Benefits of marine protected areas beyond boundaries: an evaluation for two coral reef fishes

Thesis submitted by
Thomas Dixen Mannering
in 2008

**For the research degree of Master of Science
in Marine Biology
within the School of Marine and Tropical Biology
James Cook University**

Abstract

Increases in the numbers and sizes of predatory fishes in well established no-take marine protected areas (MPAs) on coral reefs are well-known. However, few studies have investigated whether adult spillover or recruitment subsidies lead to higher adult and juvenile densities in fished areas adjacent to MPAs, compared with fished sites further away from MPAs. Our understanding of these phenomena has been limited because most MPA studies have been restricted to comparisons of MPAs and fished areas, and do not consider fished areas that do not benefit from MPAs. On the Great Barrier Reef, adults of two recreationally important coral reef fish (*Plectropomus maculatus* and *Lutjanus carponotatus*) have been observed to increase in numbers in inshore no-take areas ("green zones"). In this thesis I made a preliminary investigation of the potential for adult spillover and recruitment subsidies by comparing fished areas, near to and distant from green zones. Firstly, I examined the early age and growth of juvenile fishes at the Keppel Islands, in order to define the size of young-of-the-year (0+) and estimate settlement and spawning periods. I used this information to estimate the densities of adults and 0+ year fish within green zones, fished areas within 1km from green zones and at sites greater than 5km from the nearest protected area.

The size-age relationships for the 0+ year cohorts were determined by studies of sectioned sagittal otoliths. Juveniles were collected between October and November in 2006, and May and June in 2007. The youngest *P. maculatus* and *L. carponotatus* recruits caught were 63 (53mm FL) and 66 days old (49mm FL) respectively, but ages extended to 334 days (220mm FL) for *P. maculatus* and 345 days (183mm FL) for *L.*

2

carponotatus. Juvenile growth was rapid in both species, with *P. maculatus* and *L. carponotatus* averaging 0.96 mm d^{-1} and 0.72 mm d^{-1} respectively. The estimated PLD of *P. maculatus* was 28.6 days, while *L. carponotatus* was 33.6 days. Based on the observations from this study, recruitment surveys approximately two months after spawning would be sufficient, however, in order to include additional 0+ age cohorts, surveys would ideally take place 160 days after initial spawning.

The potential for local benefits of MPAs were examined by comparing adult and recruit densities outside MPAs, both near to and distant from the MPA boundary. Adults and juveniles of *P. maculatus* and *L. carponotatus* were surveyed at both the Keppel Islands and Palm Islands, two inshore networks of no-take MPAs on the Great Barrier Reef. Within each region, the abundance and biomass of adults and recruits were compared for three treatments: (1) Within MPAs; (2) Nearby fished areas (< 1km from MPA boundaries) and (3) distant fished areas (> 5km from MPA boundaries). Site variation accounted for the majority of differences in both adult and recruits of *P. maculatus* and *L. carponotatus*. Hence, no significant differences were found for any of the treatments. Low densities of juveniles and patchiness in their distribution appear to combine to make detecting recruitment subsidies extremely difficult. I suggest refinements of the sampling technique, as well as alternative approaches to solving this problem.

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This thesis includes some collaborative work with Prof. Geoff Jones and Dr. Craig Syms. While undertaking these collaborations, I was instrumental in the project concept and responsible for the project design, analysis and interpretation, as well as the final synthesis of results into a form suitable for publication. Data from 2006 was provided by Richard Evans and David Williamson. My collaborators provided intellectual guidance, financial support, technical instruction and editorial assistance.

Financial support for the project was provided by my supervisor Prof. Geoff Jones, MTSERF and ARC Centre of Excellence.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

Chapter 1

1.0. Introduction

Large predatory fish are highly targeted in subsistence, recreational and commercial fisheries on coral reefs (Pauly *et al.* 2002; Sadovy & Vincent 2002). Due to low stocks and reproduction, slow growth and variable recruitment, these large predatory fish are vulnerable to over-fishing (Ferreira & Russ 1995; Myers & Worm 2003; Pears *et al.,* 2006). Excessive exploitation of predatory fishes can lead to trophic cascades that impact on prey abundance and ecosystem health (Jackson *et al.*, 2001, McClanahan & Arthur 2001; Sonnenholzner *et al.,* 2007; Heithaus *et al.,* 2008). Despite traditional harvest controls such as the type of gear used, minimum catch size and total allowable catch, numbers of large predatory fishes have continued to decline in many coastal environments, resulting in the closure of fisheries (Jackson *et al.,* 2001; Frank *et al.,* 2005). In tropical countries dependent on coral reef resources, single species management strategies may be ineffective and difficult to enforce. High human population density and growth, and a high traditional dependence on fish protein in coastal communities have placed a lot of pressure on populations of large reef fishes.

Over the last 20 years the establishment of marine reserves or no-take marine protected areas (MPAs) in many tropical countries has provided a new tool to halt the decline of breeding stocks of diverse assemblages of exploited reef fishes (Halpern & Warner 2002; Russ 2002; Willis *et al.,* 2003a; Wood *et al.,* 2008). The area of coral reef

dedicated to MPAs worldwide has been steadily increasing (Wood *et al.,* 2008). For example in Australia, the establishment of the Great Barrier Reef Marine Park (GBRMP) in 1975 granted MPA status to 4.5% of the Great Barrier Reef (GBR). MPA cover along the Great Barrier Reef (GBR) increased from 4.5% to 33% in 2004 through the Representative Areas Program (RAP). Although the RAP's main purpose was to increase the protection of biodiversity in the GBRMP, the greater percentage of MPAs could potentially provide benefits to local fisheries.

MPAs have become widely acknowledged as an additional fisheries management tool primarily because they protect a portion of the spawning stock. Reef fishes are relatively sedentary (Zeller & Russ 1998; Cole *et al.,* 2000; Zeller *et al.,* 2003), so the numbers and biomass of fishes can build up rapidly within MPA boundaries (Evans & Russ 2004; Williamson *et al.,* 2004; Abesamis *et al.,* 2006b). Higher abundance of targeted reef fish within MPAs compared to fished areas provides circumstantial evidence that MPAs are working. In a review of published studies that compared abundance between protected and fished zones, 66% of cases showed abundance was greater within MPAs than outside (Halpern 2003).

In an earlier review, Russ (2002) argued that although the majority of papers suggested enhanced abundance and biomass within MPAs, only a small proportion incorporated both temporal and spatial comparisons. The average abundance of *Naso vlamingii* in a MPA at Apo Island, Philippines, increased three-fold over 20 years (Abesamis & Russ 2005). In Western Australia, abundance of *P. leopardus* increased significantly with protection from fishing, however, this only became apparent after eight years of closure to fishing (Nardi *et al.*, 2004). In the same study, closure to fishing had

13

no significant effect on the abundance of *Choerodon rubescens* within MPAs presumably because of its high mobility (Nardi *et al*., 2004). Hence, while the time taken for a build-up of fish abundance in MPAs varies, there is overwhelming evidence that provided that (a) fish are relatively sedentary, and (b) there is compliance; there will be substantial benefits to fish stocks within MPA boundaries.

Biomass studies show a greater consistent outcome than abundance, with 84% of reviewed studies displaying significantly greater biomass within MPAs than outside (Halpern 2003). However, in the majority of cases, biomass is an artifact of length. Underwater surveys along the GBR revealed greater biomass of *P. maculatus* and *L. carponotatus* when based on their estimated length (Evans & Russ 2004; Williamson *et al*., 2004). Conversely, *P. maculatus* in MPAs and fished areas along the GBR have displayed similar lengths (Ferreira & Russ 1995; Russ *et al.,* 1995). If fish biomass estimates are routinely based around length, fish with similar lengths will have similar biomass.

Protecting the spawning stock of a fishery, though important, has no direct benefit on a local fishery beyond MPA boundaries. For MPAs to be accepted by local fishing communities, the benefits must also contribute to sustainable fishing. MPAs may appear more practical to fishermen if adult fish in MPAs move across the boundaries into adjacent fished sites (spillover). However, many fished species are relatively sedentary and will not move beyond MPA boundaries. The average daily movement of *P. leopardus* observed through ultrasonic tagging was 186.6m (Zeller & Russ 1998), while observations of the mean movement of *P. leopardus*, *L. carponotatus* and *Cephalopholis cyanostigma* through use of T-bar anchor tags were less than 100m, 50m and 50m

respectively (Zeller *et al.,* 2003). However, small scale gradients in abundance or biomass of adult fish from MPAs across boundaries into adjacent fished areas have been suggested to imply spillover (Rakitan & Kramer 1996). Targeted adult reef fish abundance and biomass within the Philippines has been recorded in relation to their distance from MPAs. As distance from the MPA increased, abundance and biomass of targeted reef fish decreased, but non-target fish showed no significant decline (Abesamis *et al*. 06). Depending on the mobility of the fish species, the observed abundance and biomass gradient ranged from 100 – 350m past the MPA boundary (Russ *et al.,* 2003; 2004; Abesamis & Russ 2005; Abesamis *et al.*, 2006b). However, for adult spillover to contribute substantially to a fishery, evidence that adult numbers are augmented at greater distances from MPA boundaries is required.

The fate of the increased reproductive potential within MPA boundaries is unknown, but it is widely believed that MPAs can benefit adjacent fisheries through larval dispersal and a "recruitment subsidy" (Russ 2002; Domeier 2004). However, few studies have examined whether recruitment increases in response to fishing protection. Densities of *Stegastes partitus* larvae and recruits in St Lucia were significantly greater in a fished area than a nearby MPA (Valles *et al.,* 2001). In comparison, recruit density of *P. leopardus* increased with increasing adult abundance around the Abrolhos Islands, Western Australia. This pattern was more evident within the MPAs than adjacent fished areas suggesting a more local response (Nardi *et al.,* unpub. man.). The current empirical database is clearly too small to draw any conclusions about the likely recruitment benefits of an MPA, in spite of the massive build up of reproductive potential.

Despite the lack of evidence for MPAs creating local recruitment subsidies, recent evidence suggests larvae are capable of remaining close to their natal reef and settling in the near vicinity. Chemical mass marking of fish has proven to be an effective method of estimating the proportion of larvae that return to their birth site (Jones *et al.,* 1999; 2005; Almany *et al.,* 2007). Direct marking of *Pomacentrus ambionensis* and *Amphiprion polymnus* embryos, along with DNA genotyping, has provided estimates of local replenishment ranging from 15 – 60% (Jones *et al.,* 1999; 2005). Additionally, the larvae of *Amphiprion percula* and *Chaetodon vagabundus* tagged via maternal transmission of stable barium isotopes, have encountered local return rates of approximately 60% (Almany *et al.* 2007).

Evaluating the extent of recruitment subsidies requires a quantitative assessment of juvenile densities, inside MPAs, outside MPAs near their boundaries, and at sites sufficiently distant from MPAs so as not to receive any benefits. Nonetheless, the most common sampling designs employed for measuring the effects of MPAs include the monitoring of MPAs and adjacent areas open to fishing (see Halpern 2003). However, these two treatments are usually compared to infer how fish populations are responding within MPA boundaries. To establish whether adult fish densities or recruitment levels are higher near MPAs, this comparison is ineffective. That is, to establish the potential for adult spillover or local recruitment benefits from MPAs, sampling designs need to compare levels of spillover or recruitment outside MPAs, both near and far from MPA boundaries. The absence of near and far comparisons in most MPA studies limits their ability to assess any of the potential fishery benefits. Ultimately, recruitment subsidies

can not be sufficiently assessed unless recruit densities are compared for three treatments: within MPAs, within nearby fished areas and within distant fished areas.

Assessing the potential for recruitment subsidies requires that the current recruit cohort (fishes age 0+) can be identified and counted. This can be difficult for predatory fishes, because settlement sites, times and sizes are poorly understood, and early growth trajectories are usually minor estimates incorporated into von Bertanlanffy curves (Ferreira & Russ 1994; Newman *et al.,* 1996; 2000a). On coral reefs, juvenile densities of typical predator families such as serranids and lutjanids have seldom been monitored (Kritzer 2004; Nardi *et al.,* unpub. man.). Juveniles are often not visible at settlement and can only be observed several months after they have been on the reef. In order to identify juveniles, patterns of early growth need to be described.

The Great Barrier Reef Marine Park represents one of the most comprehensive networks of no-take coral reef protected areas, with 115,395 km^2 of the 344,400km^2 deemed "green zones". There is increasing evidence that "green zones" or no-take areas result in a rapid build up of fish numbers and biomass on inshore reefs. Increases appear to be greatest for important recreational fisheries such as coral trout (*Plectropomus* spp.) and snappers (*Lutjanidae*), while non-targeted fishes remain relatively unchanged (Evans & Russ 2004; Williamson *et al*. 2004; Russ *et al.,* 2008). There is also evidence of a return to natural trophic structure, with a decline in small prey species in protected areas (Graham *et al.,* 2003). However, while benefits within boundaries are becoming well documented there is little information on the possible impacts green zones have on adult numbers or juvenile densities in adjacent "blue zones" (fished reefs).

The overall aim of this study was to carry out a preliminary investigation into the effects of inshore green zones of the Great Barrier Reef on the abundance of adults and juveniles of two important fishes in adjacent blue zones. To achieve this, the abundance of both adults and juveniles were surveyed inside green zones, near to green zones (< 1km from a MPA boundary) and at distances greater than 5km from green zone boundaries. Clusters of green and blue zones were compared at two geographic locations; the Keppel Islands region, and the Palm Islands region, two areas subject to local recreational fishing activities.

The fish species examined were *Plectropomus maculatus* and *Lutjanus carponotatus*. These fishes are valued for their taste, and their proximity to shore makes them highly targeted by recreational fishermen. However, the large longevity and slow growth of *P. maculatus* and *L. carponotatus* make them susceptible to recruitment over-fishing. High fishing pressure removes the larger, sexually mature fish, thereby reducing the spawning stock to the point where future recruitment declines. Maintaining a healthy spawning stock of both species has received a lot of attention over the last 20 years. With the introduction of more MPAs along the GBR, many studies have shown the abundance and biomass of *P. maculatus* and *L. carponotatus* to significantly increase within the boundaries of protection. Adult spillover from these MPAs into adjacent fished areas has been suggested but not unequivocally demonstrated.

The thesis is divided into two chapters:

1) Early life history of two coral reef fish on the Great Barrier Reef (Chapter 2). This chapter examines the early growth of 0+ *P. maculatus* and *L. carponotatus*, in order to define the recruit year class for field surveys. Daily age estimates are made to quantify

size and age relationships, and daily age increments are used to calculate settlement and spawning times for juvenile fishes.

2) Evaluation of potential local adult spillover and recruitment subsidies from no-take marine protected areas on the Great Barrier Reef (Chapter 3). This chapter tests the hypothesis that areas adjacent to green zones exhibit elevated abundance of adults and 0+ juveniles, compared with sites much further from green zones. Adult and 0+ juvenile densities within green zones are also monitored to assess the potential for elevated numbers within MPA boundaries.

Chapter 2

2.0. Early life history of two coral reef fish on the Great Barrier Reef.

2.1. Abstract

Patterns of recruitment of predatory coral reef fishes are poorly understood because juveniles may be extremely cryptic for several months after settlement. In addition, because the growth rates of juvenile predators are unknown, the effective size range for assessing the magnitude and timing of recruitment is unknown. Here I examined the size-age relationships for the 0+ year cohorts of two recreationally important coral reef fish (*Plectropomus maculatus* and *Lutjanus carponotatus*) from the Keppel Islands, Great Barrier Reef. Juveniles that were collected in the field between October and November in 2006, and May and June in 2007 were measured and aged by counting daily rings on sagittal otoliths. The size and age data were used to estimate growth rates, and otolith increments were used to back-calculate settlement and spawning periods. The youngest *P. maculatus* caught was 63 days old, but 0+ recruit age reached 334 days. The youngest *L. carponotatus* recruit caught was 66 days old, while the oldest 0+ recruit was 345 days old. Juvenile growth was rapid in both species, with *P. maculatus* and *L. carponotatus* averaging 0.96 mm d^{-1} and 0.72 mm d^{-1} respectively. Spawning of both species extended through to late March. Lunar cycle was not synchronized with modal *P. maculatus* spawning dates, while *L. carponotatus* modal spawning coincided with full moon phases. The mean PLD of *P. maculatus* was estimated at 28.6 days, while *L. carponotatus*

remained within the water column on average for 5 days longer. Settlement dates of both species extended to late April. No pattern between lunar cycle and *P. maculatus* settlement was found, but full moon phases coincided with modal *L. carponotatus* settlement dates. Initial observations of juveniles indicate a one month period of cryptic behavior after settling suggesting recruit surveys should take place at least two months after spawning. However, the extended spawning period of both species suggests that additional 0+ cohorts are also present. Therefore, in order to obtain a more representative age range of recruits, surveys should take place approximately 160 days after initial spawning.

2.2. Introduction

Recruitment, or the addition of juvenile fishes to the adult habitat is widely acknowledged as an important process in the dynamics of fish populations (Russ 2002; Sale *et al.,* 2005; Cowen *et al.,* 2006). For coral reef fishes, the magnitude of recruitment can be assessed by surveying the densities of fishes shortly after settlement (Valles *et al.,* 2001). However, for predatory coral reef fishes, patterns of recruitment are poorly understood and there are few quantitative assessments (Nardi *et al.,* unpub. man.). There is increasing evidence that no-take marine protected areas result in an increase in reproductive populations of predatory fishes within their boundaries (Willis *et al.,* 2003b; Evans *et al.,* 2007). To test whether the build-up of exploited predatory fishes in marine protected areas results in recruitment subsidies in fished areas, methods for assessing the abundance of juveniles need to be developed. At present, this is hampered by a lack of

fundamental information on the age and growth of juvenile predators, and the timing of spawning and recruitment periods.

