larvae produced by adults of these two species in reserves disperse less than 5km from their natal areas. Hence, reserves with high adult numbers may make a greater contribution to nearby recruitment hotspots. The Harrison et al. (2012) study also shows that there are critical areas where recruitment hotspots are associated with larval retention areas. From a conservation perspective, identifying and protecting high recruitment, local retention areas may maximise the protection of species across generations.

There is a clear truncation of the size frequency distribution above the legal minimum size limit (MSL) in fished areas compared to reserves. This suggests that recreational fishers are having a substantial impact on the size structure of coral trout and stripey snapper populations. The presence or absence of recruitment hotspots in fished areas appears to have no effect on the abundance of these larger fishes. The dramatic decline in large *P. maculatus* in non-reserves appears to happen even at a size lower than the MSL. This suggests a level of illegal fishing of small fish outside reserves, which has been also reported in other studies (e.g. Mapstone et al. 2008; Blank and Gavin 2009; Powell et al. 2010; McLean et al. 2011; Cooke et al. 2012).

The MSL is ideally based on biological attributes such as size of maturity of each species. The MSL is usually adjusted to allow these species to reproduce on average at least once before they might be caught. However, the MSL for *E. quoyanus* is larger than the size at maturity (24 cm TL; Mapstone unpublished data). Currently, the MSL is standardised across all *Epinephelus* spp. (38 cm TL, Fisheries Act 2003), most of which are much larger than *E. quoyanus*. More biological and ecological data relating to *E. quoyanus* are needed to determine an optimal MSL, but it is likely to be lower than the current size limit.

Recruitment hotspots result in a high population density of subadults, both inside reserves and in fished areas. In designing reserve networks it will be important to include hotspots in both no-take areas for conservation purposes, and in fished areas to promote fish production. However, recruitment hotspots are clearly associated with live coral habitats of a specific type (Chapter 3; Wen et al. 2012b) and approaches to protect such nursery areas will be required for both reserve and non-reserve areas. Damaging fishing practices may also have a negative impact on the quality of recruitment habitat (Davis 1977; Bavestrello et al. 1997; Backhurst and Cole 2000; Milazzo et al. 2002; Dinsdale and Harriott 2004). Moreover, the land-based pollution and run-off could cross the boundary of marine reserves into these fragile coral reefs. Therefore, a

comprehensive management plan to preserve the recruitment hotspots of fishery target species is necessary for sustainable fisheries beyond marine reserves (Allison et al. 1998; Halpern and Warner 2003; Lubchenco et al. 2003).

Table 5-1 Two-way ANOVA of (a) adult and (b) subadult of three predatory fishes

Two factors (reserves and recruitment hotspots) of *Plectropomus maculatus*, *Lutjanus carponotatus* and *Epinephelus quoyanus* on abundance were tested.

(a) Adult

Species	Factor	F value	P vaule
<i>P. maculatus</i>	Reserves	10.62	<b>0.004*</b>
	Hotspots	6.33	<b>0.021*</b>
	Interaction	6.46	<b>0.019*</b>
<i>L. carponotatus</i>	Reserves	4.71	<b>0.042*</b>
	Hotspots	4.08	0.057
	Interaction	1.23	0.281
<i>E. quoyanus</i>	Reserves	0.38	0.546
	Hotspots	1.51	0.231
	Interaction	0.22	0.646

(b) Subadult

Species	Factor	F value	P vaule
<i>P. maculatus</i>	Reserves	2.43	0.133
	Hotspots	13.52	<b>0.001*</b>
	Interaction	2.26	0.147
<i>L. carponotatus</i>	Reserves	4.71	0.677
	Hotspots	4.08	0.073
	Interaction	1.23	0.188
<i>E. quoyanus</i>	Reserves	3.18	0.088
	Hotspots	1.97	0.174
	Interaction	1.88	0.184

Table 5-2 Paired K-S test results from reserves and recruitment hotspots

Result of paired Kolmogorov–Smirnov test from two factors: reserves and recruitment hotspots on length-frequency distribution of a) *Plectropomus maculatus*, b) *Lutjanus carponotatus* and c) *Epinephelus quoyanus*. Right upper half of each table is statistical significant value  $p$ , \*symbol means the difference between two treatment is significant different ( $\alpha < 0.05$ ). Left-bottom half of each table is the statistical distance  $D$ .  $D$  means the maximum deviation distance between two cumulative factions from two treatments.

(a) *P. maculatus*

	Res+HS	Res-HS	nRes+HS	nRes-HS
Res+HS	-	0.255	0.001*	0.026*
Res-HS	0.1238	-	0.001*	0.398
nRes+HS	0.3314	0.3884	-	0.001*
nRes-HS	0.1863	0.1409	0.3919	-

(b) *L. carponotatus*

	Res+HS	Res-HS	nRes+HS	nRes-HS
Res+HS	-	0.001*	0.001*	0.552
Res-HS	0.237	-	0.02*	0.009*
nRes+HS	0.2707	0.1882	-	0.002*
nRes-HS	0.1131	0.2518	0.2795	-

(c) *E. quoyanus*

	Res+HS	Res-HS	nRes+HS	nRes-HS
Res+HS	-	0.001*	0.001*	0.001*
Res-HS	0.5405	-	0.003*	0.028*
nRes+HS	0.3945	0.2358	-	0.594
nRes-HS	0.4044	0.1995	0.1056	-

Figure 5-1 Map of sampling sites

Four sites were in marine reserves: 2 with recruitment hotspots (hollow stars) and 2 without hotspots (hollow circles). Four sites were open to fishing: 2 with recruitment hotspots (dark star) and 2 without hotspots (dark circle).

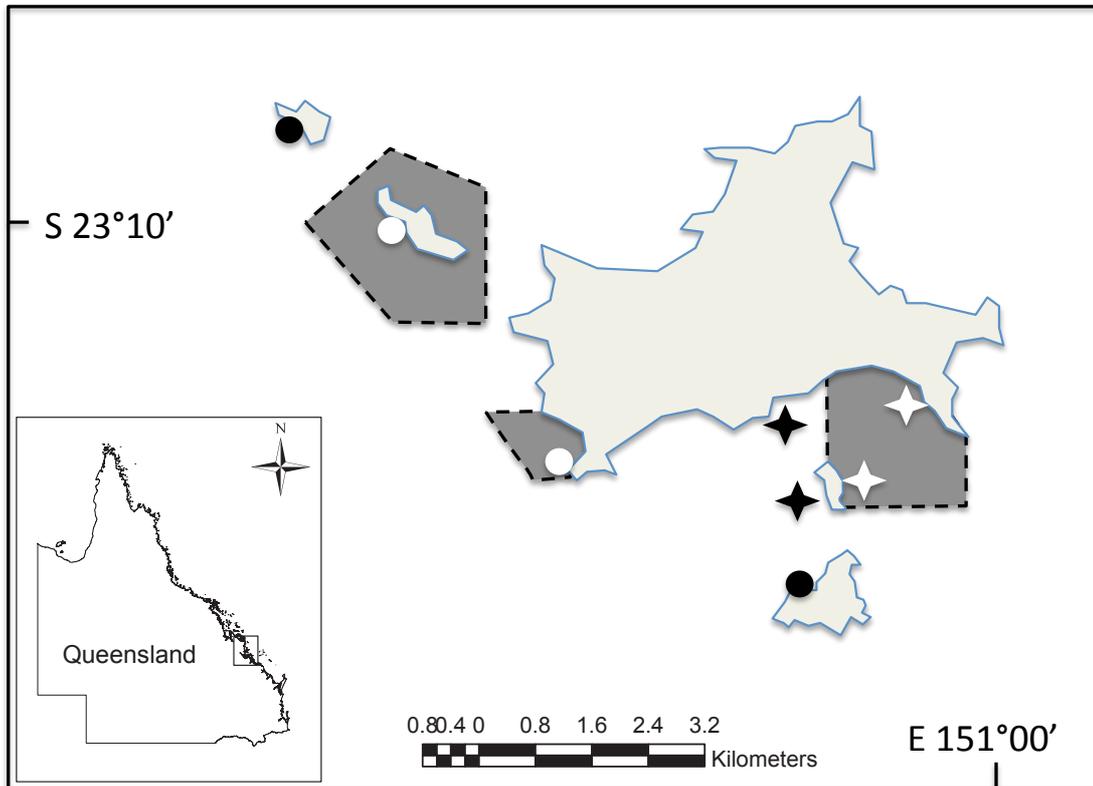
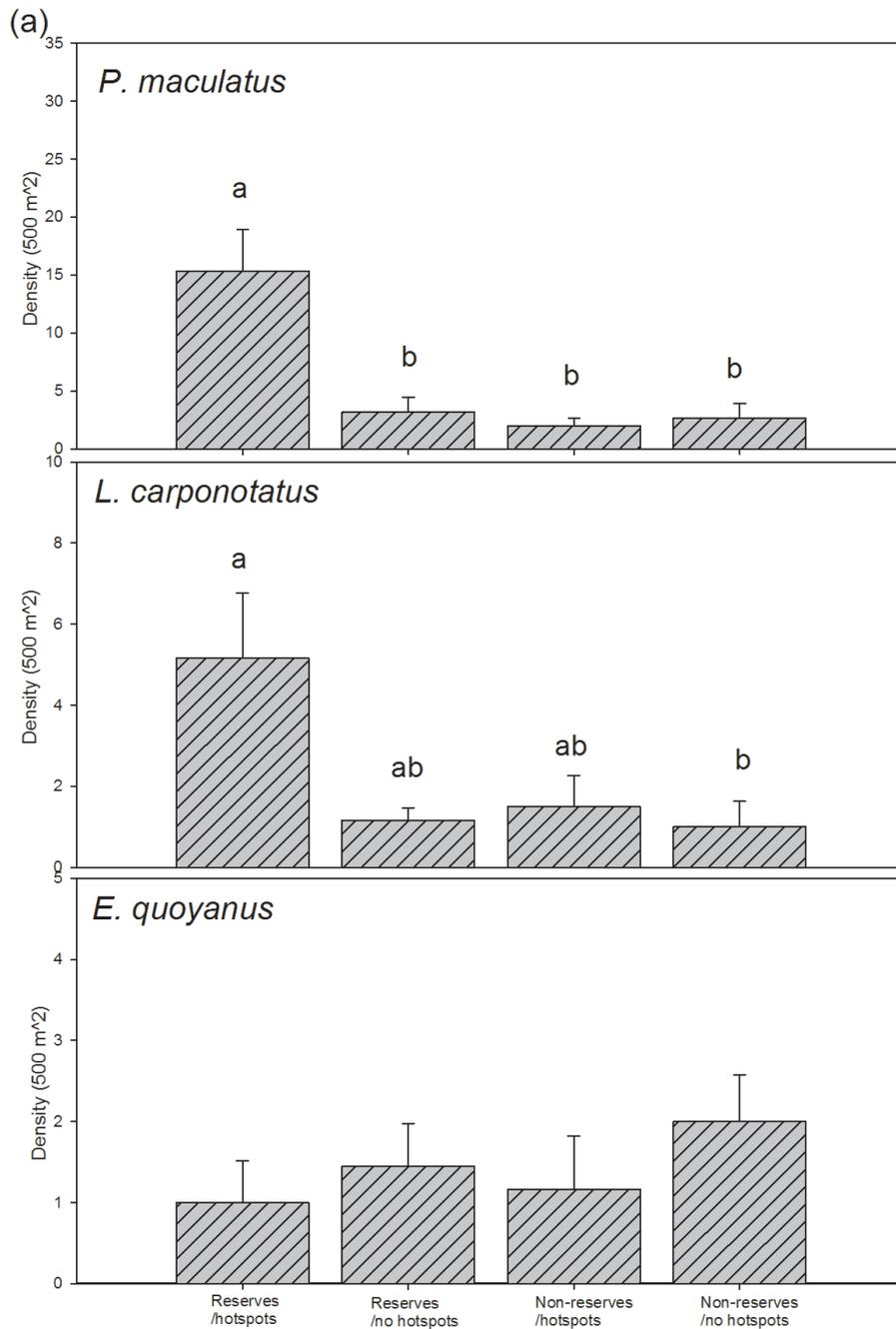


Figure 5-2 Abundance of subadult and adult among two treatment

Results of abundance of subadults and adults in reserve vs non-reserves within recruitment hotspots and non-hotspots. (a) adult, (b) subadult. Tukey's pairwise test was conducted when ANOVA  $p < 0.05$ .



