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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 tetrophthalmus*), 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 focused 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:


### 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 (23º10’S, 151º00’E) is located in the southern Great Barrier 
Reef. Sea surface temperature (SST) ranges between 18-30ºC 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 Acalá 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 (damselﬁshes), 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:

\[
1 - \frac{\text{number of individuals with empty stomachs}}{\text{total number of individuals collected}}
\]

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(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 (±SD) percentages of samples across the 4 sampling sites in two years with empty stomachs were as follows: *P. maculatus* (58.5±16.7%), *L. carponotatus* (57.2±16.3%) and *E. quoyanus* (44.5±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±16.7%; L. carponotatus: 57.2±16.3%; E. quoyanus: 44.5±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”.

<table>
<thead>
<tr>
<th>Species</th>
<th>Clam Bay (reserve)</th>
<th>Middle (reserve)</th>
<th>Halfway (open)</th>
<th>N Keppel (open)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. maculatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;49mmTL</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>50-99mmTL</td>
<td>2</td>
<td>4</td>
<td>24</td>
<td>10</td>
</tr>
<tr>
<td>100-149mmTL</td>
<td>18</td>
<td>5</td>
<td>17</td>
<td>12</td>
</tr>
<tr>
<td>150-199mmTL</td>
<td>4</td>
<td></td>
<td>8</td>
<td>5</td>
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<tr>
<td>200-249mmTL</td>
<td>13</td>
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<td>&gt;300mmTL</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. carponotatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;49mmTL</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>50-99mmTL</td>
<td>6</td>
<td>7</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>100-149mmTL</td>
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</tr>
<tr>
<td>150-199mmTL</td>
<td>11</td>
<td>4</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>200-249mmTL</td>
<td>3</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>250-299mmTL</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;300mmTL</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. quoyanus</em></td>
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<td></td>
<td></td>
</tr>
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<td>4</td>
<td>5</td>
</tr>
<tr>
<td>200-249mmTL</td>
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<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>250-299mmTL</td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;300mmTL</td>
<td>2</td>
<td></td>
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</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th></th>
<th>zone</th>
<th>site(zone)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td><em>P. maculatus</em></td>
<td>3.253</td>
<td>0.078</td>
</tr>
<tr>
<td><em>L. carponotatus</em></td>
<td>0.255</td>
<td>0.608</td>
</tr>
<tr>
<td><em>E. quoyanus</em></td>
<td>1.9</td>
<td>0.171</td>
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</tbody>
</table>

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 $\alpha = 0.05$.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P(perm)</th>
<th>Unique perms</th>
<th>P(MC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size (TL)</td>
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<td>98555</td>
<td>27.02</td>
<td>0.0001</td>
<td>9935</td>
<td>0.0001*</td>
</tr>
<tr>
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<td>5115.7</td>
<td>5115.7</td>
<td>1.1706</td>
<td>0.3159</td>
<td>719</td>
<td>0.3561</td>
</tr>
<tr>
<td>Species</td>
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<td>2.03E+05</td>
<td>1.02E+05</td>
<td>27.792</td>
<td>0.0001</td>
<td>9922</td>
<td>0.0001*</td>
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<tr>
<td>Site(Zone)</td>
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<td>3866.7</td>
<td>1.062</td>
<td>0.3714</td>
<td>9911</td>
<td>0.3633</td>
</tr>
<tr>
<td>Residual</td>
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<td>2.18E+06</td>
<td>3640.9</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Total</td>
<td>607</td>
<td>2.50E+06</td>
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2:42
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 \( \alpha = 0.05 \).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P(perm)</th>
<th>Unique perms</th>
<th>P(MC)</th>
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<td>9956</td>
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<td>57712</td>
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<td>9951</td>
<td>0.0001*</td>
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<tr>
<td>ZonexMethod</td>
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<td>3.5924</td>
<td>0.0059</td>
<td>9953</td>
<td>0.0081*</td>
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<tr>
<td>Residual</td>
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<td>39375</td>
<td>915.7</td>
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<td></td>
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</tr>
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<td>Total</td>
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<td>1.08E+05</td>
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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 \( \alpha = 0.05 \).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P(perm)</th>
</tr>
</thead>
<tbody>
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<td>3.08</td>
<td>20.697</td>
<td>0.0001*</td>
</tr>
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<td>5.177</td>
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<td>0.0001*</td>
</tr>
<tr>
<td>Size</td>
<td>5</td>
<td>11.26</td>
<td>2.252</td>
<td>34.782</td>
<td>0.0001*</td>
</tr>
<tr>
<td>Residual</td>
<td>216</td>
<td>32.15</td>
<td>0.149</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>233</td>
<td>71.21</td>
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</tbody>
</table>
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.
Ontogenetic changes in diet composition for individuals collected from no-take reserves (left panels) and open to fishing (right panels) for a) *P. maculatus*, b) *L. carponotatus* and c) *E. quoyanus*. Prey categories used to describe prey availability were reclassified into four general categories for this graph: mobile vertebrates, cryptic vertebrates, mobile invertebrates and cryptic invertebrates (See Methods).
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*= 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$^2$) 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$^2$) 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 terriginous 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 (Hc, 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 ± 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 ± 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 ± 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 ± 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 ± 2.1SE), while *P. maculatus* was most abundant on the reef base (mean = 15.9 fish per transect ± 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 ($X^2_{LI} = 682.3$, $df = 35$, $p < 0.001$), 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
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* (Quéré 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 Lutjaniidae) 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