Daily growth rings on the sectioned otoliths of juveniles provide a powerful and precise tool for estimating age and growth rates in coral reef fishes (Ferreira & Russ 1992; 1994; Newman *et al.,* 2000a; 2000b). Additionally, sectioned otoliths from young fish can also provide estimates of settlement dates, pelagic larval duration (PLD) and spawning dates (Wilson & McCormick, 1997; 1999; Zapata & Herrón 2002; Meekan *et al.,* 2006). A distinct change in contrast and width of the daily increments signals a shift from a planktonic to a benthic environment (Wilson & McCormick, 1997; 1999). Counting the number of bands from the settlement mark back to the otolith nucleus provides an estimate of the PLD of each fish (Zapata & Herrón 2002), while back-dating from the date of capture provides an estimate of the spawning date (Meekan *et al.,* 2006).

In coral reef fishes, spawning and recruitment periods are often associated with phases of the moon (Meekan *et al.,* 1993; Ferreira 1995; Samoilys 1997; Zeller 1998; Valles *et al.,* 2001). However, of the large coral reef predator species, this has only been confirmed for three species; *P. leopardus*, *P. areolatus* and *Epinephelus fuscoguttatus* (Ferreira 1995; Samoilys 1997; Zeller 1998; Pet *et al.,* 2005). Histological analysis of gonad material in *P. maculatus* and *L. carponotatus* estimated spawning periods from September to November and September to February respectively (Ferreira 1993; Kritzer 2004). However, any relationship between the lunar cycle and spawning activity of these two species is unknown.

Most of the data on the early life history of coral reef fishes comes from small species collected near the time of settlement (Victor 1986; Meekan *et al.,* 1993).

However, because of their secretive behaviour, juveniles of predatory species often cannot be observed on the reef until several months after settlement (Kaufman *et al.* 1992; Macpherson 1998). In order to identify the 0+ cohort and assess potential recruitment dynamics, it is critical to describe early patterns of age and growth. In addition, as juveniles can only be observed several months after settlement, information on PLDs is vital to determine temporal patterns of spawning and settlement.

The aim of this study was to determine the early patterns of age and growth for *P. maculatus* and *L. carponotatus* on the Great Barrier Reef. The following specific questions were addressed: (1) What is the growth trend of 0+ juveniles? (2) What is the age distribution of juveniles at the time the juvenile cohort can be sampled? (3) What are the pelagic larval durations for these two species? (4) What are the temporal patterns in recruitment and is there a lunar pattern? (5) What are the temporal patterns in spawning and is there a lunar pattern?

2.3. Materials and methods

2.3.1. Study Species

Catches of *P. maculatus* and *L. carponotatus* are among the highest from the plethora of coral reef species fished along the GBR. Both species are widely dispersed along inshore reefs, permitting easy access for recreational fishers. *P. maculatus* is one of seven *Plectropomus* species found around the world. *P. maculatus* is a slow growing, long lived monandric protogynous hermaphrodite, usually reaching transition stage on average at 4.4 years old or 35.4 cm standard length (Ferreira 1993). Female sexual

maturity is reached after two years, with spawning aggregations forming between September and December (Ferreira 1993). The maximum attainable size is 70cm total length (TL), but the minimum legal length is 38cm TL. The life demographics and hermaphroditism of *P. maculatus* make them a complicated species to manage and vulnerable to over-fishing (Williams & Russ 1991).

L. carponotatus, though not regularly caught commercially, is a valuable recreational fish (Williams & Russ 1994). *L. carponotatus* is a slow growing, long lived species with a maximum life span of 20 years. The majority of their growth occurs within the first five years, with females reaching sexual maturity after 2 years (Kritzer 2004). As with *P. maculatus*, the spawning season of *L. carponotatus* usually begins in September, but can last until February (Kritzer 2004). Minimum legal length is 25cm TL, but they can grow to 40cm TL.

2.3.2. Fish collection and examination

Forty-two *P. maculatus* and thirty-six *L. carponotatus* were collected within the surrounding blue zones of the Keppel Islands region (23^o10'S, 150^o57'E) between late October and early November, 2006 by R. D. Evans and D. H. Williamson. Forty *P. maculatus* and thirty *L. carponotatus* were collected from the blue zones in the same region between late May and early June, 2007. Prior to these occasions, density of juveniles was not sufficient for sampling. Hand spears and clove oil were used to collect juveniles of each species. Each fish was measured (FL) to the nearest mm. Two transverse incisions were made just above the eyes either side of each fish and were

extended to the opercular margins. A downward cut towards the opercular margins exposed the brain, revealing the pair of sagittal otoliths either side of the midbrain. The sagittal otoliths were removed from each fish using forceps. In cases where the otoliths were small to the naked eye, a dissecting microscope was used to aid visibility. Each otolith pair was cleaned and stored in separate marked vials. Sagittal otolith pairs were preferred because they are the largest of the three pairs found within both species. In preparation for analysis, otoliths were embedded in clear caster resin and ground to produce a 600μm thin transverse section of each otolith. Sections were polished using lapping film and mounted onto slides for examination under a microscope at 400 times magnification.

Multiple 0+ age cohorts were anticipated for both species because of the large natural variation in recruitment and the long duration of spawning. The most recent cohort was labeled the primary (1°) cohort, while earlier cohorts were labeled as secondary (2°). Cohorts were distinguished between each other through age/size ranges. Fish age was estimated from daily increment counts on their sagittal otoliths. Otolith ageing for *P. maculatus* and *L. carponotatus* has been validated from previous studies with tetracycline marking (Ferreira & Russ 1992; Cappo *et al*., 2000). The number of increments in each otolith was determined from three replicate counts. Otoliths with less than 10% difference between replicate counts were deemed suitable and their mean count was accepted. Replicates diverging by more than 10% were rejected from the analysis. The regression relationship between length measurements and corresponding age estimates was tested. Individual reef settlement dates were estimated from a distinct change in optical contrast in the daily increments. Corresponding pelagic larval durations

(PLDs) were calculated by counting the number of increments from the transition mark to the otolith nucleus. Spawning date estimates were back-calculated for individual fish by subtracting its age from the date of capture.

2.4. Results

2.4.1. Age and growth

The size of forty-two *P. maculatus* from the 2006 collection did not conform to regression line, indicating fish length is not accounted for by variation in age ($r^2 = 0.17$, Figure 1). However, the size of forty *P. maculatus* caught in 2007 increased with age ($r^2 = 0.83$, Figure 1). In 2006, *P. maculatus* ranged between 96 – 189mm FL (117 – 245 days). Two distinct age cohorts were observed in 2007. Size of the 2° 0+ age cohort ranged from 165 to 220mm FL (150 – 334 days), while the 1° 0+ cohort was between 53 and 133mm FL (63 – 147 days). The size and age range of the 2006 collection suggests that an additional cohort may have existed.

The size of thirty-six *L. carponotatus* from 2006 and thirty *L. carponotatus* collected in 2007 increased with age ($r^2 = 0.81$ and 0.92 respectively, Figure 2). Despite the regression line for the 2006 data being higher, there was only marginal difference between the two regression lines. Two distinct cohorts were observed from both the 2006 and 2007 collection. In 2006, the 2° 0+ age cohort ranged from 162 to 183mm FL (276 – 345 days), while the primary 0+ age cohort was between 75 – 130 mm FL (119 – 194 days). In 2007, the oldest cohort (2°) was comprised of 15 fish longer than 100mm FL,

while fish smaller than 100mm FL were considered to be from the most recent cohort

(1°). Age range of the 2007 collection was between 192 and 317 days for the 2° 0+ age

cohort, and 66 to 146 days for the 1° 0+ age cohort.
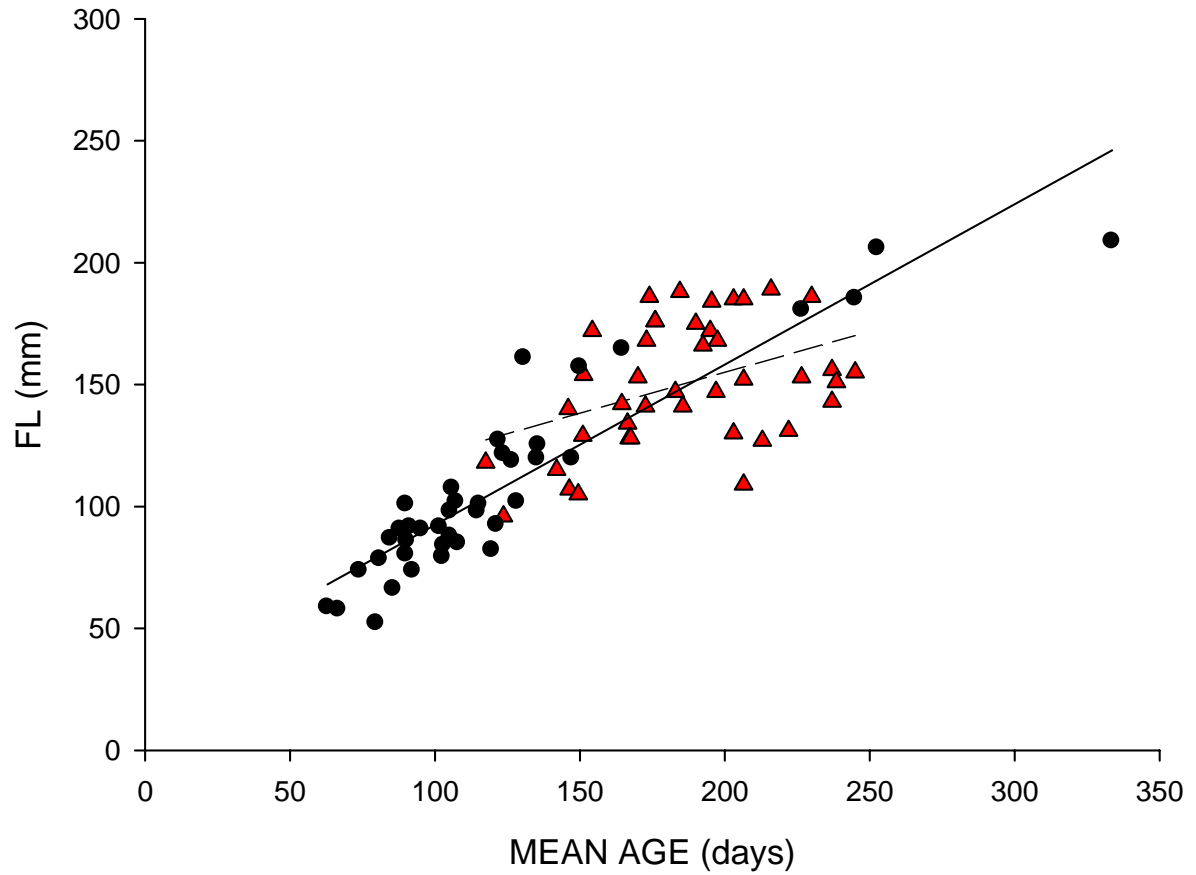
Figure 1. Relationship between age and fork length of *P. maculatus* from the Keppel Islands.

▲   = 2006 collection, 2006 FL(- - -) = 0.3358 x (age) + 87.830, r^2 = 0.1710, p = 0.0065

● = 2007 collection. 2007 FL (---) = 0.6578 x (age) + 26.604, r^2 = 0.8345, p < 0.0001
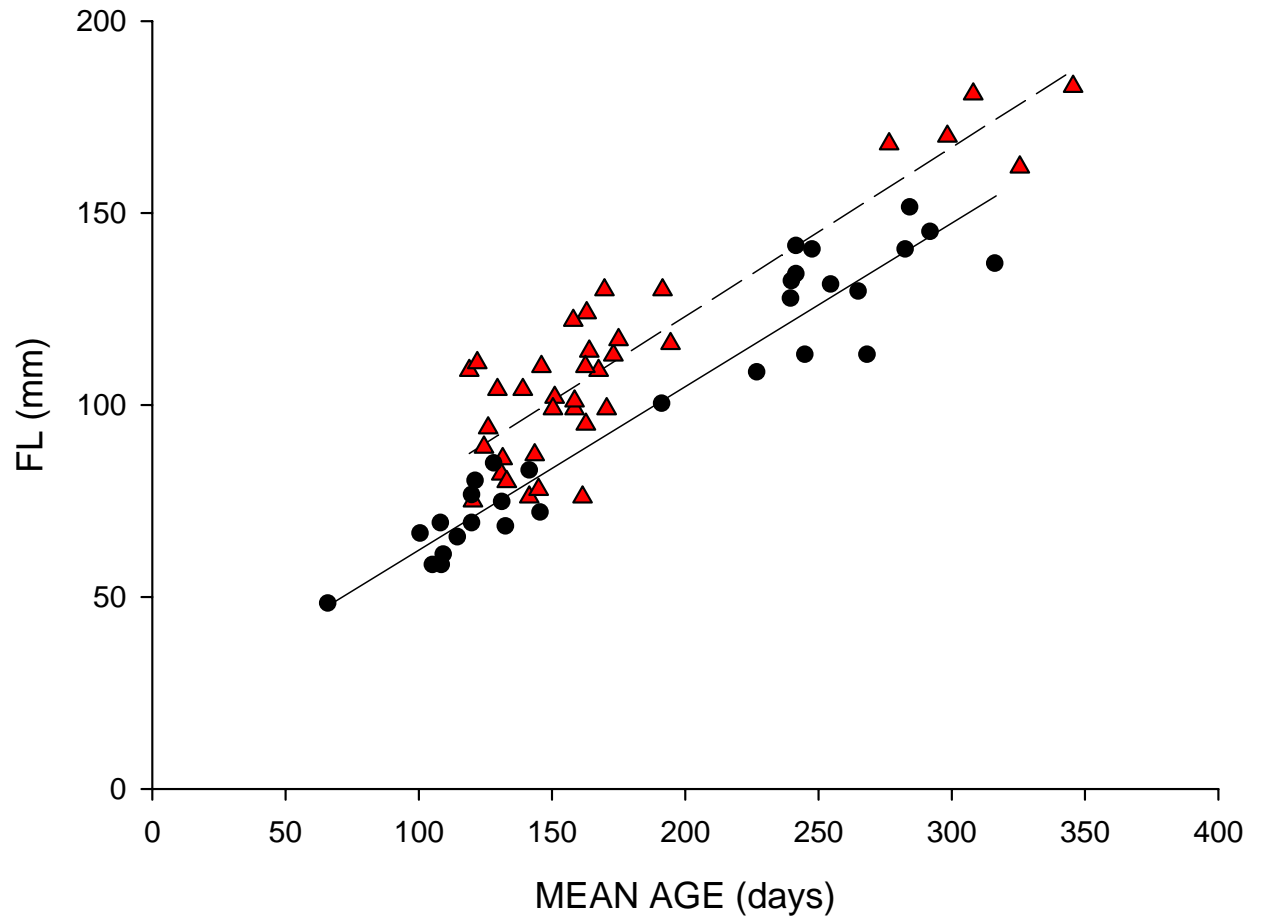
Figure 2. Relationship between age and fork length of *L. carponotatus* from the Keppel Islands.

▲ = 2006 collection, 2006 FL(- - -) = 0.4407 x (age) + 34.9024, r^2 = 0.8070, p < 0.0001

● = 2007 collection. 2007 FL (---) = 0.4261 x (age) + 19.5783, r^2 = 0.9228, p < 0.0001

2.4.2. Settlement and spawning periods

Optical contrasts were observed in the otolith increments of twenty-nine individual *P. maculatus*. Modal spawning dates for the primary cohort (1°) occurred within the second and fourth quarters of February (Figure 3). The mean PLD for *P. maculatus* was 28.6 ± 2.4 days, that corresponds to a modal reef settlement date within the fourth quarter of March (Figure 3). Spawning and settlement dates spanned throughout the lunar cycle, with no preferential phase despite higher settlement rates outside of the new and full moon periods.