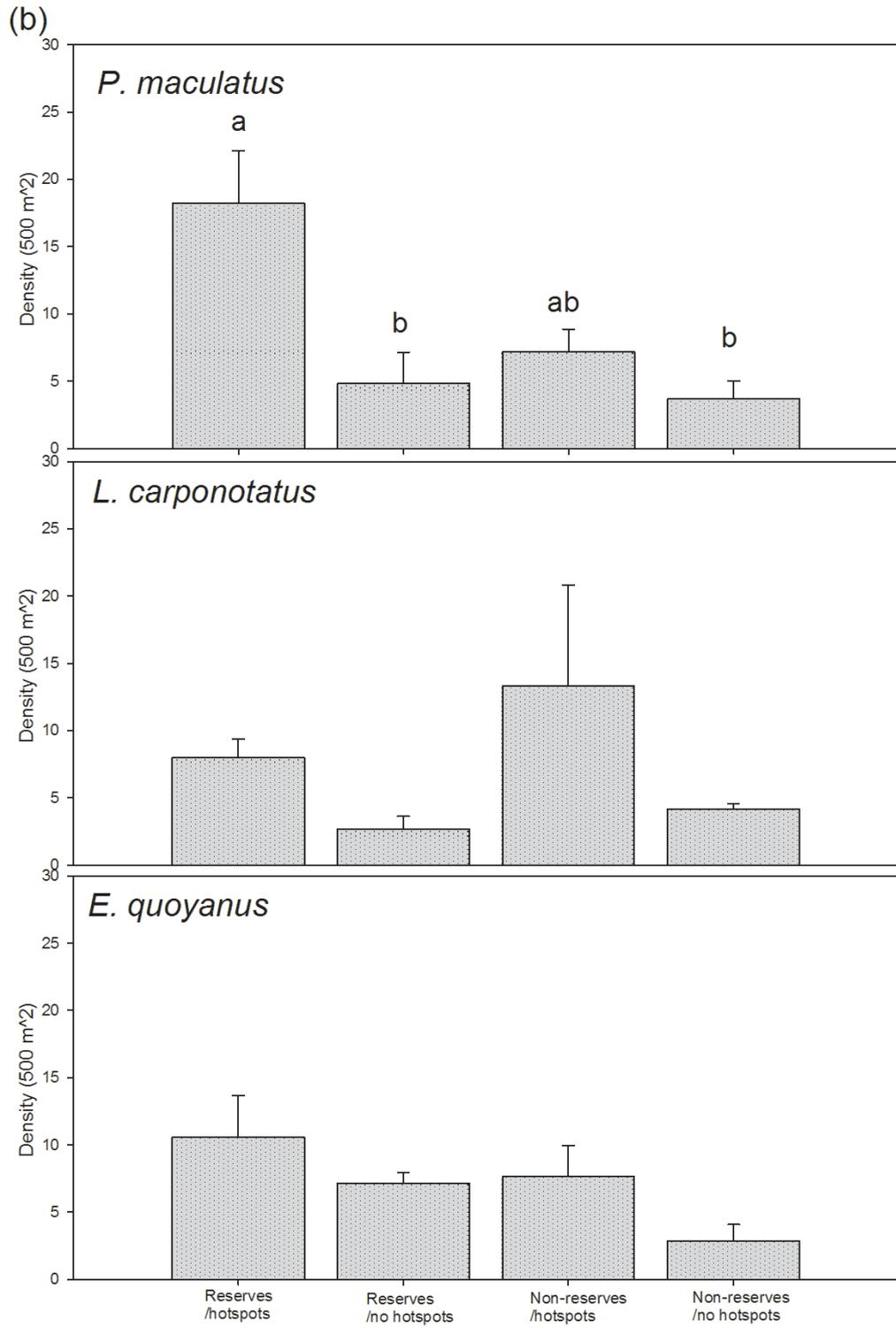
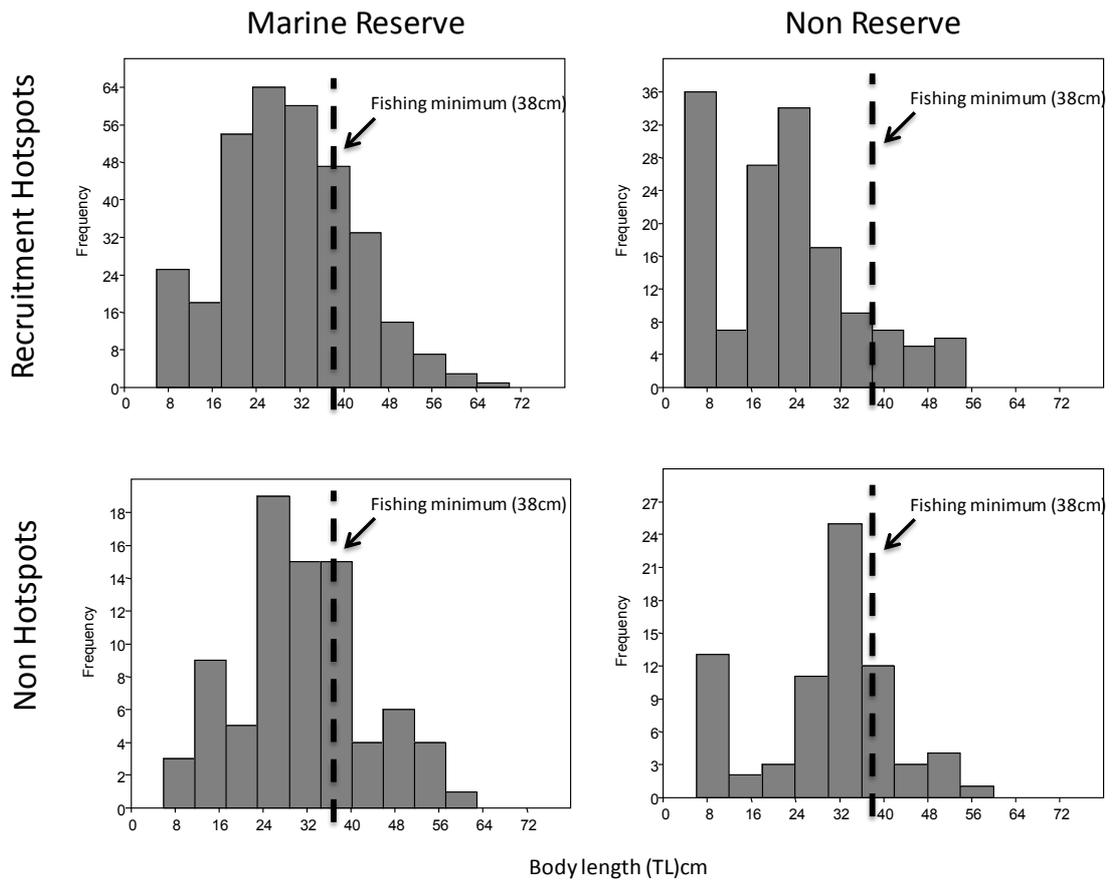


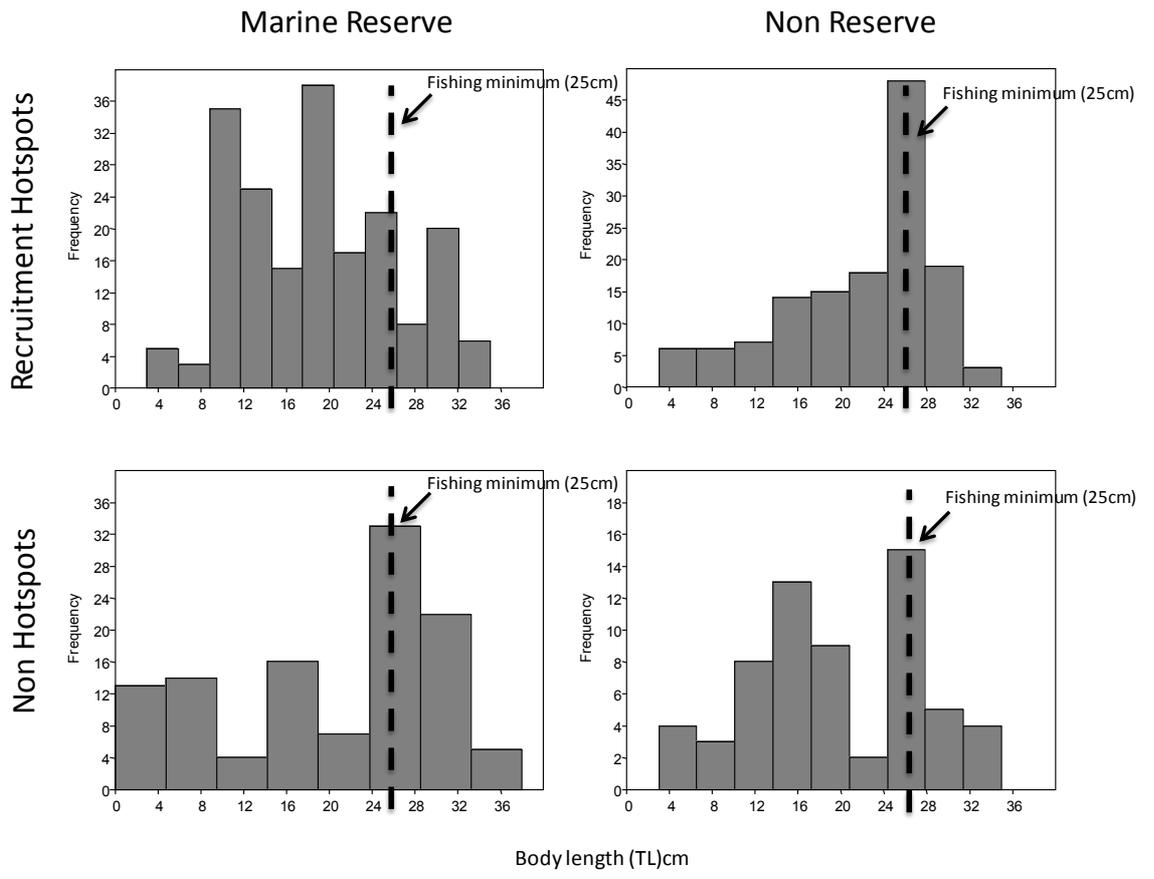
Figure 5-3 Length-frequency histogram of three species among two factors

Body length - frequency histogram of three species between two factors (reserves & recruitment hotspots). (a) *Plectropomus maculatus*, (b) *Lutjanus carponotatus*, and (c) *Epinephelus quoyanus*.

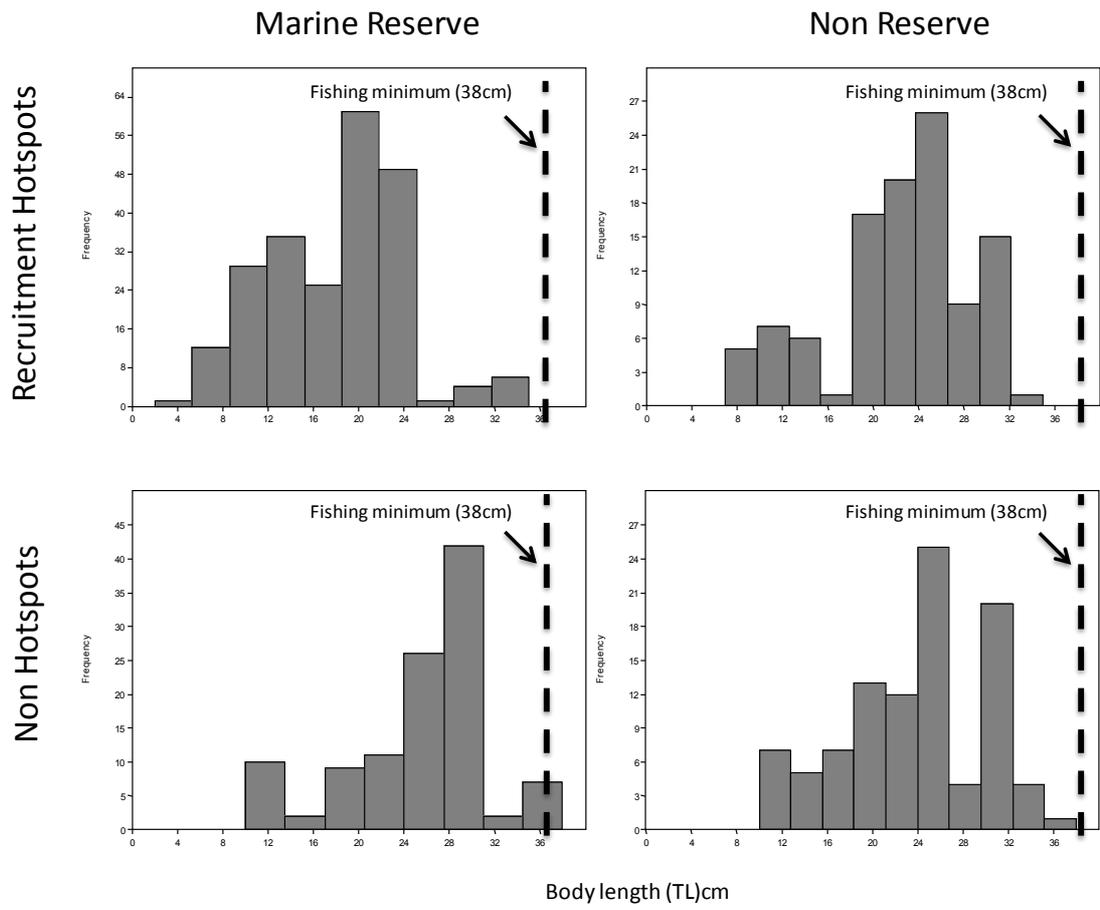
(a) *P. maculatus*



(b) *L. carponotatus*



(c) *E. quoyanus*



## CHAPTER 6 : General Conclusions

This thesis achieved the primary objective of gaining an understanding of the role of recruitment dynamics of predatory fish populations and their responses to marine reserve protection. It filled a major gap in our knowledge of the juvenile stages of 3 recreationally important fishes on the Great Barrier Reef. It advanced our knowledge of their diet, habitat selection and distribution, and identified recruitment hotspots as critical bottlenecks through which juveniles become established in reef populations. It also examined the potential for juveniles to either respond to marine reserve status or contribute to the success of reef closures. Here I highlight the major contributions made in each chapter and follow with suggestion for future research directions that follow on from this research.

### 6.1 Effects of marine reserve status on the diet of juvenile predatory fishes

In the first chapter, I examined the hypothesis that increasing abundance of fishery target species in marine reserves would have direct (consumptive) and indirect (non-consumptive) effects on their recruits, as suggested by a number of studies in places with low predator exploitation. This hypothesis was rejected. No significant differences were found in the abundance and diet of recruits (*P. maculatus*, *L. carponotatus* and *E. quoyanus*) in reserve and non-reserve areas. Only limited effects of reserve status on the diets, prey availability and prey selection were found in three focal species. Nonetheless, each species exhibited conservative dietary patterns that changed with ontogeny, and I noted increasing differences in diet among species with growth. The subtle differences in prey availability, and therefore prey selection between reserves and fished areas remain to be confirmed.

