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The Relative Roles of Recruitment and Post-recruitment Processes in the Regulation of a Coral Reef Damselfish Population.

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A thesis submitted for the degree of Doctor of Philosophy

in the Department of Marine Biology

James Cook University of North Queensland

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This thesis is dedicated to the memories of

my great uncle William Beukers

and my grandfather Ernest Beukers.

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Abstract

Assessing the processes by which populations are regulated is one of the most important goals in ecology. The local abundance of "open" marine populations may be regulated by recruitment and/or post-settlement mortality. These demographic rates could be influenced by varying levels of predation, competition and habitat structure, which may interact in complex ways. The relative importance of these factors in determining population size and structure has rarely been estimated. This thesis addresses this goal by focussing on the local dynamics of a coral reef fish *Pomacentrus moluccensis* at Lizard Island, northern Great Barrier Reef (GBR). Fundamental to this, was testing the impact of implant microtags on the growth and survivorship of *P. moluccensis*. These tags would enable the individual recognition required for mortality, migration and growth studies. Subsequently, the relative importance of recruitment, predation, habitat structure and their interactions in determining these patterns was investigated. These results were evaluated against generalisations emerging from studies on *P. moluccensis* at other locations on the GBR and other coral reef fishes.

The impact of two types of microtag on *P. moluccensis* were tested: Firstly, visible implant fluorescent (VIF) tags which provided an external marker and secondly, coded wire tags (CWT) which were not visible externally but provided individual codes. Retention rates for both microtags in new recruits of this species (10-20mm SL) were high (100%). In addition, there was no significant difference in either growth or survivorship between fish with or without microtags.

The basic life history traits and dynamics of *P. moluccensis* were assessed. Ageing *P. moluccensis* at Lizard Island by otolith increments was validated by inducing both tetracycline and stress markers on the otolith at a known time. Age and size structures varied among locations but growth rates were relatively uniform. Longevities at three sites at Lizard Island were found to be fairly similar with very few fish living longer than 6 years. This represents an extreme contrast to southern reefs where approximately 10% of individuals reached 18 years. This greatly reduced longevity at Lizard Island suggested that these populations turn over rapidly and are

more likely to be recruitment limited.

Patterns of adult and new recruit abundance were variable between sites over time at both local (transects meters to tens of meters apart) and broad (sites hundreds of meters to a few kilometers apart) scales. Recruitment to Lizard Island was up to an order of magnitude higher than recruitment recorded to the southern GBR. In contrast to the implications of reduced longevities at Lizard Island, higher recruitment is more likely to result in populations which are limited by post-settlement processes. Which would prevail?

There was evidence of variable density-dependent mortality at two spatial scales. There was no relationship between adults and new recruits in transects at four local scale sites which suggests that at this level there may be factors other than density which were also important. However, there was a significant curvilinear relationship between adult densities and new recruit densities at nine broad scale sites implying density dependence at this scale. In addition, densities of several cohorts which were widely differing in year 1 showed convergence in the following year. These results suggested that post-settlement mortality was capable of altering initial patterns laid down at recruitment.

The patterns of distribution of new recruits of *P. moluccensis* were used to assess the microhabitats with which they were most commonly associated. This species was highly associated with caespitose and corymbose acroporids, and also pocilloporid corals, but all other microhabitats were used less than would be predicted. The coral species with which *P. moluccensis* was highly associated, all show a highly complex internal structure. Could this attribute account for the observed patterns? A manipulative experiment was performed to test the effects of the peripheral branching structure of one of these coral species on the growth and survivorship of tagged *P. moluccensis*. Mortality rates were very high at all six sites around Lizard Island (67 - 93%). However, there was no significant difference in either growth or survivorship of fish between manipulated and unmanipulated coral heads.

There was significant spatial variation in predator abundance among nine sites at Lizard Island. These predator densities correlated strongly with densities of new recruits suggesting a predator aggregative effect. Predation pressure was assayed by capturing newly settled individuals and then releasing them at the same nine sites. The majority of consumed individuals were taken by either *Pseudochromis fuscus* (Pseudochromidae) or *Thalassoma lunare* (Labridae). Small cephalopholids also took a relatively high proportion which was surprising because these species often hide or are subdued in the presence of a diver. Released new recruits selected the same coral species with which the unmanipulated individuals mentioned previously were highly associated. Mortality rates varied considerably according to microhabitat with lowest mortalities from the highly selected microhabitats. There was also significant variation in the percentage cover of these microhabitats between the nine sites, suggesting that microhabitat availability could influence local survivorship patterns. Other fishes behaving aggressively towards the released new recruits of *P. moluccensis*, did not appear to be important in determining their mortality.