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<th>Species</th>
<th>Life Stage</th>
<th>Hc (corrected)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
<td>Subadults</td>
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<tr>
<td></td>
<td>Adults</td>
<td>11.19</td>
<td>0.04*</td>
</tr>
<tr>
<td><em>Lutjanus carponotatus</em></td>
<td>Recruits</td>
<td>11.07</td>
<td>0.04*</td>
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<td></td>
<td>Subadults</td>
<td>27.16</td>
<td>0.00*</td>
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<tr>
<td></td>
<td>Adults</td>
<td>8.79</td>
<td>0.32</td>
</tr>
<tr>
<td><em>Epinephalus quoyanus</em></td>
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<td></td>
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<td></td>
<td>Adults</td>
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B) Habitats

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<th>Life Stage</th>
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</thead>
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<tr>
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<td></td>
<td>Adults</td>
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<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Subadults</td>
<td>11.29</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>6.72</td>
<td>0.29</td>
</tr>
</tbody>
</table>
Microhabitat selection by carnivorous fishes at Keppel Islands. Significance of habitat selectivity was ascertained using the log-likelihood statistic ($X^2_{LI}$), 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Life stage</th>
<th>Size (cm)</th>
<th>$X^2_{LI}$</th>
<th>Copybose Acropora</th>
<th>Tabular Acropora</th>
<th>Other branching coral</th>
<th>Massive Porites</th>
<th>Other massive coral</th>
<th>Soft coral</th>
<th>Macrolgae</th>
<th>Dead branching coral</th>
<th>Carbonate pavement</th>
<th>Sand/ Rubble</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Plectropomus maculatus</em></td>
<td>Recruit</td>
<td>&lt;15</td>
<td>549.0</td>
<td>+</td>
<td>U</td>
<td>U</td>
<td>U</td>
<td>U</td>
<td>U</td>
<td>U</td>
<td>U</td>
<td>U</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>15-35</td>
<td>375.7</td>
<td>+</td>
<td>+</td>
<td>U</td>
<td>-</td>
<td>-</td>
<td>U</td>
<td>U</td>
<td>U</td>
<td>U</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>&gt;35</td>
<td>309.6</td>
<td>+</td>
<td>+</td>
<td>U</td>
<td>-</td>
<td>-</td>
<td>U</td>
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</tr>
<tr>
<td><em>Lutjanus carponotatus</em></td>
<td>Recruit</td>
<td>&lt;15</td>
<td>682.3</td>
<td>+</td>
<td>-</td>
<td>U</td>
<td>U</td>
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</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>15-30</td>
<td>342.4</td>
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<tr>
<td></td>
<td>Adult</td>
<td>&gt;30</td>
<td>316.1</td>
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<tr>
<td><em>Epinephelus quoyanus</em></td>
<td>Recruit</td>
<td>&lt;12</td>
<td>316.7</td>
<td>+</td>
<td>-</td>
<td>U</td>
<td>U</td>
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</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>12-30</td>
<td>298.2</td>
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<td>&gt;30</td>
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<td>U</td>
<td>U</td>
<td>U</td>
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</tbody>
</table>

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 (± 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 (300m²) at each location. Fishes were categorised as recruits (young of the year), subadults, or adults (sexually mature individuals) based on size.

a  *Plectropomus leopardus*

b  *Lutjanus carponotatus*

c  *Epinephelus quoyanus*
Mean (± 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.

**a. Plectropomus maculatus**

**b. Lutjanus carponotatus**

**c. Epinephelus quoyanus**

Surveys of predatory fishes at Keppel Islands revealed that significant proportions of these species were associated with live coral habitats, which were divided into consolidated substrata composed mostly of faviids. The three locations with highest availability (Table 3) accounted for >81% of live Acropora colonies located on sand (Fig. 2). However, we did not quantify the availability of specific microhabitats within consolidated substrates, and the most frequently utilised compound habitats were corymbose corals (e.g., Acropora millepora). For all three species, microhabitat preferences were recorded for recruits of *P. maculatus, L. carponotatus*, and *E. quoyanus* and especially corymbose corals (e.g., *Acropora*). However, we did not quantify the availability of specific microhabitats within consolidated substrates, and the most frequently utilised compound habitats were corymbose corals (e.g., *Acropora millepora*). For all three species, microhabitat preferences were recorded for recruits of *P. maculatus, L. carponotatus*, and *E. quoyanus*, and especially corymbose corals (e.g., *Acropora*).
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 3-4 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.

**a** *Plectropomus maculatus*

- Recruit (n = 212)
- Subadult (n = 437)
- Adult (n = 149)

**b** *Lutjanus carponotatus*

- Recruit (n = 285)
- Subadult (n = 284)
- Adult (n = 139)

**c** *Epinephelus quoyanus*

- Recruit (n = 125)
- Subadult (n = 520)
- Adult (n = 220)
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 terriginous rock).