The increased abundance of target species in marine reserves due to decreased fishery mortality is well-established (Williamson et al. 2004). However, the impact of increasing predatory fishes

in reserves on their recruits was difficult to quantify due to the rarity and cryptic behaviour of predatory recruits. The present data did not suggest that adults have major consumptive or non-consumptive effects on juveniles (but see Planes et al. 2000; Graham et al. 2003). This suggests that there is little or no impact of increasing predators on recruitment of those same predators. But further work is needed to quantify adult-juvenile encounter rates, as well as the magnitude of predation pressure on juveniles.

Differences between reserve and non-reserve areas were detected for benthocryptic prey (crustacea and fishes). This was determined from the differences in live coral coverage between reserves and non-reserves and might result from possible trophic cascades driven by increased number of predators. However, no further details or clear trophic relationships could be elucidated within the constraints of this study. Further empirical surveys and experimentation will be needed to clarify this promising topic.

The new data on the diets of juveniles indicates a number of critical prey taxa that are likely to be important in determining recruitment success and the distribution and abundance of juveniles (Jones 1986). The specific patterns of prey selection in the three predatory recruits from this study are remarkable. Benthocryptic crustacea (e.g. squat lobster-Galatheidae) and fishes (e.g. gobies-*Eviota* spp.) are important food items in the early stage of these predatory fishes. Benthocryptic animals in coral reefs have been overlooked in the majority of coral reef systems and have received little attention from both the public and researchers (but see González-Cabello and Bellwood 2009; Stella et al. 2011). This study indicates that these benthocryptic animals might play critical roles in the recovery of fishery target species and sustainable fisheries (Man et al. 1995). More data on gut contents of these predatory recruits across different regions, supported by controlled experiments, are necessary to confirm this hypothesis.

## 6.2 Patterns of recruitment and microhabitat associations for three predatory coral reef fishes

Patterns of habitat association of predatory fishes were surveyed to understand the distribution and abundance of juveniles in the reef environment. Dual-microhabitat (upper and lower) categorical analysis was first used to determine the habitat preference of predatory recruits. A combination of live corymbose *Acropora* on loose substrata (sand/rubble mix) was the most important habitat to recruits of *P. maculatus* and *L. carponotatus*. I suggest that these habitat features are critical to the recruitment of these species, a concept that has not yet been fully addressed in the literature. The benefit of choosing shelter on soft (loose) substrata rather than hard (solid) substrata is thought to relate to the availability of shelter and food resources in the former habitat. This hypothesis was examined and discussed in chapter 4 of the thesis.

Distinct ontogenetic changes in habitat preference of these three predatory fishes were confirmed in this study, but each species showed slightly different trends. *P. maculatus* move from the edge of the reef to deeper water, and associated with a large variety of microhabitats at larger sizes. *L. carponotatus* occur mostly in shallow water when young, but move to the reef flat and reef base as subadults. *L. carponotatus* also shift from using corymbose *Acropora* to tabular *Acropora* as they grow. *E. quoyanus* showed very similar ontogenetic microhabitat changes as *L. carponotatus*, but exhibited a clear ontogenetic movement from the back reef to deeper reef slope and reef base areas.

## 6.3 Role of prey availability in microhabitat preferences of juvenile coral trout

The preferred microhabitats and prey of predatory recruits were established in chapters 2 and 3 of this thesis. Among all available prey, benthocryptic crustacea and fishes constitute the largest proportion of recruits' diets. The dual-microhabitat (live corymbose *Acropora* and loose substratum) was the favoured habitat, indicating that it provides the best balance of both food and shelter for predatory recruits. Two different approaches (*in situ* prey surveys and controlled

aquarium experiments) were used to examine the role of prey and microhabitats in optimizing habitat choices. Results from the *in situ* surveys suggest that the prey fishes are strongly associated with live coral, but it is notable that prey crustacea are more abundant in loose substrata underneath both live and dead coral. I suggest that this specific habitat association maximises food availability of both prey fishes and crustacean.

Manipulative aquarium experiments were applied to verify habitat and prey selection findings from field surveys (chapter 2 & 3). Coral trout recruits preferentially chose both live and dead corymbose *Acropora* in the habitat selection experiment, which suggests that both live and dead corymbose *Acropora* fulfil the same shelter needs for recruits. In prey selection experiments, coral trout recruits consumed *Eviota zebrina* (goby) and *Aiolioops tetraphthalmus* (dartfish), which are both considered relatively slow swimmers, and therefore had the lowest ability to escape of all the experimental prey fishes. It also supported the finding in chapter 2 that *Eviota* spp. is the most common fish in the gut contents of juvenile predatory fishes. In addition, the two preferred prey species can be considered more “exposed” in the aquarium experiments relative to the damselfishes and wrasses, which consistently hid behind the coral branches and buried themselves in the sand when predators were present.

The results from the shelter and prey fish selection experiments suggest that coral trout recruits are ambush predators. Ambush predatory fishes normally hide themselves to avoid predators and to increase their chance of success in striking prey, as has been shown in the hawkfishes (family Cirrhitidae) (DeMartini 1996; Kane et al. 2009). This finding emphasises the importance of shelter (particularly corymbose *Acropora*), which could reduce the mortality rates of coral trout recruits. Although dead corymbose *Acropora* has also been used often as a preferred shelter in the aquarium experiment, lack of prey availability in dead coral from *in situ* survey data indicate that it is a poor overall choice for predatory recruits. Whether the optimal dual-microhabitats increase the survivorship/growth of predatory recruits, or whether they drive the post-settlement ontogenetic movements, are as yet unknown. Further surveys and

manipulative experiments are necessary to understand the ecological role of this optimal dual-microhabitat in the recruitment of predatory reef fishes.

#### **6.4 The importance of recruitment hotspots in determining the efficacy of marine reserve**

The optimal habitat (defined previously) was considered as areas favoured by predatory recruits both of the provision of food and shelter (chapters 2, 3, 4). Higher recruit abundances have been shown in these optimal habitats over two years of field surveys. These regions with consistently abundant recruits of predatory fishes were defined as recruitment hotspots. Here, the effects of recruitment hotspots on populations in reserves and non-reserves were verified. Those regions with recruitment hotspots and protected from fishing (i.e. reserves) demonstrated obvious juvenile replenishment and a constant adult population, as expected. However, reserves without recruitment hotspots show a low rate of replenishment and lower adult numbers than reserves with hotspots. The limited habitats preferred by recruits might be the explanation for why little to no population recovery has been found in some marine reserves (reviews in Russ and Alcala 2003; Hardt 2009). Our findings highlight the importance of successful recruitment (i.e. recruitment hotspots) for the efficacy of marine reserves.

This thesis has provided the preliminary evidence for the combined effect of recruitment hotspots and reserves on two important fishery species. Given the congruence of recruitment hotspots for these two species, it is practical to include recruitment habitat as a criterion for selecting sites for reserves. Although there are several factors that should be taken into account when designing marine reserves, this research highlights the need for the inclusion of recruitment hotspots among the criteria. As the particular characteristics of recruitment hotspots are likely to be unknown for many species, locating the recruitment hotspots of fishery important species should be an important goal for spatial fisheries management.

## 6.5 Final conclusion and future directions

A number of future research priorities can be suggested as outcomes of this research. While our empirical findings of abundance and diet of predatory recruits suggested only minimal effects from increased numbers of adult predatory fishes, more research on the direct and indirect effects of increased adult populations from different marine reserves is needed to confirm this result. The new discoveries on the habitat and prey preference of juveniles will greatly improve our understanding of the recruitment process for these important fishery species. However, further sampling from different latitudes (north to south GBR) and longitudes (inner and outer reefs) is necessary to verify the applicability of our findings to the wider GBR region. Although the combination of live coral on a sandy substratum appears to be favoured in the Keppel region, this needs to be confirmed for other locations.

Recruitment hotspots are likely to be critical for the success of marine reserves in replenishment of target fish populations. Without successful replenishment of coral reef fishes, the long-term recovery of populations in protected areas will be limited. However, this hypothesis requires further investigation. The spatial and temporal sampling in this study was limited to the Keppel islands, and a small number of marine reserves. It will be important to verify this hypothesis by sampling over a wider area to confirm the role of recruitment hotspots in natural population dynamics and the success of marine reserves.

Incorporating recruitment hotspots into reserve design may be good in theory, but how in practice can they be identified? In chapter 3, we intensively surveyed the nearshore, backreef zones where recruits and juveniles of the three study species are most common (Chapter 3; Wen et al. 2012b). Microhabitat characterization revealed that recruitment hotspots differed from similar areas that had lower recruit abundance by: a benthic substrate consisting primarily of sand and rubble (rather than reef flat); greater abundance of tabular and comrybose *Acropora* corals. A potentially profitable avenue for identifying recruitment hotspots without the need for intensive surveys would be the use of increasingly sophisticated remote sensing products and

analyses (Hochberg, 2011; and references therein). For example, high-resolution (< 1m), multispectral satellite imagery is available for many locations. Analysis of known recruitment hotspots could determine any unique characteristics or features, which could then be used to identify potential hotspots in other areas. Ground-truthing by divers of these candidate sites could both determine the accuracy of hotspot classification and provide additional data to refine the classification.

The value of identifying and incorporating recruitment hotspots into reserve design is obviously much greater if there is a high congruence among species in recruitment processes. At least in our study, the two fishery species, *P. maculatus* and *L. carponotatus*, showed similar patterns. The high recruitment areas identified here (Chapter 3; Wen et al. 2012b) and in other studies (Booth, 2000; Eagle et al. 2012) are often shallow, nearshore, backreef habitats with live corals. Such areas can be negatively impacted by a variety of stressors, including and terrestrial-sourced pollution and run-off from changing land-use practices. Therefore, comprehensive ecosystem-scale management is likely to be required to protect coral cover, recruitment hotspots and their associated fish populations and fisheries

While optimal habitats may be an important feature of recruitment hotspots, they are unlikely to be the only factor involved. Consistent larval supply to an area may also be necessary to explain the location of recruitment hotspots. The locations of spawning areas or normal spawning spots are in turn vital to determine the larval supply. Recent research by Harrison et al. (2012) in this area suggests strong links between local spawning sites and local recruitment sites in some areas. In the future, quantifying the connection of spawning aggregation and recruitment hotspots will be a major step in improving our understanding of the recruitment process, both for understanding how existing marine reserve networks operate or more effectively implementing spatial management strategies. This thesis lays the foundation to begin to complete our understanding of the life cycle and management need for some of our most significant inshore coral reef fishery resources.

## REFERENCES

- Abesamis RA, Russ GR, Alcala AC (2006) Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16:349-371
- Aburto-Oropeza O, Dominguez-Guerrero I, Cota-Nieto J, Plomozo-Lugo T (2009) Recruitment and ontogenetic habitat shifts of the yellow snapper (*Lutjanus argentiventris*) in the Gulf of California. *Marine Biology* 156:2461-2472
- Adams AJ, Ebersole JP (2002) Use of back-reef and lagoon habitats by coral reef fishes. *Marine Ecology Progress Series* 228:213-226
- Adams AJ, Dahlgren CP, Kellison GT, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (2006) Nursery function of tropical back-reef systems. *Marine Ecology Progress Series* 318:287-301
- Aguilar-Perera A, Scharer M, Nemeth M (2006) Occurrence of juvenile Nassau grouper, *Epinephelus striatus* (Teleostei : Serranidae), off Mona Island, Puerto Rico: Considerations of recruitment potential. *Caribbean Journal of Science* 42:261-265
- AIMS (2012) Weather Stations database. Australian Institute of Marine Science
- Akritis MG (1990) The rank transform method in some two-factor designs. *Journal of the American Statistical Association* 85:73-78
- Allen G, Steene R, Humann P, DeLoach N (2003) Reef fish identification: tropical Pacific. New World Publications
- Allison GW, Lubchenco J, Carr MH (1998) Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8:79-92
- Almany GR (2003) Priority effects in coral reef fish communities. *Ecology* 84:1920-1935
- Almany GR (2004a) Priority effects in coral reef fish communities of the Great Barrier Reef. *Ecology* 85:2872-2880
- Almany GR (2004b) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105-113
- Almany GR (2004c) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106:275-284
- Almany GR, Webster M (2006) The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs* 25:19-22
- Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742-744
- Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84:511-525
- Anderson MJ, Gorley R, Clarke K (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. Primer-e, Plymouth, UK 237
- Arrington DA, Winemiller KO, Loftus WF, Akin S (2002) How often do fishes "run on empty"? *Ecology* 83:2145-2151
- Ault TR, Johnson CR (1998) Relationships between habitat and recruitment of three species of damselfish (Pomacentridae) at Heron Reef, Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 223:145-166
- Ayling AM, Ayling AL (1986) A biological survey of selected reefs in the Capricorn Section of the Great Barrier Reef Marine Park. Great Barrier Reef Marine Park Authority, Townsville, Australia