Patterns of mortality appeared to be a complex interaction between recruitment, predator densities and the availability of preferred coral. Two further experiments were performed to examine these interactions. The first tested the effects of microhabitat on the behaviour of three predator species and assessed their ability to catch *P. moluccensis* new recruits in aquaria. The second tested the effects of resident predators and microhabitat on the survivorship of *P. moluccensis* on patch reefs. In both cases microhabitat modified the effects of predation. The predatory abilities of *Pseudochromis fuscus*, *Cephalopholis boenak* and *Thalassoma lunare* varied according to microhabitat. In addition, there was no difference in the survivorship of *P. moluccensis* between patch reefs with no resident predator and those consisting of high complexity corals with a resident predator. This suggested that high complexity corals may offer almost complete refuge from predation.

The factors regulating local populations of *P. moluccensis* at Lizard Island contrast with results from southern reefs where individuals were long lived and populations were found to be recruitment limited. Post-settlement processes at Lizard Island resulted in high mortality rates which varied with density and location. Both predator abundance and habitat structure were important in determining abundances of *P. moluccensis.* Hence, initial patterns of recruitment were modified by patterns of mortality to determine the size of the adult population. The difference between the northern and southern studies could be due to differences in either the scale or the locations. For example, the southern study considered processes occurring between reefs while this study looked at variation between and within sites on the same reef. Alternatively or in addition, traits specific to each location, such as the magnitude of recruitment, could be causing the differences observed. In conclusion, these results would suggest that single process theories of population regulation should be treated with caution, and instead attention should focus on the conditions which may lead to the dominance of any one process. This information would lead to the formation of universally applicable theories.

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CHAPTER 1

General Introduction

1.1 Introduction

Explaining the mechanisms by which populations are regulated is one of the fundamental aims of ecologists (Murdoch, 1994). The relative importance of density-dependent versus density-independent processes in the regulation of terrestrial populations has long been a source of debate (Haldane, 1953; Andrewartha and Birch, 1954; Varley et al., 1973; Hassell, 1985; Forrester, 1995). Early theories of population regulation were conceived with the assumption that populations were essentially "closed". In this context, early workers on insects concluded, that biotic processes which varied according to density had to be controlling populations through effects on mortality or reproduction (Nicholson, 1933). Without such regulation, it was argued on theoretical grounds, that they would eventually fluctuate to extinction (Haldane, 1953). The opposing school stressed the importance of extrinsic factors such as climate, which could maintain populations below carrying capacity (Bodenheimer, 1928; Uvarov, 1931). Smith (1935) introduced the terms density-dependent and independent to describe the action of alternative processes but this classification was subsequently rejected by those who considered that there had to be a component of density-dependence in every process (Andrewartha and Birch, 1960). However, the terminology remains, and more recently, it has been recognised that both density-dependent and independent processes could be important and variable between times, places and species (Huffaker and Messenger, 1964; MacArthur and Wilson, 1967).

Meanwhile, a similar debate about the regulation of marine populations was in progress in the fisheries literature (Hjort, 1926; Schmitt, 1930; Beverton and Holt, 1957; Slobodkin et al., 1967, Cushing and Harris, 1973). In 1914 the population, as opposed to the species, was established as the preferred unit of study (Heincke, 1889; Hjort, 1914). The two schools were split according to those who carried out theoretical versus descriptive studies (Sinclair, 1988). Theoretical ecologists emphasised the roles of processes such as predation and competition, particularly for food, and hence density-dependence (Riley, 1946; Ricker, 1954; Cushing, 1975; Lasker, 1978). The contrasting view was that regulation was due to density independent mortality during the larval stage (Sund, 1924; Carruthers et al., 1951; Iles, 1973; Sinclair et al., 1986).