Distinct changes in the otolith increment contrast were observed for all fifteen *L. carponotatus* from the 2007 1° 0+ age cohort. Modal spawning dates for the 1° cohort occurred within the first quarter of February during a full moon (Figure 4). The mean PLD for *L. carponotatus* was 33.6 ± 4.71 days. Modal reef settlement dates for the most recent cohort occurred within the second quarter of March while the moon was full (Figure 4).
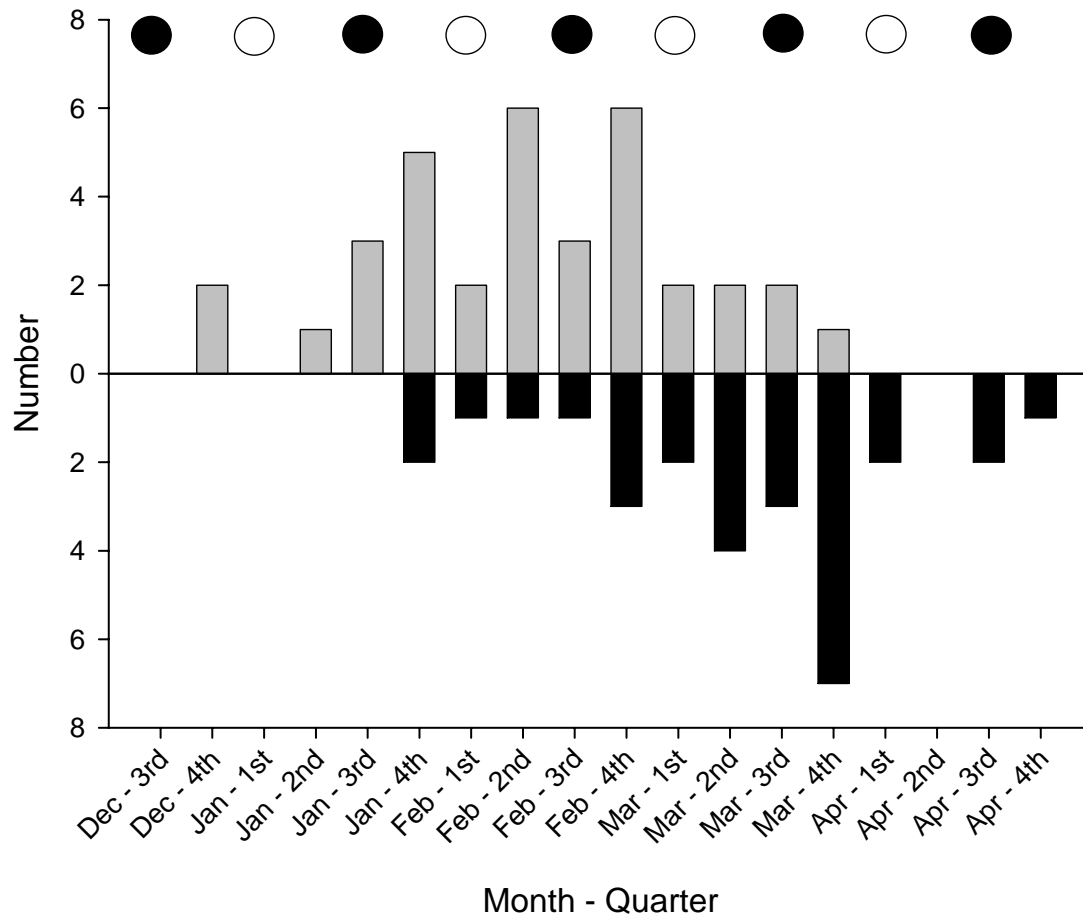
Figure 3. Spawning and settlement dates for *P. maculatus* 1° cohorts.

Grey bars = spawning, black bars = settlement, ● = new moon, ○ = full moon
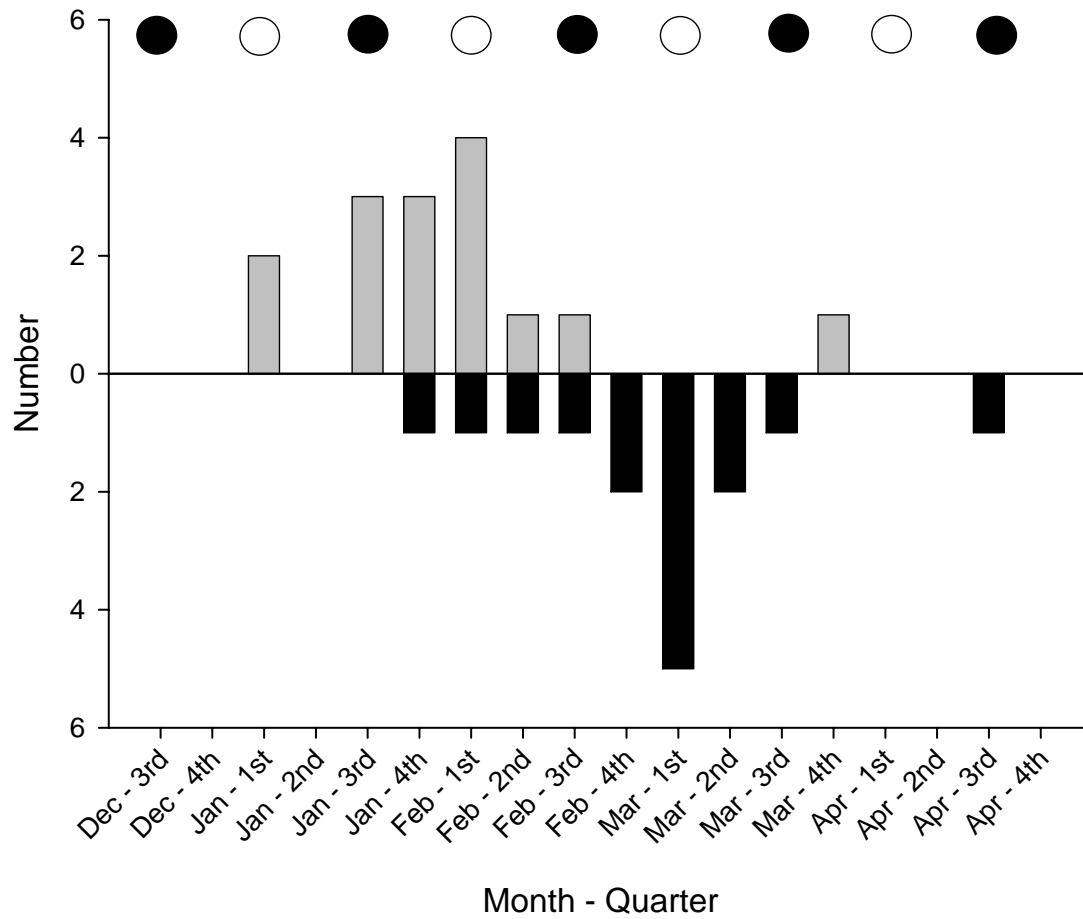
Figure 4. Spawning and settlement dates for *L. carponotatus* 1° cohorts.

Grey bars = spawning, black bars = settlement, ● = new moon, ○ = full moon

2.5. Discussion

The results from this study show that growth of juvenile *P. maculatus* and *L. carponotatus* from the Keppel Islands was rapid in the first months of their lives. This concurs with the initial high growth rates reported from annual age-based studies in *Plectropomus* and *Lutjanus* species (Ferreira & Russ 1992; 1994; Newman *et al.,* 2000b; Kritzer 2002). In particular, *L. carponotatus* growth appeared to be faster within the Keppel Islands than the combined growth rate of conspecifics from the Lizard and Palm Island regions (Kritzer 2004). *L. carponotatus* also showed similar growth trends between 2006 and 2007. High natural mortality rates during early stages of life suggest rapid growth would be advantageous because it reduces the chance of predation. The growth rate for *P. maculatus* was faster than *L. carponotatus* over equivalent age ranges.

The spawning dates estimated from this study show that *P. maculatus* and *L. carponotatus* are spawning as late as the end of March. In comparison, previous estimates on spawning periods have ranged through September to November for *P. maculatus* (Ferreira 1993), and September to March for *L. carponotatus* (Kritzer 2004). This indicates that spawning may be occurring for a longer period or later than usual for *P. maculatus*.

The spawning periods of reef fishes can be influenced by the lunar cycle. While the majority of work has concentrated on the primary target species of Australia (*P. leopardus*), additional species have been investigated. *P. areolatus* and *E. fuscoguttatus* spawning aggregations typically form during full moons between September and February in Indonesia. However, spawning aggregations of *P. areolatus* have also been

observed during new moon phases between April and July (Pet *et al.,* 2005). New moons also coincide with most *P. leopardus* spawning aggregations (Ferreira 1995; Samoilys 1997; Zeller 1998). Though no previous work has been carried out on the spawning periods of *L. carponotatus* in relation to the lunar cycle, larger ovary weight and higher proportions of ripe ovaries during new moon phases indicate that most spawning may occur during this period (Kritzer 2004). In contrast, the modal spawning of *L. carponotatus* from this study overlapped with full moon phases, while the *P. maculatus* spawning period did not discriminate between full and new moon. However, the number of fish examined within this study may not provide an adequate sample of spawning within the Keppel Islands.

Despite previous work on conspecifics, the PLD of *P. maculatus* and *L. carponotatus* has not been analysed before. The PLD for *P. leopardus* has been estimated to be 25 days (Doherty *et al.*, 1994). In comparison the average PLD for *P. maculatus* was found to be marginally longer in this study, at 28.6 days. The PLD of five lutjanid species ranged from 21.8 to 37.9 days (Zapata & Herrón 2002; Domeier 2004). Within this study, *L. carponotatus* was estimated to sit within the range found by Zapata & Herrón (2002), with an average PLD of 33.6 days.

Settlement of reef fish has also previously been linked to the lunar cycle (Meekan *et al.,* 1993; Sponaugle & Cowen 1996a; 1996b; 1997), but no previous work has been done on *P. maculatus* or *L. carponotatus*. Though no pattern between *P. maculatus* settlement and lunar phase was observed, modal *L. carponotatus* settlement did coincide with full moons. New moon settlement is predominant amongst many reef fish, but settlement during the full moon has been observed before (Booth & Beretta, 1994).

The cryptic behaviour of newly settled reef fish makes their recruitment difficult to survey. Based on the sizes of juveniles from this study, *P. maculatus* are first visible on the reef at 63 days old, while *L. carponotatus* are first observed after 66 days. The estimated PLD of *P. maculatus* was 28.6 days, while for *L. carponotatus* it was 33.6. Therefore, both species first become apparent roughly one month after settling onto the reef. Consequently, recruitment surveys could take place two months after spawning was initiated. However, only one age cohort was observed from the *P. maculatus* 2006 survey, while all other surveys observed two age cohorts. This suggests that additional cohorts were yet to settle and therefore could not be observed by sampling *P. maculatus* in October. An approximate gap of 100 days between each age cohort was apparent for both *P. maculatus* and *L. carponotatus* in the 2007 collection, as well as for the *L. carponotatus* 2006 sampling. Although initial spawning may have contributed the most to a new cohort, high pre- and post-settlement mortality may have reduced successful recruitment to insufficient levels for observation. Hence, I recommend that recruitment surveys of *P. maculatus* and *L. carponotatus* are optimized approximately 160 days after initial spawning, in order to representatively sample recruits from all age cohorts.

Aggregate spawning is common amongst many serranids and lutjanids (Domeier & Colin 1997; Samoilys 1997; Claro & Lindeman 2003; Pet *et al.,* 2005; Rhodes & Tupper 2008). The consistency in location and timing make these spawning aggregations highly susceptible to fishing. Fishing of spawning aggregations removes a large proportion of the sexually mature population and can ultimately lead to recruitment over-fishing. Two possible solutions are to impose seasonal closures that coincide with spawning or to create MPAs that encompass the spawning locations. The former requires

spawning time details, which can easily be obtained from back dating otoliths. The latter requires knowledge on spawning locations as well as any migratory paths used to reach the spawning location. For some species this presents a problem due to the relatively large number of aggregations formed (e.g. *P. leopardus*).

Existing seasonal closures for Queensland coral reef finfish fisheries occur within three, nine-day closures that coincide with the new moon phases of October, November and December. Previous work has estimated that this is the principal time for spawning aggregations of the primary finfish, *P. leopardus* (Ferreira 1995; Samoilys 1997; Zeller 1998). However, the extended spawning duration and lack of new moon spawning dominance exhibited by *P. maculatus* and *L. carponotatus* in this study suggest that seasonal closures may not be providing adequate protection for sexually mature individuals of this species.

In conclusion, this study shows that despite conspecific regional differences, the initial growth of both species is rapid, with *P. maculatus'* greater growth rate possibly attributed to its larger final size. Based on the evidence from this study, 0+ *P. maculatus* recruits are first apparent on the reef at 63 days old, while *L. carponotatus* can be observed at 66 days old. Additionally, the spawning duration of *P. maculatus* and *L. carponotatus* are longer than originally presumed. Future recruitment surveys of these two coral reef fish could take place two months after spawning, however to include any additional age cohorts, surveys would ideally occur approximately 160 days after spawning is first observed. The existing seasonal spawning closures for the Queensland coral reef finfish fisheries provide little protection for spawning individuals of both *P. maculatus* and *L. carponotatus*.

Chapter 3

3.0. Evaluation of potential local adult spillover and recruitment subsidies from no-take marine protected areas on the Great Barrier Reef

3.1. Abstract

The effectiveness of no-take marine protected areas (MPAs) in sustainable fishing is contingent upon their ability to augment fish stocks in areas accessible to fishing. Although local migration of adults across MPA boundaries has been observed, evidence for larger scale adult migration and recruitment subsidies in fished areas is lacking. Typical experimental designs in which MPAs are compared to nearby control sites are inappropriate to measure such benefits beyond MPA boundaries. In this study the potential for local benefits of MPAs were examined by comparing adult and recruit densities outside MPAs, both near to and distant from the MPA boundary. Adults and juveniles of two recreationally important predatory fishes (*P. maculatus* and *L. carponotatus*) were surveyed at both the Keppel Islands and Palm Islands, two inshore clusters of no-take MPAs on the Great Barrier Reef. In each region, the abundance and biomass of adults, as well as recruit density were compared for three treatments: (1) Within MPAs; (2) Nearby fished areas (< 1km from the MPA boundary) and (3) distant fished areas (> 5km from the MPA boundary), with four or more sites nested within each treatment. Site variation accounted for most of the variation in both adult and recruits for

both *P. maculatus* and *L. carponotatus*. That is, there was no statistically significant difference among *P. maculatus* or *L. carponotatus* for all comparisons. Hence, at the scale of the sampling design, there is no evidence of either adult spillover or recruitment subsidies. However, because of patchiness in the distributions of these predators and the low number of recruits observed, further research is needed to assess the generality of these results.

3.2. Introduction

No-take marine protected areas are widely advanced as an effective means to protect and enhance local fisheries (Lauck *et al.* 1998; Jennings 2000; Russ 2002). Within protected areas, substantial benefits of protection have been recorded, including increased adult fish abundance, size and biomass and increased larval production (Willis *et al.,* 2003b; Evans & Russ 2004; Williamson *et al*. 2004; Evans *et al.,* 2007). The combination of these factors results in higher spawning population size and greater reproductive effort than in equivalent sized areas open to fishing. However, the benefit of such MPAs acting as a tool for enhancing fisheries requires that the MPAs supplement populations beyond their boundaries (Russ 2002; Gell & Roberts 2003; Halpern *et al.,* 2004). Despite many years of research and hundreds of studies in which MPAs have been compared to fished areas, evidence for the benefits of MPAs beyond their boundaries is limited.

One obvious potential benefit of MPAs comes from the migration of adult target fish from MPAs to nearby fished areas – the spillover effect (Russ 2002; Gell & Roberts 2003; Halpern *et al.,* 2004). The benefits of spillover could be inferred from decreasing

abundance and biomass of target reef fish with increasing distance from the MPA boundary. However, the mobility of reef fish is usually limited to a home region of a few hundred meters (Zeller & Russ 1998; Zeller *et al.,* 2003). Consequently, the benefits of spillover only extend a few hundred meters from the boundaries of MPAs. For example, in the Philippines, abundance, biomass and Catch-Per-Unit-Effort (CPUE) of target fish increased over a 20 year period close to (within 300m), but not far from (300 – 500m) the MPA boundary (Russ *et al*., 2003; 2004; Abesamis & Russ 2005; Abesamis *et al.,* 2006a; 2006b). In Mombasa, Kenya, the wet mass of trap catches also declined as a function of increasing distance from a MPA (McClanahan & Mangi 2000). However, unless adult spillover occurs over substantial distances, the benefit to adjacent fisheries will be limited.

Increased size and abundance of adult fish within protected areas should result in greater larval production in MPAs (Willis *et al.,* 2003b; Evans *et al.,* 2007). If recruitment subsidies are occurring, the presence of MPAs should result in greater recruitment of juvenile fishes to fished areas through the enhanced supply of recruits from MPAs. To date, there are two examples of potential recruitment subsidies; one supporting recruitment spillover (Valles *et al.,* 2001), the other, self-recruitment (Nardi *et al.,* unpub. man.). Abundance of *Stegastes partitus* larvae and new recruits from the Soufrière Marine Management Area in St Lucia was consistently lower than in a nearby fished area (Valles *et al.* 2001). In comparison, recruit abundance of *P. leopardus* from MPAs around the Abrolhos Islands, Western Australia, was greater than nearby fished areas (Nardi *et al.* unpub. man.). These contrasting results may be due to an inappropriate

study design. The lack of information on the distance larvae disperse makes it difficult to design studies to effectively measure recruitment effects.

Coral reef fish larvae have the potential to disperse vast distances from MPAs to distant reefs. The swimming ability of some coral reef fish larvae has been estimated of speeds up to 13.7 body lengths s^{-1} (Leis & Carson-Ewart 1997). In addition, coral fish larvae can take advantage of different hydro-dynamic features by altering their position in the water column (Cowen *et al.,* 1993). Recent modeling work suggests larvae dispersal distances in the order of 10s to 100s of km, but not all models take into account larval behavior (Roberts 1997; Cowen 2002; Domeier 2004). Dispersal on this scale could possibly benefit fisheries on a regional scale as apposed to the local scale of adult spillover.