- Ayling AM, Ayling AL, Mapstone BD (1992) Possible effects of protection from fishing pressure on recruitment rates of the coral trout (*Plectropomus leopardus*: Serranidae). Proceedings of the 1991 Recruitment Workshop of the Australian Society for Fish Biology 210-215
- Bachok Z, Mansor M, Noordin R (2004) Diet composition and food habits of demersal and pelagic marine fishes from Terengganu waters, east coast of Peninsular Malaysia, NAGA, World Fish Center Quarterly 41-47
- Backhurst MK, Cole RG (2000) Biological impacts of boating at Kawau Island, north-eastern New Zealand. Journal of Environmental Management 60:239-251
- Bavestrello G, Cerrano C, Zanzi D, Cattaneo-Vietti R (1997) Damage by fishing activities to the Gorgonian coral *Paramuricea clavata* in the Ligurian Sea. Aquatic Conservation: Marine and Freshwater Ecosystems 7:253-262
- Beets J (1997) Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. Marine Ecology Progress Series 148:11-21
- Begossi A, Salivonchik S, Araujo L, Andreoli T, Clauzet M, Martinelli C, Ferreira A, Oliveira L, Silvano R (2011) Ethnobiology of snappers (Lutjanidae): target species and suggestions for management. Journal of Ethnobiology and Ethnomedicine 7:1-23
- Bell JD, Craik G, Pollard D, Russell B (1985a) Estimating length frequency distributions of large reef fish underwater. Coral Reefs 4:41-44
- Bell JD, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. Marine Ecology Progress Series 15:265-274
- Bell JD, Harmelin-Vivien ML, Galzin R (1985b) Large scale spatial variation in abundance in butterflyfishes (Chaetodontidae) on Polynesian reefs. Proceedings of the 5th International Coral Reef Symposium 5:421-426
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827-833
- Beukers JS, Jones GP (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114:50-59
- Beukers-Stewart B, Beukers-Stewart J, Jones G (2011) Behavioural and developmental responses of predatory coral reef fish to variation in the abundance of prey. Coral Reefs 30:855-864
- Beverton RJH, Holt SJ (1993) On the dynamics of exploited fish populations. American Fisheries Society
- Blank SG, Gavin MC (2009) The randomized response technique as a tool for estimating non-compliance rates in fisheries: a case study of illegal red abalone (*Haliotis rufescens*) fishing in Northern California. Environmental Conservation 36:112-119
- Blaustein L (1997) Non-consumptive effects of larval Salamandra on crustacean prey: can eggs detect predators? Oecologia 110:212-217
- Bohnsack JA (1993) Marine reserves: they enhance fisheries, reduce conflicts, and protect resources. Oceanus 36:63-71
- Bohnsack JA (1998) Application of marine reserves to reef fisheries management. Australian Journal of Ecology 23:298-304
- Booth DJ, Beretta GA (1994) Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. Coral Reefs 13:81
- Booth DJ, Brosnan DM (1995) The role of recruitment dynamics in rocky shore and coral reef fish communities. Advances in Ecological Research 26:309
- Booth DJ, Beretta GA (2002) Changes in a fish assemblage after a coral bleaching event. Marine Ecology Progress Series 245:205-212

- Booth DJ, Kingsford MJ, Doherty PJ, Beretta GA (2000) Recruitment of damselfishes in One Tree Island lagoon: persistent interannual spatial patterns. *Marine Ecology Progress Series* 202:219-230
- Bortone SA, Williams JL (1986) Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (South Florida): Gray, lane, mutton, and yellowtail snappers. [*Lutjanus griseus*; *Lutjanus synagris*; *Lutjanus analis*; *Ocyurus chrysurus*]. University of West Florida, Pensacola (USA). Dept. of Biology, United States 25
- Bouchon-Navaro Y, Bouchon C (1989) Correlations between chaetodontid fishes and coral communities of the Gulf of Aqaba (Red Sea). *Environmental Biology of Fishes* 25:47-60
- Bouchon-Navaro Y, Bouchon C, Harmelin-Vivien ML (1985) Impact of coral degradation on a chaetodontid fish assemblage, Moorea, French Polynesia Proceedings of the 5th International Coral Reef Congress 5:427-432
- Box GEP, Cox DR (1964) An analysis of transformations. *Journal of the Royal Statistical Society Series B (Methodological)* 26:211-252
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *PLoS ONE* 2:e711
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27:477-500
- Carpenter RC (1981) Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *Journal of Marine Research* 39:749-765
- Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R (1997) Relationships between coral reef substrata and fish. *Coral Reefs* 16:93-102
- Chester AJ, Thayer GW (1990) Distribution of spotted seatrout (*Cynoscion nebulosus*) and gray snapper (*Lutjanus griseus*) juveniles in seagrass habitats of Western Florida Bay. *Bulletin of Marine Science* 46:345-357
- Claudet J, Guidetti P (2010) Fishermen contribute to protection of marine reserves. *Nature* 464:673-673
- Claudet J, Osenberg C, Domenici P, Badalamenti F, Milazzo M, Falcón J, Bertocci I, Benedetti-Cecchi L, García-Charton J, Goñi R (2010) Marine reserves: fish life history and ecological traits matter. *Ecological Applications* 20:830-839
- Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Velde G (2003) Diet shifts of Caribbean grunts (Haemulidae) and snappers (Lutjanidae) and the relation with nursery-to-coral reef migrations. *Estuarine, Coastal and Shelf Science* 57:1079-1089
- Coker DJ, Pratchett MS, Munday PL (2009) Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology* 20:1204
- Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* 9:286-307
- Connell SD (1996) Variations in mortality of a coral-reef fish: links with predator abundance. *Marine Biology* 126:347-352
- Connell SD (1998a) Patterns of piscivory by resident predatory reef fish at One Tree Reef, Great Barrier Reef. *Marine and Freshwater Research* 49:25-30
- Connell SD (1998b) Effects of predators on growth, mortality and abundance of a juvenile reef-fish: evidence from manipulations of predator and prey abundance. *Marine Ecology Progress Series* 169:251-261

- Connell SD, Jones GP (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *Journal of Experimental Marine Biology and Ecology* 151:271
- Connell SD, Kingsford MJ (1998) Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs* 17:49-57
- Cooke SJ, Suski CD, Arlinghaus R, Danylchuk AJ (2012) Voluntary institutions and behaviours as alternatives to formal regulations in recreational fisheries management. *Fish and Fisheries* DOI: 10.1111/j.1467-2979.2012.00477.x
- Cowen RK (2002) Larval dispersal and retention and consequences for population connectivity. In: Sale PF (ed) *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, San Diego, pp149-170
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1:443-466
- Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science* 287:857-859
- Cowen RK, Gawarkiewicz G, Pineda J, Thorrold S, Werner F (2007) Population connectivity in marine systems: An overview. *Oceanography* 20:14-21
- Croker RA (1962) Growth and food of the gray snapper, *Lutjanus griseus* in Everglades National Park. *Transactions of the American Fisheries Society* 91:379-383
- Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227-2240
- Dahlgren CP, Eggleston DB (2001) Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. *Marine Ecology Progress Series* 217:145-156
- Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (2006) Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series* 312:291-295
- Davis GE (1977) Anchor damage to a coral reef on the coast of Florida. *Biological Conservation* 11:29-34
- Dayton PK, Sala E, Tegner MJ, Thrush S (2000) Marine reserves: parks, baselines, and fishery enhancement. *Bulletin of Marine Science* 66:617-634
- DeMartini EE (1996) Sheltering and foraging substrate uses of the arc-eye hawkfish *Paracirrhites arcatus* (Pisces: Cirrhitidae). *Bulletin of Marine Science* 58:826-837
- Depczynski M, Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series* 256:183-191
- Diggles B, Ernst I (1997) Hooking mortality of two species of shallow-water reef fish caught by recreational angling methods. *Marine and Freshwater Research* 48:479-483
- Dinsdale EA, Harriott VJ (2004) Assessing anchor damage on coral reefs: A case study in selection of environmental indicators. *Environmental Management* 33:126-139
- Doherty PJ (1981) Coral reef fishes: recruitment-limited assemblages? ICRS, Proceeding 4th International Coral Reef Symposium 2:465
- Doherty PJ (2002) Variable replenishment and the dynamics of reef fish populations *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, pp327-355
- Doherty PJ, Williams DM (1988) The replenishment of coral-reef fish populations. *Oceanography and Marine Biology* 26:487-551
- Doherty PJ, Fowler T (1994) An empirical test of recruitment limitation in a coral reef fish. *Science* 263:935
- Doherty PJ, Fowler AJ, Samoilys MA, Harris DA (1994) Monitoring the replenishment of coral trout (Pisces: Serranidae) populations. *Bulletin of Marine Science* 54:343-355

- Doherty PJ, Dufour V, Galzin R, Hixon MA, Meekan MG, Planes S (2004) High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology* 85:2422-2428
- Dorenbosch M, Verweij M, Nagelkerken I, Jiddawi N, van der Velde G (2004) Homing and daytime tidal movements of juvenile snappers (*Lutjanidae*) between shallow-water nursery habitats in Zanzibar, Western Indian Ocean. *Environmental Biology of Fishes* 70:203-209
- Duarte LO, Garcia CB (1999) Diet of the mutton snapper *Lutjanus analis* (Cuvier) from the gulf of Salamanca, Colombia, Caribbean sea. *Bulletin of Marine Science* 65:453-465
- Duffus DA, Dearden P (1990) Non-consumptive wildlife-oriented recreation: A conceptual framework. *Biological Conservation* 53:213-231
- Eagle JV, Baird AH, Jones GP, Kingsford MJ (2012) Recruitment hotspots: consistent spatial patterns in the relative abundance of coral recruits at One Tree Island, Australia. *Galaxea* (in press)
- Eggleston DB (1995) Recruitment in nassau grouper *Epinephelus striatus* - postsettlement abundance, microhabitat features, and ontogenic habitat shifts. *Marine Ecology Progress Series* 124:9-22
- Eggleston DB, Grover JJ, Lipcius RN (1998) Ontogenetic diet shifts in Nassau grouper: Trophic linkages and predatory impact. *Bulletin of Marine Science* 63:111-126
- Evans RD, Russ GR (2004) Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef, Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14:505-519
- Evans RD, Russ GR, Kritzer J (2008) Batch fecundity of *Lutjanus carponotatus* (*Lutjanidae*) and implications of no-take marine reserves on the Great Barrier Reef, Australia. *Coral Reefs* 27:179-189
- FAO (2010) The State of World Fisheries and Aquaculture. Food and Agriculture Organization of The United Nations, Rome i-xv, 1-197
- Faunce CH, Serafy JE (2007) Nearshore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*): environmental gradients and ontogenetic shifts. *Bulletin of Marine Science* 80:473-495
- Feary D, Almany G, McCormick M, Jones G (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia* 153:727-737
- Fernandes L, Day J, Kerrigan B, Breen D, De'ath G, Mapstone B, Coles R, Done T, Marsh H, Poiner I (2009) A process to design a network of marine no-take areas: Lessons from the Great Barrier Reef. *Ocean & Coastal Management* 52:439-447
- Fernandes L, Day J, Lewis A, Slegers S, Kerrigan B, Breen D, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'Ath G, Mapstone B, Marsh H, Possingham H, Ball I, Ward T, Dobbs K, Aumend J, Slater D, Stapleton K (2005) Establishing Representative No-Take Areas in the Great Barrier Reef: Large-Scale Implementation of Theory on Marine Protected Areas. *Conservation Biology* 19:1733-1744
- Ferreira B, Russ G (1992) Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces: Serranidae) from the central Great Barrier Reef, Australia. *Marine and Freshwater Research* 43:1301-1312
- Fill A, Long EY, Finke DL (2012) Non-consumptive effects of a natural enemy on a non-prey herbivore population. *Ecological Entomology* 37:43-50
- Findley JS, Findley MT (2001) Global, regional, and local patterns in species richness and abundance of butterflyfishes. *Ecological Monographs* 71:69-91

- Fisheries Act (2003) Fisheries (Coral Reef Fin Fish) Management Plan 2003. The State of Queensland, Queensland Government
- Fletcher DJ, Underwood AJ (2002) How to cope with negative estimates of components of variance in ecological field studies. *Journal of Experimental Marine Biology and Ecology* 273:89-95
- Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish. *ecology* 71:1666-1681
- Forrester GE (1995) Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. *Oecologia* 103:275
- Forrester GE, Steele MA (2004) Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology* 85:1332-1342
- Friedlander M, Parrish JD, DeFelice RC (2002) Ecology of the introduced snapper *Lutjanus kasmiva* (Forsskal) in the reef fish assemblage of a Hawaiian bay. *Journal of Fish Biology* 60:28-48
- Frisch AJ (2006) Are juvenile coral-trouts (*Plectropomus*) mimics of poisonous pufferfishes (*Canthigaster*) on coral reefs? *Marine Ecology* 27:247-252
- Frisch AJ, Van Herwerden L (2006) Field and experimental studies of hybridization between coral trouts, *Plectropomus leopardus* and *Plectropomus maculatus* (Serranidae), on the Great Barrier Reef, Australia. *Journal of Fish Biology* 68:1013-1025
- Fry G, Milton D, Van Der Velde T, Stobutzki I, Andamari R, Badrudin B, Sumiono B (2009) Reproductive dynamics and nursery habitat preferences of two commercially important Indo-Pacific red snappers *Lutjanus erythropterus* and *L. malabaricus*. *Fisheries Science* 75:145-158
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958
- Garpe KC, Ohman MC (2003) Coral and fish distribution patterns in Mafia Island Marine Park, Tanzania: fish-habitat interactions. *Hydrobiologia* 498:191-211
- Garpe KC, Yahya SAS, Lindahl U, Ohman MC (2006) Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Marine Ecology Progress Series* 315:237-247
- GBRMPA (2005) Report on the Great Barrier Reef Marine Park zoning plan 2003. pre-proofed version November 2005 Townsville: Great Barrier Reef Marine Park Authority
- Gill AB, Hart PJB (1994) Feeding behaviour and prey choice of the threespine stickleback: the interacting effects of prey size, fish size and stomach fullness. *Animal Behaviour* 47:921-932
- González-Cabello A, Bellwood DR (2009) Local ecological impacts of regional biodiversity on reef fish assemblages. *Journal of Biogeography* 36:1129-1137
- Gosliner TM, Behrens DW, Williams GC (1996) Coral reef animals of the Indo-Pacific: animal life from Africa to Hawaii exclusive of the vertebrates. Monterey: Sea Challengers
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environmental Conservation* 30:200-208
- Graham NAJ, McClanahan TR, Letourneur Y, Galzin R (2007a) Anthropogenic stressors, inter-specific competition and ENSO effects on a mauritian coral reef. *Environmental Biology of Fishes* 78:57-69
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences* 103:8425-8429

- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson JAN, Bijoux JP, Daw TM (2007b) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology* 21:1291-1300
- Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Polunin NVC, Jennings S, Chabanet P, Clark S, Spalding MD, Letourneur Y (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLoS ONE* 3:e3039
- Grorud-Colvert K, Sponaugle S (2009) Larval supply and juvenile recruitment of coral reef fishes to marine reserves and non-reserves of the upper Florida Keys, USA. *Marine Biology* 156:277-288
- Guidetti P, Milazzo M, Bussotti S, Molinari A, Murenu M, Pais A, Spanò N, Balzano R, Agardy T, Boero F, Carrada G, Cattaneo-Vietti R, Cau A, Chemello R, Greco S, Manganaro A, Notarbartolo di Sciara G, Russo GF, Tunesi L (2008) Italian marine reserve effectiveness: Does enforcement matter? *Biological Conservation* 141:699-709
- Guillaume J (2001) Nutrition and feeding of fish and crustaceans. Springer Verlag
- Hajisamae S, Ibrahim S (2008) Seasonal and spatial variations of fish trophic guilds in a shallow, semi-enclosed tropical estuarine bay. *Environmental Biology of Fishes* 82:251-264
- Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. *Ecology Letters* 5:361-366
- Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:1871-1878
- Hambäck PA, Englund G (2005) Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. *Ecology Letters* 8:1057-1065
- Hammer Ø, Harper D, Ryan P (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:9
- Harborne AR, Mumby PJ, Kappel CV, Dahlgren CP, Micheli F, Holmes KE, Sanchirico JN, Broad K, Elliott IA, Brumbaugh DR (2008) Reserve effects and natural variation in coral reef communities. *Journal of Applied Ecology* 45:1010-1018
- Hardt MJ (2009) Lessons from the past: the collapse of Jamaican coral reefs. *Fish and Fisheries* 10:143-158
- Harmelin-Vivien M, Le Diréach L, Bayle-Sempere J, Charbonnel E, García-Charton JA, Ody D, Pérez-Ruzafa A, Reñones O, Sánchez-Jerez P, Valle C (2008) Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? *Biological Conservation* 141:1829-1839
- Harrigan P, Zieman JC, Macko SA (1989) The base of nutritional support for the gray snapper (*Lutjanus griseus*): An evaluation based on a combined stomach content and stable isotope analysis. *Bulletin of Marine Science* 44:65-77
- Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, Feldheim KA, van Herwerden L, Planes S, Srinivasan M, Berumen ML, Jones GP (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology* 22:1023-1028
- Heck Jr KL, Weinstein MP (1989) Feeding habits of juvenile reef fishes associated with Panamanian seagrass meadows. *Bulletin of Marine Science* 45:629-636
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution* 23:202-210
- Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp475-508

- Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77-101
- Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946
- Hixon MA, Jones GP (2005) Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847-2859
- Holbrook SJ, Forrester GE, Schmitt RJ (2000) Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* 122:109-120
- Holland DS, Brazee RJ (1996) Marine reserves for fisheries management. *Marine Resource Economics* 11:157-172
- Holm ER (1990) Effects of density-dependent mortality on the relationship between recruitment and larval settlement. *Marine Ecology Progress Series* 60:141
- Holmes TH, McCormick MI (2010) Size-selectivity of predatory reef fish on juvenile prey. *Marine Ecology Progress Series* 399:273-283
- Holmes TH, McCormick MI (2011) Response across a gradient: behavioural reactions of newly settled fish to predation cues. *Animal Behaviour* 81:543-550
- Holt RD (1985) Population dynamics in two patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28:181
- Huey RB, Pianka ER, Vitt LJ (2001) How often do lizards “run on empty”? *Ecology* 82:1-7
- Hughes TP, Bellwood DR, Folke CS, McCook LJ, Pandolfi JM (2007) No-take areas, herbivory and coral reef resilience. *Trends in Ecology & Evolution* 22:1-3
- Hughes TP, Bellwood D, Baird A, Brodie J, Bruno J, Pandolfi J (2011) Shifting base-lines, declining coral cover, and the erosion of reef resilience: comment on Sweatman et al.(2011). *Coral Reefs* 30:653-660
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929-933
- Hutchinson N, Rhodes K (2010) Home range estimates for squaretail coral grouper, *Plectropomus areolatus* (Rüppell 1830). *Coral Reefs* 29:511-519
- IUCN (2011) IUCN red list of threatened species. IUCN
- Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New Haven
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629-637
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems *Advances in Marine Biology* 34: 201
- Jennings S, Marshall SS, Polunin NVC (1996) Seychelles' marine protected areas: comparative structure and status of reef fish communities. *Biological Conservation* 75:201-209
- Jennings S, Reynolds JD, Mills SC (1998) Life history correlates of responses to fisheries exploitation. *Biological Sciences* 265:333-339
- Jones GP (1986) Food availability affects growth in a coral reef fish. *Oecologia* 70:136-139
- Jones GP (1987) Some interactions between residents and recruits in two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* 114:169-182
- Jones GP (1988) Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* 123:115-126

- Jones GP (1990) The importance of recruitment to the dynamics of a coral reef fish population. *Ecology* 71:1691-1698
- Jones GP (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale PF (ed) *The Ecology of fishes on coral reefs*. Academic Press, New York, pp294–328
- Jones GP (1997) Relationships between recruitment and postrecruitment processes in lagoonal populations of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* 213:231-246
- Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. *Current Biology* 15:1314-1318
- Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402:802-804
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences* 101:8251-8253
- Kamukuru AT, Mgaya YD (2004) The food and feeding habits of blackspot snapper, *Lutjanus fulviflamma* (Pisces: Lutjanidae) in shallow waters of Mafia Island, Tanzania. *African Journal of Ecology* 42:49-58
- Kane CN, Brooks AJ, Holbrook SJ, Schmitt RJ (2009) The role of microhabitat preference and social organization in determining the spatial distribution of a coral reef fish. *Environmental Biology of Fishes* 84:1-10
- Kerry J, Bellwood D (2012) The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs* DOI: 10.1007/s00338-011-0859-7
- Kingsford MJ (1992) Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs* 11:193-198
- Kingsford MJ (2009) Contrasting patterns of reef utilization and recruitment of coral trout (*Plectropomus leopardus*) and snapper (*Lutjanus carponotatus*) at One Tree Island, southern Great Barrier Reef. *Coral Reefs* 28:251-264
- Kingsford MJ, Wolanski E, Choat JH (1991) Influence of tidally induced fronts and Langmuir circulations on distribution and movements of presettlement fishes around a coral reef. *Marine Biology* 109:167-180
- Kiso K, Mahyam M-I (2003) Distribution and feeding habits of juvenile and young John's snapper *Lutjanus johnii* in the Matang mangrove estuary, west coast of Peninsular Malaysia. *Fisheries Science* 69:563-568
- Kramer M, Bellwood D, Bellwood O (2012) Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. *Coral Reefs* DOI: 10.1007/s00338-012-0924-x
- Kritzer JP (2004) Sex-specific growth and mortality, spawning season, and female maturation of the stripey bass (*Lutjanus carponotatus*) on the Great Barrier Reef. *Fishery Bulletin* 102:94-107
- Kulbicki M, Bozec Y-M, Labrosse P, Letourneur Y, Mou-Tham G, Wantiez L (2005) Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. *Aquatic Living Resources* 18:231-250
- Kuwamura T, Yogo Y, Nakashima Y (1994) Population dynamics of goby *Paragobiodon echinocephalus* and host coral *Stylophora pistillata*. *Marine Ecology Progress Series* 103:17-23
- La Mesa G, Louisy P, Vacchi M (2002) Assessment of microhabitat preferences in juvenile dusky grouper (*Epinephelus marginatus*) by visual sampling. *Marine Biology* 140:175-185

- Layman CA, Silliman BR (2002) Preliminary survey and diet analysis of juvenile fishes of an estuarine creek on Andros Island, Bahamas. *Bulletin of Marine Science* 70:199-210
- Leahy SM, McCormick MI, Mitchell MD, Ferrari MCO (2011) To fear or to feed: the effects of turbidity on perception of risk by a marine fish. *Biology Letters* 7:811-813
- Lecchini D, Galzin R (2005) Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Marine Biology* 147:47-58
- Leis JM, Carson-Ewart BM (1999) In situ swimming and settlement behaviour of larvae of an Indo-Pacific coral-reef fish, the coral trout *Plectropomus leopardus* (Pisces: Serranidae). *Marine Biology* 134:51-64
- Leis JM, McCormick MI (2002) The biology, behavior, and ecology of the pelagic, larval stage of coral reef fishes. In: Sale PF (ed) *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, San Diego, pp171-199
- Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384:33-46
- Letourneur Y, Chabanet P, Vigliola L, Harmelin-Vivien M (1998) Mass settlement and post-settlement mortality of *Epinephelus merra* (Pisces: Serranidae) on Reunion coral reefs. *JMBA-Journal of the Marine Biological Association of the United Kingdom* 78:307-320
- Levin PS (1994) Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. *Environmental Biology of Fishes* 40:271-281
- Light PR, Jones GP (1997) Habitat preference in newly settled coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs* 16:117-126
- Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. *BioScience* 48:25-34
- Lipcius RN, Stockhausen WT, Eggleston DB (2001) Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics. *Marine and Freshwater Research* 52:1589-1598
- Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: The emerging science of marine reserves. *Ecological Applications* 13:3-7
- Luo J, Serafy J, Sponaugle S, Teare P, Kieckbusch D (2009) Movement of gray snapper *Lutjanus griseus* among subtropical seagrass, mangrove, and coral reef habitats. *Marine Ecology Progress Series* 380:255-269
- MacDonald JA, Shahrestani S, Weis JS (2009) Behavior and space utilization of two common fishes within Caribbean mangroves: implications for the protective function of mangrove habitats. *Estuarine, Coastal and Shelf Science* 84:195-201
- Madin EMP, Gaines SD, Warner RR (2010) Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology* 91:3563-3571
- Malcolm SB (1992) Prey defence and predator foraging. In: MJ C (ed) *Natural enemies: the population biology of predators, parasites and diseases*. Blackwell, Oxford, pp458-475
- Man A, Law R, Polunin NVC (1995) Role of marine reserves in recruitment to reef fisheries: A metapopulation model. *Biological Conservation* 71:197-204
- Mangel M (2000) On the fraction of habitat allocated to marine reserves. *Ecology Letters* 3:15-22
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) *Resource selection by animals: statistical analysis and design for field studies*. Kluwer, Boston, Massachusetts, USA
- Mannering TD (2008) Benefits of marine protected areas beyond boundaries: an evaluation for two coral reef fishes. *James Cook University*, p1-81

- Mapstone BD, Ayling A, Choat J (1999) A visual survey of demersal biota in the Cairns section of the Great Barrier Reef Marine Park. Great Barrier Reef Marine Park Authority Research Publication Series 60:1-47
- Mapstone BD, Fowler AJ (1988) Recruitment and the structure of assemblages of fish on coral reefs. *Trends in Ecology & Evolution* 3:72
- Mapstone BD, Little LR, Punt AE, Davies CR, Smith ADM, Pantus F, McDonald AD, Williams AJ, Jones A (2008) Management strategy evaluation for line fishing in the Great Barrier Reef: Balancing conservation and multi-sector fishery objectives. *Fisheries Research* 94:315-329
- Martin RA, Hammerschlag N (2012) Marine predator-prey contests: Ambush and speed versus vigilance and agility. *Marine Biology Research* 8:90-94
- McCauley D, Micheli F, Young H, Tittensor D, Brumbaugh D, Madin E, Holmes K, Smith J, Lotze H, DeSalles P, Arnold S, Worm B (2010) Acute effects of removing large fish from a near-pristine coral reef. *Marine Biology* 157:2739-2750
- McClanahan TR, Arthur R (2001) The effect of marine reserves and habitat on populations of East African coral reef fishes. *Ecological Applications* 11:559-569
- McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin* 48:327-335
- McClanahan TR, Bergman K, Huitric M, McField M, Elfving T, Nystrom M, Nordemar I (2000) Response of fishes to algae reduction on Glovers Reef, Belize. *Marine Ecology Progress Series* 206:273-282
- McClanahan TR, McField M, Huitric M, Bergman K, Sala E, Nystrom M, Nordemar I, Elfving T, Muthiga NA (2001) Responses of algae, corals and fish to the reduction of macroalgae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. *Coral Reefs* 19:367-379
- McCook LJ, Ayling T, Cappo M, Choat JH, Evans RD, De Freitas DM, Heupel M, Hughes TP, Jones GP, Mapstone B, Marsh H, Mills M, Molloy FJ, Pitcher CR, Pressey RL, Russ GR, Sutton S, Sweatman H, Tobin R, Wachenfeld DR, Williamson DH (2010) Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. *Proceedings of the National Academy of Sciences* 107:18278-18285
- McCormick M (1995) Fish feeding on mobile benthic invertebrates: influence of spatial variability in habitat associations. *Marine Biology* 121:627-637
- McIlwain JL, Jones GP (1997) Prey selection by an obligate coral-feeding wrasse and its response to small-scale disturbance. *Marine Ecology Progress Series* 155:189-198
- McLean DL, Harvey ES, Meeuwig JJ (2011) Declines in the abundance of coral trout (*Plectropomus leopardus*) in areas closed to fishing at the Houtman Abrolhos Islands, Western Australia. *Journal of Experimental Marine Biology and Ecology* 406:71-78
- Meekan MG, Milicich MJ, Doherty PJ (1993) Larval production drives temporal patterns of larval supply and recruitment of a coral reef damselfish. *Marine Ecology Progress Series* 93:217
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* 130:730
- Merriam-Webster (2005) The Merriam-Webster dictionary. Merriam-Webster Inc.
- Messmer V, Jones GP, Munday PL, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology* 92:2285-2298