Unlike many terrestrial populations, the majority of marine populations have a widely dispersing phase in their life histories followed by a more sedentary phase. As a consequence, the breeding output of the adult population does not determine the number of young individuals recruiting to the local population. In these "open" populations there is general agreement that the numbers of young joining the adults may limit that population and keep it below a level where density dependence would occur (Doherty, 1983; Hughes, 1984; Underwood and Denley, 1984; Roughgarden et al., 1985; Victor, 1986; Karlson and Levitan, 1989; Sinclair, 1991). This theory was of considerable interest for fisheries management because, if true, it would mean that stocks could easily be assessed by measuring patterns of recruitment (Gulland, 1982; Phillips, 1986; Doherty and Fowler, 1994). Whether or not recruitment has a major influence on the density or age structure of these open populations will depend on subsequent patterns of mortality in the adult environment (Warner and Hughes, 1988; Holm, 1990; Hughes,1990). Therefore, the role of recruitment cannot be assessed without also collecting information on mortality, but this has seldom been done.

In order for recruitment to be limiting, processes such as mortality and migration must remain relatively constant, both spatially and temporally, so that initial patterns of recruitment are not modified during the post-recruitment phase (Warner and Hughes, 1988; Doherty and Fowler, 1994). In addition the duration of the post-recruitment phase will be important for assessing the likely contribution of pre-and post-settlement events and for assessing reasonable time frames for studies into their effects. For example, short lived species may be regulated by different processes than long lived ones (Jones, 1991). It is more likely that patterns of abundance will match patterns of recruitment in a short lived rather than a long lived species.

Patterns of post-recruitment mortality may be influenced by various factors which make up the adult environment such as the numbers and species composition of predators and competitors, and also attributes of the habitat including resources such as the availability of food and shelter. Both predation and competition for a shared resource can influence populations (Paine, 1966; Hassell, 1978; Sih et al., 1985; Ross, 1986). They can do so directly by increasing mortality rates thus altering densities and age structures, and indirectly by altering growth or fecundity. Habitat structure may mediate the effects of these processes by providing individuals with refuges form predators and competitors. It may provide either total refuges where aggressors could not reach prey individuals or partial refuges which reduce encounter rates (Murdoch and Oaten, 1975; Christensen and Persson, 1993).

There have recently been several very comprehensive reviews which discussed the current literature on importance of recruitment, predation, competition and habitat structure in regulating coral reef fish populations (Jones, 1991; Doherty, 1991; Hixon, 1991). The relative roles of pre-settlement and post-settlement processes in shaping populations of coral reef fish has been a long lasting debate with very few conclusions being reached (Sale 1977,1978; Talbot et al., 1978; Anderson et al., 1981; Doherty 1983; Victor 1983; Ebersole 1985; Jones 1991). Most work has centred on the effects of either recruitment (recruitment limitation hypothesis) or competition (the competition hypothesis also called the resource limitation hypothesis). There has been relatively little attention directed towards predation (Hixon, 1991) or towards more pluralistic theories (Menge, 1991; Forrester, 1995).

Evidence for the recruitment limitation hypothesis has come from various sources. Firstly several studies have shown the mortality of new recruits was density independent (Connell, 1985; Harriott, 1985; Victor, 1986; Levin, 1994) which is consistent with this hypothesis. Secondly, patterns of adult and new recruit abundances have been found to correspond without any evidence of density dependence (Doherty and Williams, 1988; Doherty and Fowler, 1994). Thirdly, evidence of persistence of strong year classes has been used to demonstrate recruitment limitation but this scenario could also arise under density dependent regimes (Warner and Hughes, 1988). Negative results of studies looking for an influence of post-settlement processes (Robertson and Sheldon, 1979; Robertson et al., 1981; Sale et al., 1994) have also been used as evidence to back up this theory. However, there have been some studies which have shown that patterns of new recruit abundance have been subsequently modified (Shulman, 1985; Robertson, 1988; Jones, 1990; Forrester, 1990, 1995).