Despite having the ability to disperse vast distances, larvae may return to their natal reefs. Jones *et al.,* (1999) chemically tagged over 10 million embryos of *Pomacentrus ambionensis* around Lizard Island. After hatching, a total of 5000 juveniles were caught and their otoliths examined. Of those caught, 15 juveniles exhibited marked otoliths, indicating that between 15 – 60% of juveniles hatched around Lizard Island return to their natal reef. Mass marking of *Amphiprion percula* and *Chaetodon vagabundus* with barium isotopes also revealed around 60% of larvae returned to their birth place (Almany *et al.,* 2007). Additionally, chemical tagging and DNA genotyping of panda clownfish (*Amphiprion polymnus*) within Kimbe Bay, Papua New Guinea has also shown juveniles settling very close to their birth site, with a large proportion settling within 100m of their parent's anemone (Jones *et al.,* 2005).

To date, no literature can unequivocally prove spillover from MPAs. Uncertainty arises within the assumptions of each investigation – any difference between a MPA and a nearby fished site is due to the MPA itself. Without relevant data prior to the establishment of the MPA, as well as some form of tagging, any results obtained from subsequent data could not be certain that the MPA was the cause. Before-After-Control-Impact (BACI) experiments have been suggested as the ideal sampling method for MPA studies (Russ, 2002). However, the opportunity to monitor study sites before they become MPAs is rare.

The Great Barrier Reef Marine Park (GBRMP) was established in 1981. Following mounting evidence of increases in fish abundance within no-take areas (Evans & Russ 2004; Williamson *et al.,* 2004), the number and area of no-take MPAs was expanded in 2004. The total proportion of the GBRMP as no-take MPAs was increased from approximately 4.5% to about 33%. The planned expansion of MPAs provided a unique opportunity for sampling fished reefs before they became protected. Eighteen reefs from three inshore regions along the GBR were surveyed both before and 1.5 – 2 years after RAP was initiated. Abundance of coral trout (*Plectropomus* species) increased significantly within the Palm Islands and the Whitsundays. However, in the Keppel Islands, a decline in coral trout abundance was observed in both the MPAs and fished areas. In comparison to fished areas, the Whitsundays was the only region where abundance of coral trout increased within MPAs (Russ *et al.,* 2008). Therefore, although MPAs appeared to increase adult stocks within their boundaries, the consequences of these increased adult stocks for adjacent fished areas remains to be determined.

The overall aim of this study was to assess the potential benefits of no-take MPAs on the abundance of adult and juvenile fishes in the near vicinity of MPA boundaries. Based on data on limited adult movements and localised retention of larvae, I hypothesized that sites near MPAs should exhibit elevated densities of both adults and juveniles, in comparison with sites some distance from MPA boundaries. Adults and juveniles of two recreationally important predatory fishes (*Plectropomus maculatus* and *Lutjanus carponotatus*) were surveyed at both the Keppel Islands and Palm Islands, two inshore clusters of no-take MPAs on the Great Barrier Reef. At each island group, the abundance and biomass of adults and recruits were compared for three treatments: (1) Within MPAs; (2) Nearby fished areas (< 1km from the MPA boundary) and (3) distant fished areas (> 5 km from the MPA boundary), with at least four sites nested within each treatment.

3.3. Materials and methods

3.3.1. Study site description

Data was collected from the Keppel (23^o10'S, 150^o57'E) (Figure 5) and Palm Island (18^o34'S, 146^o29'E) (Figure 6) regions between April and June 2007. These two island regions encompass both MPAs and "blue zones" (fished areas). Both regions are inshore, easily accessible from mainland Australia and popular recreational fishing locations. As a result, both are susceptible to high levels of recreational fishing. For the purpose of this study, MPAs shall refer to areas where any form of fishing or collecting is forbidden.
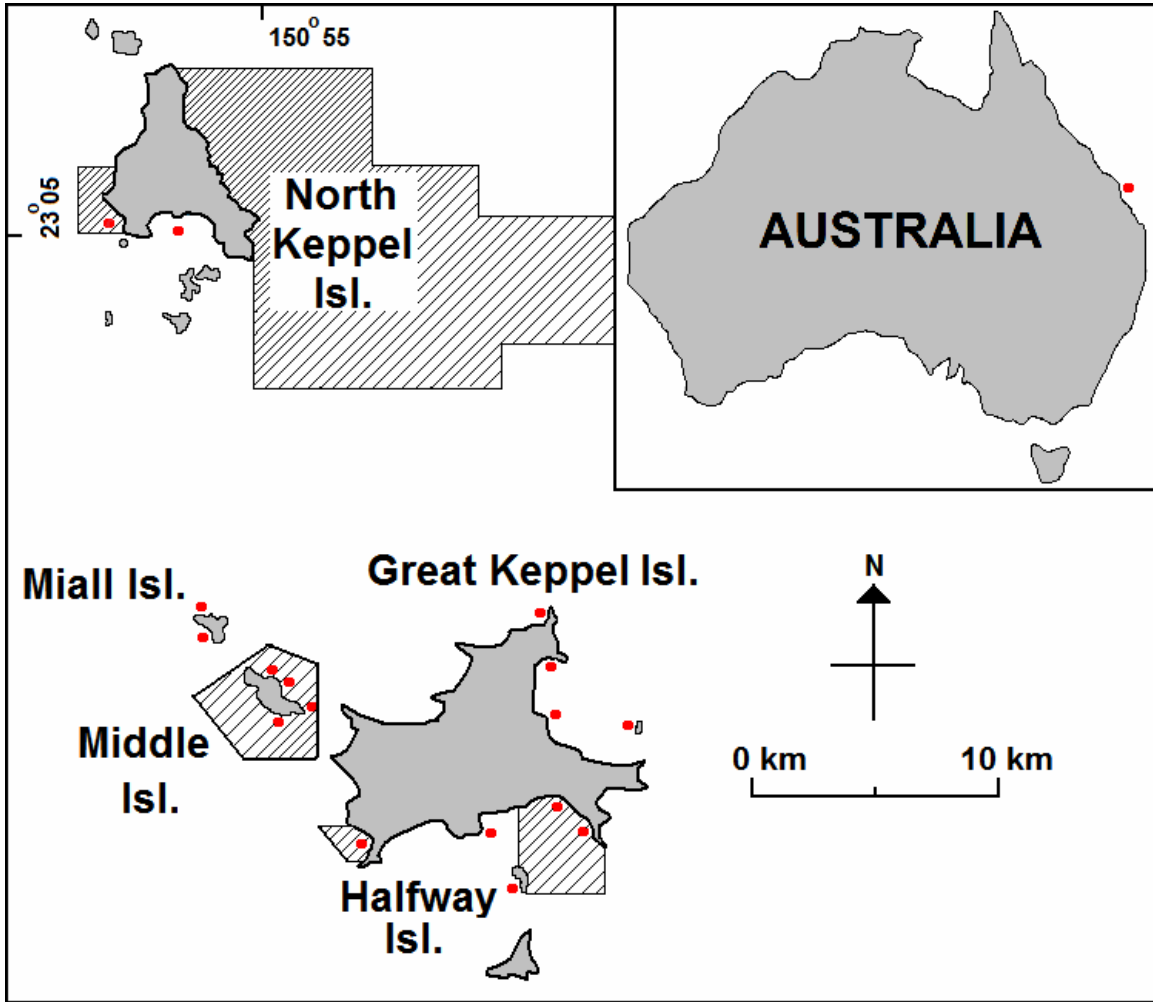
Figure 5. Map of study sites from the Keppel Island region. ● = sampling sites, ▨ = MPA zones.
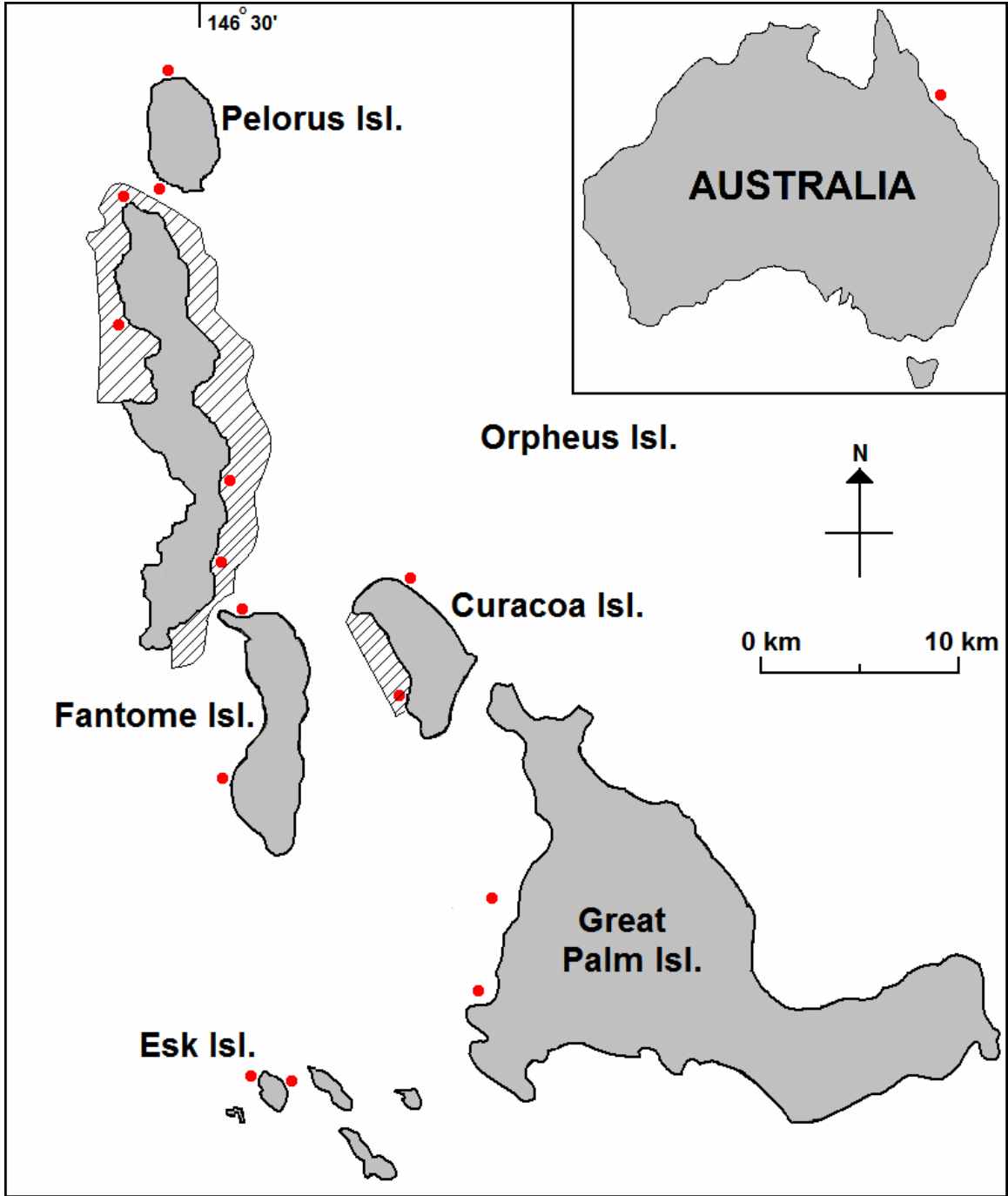
Figure 6. Map of study sites from the Palm Island region. ● = sampling sites, ▨ = MPA zones..

3.3.2. Fish surveys

Sampling was conducted within three specifically defined zones; MPAs, fished areas near (< 1 km) to MPAs and fished areas greater than 5 km from any MPA. Within each zone, a minimum of four randomly selected sites were sampled and their coordinates recorded.

Each site consisted of four underwater visual surveys (UVS), conducted within 50 x 6m transects for adults of both species. A minimum of 4m visibility was needed before any UVS took place. A two person dive team would consist of a primary diver leading each transect and recording fish observations, with the secondary diver following with a transect tape so as to minimize disturbance to fish. When observed, fish abundance was recorded and their corresponding fork length (FL) estimated. FL estimates of each fish were grouped into 50mm size categories. Size estimation was practised on models before each transect began. For simplicity, all fish observed were classed as recruits or adults based on earlier size-at-age data. Biomass of adult fish was calculated from biomass – length formulae (Moran *et al.,* 1988; Evans, pers. comm).

Habitat data was collected from the same transects used to collect fish data. The point intercept technique was used to estimate benthic cover, with benthic cover recorded every 2m along the transect tape. Benthic cover was summarised into ten different categories; live hard coral, dead coral, soft coral, rubble, sponge, invertebrates, algae, rock, sand or "other". The "other" category included any additional benthic cover not already described by the alternative nine categories.

3.3.3 Data analysis

Analysis of variance (ANOVA) was used to test for differences in the total and legal abundance and biomass of *P. maculatus* and *L. carponotatus* between MPAs, nearby fished zones and distant fished zones. In addition, differences in fish recruit cohort abundance and the benthic cover were also compared between MPAs, nearby fished zones and distant fished zones using ANOVA. The zone factor was fixed, while island and site were random and nested within zone. Young-of-the-year recruits were separated into primary (1°) and secondary (2°) cohorts for both species based on previous size-at-age studies (see chapter 2). *P. maculatus* ranging between 150 – 250mm FL were considered the 2° 0+ age cohort, while *P. maculatus* less than 150mm FL were within the 1° 0+ age cohort. The 2° 0+ age cohort of *L. carponotatus* was between 100 – 200mm FL, while *L. carponotatus* less than 100mm FL were within the 1° 0+ age cohort. All count and biomass data were square root transformed in order to satisfy the ANOVA requirements of normality and homogeneity of variances.

Initially, factors in the analysis for adult *L. carponotatus* were site, island and zone. However, as the island (zone) term was found to be non-significant for total *L. carponotatus*) within the Keppel island location (p = 0.95), the data was pooled to give more power to the analysis (Underwood 1981). This procedure was also deemed necessary for biomass of legal *P. maculatus* within the Keppel Islands (p = 0.93) and the 2° 0+ *L. carponotatus* cohort within the Keppel Islands (p = 0.97).

3.4. Results

3.4.1. Keppel Islands

There was a decreasing trend in mean density of adult *P. maculatus* from within MPAs with increasing distance from MPAs at the Keppel Island location (Figure 7a). However, the differences among means were not statistically significant (Table 1a). The trend in the densities of legal-sized *P. maculatus* was similar and were also not significant (Figure 7a, Table 1b). Legal-sized fish accounted for 61% of the total number of adults observed within MPAs, only 37% in nearby fished sites and 43% in distant fished sites. Total biomass of *P. maculatus* decreased as a function of distance from the MPA zones (Figure 7b), but the trend was not significant (Table 2a). No change in the biomass distribution was observed when only legal-sized *P. maculatus* were analysed (Figure 7b, Table 2b). In MPAs, legal-sized fish accounted for 87% of the total adult biomass, while in nearby and distant fished areas, they accounted for 67% and 85% of the biomass.

Adult densities of *L. carponotatus* were not significantly different between zones (Figure 7c, Table 3a). The greatest mean abundance of adult *L. carponotatus* was found at sites located far away from any MPAs (10.4 ± 8.1 fish per $1200m^2$), while the lowest mean abundance occurred within adjacent fished areas (7.8 ± 5.1 fish per $1200m^2$). This pattern was similar for legal-sized *L. carponotatus* (Figure 7c, Table 3b). Legal-sized *L. carponotatus* accounted for 65% of the total number of adults observed within MPAs,

40% in nearby fished sites and 62% in distant fished sites. The total biomass of adult *L. carponotatus* was not significantly different between zones (Figure 7d; Table 4a). The greatest mean total biomass was observed within distant fished zones (5.5 $\pm$ 2.8 kg/1200m^2), while the lowest was observed within nearby fished zones (2.9 $\pm$ 2.4 kg/1200m^2). No change in total biomass distribution was observed when only legal sized *L. carponotatus* were analysed (Figure 7d). Legal-sized fish accounted for 88% of the total adult biomass in MPAs, 72% in nearby fished sites and 84% in distant fished sites.

The modal length of *P. maculatus* decreased by 150mm (375 – 225mm) with increasing distance from the MPA sites (Figure 8). Modal length of *L. carponotatus* within MPAs and distant fished zones was 275mm, while in nearby fished zones it was 175mm (Figure 9).

The mean abundance of *P. maculatus* recruits from the 1° 0+ age cohort was extremely low (Figure 10a). The highest mean abundance was found within near sites (2.8 $\pm$ 5.3 fish per 1200m^2); while MPAs and distant fished sites both displayed means of less than one fish per site (0.9 $\pm$ 1.1 and 0.4 $\pm$ 0.9 fish per 1200m^2). This trend was also observed for the 2° 0+yr cohort of *P. maculatus* (Figure 10a). Neither cohorts displayed significant difference in abundance between zones (Tables 5a & b).