- Mikulas Jr JJ, Rooker JR (2008) Habitat use, growth, and mortality of post-settlement lane snapper (*Lutjanus synagris*) on natural banks in the northwestern Gulf of Mexico. *Fisheries Research* 93:77-84
- Milazzo M, Chemello R, Badalamenti F, Camarda R, Riggio S (2002) The impact of human recreational activities in marine protected areas: What lessons should be learnt in the Mediterranean Sea? *Marine Ecology* 23:280-290
- Milinski M, Heller R (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* 275:642-644
- Mitchell MD, McCormick MI, Ferrari MCO, Chivers DP (2011) Coral reef fish rapidly learn to identify multiple unknown predators upon recruitment to the reef. *PLoS ONE* 6:e15764
- Mora C, Andréfouët S, Costello MJ, Kranenburg C, Rollo A, Veron J, Gaston KJ, Myers RA (2006) Coral reefs and the global network of marine protected areas. *Science* 312:1750-1751
- Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG (2007) Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Sciences* 104:8362-8367
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98-101
- Munday PL (2000) Interactions between habitat use and patterns of abundance in coral-dwelling fishes of the Genus *Gobiodon*. *Environmental Biology of Fishes* 58:355-369
- Munday PL (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia* 128:585-593
- Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology* 10:1642-1647
- Munday PL, Wilson SK (1997) Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. *Journal of Fish Biology* 51:931-938
- Munday PL, Jones GP, Caley MJ (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Marine Ecology Progress Series* 152:227-239
- Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. *Fish and Fisheries* 9:261-285
- Munro C (2005) Diving systems. In: Eleftheriou A, McIntyre A (eds) *Methods for the study of marine benthos*. Blackwell Science Ltd, Oxford, pp112-159
- Musick JA (1999) Ecology and conservation of long-lived marine animals. *American Fisheries Society Symposium* 23:1-10
- Myers RA, Rosenberg A, Mace P, Barrowman N, Restrepo V (1994) In search of thresholds for recruitment overfishing. *ICES Journal of Marine Science: Journal du Conseil* 51:191-205
- Myers RA, Barrowman NJ (1996) Is fish recruitment related to spawner abundance? *Fishery Bulletin* 94:707-724
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280-283
- Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360:13-20
- Mysterud A, Ims RA (1998) Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435-1441

- Nakamura Y, Horinouchi M, Shibuno T, Tanaka Y, Miyajima T, Koike I, Kurokura H, Sano M (2008) Evidence of ontogenetic migration from mangroves to coral reefs by black-tail snapper *Lutjanus fulvus*: stable isotope approach. *Marine Ecology Progress Series* 355:257-266
- Nanami A, Yamada H (2008) Foraging rates and substratum selection in foraging activity of checkered snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef. *Journal of Fish Biology* 73:1484-1488
- Newman SJ, Cappo M, Williams DMB (2000) Age, growth and mortality of the stripey, *Lutjanus carponotatus* (Richardson) and the brown-stripe snapper, *L. vitta* (Quoy and Gaimard) from the central Great Barrier Reef, Australia. *Fisheries Research* 48:263-275
- Newman SJ, Williams DMB (1996) Variation in reef associated assemblages of the Lutjanidae and Lethrinidae at different distances offshore in the central Great Barrier Reef. *Environmental Biology of Fishes* 46:123-138.
- O'Leary J, Potts D, Braga J, McClanahan T (2012) Indirect consequences of fishing: reduction of coralline algae suppresses juvenile coral abundance. *Coral Reefs* 31:547-559
- Orians GH, Wittenberger JF (1991) Spatial and temporal scales in habitat selection. *The American Naturalist* 137:S29-S49
- Paddock MJ, Estes JA (2000) Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. *Ecological Applications* 10:855-870
- Pauly D (2008) Global fisheries: a brief review. *Journal of Biological Research-Thessaloniki* 9:3-9
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. *Science* 279:860-863
- Pauly D, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, Zeller D (2002) Towards sustainability in world fisheries. *Nature* 418:689 - 695
- Pimentel CR, Joyeux JC (2010) Diet and food partitioning between juveniles of mutton *Lutjanus analis*, dog *Lutjanus jocu* and lane *Lutjanus synagris* snappers (Perciformes: Lutjanidae) in a mangrove-fringed estuarine environment. *Journal of Fish Biology* 76:2299-2317
- Planes S, Galzin R, Garcia Rubies A, Goni R, Harmelin J-G, Le Direach L, Lenfant P, Quetglas A (2000) Effects of marine protected areas on recruitment processes with special reference to Mediterranean littoral ecosystems. *Environmental Conservation* 27:126-143
- Pollnac R, Christie P, Cinner JE, Dalton T, Daw TM, Forrester GE, Graham NAJ, McClanahan TR (2010) Marine reserves as linked social-ecological systems. *Proceedings of the National Academy of Sciences* 107:18262-18265
- Powell EN, Bochenek EA, DePersenaire J (2010) Evaluation of bag-and-size-limit options in the management of summer flounder *Paralichthys dentatus*. *Fisheries Research* 105:215-227
- Pratchett MS (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology* 148:373-382
- Pratchett MS, Berumen ML (2008) Interspecific variation in distributions and diets of coral reef butterflyfishes (Teleostei: Chaetodontidae). *Journal of Fish Biology* 73:1730-1747
- Pratchett MS, Wilsons SK, Baird AH (2006) Declines in the abundance of Chaetodon butterflyfishes following extensive coral depletion. *Journal of Fish Biology* 69:1269-1280
- Pratchett MS, Wilson SK, Berumen ML, McCormick MI (2004) "Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish". *Coral Reefs* 23:352-356

- Pratchett MS, Trapon M, Berumen ML, Chong-Seng K (2011) Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. *Coral Reefs* 30:183-193
- Pratchett MS, Berumen ML, Marnane MJ, Eagle JV, Pratchett DJ (2008a) Habitat associations of juvenile versus adult butterflyfishes. *Coral Reefs* 27:541-551
- Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinneri JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008b) Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences. *Oceanography and Marine Biology: an annual review* 46:251-296
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501-509
- Preisser EL, Bolnick DI, Grabowski JH (2009) Resource dynamics influence the strength of non-consumptive predator effects on prey. *Ecology Letters* 12:315-323
- Pulliam HR (1989) Individual behavior and the procurement of essential resources. In: Roughgarden J, May RM, Levin SA (eds) *Perspectives in ecological theory*. Princeton University Press, Princeton, N.J., pp25-38
- Purkis S, Graham NAJ, Riegl B (2008) Predictability of reef fish diversity and abundance using remote sensing data in Diego Garcia (Chagos Archipelago). *Coral Reefs* 27:167-178
- Quéré G, Leis J (2010) Settlement behaviour of larvae of the Stripey Snapper, *Lutjanus carponotatus*; (Teleostei: Lutjanidae). *Environmental Biology of Fishes* 88:227-238
- Randall JE (1967) Food habits of reef fishes of the West Indies. University of Miami, Institute of Marine Science
- Ritchie ME, Olff H (1999) Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* 400:557-560
- Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278:1454-1457
- Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries* 1:65-91
- Roberts CM, Polunin NVC (1993) Marine reserves: simple solutions to managing complex fisheries? *Ambio*:363-368
- Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. *Science* 294:1920-1923
- Rooker JR (1995) Feeding ecology of the schoolmaster snapper, *Lutjanus apodus* (Walbaum), from southwestern Puerto Rico. *Bulletin of Marine Science* 56:881-894
- Root RB (1967) The niche exploitation pattern of the blue-gray gnatcatcher. *Ecology Monograph* 37:317-350
- Rosenzweig ML (1991) Habitat selection and population interactions: the search for mechanism. *The American Naturalist* 137:5-28
- Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. *Science* 241:1460-1466
- Rowley RJ (1994) Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 4:233-254
- Russ GR (2002) Yet another review of marine reserves as reef fishery management tools. In: Sale PF (ed) *Coral Reef Fishes*. Academic Press, San Diego, pp421-443
- Russ GR, Alcala AC (1996a) Marine reserves: Rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* 6:947-961
- Russ GR, Alcala AC (1996b) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* 132:1-9

- Russ GR, Alcala AC (2003) Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983-2000. *Ecological Applications* 13:1553-1565
- Russ GR, Lou DC, Higgs JB, Ferreira BP (1998) Mortality rate of a cohort of the coral trout, *Plectropomus leopardus*, in zones of the Great Barrier Reef Marine Park closed to fishing. *Marine and Freshwater Research* 49:507-511
- Russ GR, Cheal AJ, Dolman AM, Emslie MJ, Evans RD, Miller I, Sweatman H, Williamson DH (2008) Rapid increase in fish numbers follows creation of world's largest marine reserve network. *Current Biology* 18:R514-R515
- Russell DJ, McDougall AJ (2005) Movement and juvenile recruitment of mangrove jack, *Lutjanus argentimaculatus* (Forsskål), in northern Australia. *Marine and Freshwater Research* 56:465-475
- Rutherford ES, Schmidt TW, Tilmant JT (1989) Early life history of spotted seatrout (*Cynoscion nebulosus*) and gray snapper (*Lutjanus griseus*) in Florida Bay, Everglades National Park, Florida. *Bulletin of Marine Science* 44:49-64
- Ruttenberg BI, Hamilton SL, Walsh SM, Donovan MK, Friedlander A, DeMartini E, Sala E, Sandin SA (2011) Predator-induced demographic shifts in coral reef fish assemblages. *PLoS ONE* 6:e21062
- Sadovy Y (2000) Regional survey for fry/fingerling supply and current practices for grouper mariculture: evaluating current status and long-term prospects for grouper mariculture in South East Asia final report to the collaborative APEC Grouper Research and Development Network (FWG 01/99) pp1-89
- Sadovy Y (2001) Summary of regional survey of fry/fingerling supply for grouper mariculture in Southeast Asia. *SPC Live Reef Fish Information Bulletin* 8:22-29
- Sadovy Y (2005) Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. *Fish and Fisheries* 6:167-185
- Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002) A general model for designing networks of marine reserves. *Science* 298:1991-1993
- Sale PF, Doherty P, Eckert G, Douglas W, Ferrell D (1984) Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia* 64:191-198
- Sale PF (1976) The effect of territorial adult pomacentrid fishes on the recruitment and survival of juveniles on patches of coral rubble. *Journal of Experimental Marine Biology and Ecology* 24:297
- Sale PF (1977) Maintenance of high diversity in coral reef fish communities. *The American Naturalist* 111:337-359
- Sale PF (1979) Recruitment, loss and coexistence in a guild of territorial coral reef fishes. *Oecologia* 42:159-177
- Sale PF (1980) Assemblages of fish on patch reefs predictable or unpredictable? *Environmental Biology of Fishes* 5:243
- Sale PF (2004) Connectivity, recruitment variation, and the structure of reef fish communities. *Integrative and Comparative Biology* 44:390-399
- Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution* 20:74-80
- Samoilys M (1988) Abundance and species richness of coral reef fish on the Kenyan coast: the effects of protective management and fishing. *ICRS: Proceedings of the 6th International Coral Reef Symposium* 2:261-266
- Samoilys M (1997) Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. *Coral Reefs* 16:151-158

- Sano M, Shimizu M, Nose Y (1984) Changes in structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. *Pacific Science* 38:51-79
- Sano M, Shimizu M, Nose Y (1987) Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Marine Ecology Progress Series* 37:191-199
- Schellekens T, Roos André Md, Persson L (2010) Ontogenetic diet shifts result in niche partitioning between two consumer species irrespective of competitive abilities. *The American Naturalist* 176:625-637
- Schmitt RJ, Holbrook SJ (2000) Habitat-limited recruitment of coral reef damselfish. *Ecology* 81:3479-3494
- Scott DW (1979) On optimal and data-based histograms. *Biometrika* 66:605-610
- Shulman MJ (1984) Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* 74:85-109
- Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66:1056-1066
- Shulman MJ, Ogden JC, Ebersole JP, McFarland WN, Miller SL, Wolf NG (1983) Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* 64:1508-1513
- Silverman BW (1986) Density estimation for statistics and data analysis. Chapman & Hall/CRC
- Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research. WH Freeman and Company, New York
- Sonnenholzner JI, Ladah LB, Lafferty KD (2007) Cascading effects of fishing on Galapagos rocky reef communities. *Marine Ecology Progress Series* 343:77-85
- Sponaugle S, Cowen RK (1996) Larval supply and patterns of recruitment for two caribbean reef fishes *Stegastes partitus*. *Marine and Freshwater Research* 47:433-447
- St John J (1999) Ontogenetic changes in the diet of the coral reef grouper *Plectropomus leopardus* (Serranidae): patterns in taxa, size and habitat of prey. *Marine Ecology Progress Series* 180:233-246
- St John J, Russ GR, Brown IW, Squire LC (2001) The diet of the large coral reef serranid *Plectropomus leopardus* in two fishing zones on the Great Barrier Reef, Australia. *Fishery Bulletin* 99:180-192
- Stella JS, Pratchett MS, Hutchings PA, Jones GP (2011) Coral-associated invertebrates: diversity, ecology importance and vulnerability to disturbance. *Oceanography and Marine Biology: an annual review* 49:43-104
- Stephens MA (1970) Use of the Kolmogorov-Smirnov, Cramér-Von Mises and related statistics without extensive tables. *Journal of the Royal Statistical Society Series B (Methodological)* 32:115-122
- Stewart BD, Jones GP (2001) Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Marine Biology* 138:383-397
- Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402:799-802
- Sweatman HPA (1988) Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. *Journal of Experimental Marine Biology and Ecology* 124:163-174
- Sweatman HPA (1985) The influence of adults of some coral reef fishes on larval recruitment. *Ecological Monographs* 55:469-485
- Sweatman HPA (1993) Tropical snapper (Lutjanidae) that is piscivorous at settlement. *Copeia* 1993:1137-1139

- Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81:2714-2729
- Szedlmayer S, Conti J (1999) Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. *Fishery Bulletin* 97:626-635
- Tolimieri N (1995) Effects of microhabitat characteristics on the settlement and recruitment of a coral-reef fish at two spatial scales. *Oecologia* 102:52-63
- Tupper M (2007) Identification of nursery habitats for commercially valuable humphead wrasse *Cheilinus undulatus* and large groupers (Pisces: Serranidae) in Palau. *Marine Ecology Progress Series* 332:189-199
- Valles H, Sponaugle S, Oxenford H (2001) Larval supply to a marine reserve and adjacent fished area in the Soufriere Marine Management Area, St Lucia, West Indies. *Journal of Fish Biology* 59:152-177
- Valles H, Kramer DL, Hunte W (2008) Temporal and spatial patterns in the recruitment of coral-reef fishes in Barbados. *Marine Ecology Progress Series* 363:257-272
- Victor BC (1983) Recruitment and population dynamics of a coral reef fish. *Science* 219:419-420
- Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecological Monographs* 56:145-160
- Vinson MR, Angradi TR (2010) Stomach emptiness in fishes: sources of variation and study design implications. *Reviews in Fisheries Science* 19:63-73
- Vogele LE, Boyer RL, Heard WR (1971) A portable underwater suction device. *The Progressive Fish-Culturist* 33:62-63
- Walters CJ, Juanes F (1993) Recruitment limitation as a consequence of natural-selection for use of restricted feeding habitats and predation risk-taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2058-2070
- Wand M (1997) Data-based choice of histogram bin width. *American Statistician*:59-64
- Warner RR, Swearer SE, Caselle JE (2000) Larval accumulation and retention: implications for the design of marine reserves and essential habitat. *Bulletin of Marine Science* 66:821-830
- Watson M, Munro JL (2004) Settlement and recruitment of coral reef fishes in moderately exploited and overexploited Caribbean ecosystems: implications for marine protected areas. *Fisheries Research* 69:415-425
- Wen, C., Almany, G.R., Williamson, D.H., Pratchett, M.S., Jones, G.P., 2012a Evaluating the effects of marine reserves on diet, prey availability and prey selection by juvenile predatory fishes. *Marine Ecology Progress Series* 469: 133-144.
- Wen, C., Pratchett, M.S., Almany, G.R., Jones, G.P., 2012b. Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia. *Coral Reefs* doi: 10.1007/s00338-012-0985-x
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interaction in size structured population. *Annual Review of Ecology and Systematics* 15:393-425
- Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill - the foraging rate predation risk trade-off. *Ecology* 69:1352-1366
- Werner EE, Mittelbach GG, Hall DJ, Gilliam JF (1983) Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology*:1525-1539
- Westmacott S, Teleki K, Wells S, West J (2000) Management of Bleached and Severely Damaged Coral Reefs. IUCN, Gland, Switzerland, and Cambridge, UK.

- Williams DMB, Russ GR (1994) Review of data on fishes of commercial and recreational fishing interest in the Great Barrier Reef: a report to the Great Barrier Reef Marine Park Authority. Great Barrier Reef Marine Park Authority
- Williams DMB, Sale PF (1981) Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within "One Tree Lagoon", Great Barrier Reef. *Marine Biology* 65:245-253
- Williamson DH, Russ GR, Ayling AM (2004) No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environmental Conservation* 31:149-159
- Wilson SK, Fisher R, Pratchett M, Graham N, Dulvy N, Turner R, Cakacaka A, Polunin N (2010a) Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecological Applications* 20:442-451
- Wilson SK, Fisher R, Pratchett M, Graham N, Dulvy N, Turner R, Cakacaka A, Polunin N, Rushton S (2008) Exploitation and habitat degradation as agents of change within coral reef fish communities. *Global Change Biology* 14:2796-2809
- Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* 12:2220-2234
- Wilson SK, Depczynski M, Fisher R, Holmes TH, O'Leary RA, Tinkler P (2010b) Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: the importance of coral and algae. *PLoS ONE* 5:e15185
- Witte F, Goldschmidt T, Wanink J, Oijen M, Goudswaard K, Witte-Maas E, Bouton N (1992) The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes* 34:1-28
- Wolanski E, Doherty P, Carleton J (1997) Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. *Naturwissenschaften* 84:262-268
- Wood LJ, Fish L, Laughren J, Pauly D (2008) Assessing progress towards global marine protection targets: shortfalls in information and action. *Oryx* 42:340-351
- Worm B, Sandow M, Oschlies A, Lotze HK, Myers RA (2005) Global patterns of predator diversity in the open oceans. *Science* 309:1365-1369
- Zar JH (1999) *Biostatistical analysis*. Prentice Hall New Jersey
- Zeller DC (1997) Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Marine Ecology Progress Series* 154:65-77
- Zeller DC (2002) Tidal current orientation of *Plectropomus leopardus* (Serranidae). *Coral Reefs* 21:183-187
- Zeller DC, Russ GR (1998) Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae)). *Canadian Journal of Fisheries and Aquatic Sciences* 55:917-924

**APPENDIX I Reviews on habitats and diets study of three predatory genera**  
*Plectropomus* (Serranidae), *Epinephelus* (Epinephelidae) and *Lutjanus* (Lujanidae). Some papers did not indicate how they measured the size of fishes, i.e. standard length (SL) or total length (TL) or fork length (FL).

Predatory fish	Location	Diet	Habitat	size (mm)	Reference
Serranidae					
Most Serranidae	One tree, GBR		Live coral abundant location		(Silverman 1986)
<i>P. areolatus</i>	Pohnpei, Federated States of Micronesia		Coral reef-rich lagoon of seaward reef.	479 ± 19 TL for females and 559 ± 33 TL for males	(Hutchinson and Rhodes 2010)
<i>P. leopardus</i>	Northern GBR		Rubble substrata	Recruit juvenile	(Light and Jones 1997)
<i>P. leopardus</i>	One tree, GBR		Reef slope & seaward edge lagoon	Recruit	(Kingsford 2009)
<i>P. leopardus</i>	Northern GBR	Ontogeny (benthic dwelling crustacean to pure fish prey)		47-573	(St John 1999)
<i>P. leopardus</i>	One Tree, GBR	Spatial, temporal and size variation in diet. (Invertebrate to fish)		10-289	(Kingsford 1992)
<i>P. leopardus</i>	Northern GBR	Mainly fish (Pomacentridae 25.3%; Labridae 19.9% Clupeidae 16.6% and others)		130-585 FL	(St John et al. 2001)
<i>P. leopardus</i>	Lizard Island		Patch & fringe reef (home range)	376-675	(Zeller 1997)
<i>P. leopardus</i>	Lizard Island		Dead and live coral (vertical reef wall & deep reef edge)	160-175	(Leis and Carson-Ewart 1999)
<i>P. leopardus</i>	Lizard Island		Up-current coral bommies	376-675	(Zeller 2002)
<i>P. leopardus</i>	Southern GBR		Coral bommies of leeward slope	330-660	(Samoilys 1997)
<i>P. leopardus</i>	New Caledonia	Mainly fish (88%), other crustacean and molluscs		240-790	(Kulbicki et al. 2005)
<i>P. leopardus</i> & <i>P. maculatus</i>	Northern GBR		Most from southeast corner of reefs. Shallow (1m) more than deep (20m).	16.8± 0.19, 25.2± 0.9	(Doherty et al. 1994)
Epinephelidae					
<i>E. adscensionis</i>	Puerto Rico and Virgin Islands	Crab (66.7%), fish (20.1%) and shrimp (4.4%)		122 – 395 SL	(Randall 1967)
<i>E. adscensionis</i> , <i>E. cruentatus</i> , <i>E. fulvus</i> , <i>E. guttatus</i> , <i>E. striatus</i>	US Virgin Islands, Caribbean Sea		Mainly inhabit patch-reef and few at back-reef. <i>E. guttatus</i> also use algal plain habitat.	Large juvenile (>50).	(Adams and Ebersole 2002)
<i>E. areolatus</i>	New Caledonia	Fish (38%), crab (46%) and shrimp (12%)		210-330	(Kulbicki et al. 2005)
<i>E. coeruleopunctatus</i>	New Caledonia	Fish (20%), crab (60%) and shrimp (20%)		220-690	(Kulbicki et al. 2005)

<i>E. coioides</i>	New Caledonia	Fish (37%), crab (37%) and shrimp (13%) and molluscs (13%)		290-290	(Kulbicki et al. 2005)
<i>E. coioides</i>	Gulf of Thailand	Shrimp (54%), fish (33%) and amphipod (11%)	Shallow seagrass-mangrove	85 ±34 SL	(Hajisamae and Ibrahim 2008)
<i>E. cyanopodus</i>	New Caledonia	Fish (56%), crab (24%) and other invertebrate		240-670	(Kulbicki et al. 2005)
<i>E. fasciatus</i>	New Caledonia	Fish (18%), crab (63%) and other invertebrate		120-330	(Kulbicki et al. 2005)
<i>E. guttatus</i>	Puerto Rico and Virgin Islands	Crab (39.5%), fish (21.1%), stomatopods (16.6%) and shrimp (10.5%)		82-450 SL	(Randall 1967)
<i>E. itajara</i>	Panama		Mangrove and estuarine	juvenile	(Hutchinson and Rhodes 2010)
<i>E. itajara</i>	Gulf of Mexico		Mangrove	juvenile	(Zeller 1997)
<i>E. itajara</i>	Puerto Rico and Virgin Islands	Spiny lobster (45.6%), scyllarid lobster (23.3%), fishes (13.3%) and crabs (12.2%)		1250-1650 SL	(Randall 1967)
<i>E. macrospilos</i>	New Caledonia	Fish (24%), crab (56%) and other invertebrate		200-370	(Kulbicki et al. 2005)
<i>E. maculatus</i>	New Caledonia	Fish (36%), crab (29%) and other invertebrate		190-520	(Kulbicki et al. 2005)
<i>E. malabaricus</i>	New Caledonia	Fish (24%), crab (62%) and other invertebrate		160-1000	(Kulbicki et al. 2005)
<i>E. marginatus</i>	Mediterranean		Cavities, recesses, flat or sub-horizontal rocky substrates	70-300 TL	(La Mesa et al. 2002)
<i>E. merra</i>	Reunion Island, southwestern Indian Ocean	Fishes (42.9%, cannibalism), tanaids (21.4%), shrimps (21.4%), copepods (7.1%) and amphipods (7.1%)	Back reef and inner reef flat	39.7 ±1.5 SL	(Letourneur et al. 1998)
<i>E. merra</i>	Moorea Island, French Polynesia		Ontogenetic habitat shift from fringing reef to barrier reef after 40mm threshold	19-65 TL	(Lecchini and Galzin 2005)
<i>E. merra</i>	New Caledonia	Fish (30%), crab (38%), shrimp (18%) and other invertebrate		110-240	(Kulbicki et al. 2005)
<i>E. morio</i>	Puerto Rico and Virgin Islands	Unid. crustacean (50%), crabs (33.3%) and fishes (16.7%)		228 -340 SL	(Randall 1967)
<i>E. polyphemadion</i>	New Caledonia	Fish (43%), crab (47%) other invertebrate		220-590	(Kulbicki et al. 2005)
<i>E. quayanus</i>	One Tree Island, GBR	Fish (52%, main blenniidae), crab (48%)		163-364	(Connell 1998b)
<i>E. striatus</i>	Caribbean, Gulf of Mexico		Ontogenetic shift from macroalgal-Porites spp. clumps to patch-reef	25 to 150	(Eggleston 1995)