There have been very few studies on the mortality rates of coral reef fish, but these few show mortality to be highest during the early post-settlement stage (Aldenhoven, 1986; Victor, 1986; Eckert, 1987; Meekan, 1988; Sale and Ferrell, 1988). If predation is making a significant impact on abundance of populations of coral reef fish, this may be occurring in this time period. However, at present we do not even know which predator species are preying on a given prey species (Choat, 1982; Jones, 1991, Kingsford, 1992). The effects of predatory fish on the mortality rates of their prey have been well documented in other aquatic environments (Orth, 1977; Werner et al., 1983; Summerston and Peterson, 1984; Virnstein et al., 1984; Holbrook and Schmitt, 1988; Sih et al., 1992). In freshwater studies predator presence has been shown to decrease time feeding and there was also a decrease in growth rates (Feltmate and Williams, 1991; Tabor and Wurtsbaugh, 1991; Fraser and Giliam, 1992). If predation pressure were size specific then this decrease in growth rates could increase mortality due to predation (Mapstone and Fowler 1988; Doherty and Williams 1988).

While there is much correlative evidence showing several attributes of habitat, including structure may be important in determining adult densities (Luckhurst and Luckhurst, 1978; Thresher, 1983; Bell and Galzin, 1984; Roberts and Ormond, 1987; Sano et al., 1987) there has been little experimental work on these effects on coral reef fish. Several studies have shown that refuges may be limiting (Shulman, 1984; Hixon and Beets, 1989, 1993; Buchheim and Hixon, 1992). In addition, Shulman, (1985) showed that observed patterns in the distribution of juveniles were probably due to availability of shelter and encounter rates with predators. Other work has found the opposite to be the case (Robertson and Sheldon, 1979; Robertson et al., 1981).

The importance of each process must be evaluated against the magnitude of other processes. (Hairston et al., 1960; Menge and Sutherland, 1987; Power, 1992). Indeed, these processes may interact to determine the distribution and abundances of organisms (Keough, 1988; Mapstone and Fowler, 1988; Warner and Hughes, 1988; Forrester, 1995) and may vary temporally, spatially and according to the spatial scale of interest (Roberts and Ormond, 1987; Williams, 1991). This may lead to variability within a species both in terms of the factors regulating populations and life history characteristics. Therefore, what is most important is to determine the most important factors under a specific range of conditions. It is only with this kind of information that theories will be formed which are non trivial and will provide the basis of general predictions.

1.2 Natural history of *Pomacentrus moluccensis* (Bleeker), synonym *Pomacentrus popei*

Pomacentrus moluccensis, is an abundant damselfish which is widely distributed throughout the Indo-Pacific. Duration of the larval phase varies from 19.9 ± 1.66days ($\bar{x} \pm sd$) and standard length at settlement has been shown to be 10.7 ± 0.37mm ($\bar{x} \pm sd$) for this species at Palau in the Western Pacific (Wellington and Victor, 1989). This species has been shown to settle preferentially in live branched coral (Eckert, 1984; Sale et al., 1984) and the distribution of live corals has been shown to largely determine patterns in the distribution and abundance of recruit *P. moluccensis* at small scales (Sale et al., 1984). In addition, new recruits of *P. moluccensis* may use chemical cues to avoid coral heads where there are potential competitors (Sweatman, 1988). Adults of this species have also been found to occur only in areas of living coral (Mapstone, 1988; Sale et al., 1994). All these habitat studies were carried out at One Tree Island on the Great Barrier Reef (GBR), Australia. Mortality rates have also been gauged for *P. moluccensis* at One Tree island at 56% during the first post-recruitment year (Mapstone, 1988). Sale and Ferrell, (1988) found that on patch reefs in One Tree Lagoon this pomacentrid had a loss of 50% in the first two weeks, but thereafter survivorship was very high. At One Tree Reef, 10% of the population was estimated to be more than 18 years old (Mapstone, 1988). It has been shown that individuals of this species can be aged at One Tree Island in the southern GBR and John Brewer Reef in the central GBR using otolith increments (Fowler, 1990; Fowler and Doherty, 1992). This is contrary to findings for another pomacentrid, *Pomacentrus wardi*, in which ageing by otoliths was only possible at the southern-most of the two locations (Fowler and Doherty, 1992). Recently, Doherty and Fowler, (1994) have demonstrated that *P. moluccensis* is recruitment limited on patch reefs in the southern GBR. A nine year data set showed that adult density varied linearly with density of new recruits measured in April. They also reconstructed the age structure and compared it to known patterns of recruit abundance over the nine years. They observed persistence of large cohorts.