![Graph showing frequency of use of different compound microhabitats by recruits](image)

- **Plectopomus maculatus** \((n=149)\)
- **Lutjanus carponotatus** \((n=200)\)
- **Epinephalus quoyanus** \((n=168)\)
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 (Mysterud 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-
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 m². 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 deal 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 tetrophthalmus* (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. tetrophthalmus*). 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 ± 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. tetrophthalmus*) 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;
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$^2$ ± 9.6 SE) and crustaceans (726.8 individuals per m$^2$ ±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$^2$ ±55 SE) was more than twice that recorded for live corals on the consolidated reef substratum (120 individuals per m$^2$ ±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 (±0.19 SE) individuals of *A. tertrophthalmus* (representing 48.3%) were consumed across the 25 feeding trials, compared to 1.67 (±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 pre fishes. The differential consumption of prey species was largely relate 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 1-3 cm 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)

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
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<td>1</td>
<td>1542</td>
<td>3.566</td>
<td>0.066</td>
</tr>
<tr>
<td>Habitat</td>
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<td>4</td>
<td>12200</td>
<td>28.210</td>
<td>0.000</td>
</tr>
<tr>
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<td>1712</td>
<td>3.959</td>
<td>0.008</td>
</tr>
<tr>
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</tr>
<tr>
<td>Total</td>
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<td>49</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(b)

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
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<td>1</td>
<td>0.000</td>
<td>0.001</td>
<td>0.970</td>
</tr>
<tr>
<td>Habitat</td>
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<td>7.355</td>
<td>61.630</td>
<td>0.000</td>
</tr>
<tr>
<td>Interaction</td>
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<td>0.230</td>
<td>1.931</td>
<td>0.124</td>
</tr>
<tr>
<td>Error</td>
<td>4.774</td>
<td>40</td>
<td>0.119</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>35.110</td>
<td>49</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Mean (±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 (±SE) occupancy of five microhabitats by juvenile coral trout (N = 30).

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

Mean (± 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; Samoilys 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
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 fellows: *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; Samoilys 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

<table>
<thead>
<tr>
<th>Species</th>
<th>Factor</th>
<th>F value</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. maculatus</em></td>
<td>Reserves</td>
<td>10.62</td>
<td>0.004*</td>
</tr>
<tr>
<td></td>
<td>Hotspots</td>
<td>6.33</td>
<td>0.021*</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>6.46</td>
<td>0.019*</td>
</tr>
<tr>
<td><em>L. carponotatus</em></td>
<td>Reserves</td>
<td>4.71</td>
<td>0.042*</td>
</tr>
<tr>
<td></td>
<td>Hotspots</td>
<td>4.08</td>
<td>0.057</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>1.23</td>
<td>0.281</td>
</tr>
<tr>
<td><em>E. quoyanus</em></td>
<td>Reserves</td>
<td>0.38</td>
<td>0.546</td>
</tr>
<tr>
<td></td>
<td>Hotspots</td>
<td>1.51</td>
<td>0.231</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>0.22</td>
<td>0.646</td>
</tr>
</tbody>
</table>

(b) Subadult

<table>
<thead>
<tr>
<th>Species</th>
<th>Factor</th>
<th>F value</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. maculatus</em></td>
<td>Reserves</td>
<td>2.43</td>
<td>0.133</td>
</tr>
<tr>
<td></td>
<td>Hotspots</td>
<td>13.52</td>
<td>0.001*</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>2.26</td>
<td>0.147</td>
</tr>
<tr>
<td><em>L. carponotatus</em></td>
<td>Reserves</td>
<td>4.71</td>
<td>0.677</td>
</tr>
<tr>
<td></td>
<td>Hotspots</td>
<td>4.08</td>
<td>0.073</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>1.23</td>
<td>0.188</td>
</tr>
<tr>
<td><em>E. quoyanus</em></td>
<td>Reserves</td>
<td>3.18</td>
<td>0.088</td>
</tr>
<tr>
<td></td>
<td>Hotspots</td>
<td>1.97</td>
<td>0.174</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>1.88</td>
<td>0.184</td>
</tr>
</tbody>
</table>
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*

<table>
<thead>
<tr>
<th></th>
<th>Res+HS</th>
<th>Res-HS</th>
<th>nRes+HS</th>
<th>nRes-HS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Res+HS</td>
<td>-</td>
<td>0.255</td>
<td>0.001*</td>
<td>0.026*</td>
</tr>
<tr>
<td>Res-HS</td>
<td>0.1238</td>
<td>-</td>
<td>0.001*</td>
<td>0.398</td>
</tr>
<tr>
<td>nRes+HS</td>
<td>0.3314</td>
<td>0.3884</td>
<td>-</td>
<td>0.001*</td>
</tr>
<tr>
<td>nRes-HS</td>
<td>0.1863</td>
<td>0.1409</td>
<td>0.3919</td>
<td>-</td>
</tr>
</tbody>
</table>

(b) *L. carponotatus*

<table>
<thead>
<tr>
<th></th>
<th>Res+HS</th>
<th>Res-HS</th>
<th>nRes+HS</th>
<th>nRes-HS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Res+HS</td>
<td>-</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.552</td>
</tr>
<tr>
<td>Res-HS</td>
<td>0.237</td>
<td>-</td>
<td>0.02*</td>
<td>0.009*</td>
</tr>
<tr>
<td>nRes+HS</td>
<td>0.2707</td>
<td>0.1882</td>
<td>-</td>
<td>0.002*</td>
</tr>
<tr>
<td>nRes-HS</td>
<td>0.1131</td>
<td>0.2518</td>
<td>0.2795</td>
<td>-</td>
</tr>
</tbody>
</table>