A total of only nine *L. carponotatus* recruits from the 1° 0+ age cohort were observed in UVS around the Keppel Islands. These low observations of *L. carponotatus* recruits reduced the site mean to below one fish per 1200m^2 (Figure 10b). *L. carponotatus* recruits from the 1° 0+ age cohort were rarely observed in the majority of sites, resulting in a large variation between sites that did contain recruits from the primary cohort. Nearby fished sites showed the largest mean abundance (0.6 $\pm$ 1.1 fish per

1200m^2), while mean abundance in MPAs and distant fished sites was 0.2 $\pm$ 0.6 and 0.2 $\pm$ 0.4 fish per 1200m^2 respectively. The 2° 0+ age cohort of *L. carponotatus* recruits exhibited the same trend as *L. carponotatus* recruits from the 1° 0+ age cohort (Figure 10b), with the largest mean abundance within nearby fished sites (3 $\pm$ 2.7 fish per 1200m^2), followed by MPAs (2.1 $\pm$ 2.0 fish per 1200m^2) and distant fished sites (2 $\pm$ 2.1 fish per 1200m^2). Neither cohort showed any significant difference in abundance between zones (Tables 6a & b).
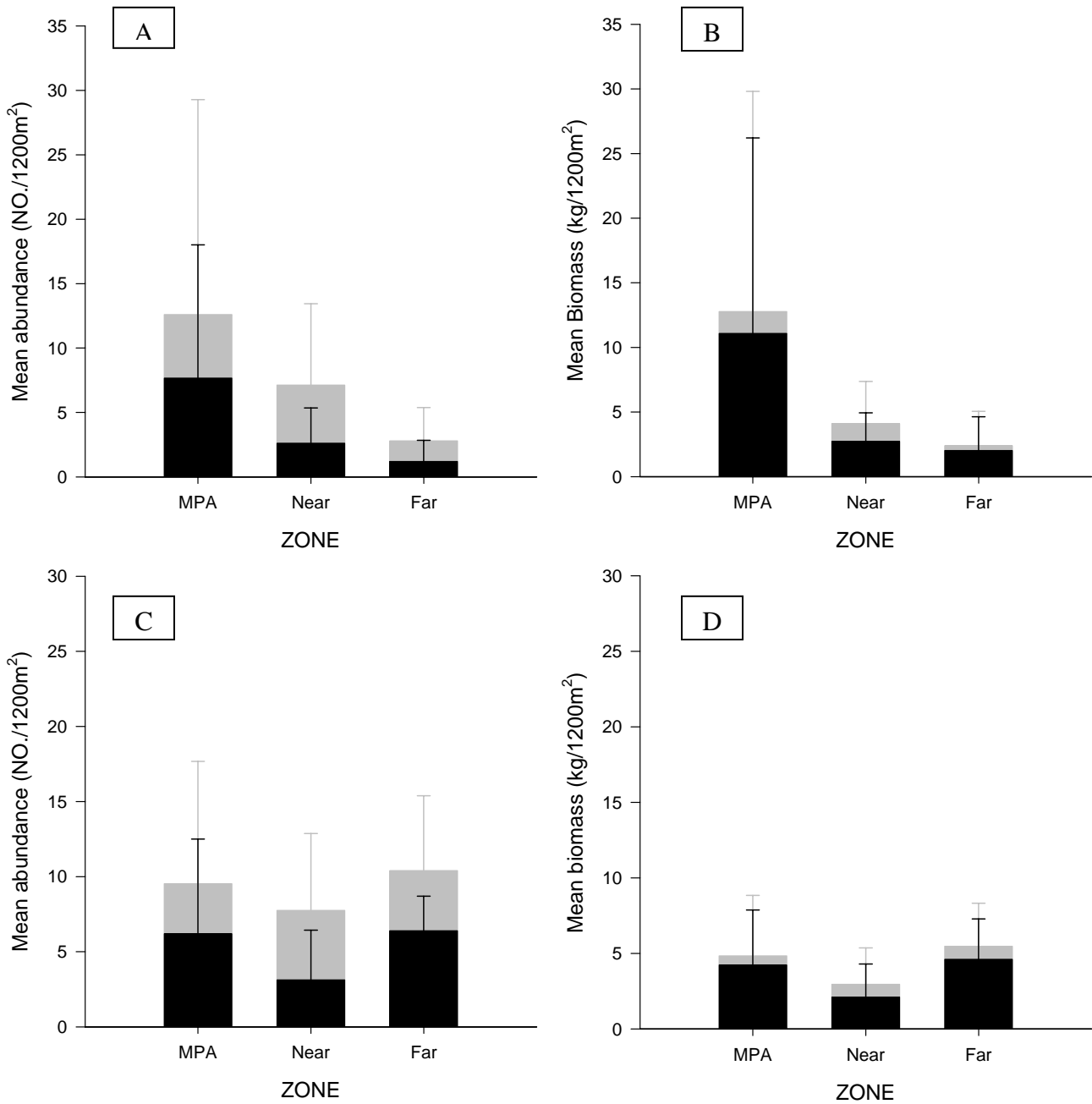
Figure 7. Mean (+S.E.) total *P. maculatus* adult abundance and legal-sized *P. maculatus* abundance from the Keppel Islands (A). Mean (+S.E.) total *P. maculatus* adult biomass and legal-sized *P. maculatus* biomass from the Keppel Islands (B). Mean (+S.E.) total *L. carponotatus* adult abundance and legal-sized *L. carponotatus* abundance from the Keppel Islands (C). Mean (+S.E.) total *L. carponotatus* adult biomass and legal-sized *L. carponotatus* biomass from the Keppel Islands (D). Light bars = total, dark bars = legal.

Table 1a. Abundance of *P. maculatus* from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	7.47	2	3.73	1.62	0.38
Island (zone)	13.8	5	2.76	0.88	0.53
Site (island x zone)	26.74	9	2.97	3.43	<0.01*
Error	82.39	95	0.87		

Table 1b. Abundance of legal-sized *P. maculatus* from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	6.76	2	3.38	11.3	0.53
Island (zone)	4.2	5	0.84	0.4	0.84
Site (island x zone)	17.85	9	1.98	3.2	<0.01*
Error	58.87	95	0.62		

Table 2a. Biomass of *P. maculatus* from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	9241.84	2	4620.92	6.33	0.41
Island (zone)	7716.2	5	1543.24	0.47	0.79
Site (island x zone)	28096.5	9	3121.83	3.46	<0.01*
Error	85683.7	95	901.93		

Table 2b. Biomass of legal-sized *P. maculatus* from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	10222.42	2	5111.21	2.57	0.12
Site (island x zone)	30490.65	14	2177.9	2.41	<0.01*
Error	85659.97	95	901.68		

Table 3a. Abundance of *L. carponotatus* from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	1.52	2	0.76	0.74	0.49
Site (island x zone)	15.27	14	1.09	1.65	0.08
Error	62.9	95	0.66		

Table 3b. Abundance of legal-sized *L. carponotatus* from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	7.47	2	3.73	1.62	0.38
Island (zone)	13.8	5	2.76	0.88	0.53
Site (island x zone)	26.74	9	2.97	3.43	<0.01*
Error	82.39	95	0.87		

Table 4a. Biomass of *L. carponotatus* from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	9241.84	2	4620.92	6.33	0.41
Island (zone)	7716.2	5	1543.24	0.47	0.79
Site (island x zone)	28096.5	9	3121.83	3.46	<0.01*
Error	85683.7	95	901.93		

Table 4b. Biomass of legal-sized *L. carponotatus* from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	3295.44	2	1647.72	6.17	0.13
Island (zone)	1521.44	5	304.29	0.69	0.65
Site (island x zone)	3963.1	9	440.34	1.05	0.41
Error	39963.49	95	420.67		
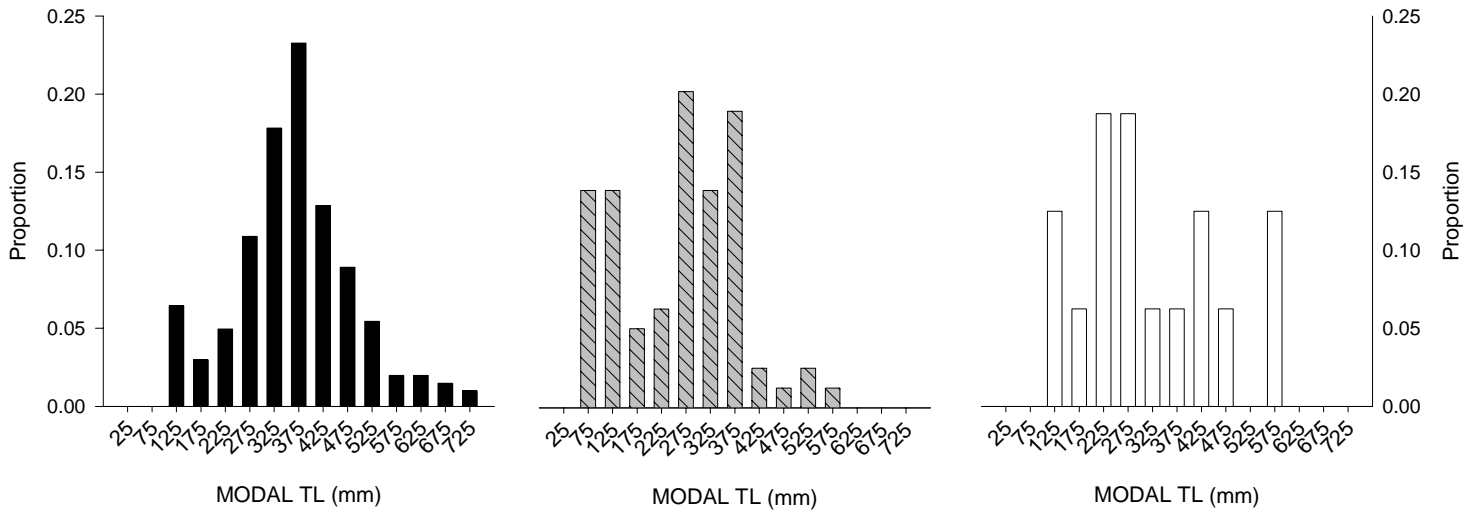
Figure 8. Size distribution of *P. maculatus* from the Keppel Island region.

Dark bars = MPAS, grey bars = near sites, white bars = far sites.
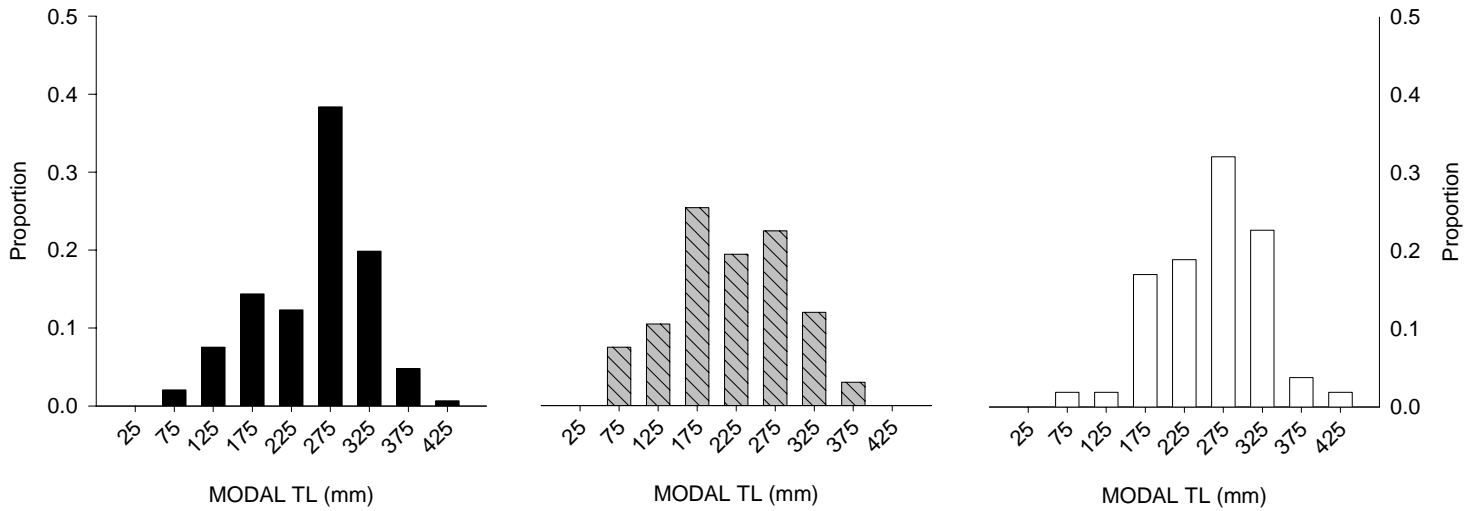
Figure 9. Size distribution of *L. carponotatus* from the Keppel Island region.

Dark bars = MPAS, grey bars = near sites, white bars = far sites.
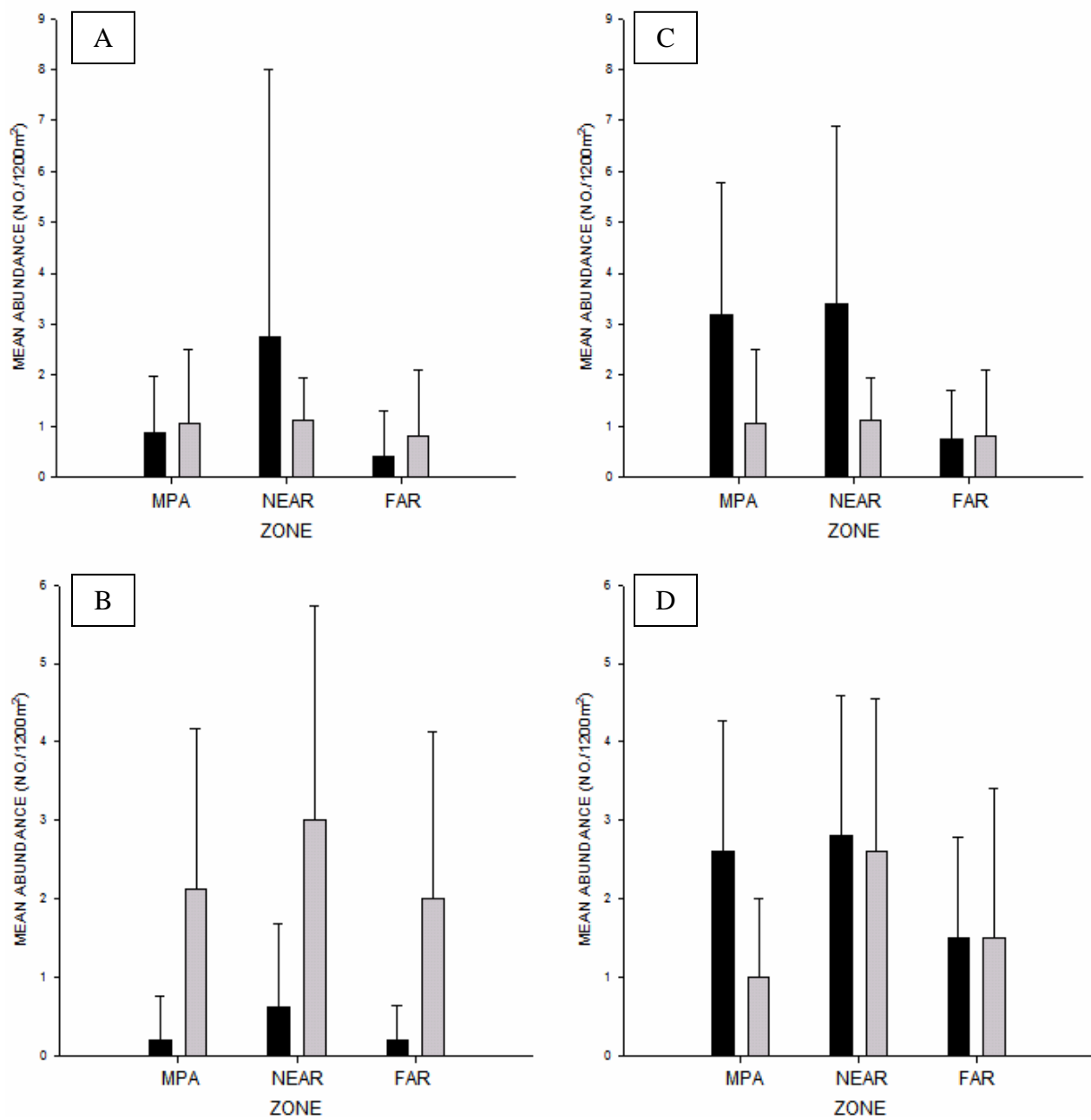
Figure 10. Mean (+ SE) abundance of *P. maculatus* (a) and *L. carponotatus* (b) recruits from the Keppel Island region. Mean (+ SE) abundance of *P. maculatus* (c) and *L. carponotatus* (d) recruits from the Palm Island region. Dark bars = primary cohort, grey bars = secondary cohort.