1.3 Thesis Synopsis

There were two main aims to this thesis. The first was to quantify life history traits, population dynamics, distribution and abundance of *P. moluccensis* at Lizard Island, in the northern GBR. The second aim was to investigate the relative contribution of patterns of recruitment, predation and habitat attributes in forming these characteristics of *P. moluccensis* populations. These results were then compared to those obtained for this species in other locations on the GBR.

In chapter two methods which were applicable to more than one chapter are discussed. The most important result of that chapter was the assessment of the most efficient transect size and number of replicates required per site to give a precision of 0.15.

Recognition of cohorts and individuals was needed for two reasons: Firstly an external marker was needed to enable recapture of individuals for otolith validation, and secondly to obtain reliable mortality estimates from recapture data. The most common method employed for coral reef fish is tagging. It has not previously been possible to tag very small individuals such as new recruits due to the small size of the fish and the relatively large tag size. A need was recognised to show empirical evidence that any method of tagging used did not affect attributes that were subsequently to be measured such as survivorship and growth rates. Chapter 3 validated the use of implant microtags and showed that there was negligible impact on growth and survivorship of new recruits.

The basic life history traits of *P. moluccensis* were investigated in chapter 4. As stated previously, ageing using otolith increments had already been validated for this species at two locations in the southern and central GBR. This study extended that range to include the northern GBR thus making this species ideal for latitudinal comparisons in demography and population regulation. Longevities were consistent between three sites at 6 years old contrasting with previous figures from southern reefs showing longevities of up to 18 years old. However, growth rates between latitudes were very similar.

Chapter 5 investigated population demographic variables, specifically recruitment and mortality and their relative importance in determining patterns in the distribution and abundance of adult *P. moluccensis*. There was a poor relationship between adults and new recruits along transects at four local scale sites. At a broader scale, adult and new recruit densities and percent mortality were all shown to be significantly variable between three zones, with three sites per zone. There were significant curvilinear relationships between adult and new recruit density, and between percent mortality and new recruit density at these nine sites. This showed density dependence at site level and suggested an important role of post-settlement processes at this scale. These processes were assessed further in the following chapters.

The habitat associations of *P. moluccensis* were assessed in chapter 6. New recruits of this species were highly associated with pocilloporids and some acroporids all of which have a complex structure. An experiment was performed to see if there was any effect of altering the structure in the peripheral branches of coral heads (these were readily manipulated) on growth and survivorship during the first reef associated year. All individuals in this experiment were tagged and mortality rates were surprisingly high. However, there was no effect of the manipulations on either growth or survivorship. The restricted distribution of this species implied an important influence of microhabitat but the exact attributes accounting for this distribution were elusive.

The role of predators and predator densities was investigated in chapter 7. Densities of predators were significantly different between sites and correlated very strongly with new recruit abundances. It is widely acknowledged that recruitment is highly spatially and temporally variable. The majority of these predators had recruited in previous years so it seemed unlikely that these patterns would be due to recruitment. There was, therefore, a strong implication that predators had aggregated where new recruit densities were high. An experiment was performed to assay predation pressure on *P. moluccensis* and an interaction between predation and habitat was suggested. Mortality rates from different microhabitats were very different with the lowest values being from those coral species with which *P. moluccensis* was found to be highly associated in chapter 6.

The hypothesis that both predator abundance and habitat structure could influence the distribution and abundance of *P. moluccensis* was tested in chapter 8. Two experiments were performed, the first to test the effects of three microhabitats of different complexity on the behaviour and predatory abilities of three predator species. The second tested the effects of resident predators and microhabitat complexity on the survivorship of *P. moluccensis* new recruits on patch reefs over a two month period. In both experiments microhabitat complexity modified the impact of the predators and *P. moluccensis* survivorship was significantly higher in the complex microhabitats.

The implications and conclusions from each chapter are considered in the General Discussion, chapter 9.

CHAPTER 2

General methods and techniques

2.1 Study site

Lizard Island, is located in the Cairns section of the Great Barrier Reef Marine Park, Queensland (14°40'S 145°27'E) . It lies approximately 30 km off the coast of Cape York from Lookout Point, and 17 km west of the outer barrier reef. It is surrounded by shallow fringing reefs with reef flats of 2m - 4m depth. It is connected to two smaller granite islands by reef which forms a protected lagoonal area of varying depths. This lagoon is mostly sand bottomed interspersed with patch reefs and some contiguous reef. Between March and November tradewinds blow from the south east. Over the summer period winds are mostly lighter and blow from the north west (Fig 1).