(c) *E. quoyanus*

<table>
<thead>
<tr>
<th></th>
<th>Res+HS</th>
<th>Res-HS</th>
<th>nRes+HS</th>
<th>nRes-HS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Res+HS</td>
<td>-</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.001*</td>
</tr>
<tr>
<td>Res-HS</td>
<td>0.5405</td>
<td>-</td>
<td>0.003*</td>
<td>0.028*</td>
</tr>
<tr>
<td>nRes+HS</td>
<td>0.3945</td>
<td>0.2358</td>
<td>-</td>
<td>0.594</td>
</tr>
<tr>
<td>nRes-HS</td>
<td>0.4044</td>
<td>0.1995</td>
<td>0.1056</td>
<td>-</td>
</tr>
</tbody>
</table>
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).
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*

Marine Reserve

Non Reserve

Recruitment Hotspots

Non Hotspots

Body length (TL) cm

Fishing minimum (25cm)
(c) *E. quoyanus*

**Marine Reserve**

**Non Reserve**

**Recruitment Hotspots**

**Non Hotspots**

Fishing minimum (38cm)

Body length (TL) cm
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 *Aioliops tetrophthalmus* (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.
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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).

<table>
<thead>
<tr>
<th>Predatory fish</th>
<th>Location</th>
<th>Diet</th>
<th>Habitat</th>
<th>size (mm)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Serranidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Most Serranidae</td>
<td>One tree, GBR</td>
<td>Live coral abundant location</td>
<td></td>
<td></td>
<td>(Silverman 1986)</td>
</tr>
<tr>
<td><em>P. areolatus</em></td>
<td>Pohnpei, Federated States of Micronesia</td>
<td>Coral reef-rich lagoon of seaward reef.</td>
<td>479 ± 19 TL for females and 559 ± 33 TL for males</td>
<td>(Hutchinson and Rhodes 2010)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>Northern GBR</td>
<td>Rubble substrata</td>
<td>Recruit juvenile</td>
<td>(Light and Jones 1997)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>One tree, GBR</td>
<td>Ontogeny (benthic dwelling crustacean to pure fish prey)</td>
<td></td>
<td>(St John 1999)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>One Tree, GBR</td>
<td>Spatial, temporal and size variation in diet. (Invertebrate to fish)</td>
<td></td>
<td>(Kingsford 1992)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>Northern GBR</td>
<td>Mainly fish (Pomacentridae 25.3%; Labridae 19.9% Clupeidae 16.6% and others)</td>
<td>Recruit</td>
<td>(St John et al. 2001)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>Lizard Island</td>
<td>Patch &amp; fringe reef (home range)</td>
<td></td>
<td>(Zeller 1997)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>Lizard Island</td>
<td>Dead and live coral (vertical reef wall &amp; deep reef edge)</td>
<td></td>
<td>(Leis and Carson-Ewart 1999)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>Lizard Island</td>
<td>Up-current coral bommies</td>
<td></td>
<td>(Zeller 2002)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>Southern GBR</td>
<td>Coral bommies of leeward slope</td>
<td></td>
<td>(Samoilys 1997)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em></td>
<td>New Caledonia</td>
<td>Mainly fish (88%), other crustacean and molluscs</td>
<td></td>
<td>(Kulbicki et al. 2005)</td>
<td></td>
</tr>
<tr>
<td><em>P. leopardus</em> &amp; <em>P. maculatus</em></td>
<td>Northern GBR</td>
<td>Most from southeast corner of reefs. Shallow (1m) more than deep (20m).</td>
<td></td>
<td>(Doherty et al. 1994)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Epinephelidae</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. adscensionis</em></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Crab (66.7%), fish (20.1%) and shrimp (4.4%)</td>
<td></td>
<td>122 – 395 SL</td>
<td>(Randall 1967)</td>
</tr>
<tr>
<td><em>E. areolatus</em></td>
<td>New Caledonia</td>
<td>Fish (38%), crab (46%) and shrimp (12%)</td>
<td></td>
<td>210-330</td>
<td>(Kulbicki et al. 2005)</td>
</tr>
<tr>
<td><em>E. coeruleopunctatus</em></td>
<td>New Caledonia</td>
<td>Fish (20%), crab (60%) and shrimp (20%)</td>
<td></td>
<td>220-690</td>
<td>(Kulbicki et al. 2005)</td>
</tr>
<tr>
<td>Species</td>
<td>Location</td>
<td>Diet</td>
<td>Size Range</td>
<td>Reference</td>
<td></td>
</tr>
<tr>
<td>-------------</td>
<td>---------------------------</td>
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<td></td>
</tr>
<tr>
<td><em>E. coioides</em></td>
<td>New Caledonia</td>
<td>Fish (37%), crab (37%) and shrimp (13%) and molluscs (13%)</td>
<td>290-290</td>