Table 5a. Abundance of the 1° *P. maculatus* 0+ age cohort from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	3.61	2	1.81	0.71	0.54
Island (zone)	10.61	5	2.12	6.95	<0.01*
Site (island x zone)	2.65	9	0.29	1.83	0.07
Error	15.31	95	0.16		

Table 5b. Abundance of the 2° *P. maculatus* 0+ age cohort from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	0.14	2	0.07	0.21	0.82
Island (zone)	1.77	5	0.35	1.16	0.41
Site (island x zone)	2.68	9	0.3	1.55	0.14
Error	18.24	95	0.19		

Table 6a. Abundance of the 1° *L. carponotatus* 0+ age cohort from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	0.25	2	0.13	0.5	0.64
Island (zone)	1.1	5	0.22	3.07	0.08
Site (island x zone)	0.64	9	0.07	1.05	0.4
Error	6.42	95	0.07		

Table 6b. Abundance of the 2° *L. carponotatus* 0+ age cohort from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	0.85	2	0.43	0.69	0.52
Site (island x zone)	9.5	14	0.68	2.27	0.01*
Error	28.44	95	0.3		

3.4.2. Palm Islands

The mean density of adult *P. maculatus* was not significantly affected by protection (Figure 11a). The greatest mean abundance of *P. maculatus* was within MPAs (10.6 $\pm$ 3.1 fish per 1200m^2). However, unlike the Keppel Islands location, the lowest mean abundance was within adjacent sites (7.2 $\pm$ 5.7 fish per 1200m^2). Excluding observations of *P. maculatus* under the legal catch size resulted in greater similarity of mean abundances between zones. The mean abundance of legal-sized *P. maculatus* was lowest in far sites rather than near sites, but the difference between the two zones was only 0.3 fish per 1200m^2. No significant difference in the total or legal mean abundance of *P. maculatus* was observed between zones (Tables 7a & b). Legal-sized *P. maculatus* accounted for 42% of the total number of adults observed in MPAs, 50% in nearby fished sites and 36% in distant fished sites. Mean biomass of *P. maculatus* was greatest within MPA sites (12.1 $\pm$ 7.4 kg/1200m^2), but relatively similar mean biomasses were also observed in nearby and distant fished sites (9.24 $\pm$ 4.2 and 9.85 $\pm$ 11.6 kg/1200m^2 respectively). This pattern of distribution was also seen for the biomass of legal-size *P. maculatus* (Figure 11b). No significant difference in *P. maculatus* biomass was recorded, regardless of size (Table 8a & b). Legal-sized *P. maculatus* accounted for 87% of the total biomass observed in MPAs, while in both nearby and distant fished sites, 90% of the adult biomass was comprised of legal-sized *P. maculatus.*

In comparison to *P. maculatus*, abundance of adult *L. carponotatus* increased with increasing distance from MPAs (Figure 11c). Abundance within far sites (17.8 $\pm$ 7.6 fish per 1200m^2), though 37% greater than MPA sites (11.2 $\pm$ 4.7 fish per 1200m^2) and 30%

greater than near sites (12.4 $\pm$ 7.4 fish per 1200m^2), was not significant (Table 9a). Legal-sized *L. carponotatus* showed no change in mean distribution, nor was any significant difference in abundance observed between zones (Table 9b). Legal-sized *L. carponotatus* accounted for 87% of the total adult density observed within the MPAs, 76% in nearby fished sites and 89% in distant fished sites. Distance from fishing protection had no significant effect on the mean biomass of *L. carponotatus* (Figure 11d, Table 10a). The greatest mean biomass of *L. carponotatus* was within distant fished sites (20.7 $\pm$ 7.8 kg/1200m^2). The lowest mean biomass was found within MPA sites (8.5 $\pm$ 3.6 kg/1200m^2), but was relatively similar to the mean biomass inside nearby fished sites (9.9 $\pm$ 5.8 kg/1200m^2). Legal-sized *L. carponotatus* biomass showed the same pattern as total biomass, and was also not significantly affected by distance from fishing protection (Table 10b). Legal-sized *L. carponotatus* accounted for the majority of total biomass in MPAs, nearby fished sites and distant fished sites (94%, 97% and 98% respectively).

The largest modal length for *P. maculatus* was within the distant fished sites (175mm), while both MPAs and nearby fished sites had modal lengths of 125mm (Figure 12). Distant fished sites also contained the greatest modal length of *L. carponotatus* (375mm) with the majority of fish falling into the three largest size categories. Modal length of *L. carponotatus* within MPAs and nearby fished sites was 325mm (Figure 13).

Mean abundance of *P. maculatus* recruits from the 1° 0+ age cohort was greatest within nearby fished sites (3.4 $\pm$ 3.5 fish per 1200m^2), but was closely followed by MPA sites (3.2 $\pm$ 2.6 fish per 1200m^2), while only 0.8 $\pm$ 0.9 fish per 1200m^2 were observed within distant fished sites (Figure 10c). In contrast, the abundance of the 2° 0+ age cohort was greatest within distant fished sites (4.0 $\pm$ 2.4 fish per 1200m^2), followed by MPAs

(2.8 $\pm$ 1.3 fish per 1200m^2) and nearby fished sites (1.6 $\pm$ 3.0 fish per 1200m^2). Differences in mean abundance between zones were not significant for either cohort (Tables 11a & b).

Greater numbers of *L. carponotatus* recruits from the 1° 0+ age cohort were present within the Palm Islands compared to the Keppel Islands, with relatively similar values in MPAs and nearby fished sites (2.6 $\pm$ 1.7 and 2.8 $\pm$ 1.8 fish per 1200m^2 respectively). The lowest mean abundance (1.5 $\pm$ 1.3 fish per 1200m^2) was in distant fished sites (Figure 10d). Within the subsequent cohort, the greatest mean abundance (2.6 $\pm$ 1.9 fish per 1200m^2) was still within nearby fished sites. However, the lowest mean abundance (1.0 $\pm$ 1.0 fish per 1200m^2) was within MPAs (Figure 10d). There was no significant difference in abundance between zones for either of the cohorts (Table 12a & b).
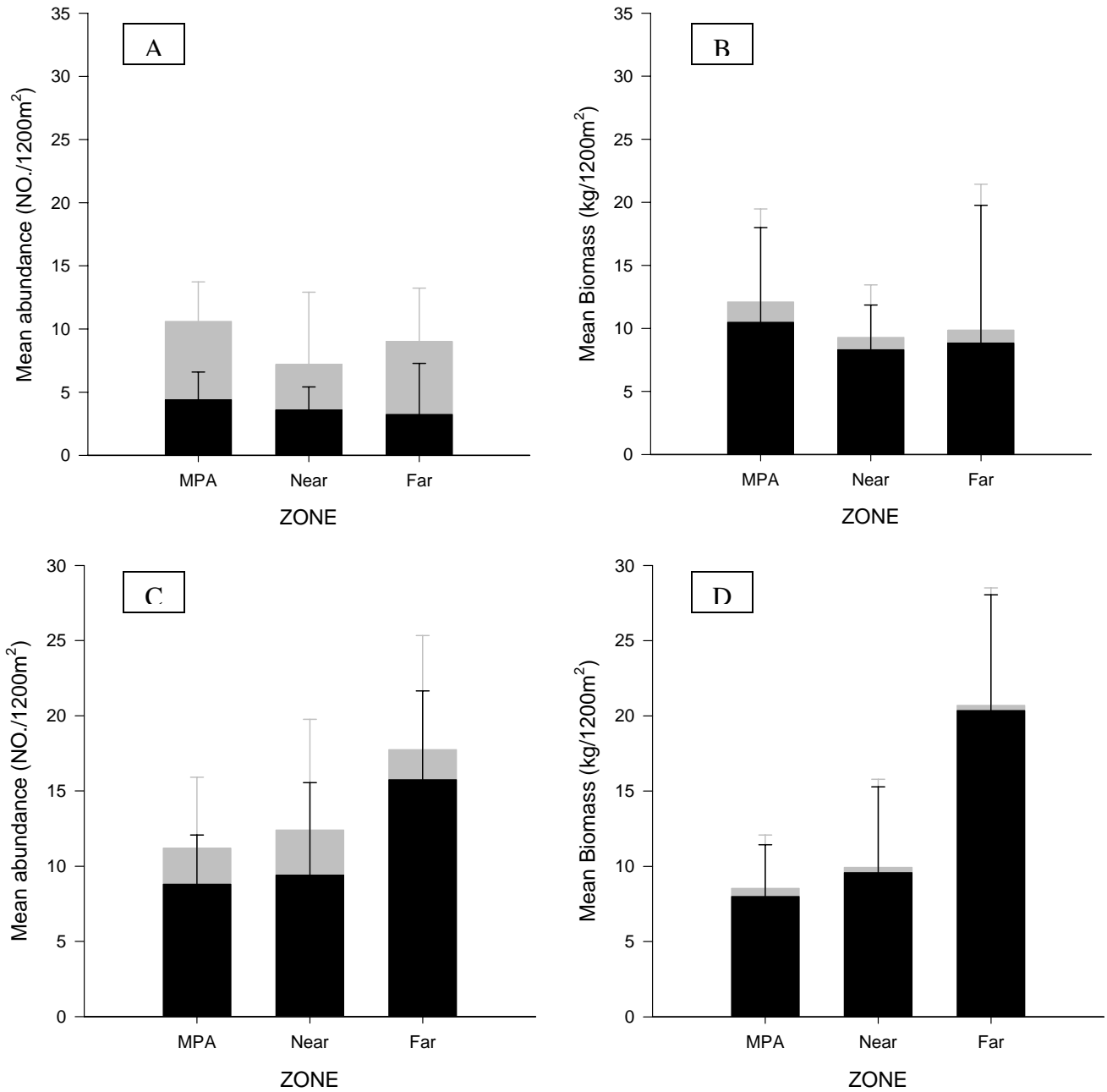
Figure 11. Mean (+S.E.) total *P. maculatus* adult abundance and legal-sized *P. maculatus* abundance from the Palm Islands (A). Mean (+S.E.) total *P. maculatus* adult biomass and legal-sized *P. maculatus* biomass from the Palm Islands (B). Mean (+S.E.) total *L. carponotatus* adult abundance and legal-sized *L. carponotatus* abundance from the Palm Islands (C). Mean (+S.E.) total *L. carponotatus* adult biomass and legal-sized *L. carponotatus* biomass from the Palm Islands (D). Light bars = total, dark bars = legal.

Table 7a. Abundance of *P. maculatus* from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	1.65	2	0.83	1.71	0.34
Island (zone)	2.15	4	0.54	0.6	0.68
Site (island x zone)	6.31	7	0.9	2.04	0.07
Error	18.51	42	0.44		

Table 7b. Abundance of legal-sized *P. maculatus* from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	0.1	2	0.05	0.05	0.95
Island (zone)	4.04	4	1.01	1.68	0.26
Site (island x zone)	4.21	7	0.6	1.34	0.25
Error	18.81	42	0.45		

Table 8a. Biomass of *P. maculatus* from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	330.99	2	165.5	0.06	0.94
Island (zone)	9706.78	4	2426.69	1.73	0.28
Site (island x zone)	9843.22	7	1406.17	1.54	0.18
Error	38425.4	42	914.89		

Table 8b. Biomass of legal-sized *P. maculatus* from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	44.67	2	22.34	0.01	0.99
Island (zone)	11145.77	4	2786.44	1.89	0.22
Site (island x zone)	10331.65	7	1475.95	1.23	0.31
Error	50347.38	42	1198.75		

Table 9a. Abundance of *L. carponotatus* from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	0.76	2	0.38	0.35	0.73
Island (zone)	4.21	4	1.05	1.3	0.36
Site (island x zone)	5.67	7	0.81	0.93	0.5
Error	36.74	42	0.87		

Table 9b. Abundance of legal-sized *L. carponotatus* from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	1.44	2	0.72	1.37	0.38
Island (zone)	2.14	4	0.54	0.9	0.51
Site (island x zone)	4.18	7	0.6	0.55	0.79
Error	45.45	42	1.08		

Table 10a. Biomass of *L. carponotatus* from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	3964.9	2	1982.5	2.41	0.23
Island (zone)	3191.8	4	798	1.29	0.36
Site (island x zone)	4336.7	7	619.5	0.64	0.72
Error	40947.6	42	974.9		

Table 10b. Biomass of legal-sized *L. carponotatus* from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	4381.4	2	2190.7	3.37	0.17
Island (zone)	2626.3	4	656.6	0.93	0.5
Site (island x zone)	4928.3	7	704	0.62	0.74
Error	47632.9	42	1134.1		
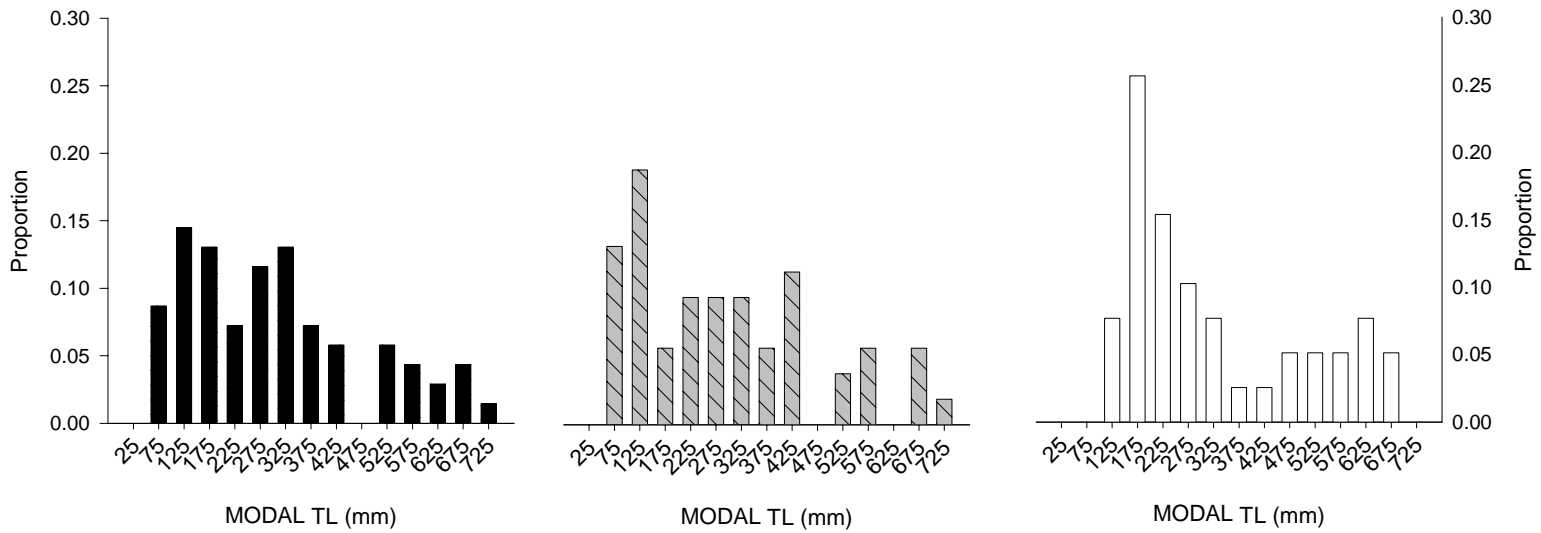
Figure 12. Size distribution of *P. maculatus* from all zones in the Palm Islands region.

Dark bars = MPA, grey bars = near sites, white bars = far sites.
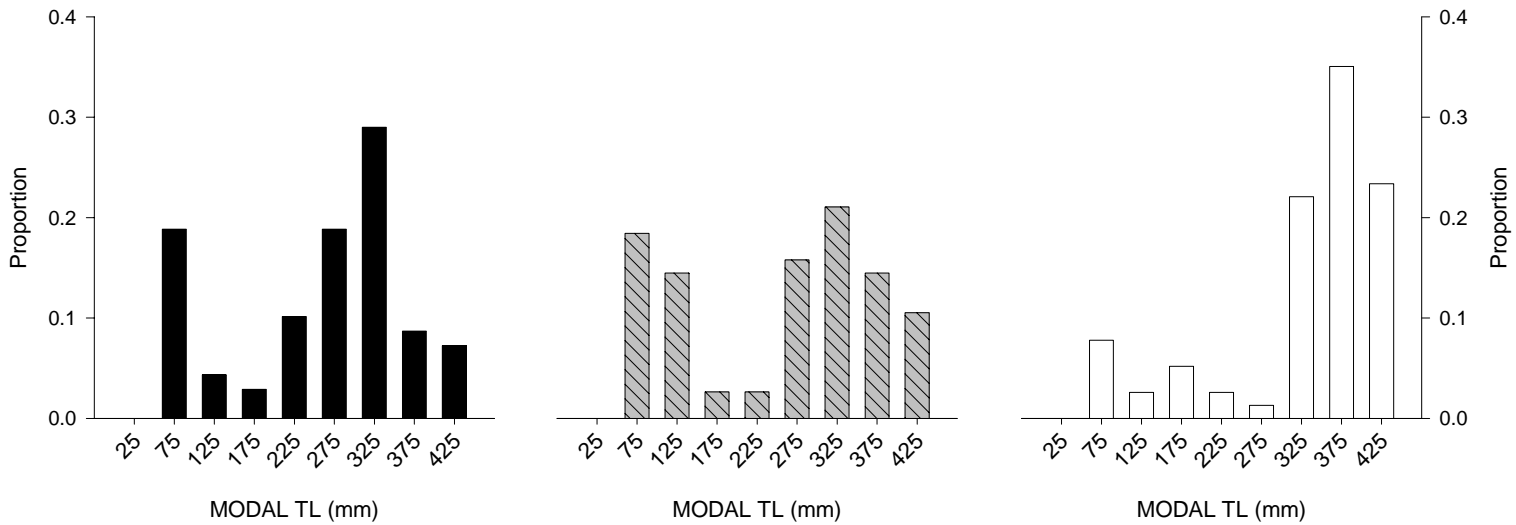
Figure 13. Size distribution of *L. carponotatus* from all zones in the Palm Islands region.

Dark bars = MPA, grey bars = near sites, white bars = far sites.