<i>E. striatus</i>	Bahama		Ontogenetic shift from algal-rich clumps to adjacent macroalgae covered coral <i>Porites porites</i>	35-75 TL	(Dahlgren and Eggleston 2000)
<i>E. striatus</i>	Bahama	Ontogenetic diet shift from brachyuran crab to fish		<200, 200-300, >300 (no clear size range)	(Eggleston et al. 1998)
<i>E. striatus</i>	Panama	Porcellanid and xanthid crab and minor fish	Seagrass meadows	50-190 TL	(Heck Jr and Weinstein 1989)
<i>E. striatus</i>	Puerto Rico and Virgin Islands	Fishes (54%), crabs (22.5%), stomatopods (5.5%), cephalopods (5.2%) and shrimps (5%)		170-686 SL	(Randall 1967)
Lutjanidae					
Most Lutjanidae	One Tree Island, GBR		Live coral abundant location		(Silverman 1986)
<i>L. adetii</i>	New Caledonia	Fish (29%), crab (41%), shrimp (16%) and other invertebrate		190-510	(Kulbicki et al. 2005)
<i>L. analis</i>	Puerto Rico and Virgin Islands	Crabs (44.4%), fishes (29.8%) and gastropods (13%)		204-620 SL	(Randall 1967)
<i>L. analis</i>	US Virgin Islands, Caribbean Sea		Wild distribution from patch-reef, sea grass, algal plain, sand and back-reef.	Large juvenile (>50).	(Adams and Ebersole 2002)
<i>L. analis</i>	Gulf of Salamanca, Caribbean Sea	Ontogenetic diet shifts from small crustacean dominant (<250mm) to fish and variety of invertebrates (300- >400mm)		85 to 460 SL	(Reviews in Duarte and Garcia 1999) <sup>§</sup>
<i>L. analis</i>	Brazil, Atlantic Ocean	Mainly fish, some mollusks		300-520 TL	(Begossi et al. 2011)
<i>L. analis</i>	Brazil	Mainly shrimp (39.11%), and crab (28.48%)		122 ±60 ; range 20 to 249	(Pimentel and Joyeux 2010)
<i>L. analis</i> & <i>L. griseus</i>	Panama	Porcellanid and xanthid crab		30-149 TL	(Heck Jr and Weinstein 1989)
<i>L. apodus</i>	Puerto Rico and Virgin Islands	Fishes (60.7%), crabs (22.2%), unid. crustacean (6%)		125-445 SL	(Randall 1967)
<i>L. apodus</i>	US Virgin Islands, Caribbean Sea		Only found in patch-reef and back-reef	Large juvenile (>50).	(Adams and Ebersole 2002)
<i>L. apodus</i>	Puerto Rico	Ontogenetic shift from crustacean (amphipods and crabs) to fish and other crustacean.	Feeding are ontogenetically shift from mangrove (≤70) to coral reef-mangrove both habitats (>70)	≤70 FL and >70 FL	(Rooker 1995)

<i>L. apodus</i>	Honduras, Caribbean		Ontogenetic habitats from under the shelter of mangrove root system to further outside and close to substrate.	70 – 200 TL	(MacDonald et al. 2009)
<i>L. apodus</i>	Caribbean	Ontogenetic diet shift from small crustacean to large decapoda	Ontogenetic migrant from mangrove nursery to reef habitats.	<25 to 225	(Cocheret de la Morinière et al. 2003)
<i>L. apodus</i>	Andros Island, Bahamas	Decapoda ( <i>Panopeus sp.</i> and <i>Mithras sp.</i> , 49%), other benthos and fishes		106 ±30 SL	(Layman and Silliman 2002)
<i>L. argentimaculatus</i>	Okinawa, Japan	Estuary-source crab in small juvenile. Fishes in large juvenile	Mangrove	66-189 SL	(Nakamura et al. 2008)
<i>L. argentimaculatus</i>	Northern Australia		Ontogenetic movement from inshore riverine, mangrove habitat to off shore reef habitats.	380 to 548 FL	(Russell and McDougall 2005)
<i>L. argentimaculatus</i>	New Caledonia	Fish (11%), crab (81%) and shrimp (8%)		150-530	(Kulbicki et al. 2005)
<i>L. argentiventris</i>	Gulf of California		Ontogenetic habitat shift from mangrove (root) to shallow reef then deep reef	16.9-126.2 SL; mean: 55.2 ±1.7 SL	(Aburto-Oropeza et al. 2009)
<i>L. bohar</i>	New Caledonia	Fish (61%), crab (9%), other mollusks (16%) and other invertebrate		170-750	(Kulbicki et al. 2005)
<i>L. campechanus</i>	Gulf of Mexico		Inner of shelf	17.4 SL	(Szedlmayer and Conti 1999)
<i>L. carponotatus</i>	One Tree Island, GBR	Fish (48%, most blenniidae), crab (29%), other crustacean (10%), other (13%)		200-346	(Connell 1998b)
<i>L. carponotatus</i>	One Tree Island, GBR		Lagoon live coral	80-120(recruits)	(Kingsford 2009)
<i>L. carponotatus</i>	Lizard Island, GBR		Hard and soft coral (58%), topographic reef features (29%) and sand and rubble (13%)	17-22 SL	(Quéré and Leis 2010)
<i>L. cyanopterus</i>	Puerto Rico and Virgin Islands	Fishes (100%)		410 – 990 SL	(Randall 1967)
<i>L. decussatus</i>	Okinawa, Japan		Live branch coral as feeding ground	<150 TL	(Nanami and Yamada 2008)
<i>L. erythropterus</i> & <i>L. malabaricus</i>	Northern Australia & Indonesia		Inshore, estuarine; silty, muddy coarse sand/rubble	Age-0 recruits	(Fry et al. 2009)
<i>L. fulviflamma</i>	One Tree Island, GBR	Fish (36%), crab (52%), other crustacean (12%)		182-360	(Connell 1998b)

<i>L. fulviflamma</i>	Mafia Island, Tanzania	Ontogenetic diet shift from crab, decapoda and Stomatopoda to increasing fish item and decrease decapoda and stomatopoda		90-297 TL	(Kamukuru and Mgaya 2004)
<i>L. fulviflamma</i> & <i>L. ehrenbergii</i>	Zanzibar island, Tanzania		Inter-tide movement between seagrass and shelter notches	90-180 TL (juvenile)	(Dorenbosch et al. 2004)
<i>L. fulviflammus</i>	New Caledonia	Fish (44%), crab (33%), shrimp (17%) and other invertebrate		70-330	(Kulbicki et al. 2005)
<i>L. fulvus</i>	Okinawa, Japan	Juvenile collected from mangrove have estuary-source crustacean. Juvenile from reef have reef-source crustacean (Xanthidae and Calathea spp.)	Mangrove and coral reefs habitats (with stable isotope evidence)	42-205 SL	(Nakamura et al. 2008)
<i>L. fulvus</i>	New Caledonia	Fish (15%), crab (72%), shrimp (9%) and other invertebrate		80-280	(Kulbicki et al. 2005)
<i>L. gibbus</i>	Okinawa, Japan		Holes on top of coral patch (hard substratum) in seagrass bed	Recruits (<40 TL)	(Nanami and Yamada 2008)
<i>L. gibbus</i>	Okinawa, Japan	Small individual (54-77mm SL) consume shrimp and isopods; large fish (142-275 mm SL) consumed reef-source crab (Xanthidae)	Coral reefs	54-275 SL	(Nanami and Yamada 2008)
<i>L. gibbus</i>	New Caledonia	Fish (20%), crab (32%), other crustacean and mollusks		170-390	(Kulbicki et al. 2005)
<i>L. gibbus</i>	Peninsular Malaysia	Squid (90%), other fish		210-1110	(Kulbicki et al. 2005)
<i>L. griseus</i>	Puerto Rico and Virgin Islands	Crabs (40%), fishes (39.1%) and shrimps (13.2%). Ontogenetic diet shift from amphipod, shrimp and copepod to large crustacean and fishes.	Seagrass bed	120 – 400 SL	(Reviews in Randall 1967)
<i>L. griseus</i>	Florida Bay	Fish and shrimp (sea grass) or fish, shrimp and crab (mangrove)	Seagrass and mangrove	No mentioned size, probably adult	(Harrigan et al. 1989)
<i>L. griseus</i>	Florida Bay		Seagrass rich ( <i>Tihalassia testudinum</i> ) basin and ( <i>Syringodium</i> ) channels	Juvenile (mean: 98 and 94)	(Chester and Thayer 1990)
<i>L. griseus</i>	Florida Bay		Seagrass beds and mangrove region with Hatodule and Syringodium	17-332 FL	(Reviews in Rutherford et al. 1989)
<i>L. griseus</i>	Florida Keys	Crustacean (61.6%) and fishes (34%)		81-456 FL	(Crocker 1962)

<i>L. griseus</i>	Florida coast		Ontogenetic habitat use from seagrass (recruits) to mangrove (10-12cm TL)	7.8 TL(when settled) to 100-120 TL	(Faunce and Serafy 2007)
<i>L. griseus</i>	Florida Keys		Seasonal migration between inshore seagrass bed, mangrove and offshore coral reefs	240 – 358 TL	(Luo et al. 2009)
<i>L. griseus</i>	Andros Island, Bahamas	Decapoda ( <i>Callinectes</i> spp. and <i>Panopeus</i> sp., 54%), other benthos and fishes		109 ±32 SL	(Layman and Silliman 2002)
<i>L. griseus</i> ; <i>L. synagris</i> ; <i>L. analis</i>	Florida Bay	Small benthic fish and crustacean	Inshore shallow seagrass habitats	Juvenile (50) and adult (400 to 900)	(Reviews in Bortone and Williams 1986)
<i>L. jocu</i>	Puerto Rico and Virgin Islands	Fishes (60.7%), crabs (15.4%), octopuses (7%) and spiny lobsters (6.6%)		190-630 SL	(Randall 1967)
<i>L. jocu</i>	Brazil	Crab (43.81%), fish (24.39%)		143±49; range 17 to 237	(Pimentel and Joyeux 2010)
<i>L. johnii</i>	Malay Peninsula	Mainly crab and shrimp. Large size increase crab in diet		34 – 211 TL	(Kiso and Mahyam 2003)
<i>L. kasmira</i>	New Caledonia	Fish (13%), crab (43%), other crustacean and mollusks		160-220	(Kulbicki et al. 2005)
<i>L. kasmira</i>	Island of Kauai, Hawaii		Recruits happen in small rubble below reef slope, subadult and adult abundant at soft bottom next to reef edge.	From 40 to 240 SL (mean: 145.8 to 163.4 SL)	(Friedlander et al. 2002)
<i>L. mabogoni</i>	Puerto Rico and Virgin Islands	Fishes (75%), shrimp (12.5%), octopuses (9.4%)		135-295 SL	(Randall 1967)
<i>L. mahogoni</i>	US Virgin Islands, Caribbean Sea		Wild distribution on most of the size classes, especially small one. From patch-reef, rubble, sea grass, algal plain, sand and back-reef.	Small to large juvenile (<30 to >50)	(Adams and Ebersole 2002)
<i>L. malabaricus</i>	Peninsular Malaysia	Ponyfish (42%), squid (23%), threadfin bream (17%)		340-640	(Bachok et al. 2004)
<i>L. quinquelineatus</i>	New Caledonia	Fish (17%), crab (33%), shrimp (10%), other molluscus, crustacean and worm		130-230	(Kulbicki et al. 2005)
<i>L. russelli</i>	Gulf of Thailand	Shrimp (59%), amphipod (22%)	Shallow seagrass-mangrove	78±28 SL	(Hajisamae and Ibrahim 2008)
<i>L. russellii</i>	New Caledonia	Fish (57%), crab (13%) and shrimp (30%)		110-310	(Kulbicki et al. 2005)
<i>L. sangulneus</i>	Peninsular Malaysia	Round scad (94%), squid (5%)		210-740	(Bachok et al. 2004)

<i>L. sebae</i>	New Caledonia	Fish (26%), crab (38%), and other crustacean (27%)		250-770	(Kulbicki et al. 2005)
<i>L. synagris</i>	Puerto Rico and Virgin Islands	Crabs (50%), stomatopods (50%). Ontogenetic diet shift from amphipod, copepods, shrimp and copepod to large crustacean and fishes.		148-280 SL	(Reviews in Randall 1967)
<i>L. synagris</i>	US Virgin Islands, Caribbean		Only large class found in back-reef	Large juvenile (>50).	(Adams and Ebersole 2002)
<i>L. synagris</i>	Brazil, Atlantic Ocean	Few fish, mainly crustacean		350 – 560 TL	(Begossi et al. 2011)
<i>L. synagris</i>	Brazil	Shrimp (38.41%), amphipod (29.18%)		77±33; range 18 to 162	(Pimentel and Joyeux 2010)
<i>L. synagris</i>	Gulf of Mexico		Inshore mud and shell ridge (of natural banks) have higher abundance	28.0±3.6 to 44.2±1.2	(Mikulas Jr and Rooker 2008)
<i>L. vita</i>	New Caledonia	Fish (47%), crab (21%), shrimp (18%) and other crustacean		100-390	(Kulbicki et al. 2005)
<i>L. vivanus</i>	Brazil, Atlantic Ocean	Half fish and half crustacean		250 – 410 TL	(Begossi et al. 2011)

§: Duarte et al (1999) address some references that cannot be accessed due to non-English written documents.

## **APPENDIX II Journal articles published during PhD Candidature**

Leis JM, Piola RF, Hay AC, Wen C, Kan KP (2009) Ontogeny of behaviour relevant to dispersal and connectivity in the larvae of two non-reef demersal, tropical fish species. *Marine and Freshwater Research* 60:211-223

Wen CKC, Pratchett MS, Shao KT, Kan KP, Chan BKK (2010) Effects of habitat modification on coastal fish assemblages. *Journal of Fish Biology* 77:1674-1687

THIS ARTICLE HAS BEEN REMOVED DUE  
TO COPYRIGHT RESTRICTIONS

Leis JM, Piola RF, Hay AC, Wen C, Kan KP (2009) Ontogeny of behaviour relevant to dispersal and connectivity in the larvae of two non-reef demersal, tropical fish species. *Marine and Freshwater Research* 60:211-223.

























THIS ARTICLE HAS BEEN REMOVED DUE  
TO COPYRIGHT RESTRICTIONS

Wen CKC, Pratchett MS, Shao KT, Kan KP, Chan BKK (2010)  
Effects of habitat modification on coastal fish assemblages. *Journal  
of Fish Biology* 77:1674-1687.

