<td>(Kulbicki et al. 2005)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gulf of Thailand</td>
<td>Shrimp (54%), fish (33%) and amphipod (11%)</td>
<td>Shallow seagrass-mangrove</td>
<td>85 ±34 SL</td>
<td>(Hajisamae and Ibrahim 2008)</td>
</tr>
<tr>
<td><em>E. cyanopodus</em></td>
<td>New Caledonia</td>
<td>Fish (56%), crab (24%) and other invertebrate</td>
<td>240-670</td>
<td>(Kulbicki et al. 2005)</td>
<td></td>
</tr>
<tr>
<td><em>E. fasciatus</em></td>
<td>New Caledonia</td>
<td>Fish (18%), crab (63%) and other invertebrate</td>
<td>120-330</td>
<td>(Kulbicki et al. 2005)</td>
<td></td>
</tr>
<tr>
<td><em>E. guttatus</em></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Crab (39.5%), fish (21.1%), stomatopods (16.6%) and shrimp (10.5%)</td>
<td>82-450 SL</td>
<td>(Randall 1967)</td>
<td></td>
</tr>
<tr>
<td><em>E. itajara</em></td>
<td>Panama</td>
<td>Mangrove and estuarine juvenile</td>
<td></td>
<td>(Hutchinson and Rhodes 2010)</td>
<td></td>
</tr>
<tr>
<td><em>E. itajara</em></td>
<td>Gulf of Mexico</td>
<td>Mangrove juvenile</td>
<td></td>
<td>(Zeller 1997)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Spiny lobster (45.6%), scyllarid lobster (23.3%), fishes (13.3%) and crabs (12.2%)</td>
<td>1250-1650 SL</td>
<td>(Randall 1967)</td>
<td></td>
</tr>
<tr>
<td><em>E. maculatus</em></td>
<td>New Caledonia</td>
<td>Fish (24%), crab (56%) and other invertebrate</td>
<td>200-370</td>
<td>(Kulbicki et al. 2005)</td>
<td></td>
</tr>
<tr>
<td><em>E. malabaricus</em></td>
<td>New Caledonia</td>
<td>Fish (24%), crab (62%) and other invertebrate</td>
<td>160-1000</td>
<td>(Kulbicki et al. 2005)</td>
<td></td>
</tr>
<tr>
<td><em>E. marginatus</em></td>
<td>Mediterranean</td>
<td>Fishes (42.9%, cannibalism), tanaids (21.4%), shrimps (21.4%), copepods (7.1%) and amphipods (7.1%)</td>
<td>70-300 TL</td>
<td>(La Mesa et al. 2002)</td>
<td></td>
</tr>
<tr>
<td><em>E. merra</em></td>
<td>Reunion Island, south-western Indian Ocean</td>
<td>Fishes (42.9%, cannibalism), tanaids (21.4%), shrimps (21.4%), copepods (7.1%) and amphipods (7.1%)</td>
<td>Back reef and inner reef flat</td>
<td>39.7 ±1.5 SL</td>
<td>(Letourneur et al. 1998)</td>
</tr>
<tr>
<td></td>
<td>Moorea Island, French Polynesia</td>
<td>Fishes (42.9%, cannibalism), tanaids (21.4%), shrimps (21.4%), copepods (7.1%) and amphipods (7.1%)</td>
<td>Ontogenetic habitat shift from fringing reef to barrier reef after 40mm threshold</td>
<td>19-65 TL</td>
<td>(Lecchini and Galzin 2005)</td>
</tr>
<tr>
<td><em>E. merra</em></td>
<td>New Caledonia</td>
<td>Fish (30%), crab (38%), shrimp (18%) and other invertebrate</td>
<td>110-240</td>
<td>(Kulbicki et al. 2005)</td>
<td></td>
</tr>
<tr>
<td><em>E. morio</em></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Unid. crustacean (50%), crabs (33.3%) and fishes (16.7%)</td>
<td>Unid. crustacean (50%), crabs (33.3%) and fishes (16.7%)</td>
<td>228 -340 SL</td>
<td>(Randall 1967)</td>
</tr>
<tr>
<td><em>E. polyphexadion</em></td>
<td>New Caledonia</td>
<td>Fish (43%), crab (47%) and other invertebrate</td>
<td>220-590</td>
<td>(Kulbicki et al. 2005)</td>
<td></td>
</tr>
<tr>
<td><em>E. quayanus</em></td>
<td>One Tree Island, GBR</td>
<td>Fish (52%, main bleniiidae), crab (48%)</td>
<td>163-364</td>
<td>(Connell 1998B)</td>
<td></td>
</tr>
<tr>
<td><em>E. striatus</em></td>
<td>Caribbean, Gulf of Mexico</td>
<td>Fish (52%), main bleniiidae, crab (48%)</td>
<td>Ontogenetic shift from macroalgal-Porites spp. clumps to patch-reef</td>
<td>25 to 150</td>
<td>(Eggleston 1995)</td>
</tr>
<tr>
<td><strong>E. striatus</strong></td>
<td>Bahama</td>
<td>Ontogenetic shift from algal-rich clumps to adjacent macroalgae covered coral <em>Porites porites</em></td>
<td>35-75 TL</td>
<td>(Dahlgren and Eggleston 2000)</td>
<td></td>
</tr>
<tr>
<td><strong>E. striatus</strong></td>
<td>Bahama</td>
<td>Ontogenetic diet shift from brachyuran crab to fish</td>
<td>&lt;200, 200-300, &gt;300 (no clear size range)</td>
<td>(Eggleston et al. 1998)</td>
<td></td>
</tr>
<tr>
<td><strong>E. striatus</strong></td>
<td>Panama</td>
<td>Porcellanid and xanthid crab and minor fish</td>
<td>Seagrass meadows</td>
<td>50-190 TL</td>
<td>(Heck Jr and Weinstein 1989)</td>
</tr>
<tr>
<td><strong>E. striatus</strong></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Fishes (54%), crabs (22.5%), stomatopods (5.5%), cephalopods (5.2%) and shrimps (5%)</td>
<td></td>
<td>170-686 SL</td>
<td>(Randall 1967)</td>
</tr>
</tbody>
</table>