Table 11a. Abundance of the 1° *P. maculatus* 0+ age cohort from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	1.89	2	0.95	1.51	0.35
Island (zone)	2.49	4	0.62	1.07	0.44
Site (island x zone)	4.08	7	0.58	1.52	0.19
Error	16.16	42	0.38		

Table 11b. Abundance of the 2° *P. maculatus* 0+ age cohort from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	2.29	2	1.15	2.4	0.25
Island (zone)	2.03	4	0.51	0.72	0.6
Site (island x zone)	4.93	7	0.7	2.32	0.04
Error	12.77	42	0.3		

Table 12a. Abundance of the 1° *L. carponotatus* 0+ age cohort from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	0.41	2	0.21	0.33	0.74
Island (zone)	2.35	4	0.59	1.85	0.22
Site (island x zone)	2.22	7	0.32	0.94	0.49
Error	14.23	42	0.34		

Table 12b. Abundance of the 2° *L. carponotatus* 0+ age cohort from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	0.94	2	0.47	1.67	0.34
Island (zone)	1.19	4	0.3	0.71	0.61
Site (island x zone)	2.94	7	0.42	1.49	0.2
Error	11.86	42	0.28		

3.4.3. Benthic cover

Live coral cover (LCC), both hard and soft, showed no significant difference between zones at the Keppel or Palm Island locations (Table 13a & b). MPAs within the Keppel Islands had the lowest LCC (35%), while both nearby and distant fished sites averaged over 50% LCC (Figure 14). In the Palm Islands, nearby fished sites had the lowest LCC (37%). MPAs and distant fished sites within the Palm Islands both averaged 40% LCC (Figure 14). There was significant variation among sites within both locations (Table 13a & b).
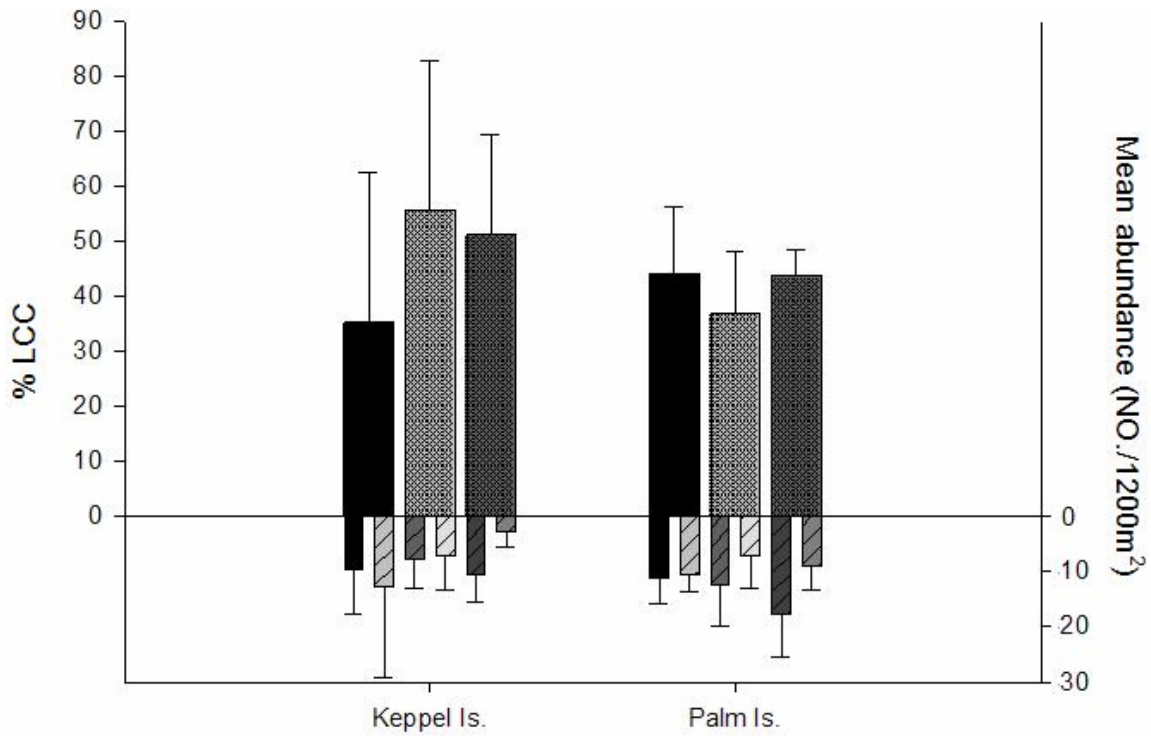
Figure 14 . Mean (+ SE) percent of live coral cover with mean abundance of adult fish from the Keppel and Palm Island regions.

■ = MPA LCC, ▨ = near sites LCC, ▨ = far sites LCC, ■ = mean MPA abundance of *L. carponotatus*, ▨ = mean MPA abundance of *P. maculatus*, ▨ = mean near abundance of *L. carponotatus*, ▨ = mean near abundance of *P. maculatus,* ▨ = mean far abundance of *L. carponotatus,* ▨ = mean far abundance of *P. maculatus*. .

Table 13a. Abundance of live coral cover from the Keppel Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	90.37	2	45.19	0.26	0.79
Island (zone)	970.22	5	194.04	1.12	0.42
Site (island x zone)	1452.73	9	161.41	8.77	>0.01*
Error	1749.13	95	18.41		

Table 13b. Abundance of live coral cover from the Palm Islands. (*) indicate a significant result.

Source of Variation	SS	DF	MS	F	p
Zone	47.64	2	23.82	1.74	0.36
Island (zone)	64.08	4	16.02	0.5	0.74
Site (island x zone)	224.81	7	32.12	6.11	>0.01*
Error	220.75	42	5.26		

3.5. Discussion

Well established and enforced MPAs should increase the abundance, size, biomass and reproductive output of targeted fish within their boundaries (Russ 2002; Halpern & Warner 2002). However, if MPAs are to contribute to sustainable harvesting, there must be a net migration of individuals of exploited fish species to areas outside of the MPA boundaries. To date, studies of adult spillover have found that the distance travelled by the migrating fish only occurs over a couple of hundred meters (Russ & Alcala 96; Russ *et al.* 2003; 2004; Abesamis *et al.* 2006b). Spillover at this small spatial scale would primarily benefit local communities in a position to "fish the boundary". Here I looked for evidence that adult spillover could occur on a larger spatial scale of kilometres rather than meters. If adult spillover does not expand past 200m, larval migration would seem to be the only possible means by which MPAs can benefit the broader areas open to fishing. I also looked for evidence, based on densities of 0+ yr fish, that no-take MPAs may augment recruitment near their boundaries.

This study did not demonstrate that MPAs within the Keppel and Palm Island regions provide the anticipated external benefits for local fisheries. In fact, evidence for an increase in adult densities inside MPAs was not observed either. If spillover was taking place, abundance and biomass of *P. maculatus* and *L. carponotatus* should have been higher adjacent to MPAs, compared with sites over 5km away, which was not the case. There was no indication of either adult spillover or recruitment subsidies at this scale. MPA status had no significant effect on the recruit abundance (both cohorts) of either *P. maculatus* or *L. carponotatus* from both locations.

Although similar levels of abundance in *Plectropomus* species and *L. carponotatus* between open and closed sites have been observed along the GBR previously (Zeller & Russ 1998, Evans & Russ 2004), the majority of literature concerning these fish suggests significant differences between these two zones (Craik 1981, Evans & Russ 2004, Nardi *et al.* 2004, Williamson *et al.* 2004, Begg *et al.* 2005; Russ *et al.,* 2008). The results from this study agree with the former observation, whereby no significant difference in abundance of *P. maculatus* or *L. carponotatus* occurred regardless of fishing protection or location. Despite previous studies reporting a significant gradient decline in target fish abundance with increasing distance from a MPA in the Philippines (Russ & Alcala 1996; Abesamis & Russ 2005; Abesamis *et al*., 2006a); this was not the case in this study. Only *P. maculatus* from the Keppel Island location showed a decline in abundance with increasing distance from the MPAs, but because of high site variation, no significant difference between treatments was observed.

Abundance observations alone are inefficient in determining whether or not MPAs are working. High fishing pressure may reduce the number of large fish to the extent that juvenile fish no longer need to compete for space and, therefore become more plentiful (Roberts & Polunin 1991; 1992). Hence, decreasing biomass with increasing distance is also used as an indicator of spillover. This trend was recorded around Apo Island in the Philippines where biomass of *Naso vlamingii* was 40 times greater close to (200m), but not far from (250 – 500m) the boundary of the MPA over an 18 year period (Russ *et al.* 2003). The CPUE of additional target fish was also reported to be significantly greater close to the boundary of the MPA off Apo Island compared to far from it (Russ *et al*. 2003; 2004; Abesamis *et al.* 06a), while the total wet mass of trap

catch also declined as a function of distance from the Mombasa MPA, Kenya (McClanahan & Mangi 2000). With the exception of one case, the results from this study showed no evidence of fish biomass decreasing with increasing distance from MPAs. This gradient was not significant, and as biomass was estimated from length and abundance, it can be attributed to the abundance gradient also recorded.

In 2004, the RAP applied protective status to numerous locations along the GBR, and increased marine national park coverage to about 33%. A number of these newly protected sites were situated within the Keppel and Palm Island locations, and were subsequently used during this study. However, the protective efficacy of a MPA has been linked to the length of protective status. Russ *et al.* (1995) observed no significant difference in mean size of coral trout between protected and fished zones, despite six years of protection. In Western Australia, no significant difference in the abundance of *P. leopardus* was observed after three years of protection from fishing. However, after a further five years, the abundance within closed zones had increased by up to 15 times that of open zones (Nardi *et al*, 2004). Paddack & Estes (2000) compared the sizes of six species of rockfish (*Sebastes* spp.) between three MPAs and nearby fished sites off the coast of California over three years. Point Lobos State Reserve was designated a MPA in 1963, Hopkins Marine Life Refuge was founded in 1984 and Big Creek Marine Ecological Reserve was established the same year of their investigation (1994). Therefore, Point Lobos State Reserve had been established for 21 years, and Hopkins Marine Life Refuge 10 years prior to the study. In comparison, Big Creek Marine Ecological Reserve had only been founded the same year the study commenced. All six species of rockfish were significantly larger within Hopkins Marine Life Refuge and

Point Lobos State Reserve over the three year study. In contrast, the same species of fish showed no variation in size between Big Creek Marine Ecological Reserve and nearby fished sites (Paddack & Estes 2000). Therefore, including recently introduced MPAs as study sites may explain the large variation observed between sites. Three years of protection from fishing may not have been adequate to noticeably affect the abundance and biomass of reef fish within the boundaries of the MPA.

Based on a density-dependent theory of spillover (Abesamis & Russ 2005), recently established MPAs where initial fishing pressure was not extremely high, would fail to increase the adult stock, thereby reducing the possibility of spillover to adjacent fished reefs. In addition, as the majority of reef fish are relatively sedentary (Zeller & Russ 1998; Cole *et al.,* 2000; Zeller *et al.,* 2003), the spatial scale set for nearby fished sites may have been too great to observe spillover.

Concern should lie not just in the spawning stock, or "source" of recruits, but in the sites (or sinks) that they settle (Roberts 1995; Crowder *et al.* 2000; Murawski *et al.* 2000). Large variations in fish abundance can be due to large inconsistencies in recruitment (Doherty 1991). Protection of settling larvae would increase recruitment to species populations that have been deemed recruitment limited, and reduce chances of stock collapse. Survival of haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) recruits improved when MPAs were designed based on patterns of spawning sites and juvenile incidence in New England. Before these MPAs were introduced, seasonal closed areas were having little effect on fish stocks (Murawski *et al.* 2000).

So far the published evidence for recruitment subsidies is contradictory. Nardi *et al.* (unpub. man.) showed the abundance of *P. leopardus* recruits to be greater within

MPAs compared to fished sites around the Abrolhos Islands, Western Australia. In contrast, *Stegastes partitus* recruit abundance around St. Lucia, Caribbean, were significantly greater in the fished site compared to the MPA (Valles *et al.* 2001). The former study suggests recruitment is localised while the latter implies recruits disperse.

The results from this study suggest that MPAs had no effect on recruit distribution of *P. maculatus* and *L. carponotatus*. However, there are a number of reasons as to why a recruitment subsidy may have been present, but not detected. Firstly, if the MPA has not been established long enough, no increase in spawning stock would occur, and hence no increase in the production of larvae. Secondly, natural paucity of recruitment may have been responsible for the low number of recruits observed within this study. Lastly, inadequate knowledge of dispersal distances of *P. maculatus* and *L. carponotatus* larvae, as well as the large cover of MPA networks now present on the GBR, made selecting appropriate distant fished sample sites difficult and possibly erroneous.

Increased larval production within MPAs creates "sources" of potential new recruits. Future studies on recruitment subsidies need a greater understanding of the settlement sites, or "sinks", of the species involved. Mass chemical tagging of larvae, as well as DNA genotyping can provide background on the connectivity between these "sources" and "sinks". Large (100 – 200m), fixed transects within these "sinks" should provide adequate sampling of recruitment. Comparisons of recruit density between MPAs and "sinks" over a number of years would provide estimates of recruitment subsidy and their temporal variability.

Data collection on a temporal scale is important as it removes any suggestion that the results obtained were already present before the establishment of the MPA. To

unequivocally determine whether MPAs enhance fish populations outside of their boundaries requires a BACI sampling design (Russ 2002). This requires collection of data in MPAs and fished sites, before and after protection from fishing is established. Due to the lack of availability of new MPAs, only one study has attempted to use the BACI design (Russ *et al.,* 2008). However, for a successful BACI design, sampling needs to occur over a longer period of time than Russ *et al.,* (2008) carried out.

This study provides an insight into the supposed benefits MPA have on targeted coral reef fish. In particular, a much needed account on the empirical findings of fish recruitment in relation to MPAs is presented. Comparisons between zones were over-shadowed by large site variation in each assessment. Hence, no significant differences were found for *P. maculatus* and *L. carponotatus* in any of the treatments.

Though no study to date has been able to unequivocally state whether or not spillover occurs, by factoring in distant fished sites as a control, comparisons between zones were more acceptable. Ideally, a BACI design would have been applied, but no new MPAs were being established at the time of sampling. Clearly, the natural annual variability in recruitment requires observations based over a temporal scale, rather than the "snap-shot" experienced in this study. Nevertheless, for marine parks to be fully accepted into the fishing community as a justifiable means of management, benefits need to transpire on a regular basis. Understanding connectivity between sources and sinks will help establish if spillover and recruitment subsidies occur.

4.0. Conclusion

Marine fisheries management is a complex and evolving process that increasingly relies on multiple strategies to sustain multi-species harvests. Marine protected areas (MPAs) are one tool available to fisheries managers. MPAs prohibit fishing within a locale in order to protect spawning stock, whilst also providing fisheries independent data and acting as a buffer against unexpected outcomes. In addition, spillover of adults and larvae from the MPA boundary could augment nearby fished populations. Attempts to show adult spillover by comparing abundance or biomass between MPAs and adjacent fished areas, though plentiful, do not include a control site (i.e. a site that is not affected by the MPA study site). The two studies that have investigated recruitment in relation to MPAs also used this inappropriate sampling design. These studies can not truly assess the potential benefits of MPAs. Evaluating spillover requires quantative assessment of adult and recruit densities inside the MPAs, nearby the MPAs and at fished sites sufficiently distant from the MPAs so as not to receive any benefits. This study provides information on the early life history of two recreationally important finfish species (*P. maculatus* and *L. carponotatus*), specifically when they are first perceptible on the reef. In addition, the abundance and biomass of adults and recruits from the Keppel and Palm Island regions were compared between three treatments: (1) within MPAs; (2) nearby fished areas and (3) distant fished areas.

Correctly identifying larvae in situ is near impossible. Hence, establishing the size recruits are first observed on the reef is important for evaluating evidence of recruitment subsidies. Results from this study show *P. maculatus* and *L. carponotatus* are first

observed on the reef at 60mm FL (63 days old) and 49mm FL (66 days old) respectively. Recruit size reached 217mm FL (253 days old) for *P. maculatus* and 162mm FL (285 days old) for *L. carponotatus* because of older 0+ age cohorts. PLD estimates of *P. maculatus* and *L. carponotatus* were 28.6 days and 33.6 days respectively. Therefore after settlement, the recruits were hiding amongst the coral for around one month (~ 33 – 35 days). Based on this evidence, recruitment surveys two months after spawning is observed would be satisfactory. However, in order to include older 0+ age cohorts, recruitment surveys would optimally take place approximately 160 days after initial spawning.

MPAs are expected to increase the abundance and biomass of target fish within their boundaries. This was not the case for either species from the Keppel and Palm Island regions, where no difference in abundance or biomass between MPAs and fished sites was observed. This result was unexpected, given that previous studies have reported significantly greater abundance and biomass of *Plectropomus* species and *L. carponotatus* within MPAs from the same localities (Evans & Russ 2004; Williamson *et al.,* 2004; Russ *et al.,* 2008). It is possible that sites located within RAP established MPAs may not have been protected long enough for benefits to become apparent, therefore confounding the results.

Greater abundance and biomass with increasing proximity to the MPA boundary are putative indicators of adult spillover (Russ *et al*., 2003; 2004; Abesamis & Russ 2005; Abesamis *et al.,* 2006a; 2006b). In this study, large variation between sites accounted for the majority of differences between treatments. Therefore, no difference in abundance or

biomass of *P. maculatus* or *L. carponotatus* between MPAs, nearby fished sites and distant fished sites was found.

As with abundance and biomass within MPAs, spillover of adult fish is unlikely to occur if the MPA has not been established long enough. In addition, the migration of adult fish from protected to unprotected sites is largely dependent on their mobility. The majority of fish are relatively sessile organisms; rarely moving outside a home range of 200m (Zeller & Russ 1998; Cole *et al.,* 2000; Zeller *et al.,* 2003). In this study, the distance between protected and fished sites was greater than the average home range of most coral reef fish. Consequently, although spillover may have been occurring, it may not have reached nearby fished sites.