**Lutjanidae**

<table>
<thead>
<tr>
<th>Most Lutjanidae</th>
<th>One Tree Island, GBR</th>
<th>Live coral abundant location</th>
<th>(Silverman 1986)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>L. adetii</strong></td>
<td>New Caledonia</td>
<td>Fish (29%), crab (41%), shrimp (16%) and other invertebrate</td>
<td>190-510</td>
</tr>
<tr>
<td><strong>L. analis</strong></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Crabs (44.4%), fishes (29.8%) and gastropods (13%)</td>
<td>204-620 SL</td>
</tr>
<tr>
<td><strong>L. analis</strong></td>
<td>Gulf of Salamanca, Caribbean Sea</td>
<td>Ontogenetic diet shifts from small crustacean dominant (&lt;250mm) to fish and variety of invertebrates (300- &gt;400mm)</td>
<td>85 to 460 SL</td>
</tr>
<tr>
<td><strong>L. analis</strong></td>
<td>Brazil, Atlantic Ocean</td>
<td>Mainly fish, some mollusks</td>
<td>300-520 TL</td>
</tr>
<tr>
<td><strong>L. analis</strong></td>
<td>Brazil</td>
<td>Mainly shrimp (39.11%), and crab (28.48%)</td>
<td>122 ±60 ; range 20 to 249</td>
</tr>
<tr>
<td><strong>L. analis &amp; L. griseus</strong></td>
<td>Panama</td>
<td>Porcellanid and xanthid crab</td>
<td>30-149 TL</td>
</tr>
<tr>
<td><strong>L. apodus</strong></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Fishes (60.7%), crabs (22.2%), unid. crustacean (6%)</td>
<td>125-445 SL</td>
</tr>
<tr>
<td><strong>L. apodus</strong></td>
<td>US Virgin Islands, Caribbean Sea</td>
<td>Only found in patch-reef and back-reef</td>
<td>Large juvenile (&gt;50).</td>
</tr>
<tr>
<td><strong>L. apodus</strong></td>
<td>Puerto Rico</td>
<td>Ontogenetic shift from crustacean (amphipods and crabs) to fish and other crustacean.</td>
<td>Feeding are ontogenetically shift from mangrove (≤70) to coral reef-mangrove both habitats (&gt;70)</td>
</tr>
<tr>
<td>Species</td>
<td>Location</td>
<td>Habitat Details</td>
<td>Size Range</td>
</tr>
<tr>
<td>-----------------</td>
<td>---------------------------------</td>
<td>---------------------------------------------------------------------------------</td>
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</tr>
<tr>
<td><em>L. apodus</em></td>
<td>Honduras, Caribbean</td>
<td>Ontogenetic habitats from under the shelter of mangrove root system to further outside and close to substrate.</td>
<td>70 – 200 TL</td>
</tr>
<tr>
<td><em>L. apodus</em></td>
<td>Caribbean</td>
<td>Ontogenetic diet shift from small crustacean to large decapoda</td>
<td>&lt;25 to 225 TL</td>
</tr>
<tr>
<td><em>L. apodus</em></td>
<td>Andros Island, Bahamas</td>
<td>Decapoda (<em>Panopeus sp.</em> and <em>Mithras sp.</em>, 49%), other benthos and fishes</td>
<td>106 ±30 SL</td>
</tr>
<tr>
<td><em>L. argentinamaculatus</em></td>
<td>Okinawa, Japan</td>
<td>Estuary-source crab in small juvenile. Fishes in large juvenile</td>
<td>Mangrove 66-189 SL</td>
</tr>
<tr>
<td><em>L. argentinamaculatus</em></td>
<td>Northern Australia</td>
<td>Ontogenetic movement from inshore riverine, mangrove habitat to off-sho reef habitats.</td>
<td>380 to 548 FL</td>
</tr>
<tr>
<td><em>L. argentinamaculatus</em></td>
<td>New Caledonia</td>
<td>Fish (11%), crab (81%) and shrimp (8%)</td>
<td>150-530 SL</td>
</tr>
<tr>
<td><em>L. argentinaventris</em></td>
<td>Gulf of California</td>
<td>Ontogenetic habitat shift from mangrove (root) to shallow reef then deep reef</td>
<td>16.9-126.2 SL; mean: 55.2 ±1.7 SL</td>
</tr>
<tr>
<td><em>L. bohar</em></td>
<td>New Caledonia</td>
<td>Fish (61%), crab (9%), other mollusks (16%) and other invertebrate</td>
<td>170-750 SL</td>
</tr>
<tr>
<td><em>L. campechanus</em></td>
<td>Gulf of Mexico</td>
<td>Inner of shelf</td>
<td>17.4 SL</td>
</tr>
<tr>
<td><em>L. carponotatus</em></td>
<td>One Tree Island, GBR</td>
<td>Fish (48%, most blenniidae), crab (29%), other crustacean (10%), other (13%)</td>
<td>200-346 SL</td>
</tr>
<tr>
<td><em>L. carponotatus</em></td>
<td>One Tree Island, GBR</td>
<td>Lagoon live coral</td>
<td>80-120(recruits)</td>
</tr>
<tr>
<td><em>L. carponotatus</em></td>
<td>Lizard Island, GBR</td>
<td>Hard and soft coral (58%), topographic reef features (29%) and sand and rubble (13%)</td>
<td>17-22 SL</td>
</tr>
<tr>
<td><em>L. cyanopterus</em></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Fishes (100%)</td>
<td>410 – 990 SL</td>
</tr>
<tr>
<td><em>L. decussatus</em></td>
<td>Okinawa, Japan</td>
<td>Live branch coral as feeding ground</td>
<td>&lt;150 TL</td>
</tr>
<tr>
<td><em>L. erythropterus</em> &amp; <em>L. malabaricus</em></td>
<td>Northern Australia &amp; Indonesia</td>
<td>Inshore, estuarine; silty, muddy coarse sand/rubble</td>
<td>Age-0 recruits</td>
</tr>
<tr>
<td><em>L. fulviflamma</em></td>
<td>One Tree Island, GBR</td>
<td>Fish (36%), crab (52%), other crustacean (12%)</td>
<td>182-360 SL</td>
</tr>
<tr>
<td>Species</td>
<td>Location</td>
<td>Diet Description</td>
<td>Size (TL)</td>
</tr>
<tr>
<td>-----------------</td>
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</tr>
<tr>
<td><em>L. fulviflamma</em></td>
<td>Mafia Island, Tanzania</td>
<td>Ontogenetic diet shift from crab, decapoda and Stomatopoda to increasing fish item and decrease decapoda and stomatopoda</td>
<td>90-297</td>
</tr>
<tr>
<td><em>L. fulviflamma</em> &amp; <em>L. ehrenbergii</em></td>
<td>Zanzibar island, Tanzania</td>
<td>Inter-tide movement between seagrass and shelter notches</td>
<td>90-180 TL</td>
</tr>
<tr>
<td><em>L. fulviflamma</em></td>
<td>New Caledonia</td>
<td>Fish (44%), crab (33%), shrimp (17%) and other invertebrate</td>
<td>70-330</td>
</tr>
<tr>
<td><em>L. fulvus</em></td>
<td>Okinawa, Japan</td>
<td>Juvenile collected from mangrove have estuary-source crustacean. Juvenile from reef have reef-source crustacean (Xanthidae and Calathea spp.)</td>
<td>42-205 SL</td>
</tr>
<tr>
<td><em>L. fulvus</em></td>
<td>New Caledonia</td>
<td>Holes on top of coral patch (hard substratum) in seagrass bed</td>
<td>80-280</td>
</tr>
<tr>
<td><em>L. gibbus</em></td>
<td>Okinawa, Japan</td>
<td>Small individual (54-77mm SL) consume shrimp and isopods; large fish (142-275 mm SL) consumed reef-source crab (Xanthidae)</td>
<td>54-275 SL</td>
</tr>
<tr>
<td><em>L. gibbus</em></td>
<td>New Caledonia</td>
<td>Fish (20%), crab (32%), other crustacean and mollusks</td>
<td>170-390</td>
</tr>
<tr>
<td><em>L. gibbus</em></td>
<td>Peninsular Malaysia</td>
<td>Squid (90%), other fish</td>
<td>210-1110</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Crabs (40%), fishes (39.1%) and shrimps (13.2%). Ontogenetic diet shift from amphipod, shrimp and copepod to large crustacean and fishes.</td>
<td>120 – 400 SL</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Florida Bay</td>
<td>Fish and shrimp (sea grass) or fish, shrimp and crab (mangrove)</td>
<td>No</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Florida Bay</td>
<td>Seagrass and mangrove</td>
<td>No</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Florida Bay</td>
<td>Seagrass rich (<em>Tihalassia testudinum</em>) basin and (<em>Syringodium</em>) channels</td>
<td>Juvenile (mean: 98 and 94)</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Florida Bay</td>
<td>Seagrass beds and mangrove region with Hatodule and <em>Syringodium</em></td>
<td>17-332 FL</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Florida Keys</td>
<td>Crustacean (61.6%) and fishes (34%)</td>
<td>81-456 FL</td>
</tr>
<tr>
<td>Species</td>
<td>Location</td>
<td>Habitat/Behavior</td>
<td>Size/Additional Info</td>
</tr>
<tr>
<td>--------------------</td>
<td>-------------------------------</td>
<td>----------------------------------------------------------------------------------</td>
<td>--------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Florida coast</td>
<td>Ontogenetic habitat use from seagrass (recruits) to mangrove (10-12cm TL)</td>
<td>7.8 TL (when settled) to 100-120 TL</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Florida Keys</td>
<td>Seasonal migration between inshore seagrass bed, mangrove and offshore coral reefs</td>