This study did not find any difference in recruit density between the three treatments. The lack of support for recruitment subsidies may have been due to undeveloped MPAs and low recruit numbers, but it is most likely that insufficient knowledge of settlement sites was a key factor. The paucity of available evidence regarding recruitment and MPAs does little to answer the question; are MPA larvae augmenting nearby fished areas, with only one study providing evidence for recruitment spillover (Valles *et al.,* 2001), while another provides evidence for local retention (Nardi *et al.,* unpub. man.).

Establishing the levels of connectivity between MPA networks is imperative for establishing efficient networks of MPAs. Information on spawning and settlement locations are vital for efficient placement of MPAs. Chemical tagging of larvae can provide estimates of self-recruitment (Jones *et al.* 1999; 2005; Almany *et al.,* 2007), but do not provide details of the larvae that are unaccounted for. Do they disperse and settle

in other locations or are they lost to high levels of larval mortality? DNA genotyping of reef finfish could be used to track genetic migration in reef fish. However, care must be taken not to assume that genetic variation is only due to dispersal of genes. Random mutation, as well as selective variation from fisheries, may influence the genetic structure of a population (Mora & Sale 2002).

Although no significant differences in any of the three treatments were found, this study does provide preliminary findings on the size of early recruits as well as the optimum time for recruit surveys. Future investigations into recruitment subsidies should use mass chemical tagging of larvae, in conjunction with DNA genotyping, to acquire a greater understanding of sources and sinks. Once an appropriate spatial scale is determined, periodic surveys of permanent transects within these sources and sinks will provide estimates of MPA based recruitment subsidies.

5.0. Bibliography

Abesamis, R. A., and G. R. Russ. 2005. Density-dependent spillover from a MPA: long-term evidence. Ecological Applications **15**: 1798 – 1812.

Abesamis, R. A., A. C. Alcala, and G. R. Russ. 2006a. How much does the fishery at Apo Island benefit from spillover of adult fish from the adjacent marine reserve? Fisheries Bulletin **104**: 360-375.

Abesamis, R. A., G. R. Russ, and A. C. Alcala. 2006b. Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. Aquatic Conservation: Marine and Freshwater Ecosystems **16**: 349 – 371.

Almany, G. R., M. L. Berumen, S. R. Thorrold, S. Planes, and G. P. Jones. 2007. Local replenishment of coral reef fish populations in a marine reserve. Science **316**: 742 – 744.

Begg, G. A., B. D. Mapstone, A. J. Williams, S. Adams, C. R. Davies, and D. C. Lou. 2005. Multivariate life-history indices of exploited coral reef fish populations used to measure the performance of no-take zones in a marine protected area. Canadian Journal of Fisheries and Aquatic Sciences **62**: 679-692.

Booth, D. J. and G. A. Beretta. 1994. Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. Coral Reefs **13**: 81 – 89.

Cappo, M., P. Eden, S. J. Newman, and S. Robertson. 2000. A new approach of validation of periodicity and timing of opaque zone formation in the otoliths of eleven species of Lutjanus from the central Great Barrier Reef. Fishery Bulletin **98**: 474 - 488.

Claro, R., and K. C. Lindeman. 2003. Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. Gulf Caribbean Research **14**: 91 – 106.

Cole, R. G., E. Villouta, and R. J. Davidson. 2000. Direct evidence of limited dispersal of the reef fish *Parapercis colias* (Pinguipedidae) within a marine reserve and adjacent fished areas. Aquatic Conservation: Marine and Freshwater Ecosystems **10**: 421 – 436.

Cowen, R. K. 2002. Larval dispersal and retention and consequences for population connectivity. In: Coral reef fishes: dynamics and diversity in a complex ecosystem, Ed. P. F. Sale, pp. 149 – 170. San Diego, USA: Academic Press.

Cowen, R. K., J. A. Hare, and M. P. Fahay. 1993. Beyond hydrography – can physical processes explain larval fish assemblages within the middle Atlantic Bight? Bulletin of Marine Science **53**: 567-587.

Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. Science **311**: 522 – 527.

Craik, G. J. S. 1981. Underwater survey of coral trout *Plectropomus leopardus*, (Serranidae) populations in the Capricornia section of the Great Barrier Reef Marine Park. In: Proceedings of the 4th International Coral Reef Symposium, Vol. 1, pp 53 – 58.

Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting MPAs. Bulletin of Marine Science **66**: 799-820.

Doherty, P. J. 1991. Spatial and temporal patterns in recruitment. In: The ecology of fishes on coral reefs, Ed. P. F. Sale, pp 601 – 635. San Diego, USA: Academic Press.

Doherty, P. J., A. J. Fowler, M. A. Samoilys, and D. A. Harris. 1994. Monitoring the replenishment of coral trout (Pisces: Serranidae) populations. Bulletin of Marine Science **54**: 343 – 355.

Domeier, M. L. 2004. A potential larval recruitment pathway originating from a Florida marine protected area. Fisheries Oceanography **13**: 287 – 294.

Domeier, M. L., and P. L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. Bulletin of Marine Science **60**: 698 – 726.

Evans, R. D., and G. R. Russ. 2004. Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef, Australia. Aquatic Conservation: Marine and Freshwater Ecosystems **14**: 505-519.

Evans, R. D., G. R. Russ, and J. P. Kritzer. 2007. Batch fecundity of *Lutjanus carponotatus* (Lutjanidae) and implications of no-take marine reserves in the Great Barrier Reef, Australia. Coral Reefs **27**: 179 – 189.

Ferreira, B. P. 1993. Reproduction of the inshore coral trout *Plectropomus maculatus* (Perciformes: Serranidae) from the Central Great Barrier Reef, Australia. Journal of Fish Biology **42**: 831 – 844.

Ferreira, B. P. 1995. Reproduction of the common coral trout *Plectropomus leopardus* (Serranidae: Epinephelinae) from the central and northern Great Barrier Reef, Australia. Bulletin of Marine Science **56**: 653 – 669.

Ferreira, B. P., and G. R. Russ. 1992. Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces: Serranidae) from the Central Great Barrier Reef, Australia. Australian Journal of Marine and Freshwater Research **43**: 1391 – 1312.

Ferreira, B. P., and G. R. Russ. 1994. Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus*, (Lacepede 1802) from Lizard Island, Northern Great Barrier Reef. Fishery Bulletin **92**: 46 – 57.

Ferreira, B. P., and G. R. Russ. 1995. Population structure of the leopard coral grouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia. Fishery Bulletin **93**: 629 – 642.

Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly Cod-dominated ecosystem. Science **308**: 1621 – 1623.

Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of MPAs. Trends in Ecology and Evolution **18**: 448 – 455.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. 2003. Environmental Conservation **30**: 200 – 208.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5**: 361 – 366.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications **13**: S117 – S137.

Halpern, B. S., S. D. Gaines, and R. R. Warner. 2004. Confounding effects of the export of production and the displacement of fishing effort from marine reserves. Ecological Applications **14**: 1248 – 1256.

Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution **23**: 202 – 210.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourgue, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293**: 629 – 638.

Jennings, S. 2000. Patterns and prediction of population recovery in marine reserves. Reviews in Fish Biology and Fisheries **10**: 209-231.

Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. Nature **402**: 802 – 804.

Jones, G. P., S. Planes, and S. R. Thorrold. 2005. Coral reef fish larvae settle close to home. Current Biology **15**: 1314 – 1318.

Kaufman, L., J. Ebersole, J. Beets, and C. C. McIvor. 1992. A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. Environmental Biology of Fishes **34**: 109 – 118.

Kritzer, J. P. 2002. Variation in the population biology of stripey bass *Lutjanus carponotatus* within and between two island groups on the Great Barrier Reef. Marine Ecology Progress Series **243**: 191 – 207.

Kritzer, J. P. 2004. Sex-specific growth and mortality, spawning season, and female maturation of the stripey bass (*Lutjanus carponotatus*) on the Great Barrier Reef. Fishery Bulletin **102**: 94 – 107.

Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through MPAs. Ecological Applications **8**: S72-S78.

Leis, J.M., and B. M. Carson-Ewart. 1997. In situ swimming speeds of the late larvae of some Indo-Pacific coral reef fishes. Marine Ecology Progress Series **159**: 165-174.

McClanahan, T. R., and S. Mangi. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecological Applications **10**: 1792-1805.

McClanahan, T. R., and R. Arthur. 2001. The effect of marine reserves and habitat on populations of East African coral reef fishes. Ecological Applications **11**: 559 – 569.

Macpherson, E. 1998. Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. Journal of Experimental Marine Biology and Ecology **220**: 127 – 150.

Meekan, M. G, M. J. Milicich, and P. J. Doherty. 1993. Larval production drives temporal patterns of larval supply and recruitment of a coral reef damselfish. Marine Ecology Progress Series **93**: 217 – 225.

Meekan, M. G., L. Vigliola, A. Hansen, P. J. Doherty, A. Halford, and J. H. Carleton. 2006. Bigger is better: size-selective mortality throughout the life history of a fast-growing clupeid, *Spratelloides gracilis*. Marine Ecology Progress Series **317**: 237 – 244.

Mora, C., and P. F. Sale. 2002. Are populations of coral reef fish open or closed? Trends in Ecology and Evolution **17**: 422 – 428.

Moran, M., J. Jenke, C. Burton, and D. Clarke. 1988. The Western Australian trap and line fishery on the Northwest Shelf. Western Australia Marine Research Laboratories. FIRTA. Project 86/28, Final report. 79 pp.

Murawski, S. A., R. Brown, H. –L. Lai, P. J. Rago, and L. Hendrickson. 2000. Large-scale closed areas as a fishery management tool in temperate marine systems: the Georges Bank experience. Bulletin of Marine Science **66**: 775-798.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature **423**: 280 – 283.

Nardi, K., G. P. Jones, M. J. Moran, and Y. W. Cheng. 2004. Contrasting effects of marine protected areas on the abundance of two exploited reef fishes at the sub-tropical Houtman Abrolhos Islands, Western Australia. Environmental Conservation **31**: 160-168.

Newman, S. J., D. McB. Williams, and G. R. Russ. 1996. Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the Central Great Barrier Reef, Australia. Marine and Freshwater Research **47**: 575 – 584.

Newman, S. J., M. Cappo, and D. McB. Williams. 2000a. Age, growth, mortality rates and corresponding yield estimates using otoliths of the tropical red snappers, *Lutjanus erythropterus*, *L. malabaricus* and *L. sebae*, from the central Great Barrier Reef. Fisheries Research **48**: 1 – 14.

Newman, S. J., M. Cappo, and D. McB. Williams. 2000b. Age, growth and mortality of the stripey, *Lutjanus carponotatus* (Richardson) and the brown-stripe snapper, *L. vitta* (Quoy and Gaimard) from the central Great Barrier Reef, Australia. Fisheries Research **48**: 263 – 275.

Paddack, M. J., and J. A. Estes. 2000. Kelp forest fish populations in MPAs and adjacent exploited areas of Central California. Ecological Applications **10**: 855 – 870.

Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumalila, C. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. Nature **418**: 689 – 695.

Pears, R. J., J. H. Choat, B. D. Mapstone, and G. A. Begg. 2006. Demography of a large grouper, *Epinephelus fuscoguttatus*, from Australia's Great Barrier Reef: implications for fishery management. Marine Ecology Progress Series **307**: 259 – 272.

Pet, J. S., P. J. Mous, A. H. Muljadi, Y. J. Sadovy, and L. Squire. 2005. Aggregations of *Plectropomus areolatus* and *Epinephelus fuscoguttatus* (groupers, Serranidae) in the Komodo National Park, Indonesia: monitoring and implications for management. Environmental Biology of Fishes **74**: 209 – 218.

Rakitan, A., and D. L. Kramer. 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. Marine Ecology Progress Series **131**: 97 – 113.

Rhodes, K. L., and M. H. Tupper. 2008. The vulnerability of reproductively active squaretail coral grouper (*Plectropomus areolatus*) to fishing. Fishery Bulletin **106**: 194 – 203.

Roberts, C. M. 1995. Rapid build-up of fish biomass in a Caribbean MPA. Conservation Biology **9**: 815-826.

Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. Science **278**: 1454 – 1457.

Roberts, C. M., and N. V. C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries **1**: 65 – 91.

Roberts, C. M., and N. V. C. Polunin. 1992. Effects of the marine reserve protection on northern Red Sea fish populations. In: Proceedings of the Seventh International Coral Reef Symposium, Vol. 2, pp. 969 – 977.

Russ, G. R. 2002. Yet another review of marine reserves as reef fisheries management tools. In: Coral reef fishes: dynamics and diversity in a complex ecosystem, Ed. P. F. Sale, pp. 421-443. San Diego, USA: Academic Press.

Russ, G. R., and A. C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series **132**: 1-9.

Russ, G. R., D. C. Lou, and B. F. Ferreira. 1995. A long-term study on population structure of coral trout on reefs open and closed to fishing in the central Great Barrier Reef. Technical Report 3, CRC Reef Research Centre, Townsville, Queensland, Australia: 30pp.

Russ, G. R., A. C. Alcala, and A. P. Maypa. 2003. Spillover from marine reserves: the case of *Naso vlamingii* at Apo Island, the Philippines. Marine Ecology Progress Series **264**: 15 – 20.

Russ, G. R., A. C. Alcala, A. P. Maypa, H. P. Calumpong, and A. T. White. 2004. Marine reserve benefits local fishery. Ecological Applications **14**: 597 – 606.

Russ, G. R., A. J. Cheal, A. M. Dolman, M. J. Emslie, R. D. Evans, I. Miller, H. Sweatman, and D. H. Williamson. 2008. Rapid increase in fish numbers follows creation of world's largest marine reserve network. Current Biology **18**: R514 – R515.

Sadovy, Y. J., and A. C. J. Vincent. 2002. Ecological issues and the trades in live reef fishes. In: Coral reef fishes: dynamics and diversity in a complex ecosystem, Ed. P. F. Sale, pp. 391 - 420. San Diego, USA: Academic Press.

Sale, P. F., R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution **20**: 74 – 80.

Samoilys, M. A. 1997. Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) on the northern Great Barrier Reef. Marine Ecology Progress Series **160**: 149 – 159.

Sonnenholzner, J. I., L. B. Ladah, and K. D. Lafferty. 2007. Cascading effects of fishing on Galapagos rocky reef communities. Marine Ecology Progress Series **343**: 77 – 85.

Sponaugle, S., and R. K. Cowen. 1996a. Nearshore patterns of larval supply to Barbados, West Indies. Marine Ecology Progress Series **133**: 13 – 28.

Sponaugle, S., and R. K. Cowen. 1996b. Larval supply and patterns of recruitment for two Caribbean fishes, *Stegastes partitus* and *Acanthurus bahianus*. Marine and Freshwater Research **47**: 433 – 447.

Sponaugle, S., and R. K. Cowen. 1997. Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). Ecological Monographs **67**: 177 – 202.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology: an Annual Review **19**: 513 – 605.

Valles, H., S. Sponaugle, and H. A. Oxenford. 2001. Larval supply to a marine reserve and adjacent fished area in the Soufrière Marine Management Area, St. Lucia, West Indies. Journal of Fish Biology **59**: S152-S177.

Victor, B.C. 1986. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Marine Biology **90**: 317 – 326.

Williams, D. McB., and G. R. Russ. 1991. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef. Report to the Great Barrier Reef Marine Park Authority, Townsville, Queensland.

Williams, D. McB., and G. R. Russ. 1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef, Vol. 1. Great Barrier Reef Marine Park Authority Research Publication No. 33, 106pp.

Williamson, D. H., G. R. Russ, and A. M. Ayling. 2004. No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. Environmental Conservation **3**: 149-159.

Willis, T. J., R. B. Millar, and R. C. Babcock. 2003a. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in Northern New Zealand marine reserves. Journal of Applied Ecology **40**: 214 – 227.

Willis, T. J., R. B. Millar, R. C. Babcock, and N. Tolimieri. 2003b. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? Environmental Conservation **30**: 97 – 103.

Wilson, D. T., and M. I. McCormick. 1997. Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. Marine Ecology Progress Series **153**: 259 – 271.

Wilson, D. T., and M. I. McCormick. 1999. Microstructure of settlement-marks in the otoliths of tropical reef fishes. Marine Biology **134**: 29 – 41.

Wood L.J., L. Fish, J. Laughren, and D. Pauly. 2008 Assessing progress towards global marine protection targets: shortfalls in information and action. Oryx **42**: 340-351.

Zapata, F. A., and P. A. Herrón. 2002. Pelagic larval duration and geographic distribution of tropical eastern Pacific snappers (Pisces: Lutjanidae). Marine Ecology Progress Series **230**: 295 – 300.

Zeller, D. C. 1998. Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. Marine Ecology Progress Series **162**: 253 – 263.

Zeller, D. C., and G. R. Russ. 1998. Marine reserves: patterns of adult movement of coral trout (*Plectropomus leopardus* (Serranidae)). Canadian Journal of Fishery and Aquatic Science **55**: 917 – 924.

Zeller, D. C., S. L. Stoute, and G. R. Russ. 2003. Movements of reef fishes across marine reserve boundaries: effects of manipulating a density gradient. Marine Ecology Progress Series **254**: 269 – 280.