<td>240 – 358 TL</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>Andros Island, Bahamas</td>
<td>Decapoda (<em>Callinectes</em> spp. and <em>Panopeus</em> sp., 54%), other benthos and fishes</td>
<td>109 ±32 SL</td>
</tr>
<tr>
<td><em>L. griseus; L. synagris; L. analis</em></td>
<td>Florida Bay</td>
<td>Small benthic fish and crustacean</td>
<td>Inshore shallow seagrass habitats</td>
</tr>
<tr>
<td><em>L. jocu</em></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Fishes (60.7%), crabs (15.4%), octopuses (7%) and spiny lobsters (6.6%)</td>
<td>190-630 SL</td>
</tr>
<tr>
<td><em>L. jocu</em></td>
<td>Brazil</td>
<td>Crab (43.81%), fish (24.39%)</td>
<td>143±49; range 17 to 237</td>
</tr>
<tr>
<td><em>L. johnii</em></td>
<td>Malay Peninsula</td>
<td>Mainly crab and shrimp. Large size increase crab in diet</td>
<td>34 – 211 TL</td>
</tr>
<tr>
<td><em>L. kasmira</em></td>
<td>New Caledonia</td>
<td>Fish (13%), crab (43%), other crustacean and mollusks</td>
<td>160-220</td>
</tr>
<tr>
<td><em>L. kasmiva</em></td>
<td>Island of Kauai, Hawaii</td>
<td>Recruits happen in small rubble below reef slope, subadult and adult abundant at soft bottom next to reef edge</td>
<td>From 40 to 240 SL (mean: 145.8 to 163.4 SL)</td>
</tr>
<tr>
<td><em>L. mabogoni</em></td>
<td>Puerto Rico and Virgin Islands</td>
<td>Fishes (75%), shrimp (12.5%), octopuses (9.4%)</td>
<td>135-295 SL</td>
</tr>
<tr>
<td><em>L. mahogoni</em></td>
<td>US Virgin Islands, Caribbean Sea</td>
<td>Wild distribution on most of the size classes, especially small one. From patch-reef, rubble, sea grass, algal plain, sand and back-reef.</td>
<td>Small to large juvenile (&lt;30 to &gt;50)</td>
</tr>
<tr>
<td><em>L. malabaricus</em></td>
<td>Peninsular Malaysia</td>
<td>Ponyfish (42%), squid (23%), threadfin bream (17%)</td>
<td>340-640</td>
</tr>
<tr>
<td><em>L. quinquelineatus</em></td>
<td>New Caledonia</td>
<td>Fish (17%), crab (33%), shrimp (10%), other mollusus, crustacean and worm</td>
<td>130-230</td>
</tr>
<tr>
<td><em>L. russelli</em></td>
<td>Gulf of Thailand</td>
<td>Shrimp (59%), amphipod (22%)</td>
<td>Shallow seagrass-mangrove</td>
</tr>
<tr>
<td><em>L. russellii</em></td>
<td>New Caledonia</td>
<td>Fish (57%), crab (13%) and shrimp (30%)</td>
<td>110-310</td>
</tr>
<tr>
<td><em>L. sangulneus</em></td>
<td>Peninsular Malaysia</td>
<td>Round scad (94%), squid (5%)</td>
<td>210-740</td>
</tr>
<tr>
<td>L. sebae</td>
<td>New Caledonia</td>
<td>Fish (26%), crab (38%), and other crustacean (27%)</td>
<td>250-770</td>
</tr>
<tr>
<td>-------------</td>
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<td>---------------------------------------------------</td>
<td>---------</td>
</tr>
<tr>
<td>L. synagris</td>
<td>Puerto Rico and Virgin Islands</td>
<td>Crabs (50%), stomatopods (50%). Ontogenetic diet shift from amphipod, copepods, shrimp and copepod to large crustacean and fishes.</td>
<td>148-280 SL</td>
</tr>
<tr>
<td>L. synagris</td>
<td>US Virgin Islands, Caribbean</td>
<td>Only large class found in back-reef</td>
<td>Large juvenile (&gt;50).</td>
</tr>
<tr>
<td>L. synagris</td>
<td>Brazil, Atlantic Ocean</td>
<td>Few fish, mainly crustacean</td>
<td>350 – 560 TL</td>
</tr>
<tr>
<td>L. synagris</td>
<td>Brazil</td>
<td>Shrimp (38.41%), amphipod (29.18%)</td>
<td>77±33; range 18 to 162</td>
</tr>
<tr>
<td>L. synagris</td>
<td>Gulf of Mexico</td>
<td>Inshore mud and shell ridge (of natural banks) have higher abundance</td>
<td>28.0±3.6 to 44.2±1.2</td>
</tr>
<tr>
<td>L. vita</td>
<td>New Caledonia</td>
<td>Fish (47%), crab (21%), shrimp (18%) and other crustacean</td>
<td>100-390</td>
</tr>
<tr>
<td>L. vivanus</td>
<td>Brazil, Atlantic Ocean</td>
<td>Half fish and half crustacean</td>
<td>250 – 410 TL</td>
</tr>
</tbody>
</table>

§: 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


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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.