In chapters 4 and 5 comparisons are made with studies from two other locations on the Great Barrier Reef (GBR), the Capricorn Bunker group are seven reefs in the southern GBR and John Brewer Reef is in the central GBR (Fig 2). The Capricorn Bunker group are approximately 1200km south of Lizard Island.

2.2 Techniques for capturing fish

Fish had to be captured both for tagging (Chs 3 - 6) and for all experiments (Chs 6 - 8). *Pomacentrus moluccensis* were captured using a large polythene bag and fish anaesthetic. 20ml quinaldine was diluted with 500ml low grade ethanol in a trigger spray bottle. In the field fish were herded into their resident coral head and the large polyethylene bag placed over it ensuring that there were no gaps left open. Then the quinaldine was squirted directly at the fish until they were knocked unconscious and could be collected either by hand or in a net.

Predators also had to be caught for two experiments (Chs 7 & 8). They were collected in different ways according to species. *Cephalopholis boenak* and *Pseudochromis fuscus* were chased into a hole in the reef and then quinaldine was squirted into it while all exits from the hole were carefully scanned. The fish may be very drowsy on exiting the hole in which case it would be easily captured with a hand net or may exit rather more quickly in which case the whole procedure would be repeated again until it was collected or lost!

Thalassoma lunare were captured using a large polyethylene bag and a drawstring. The rope was wrapped over the entrance to the bag and threaded through a lead weight at the bottom. At least 5m of rope was left on each side with a diver holding it. coral rubble and sand was placed inside the bag and left to settle for 5 minutes. Then bait usually of pilchards was placed inside the bag. When a *T. lunare* entered the bag past the draw-string both divers pulled on the rope as quickly as possible to close the entrance.

2.3 Verification of optimum transect length for abundance data

2.3.1 Methods

Optimal transect size for *P. moluccensis* was assessed using transect lengths of 5, 10 and 15m. Each length was repeated ten times. Individuals of *P. moluccensis* were counted along each transect within a 1m width which was assessed using a measuring stick. This was carried out at two sites in the Lizard Island area, on the reef slopes of Palfrey Island and Turtle Bay. The following equation (sensu Pringle, 1984; Andrew and Mapstone, 1987) was used to calculate the sample size required to give a precision of 0.15.

$$n = \left(\frac{sd}{p \ x \ \bar{X}} \right)^2$$

Where

n = number of replicates

sd = standard deviation

x = mean

p = precision

The most efficient transect size was calculated from the following equation:

$$T = n \times t$$

Where

T = total time required for a precision of 0.15

n = number of replicates required for a precision of 0.15

t = time taken to complete one transect

2.3.2 Results and Conclusion

The results varied between sites. A precision of 0.15 was considered to be sufficient for assessing the abundance of *P. moluccensis.* At Palfrey Island the most efficient transect size was 10m and the required number of replicates was seven (Table 1). However, at Turtle Bay 5m transects were most efficient to give a precision of 0.15. It was decided to take the most conservative estimate which was transect size 10m. At Turtle Bay eleven transects were required to give a precision of 0.15 and so this being the largest was chosen. In all chapters twelve transects were used as the number of replicates to allow for possible variation at other sites.

Table 1 Calculations for the number of transects of each of three sizes required for a precision of 0.15 at two sites, and the efficiency of each transect size. Mean density and sd are the mean and standard deviation of the number of fish on 10 transects of the specified length.

	Palfrey			Turtle		
	5m	10m	15m	5m	10m	15m
mean density(m^2)	3.00	2.41	2.13	2.86	2.54	2.63
sd	2.03	0.93	0.81	1.27	1.22	1.46
n	20.35	6.62	6.39	8.74	10.24	13.82
real n	**21**	**7**	**7**	**9**	**11**	**14**
mean t (mins)	6.00	10.6	16.50	3.44	4.58	4.54
T	**127**	**75**	**116**	**31**	**51**	**64**

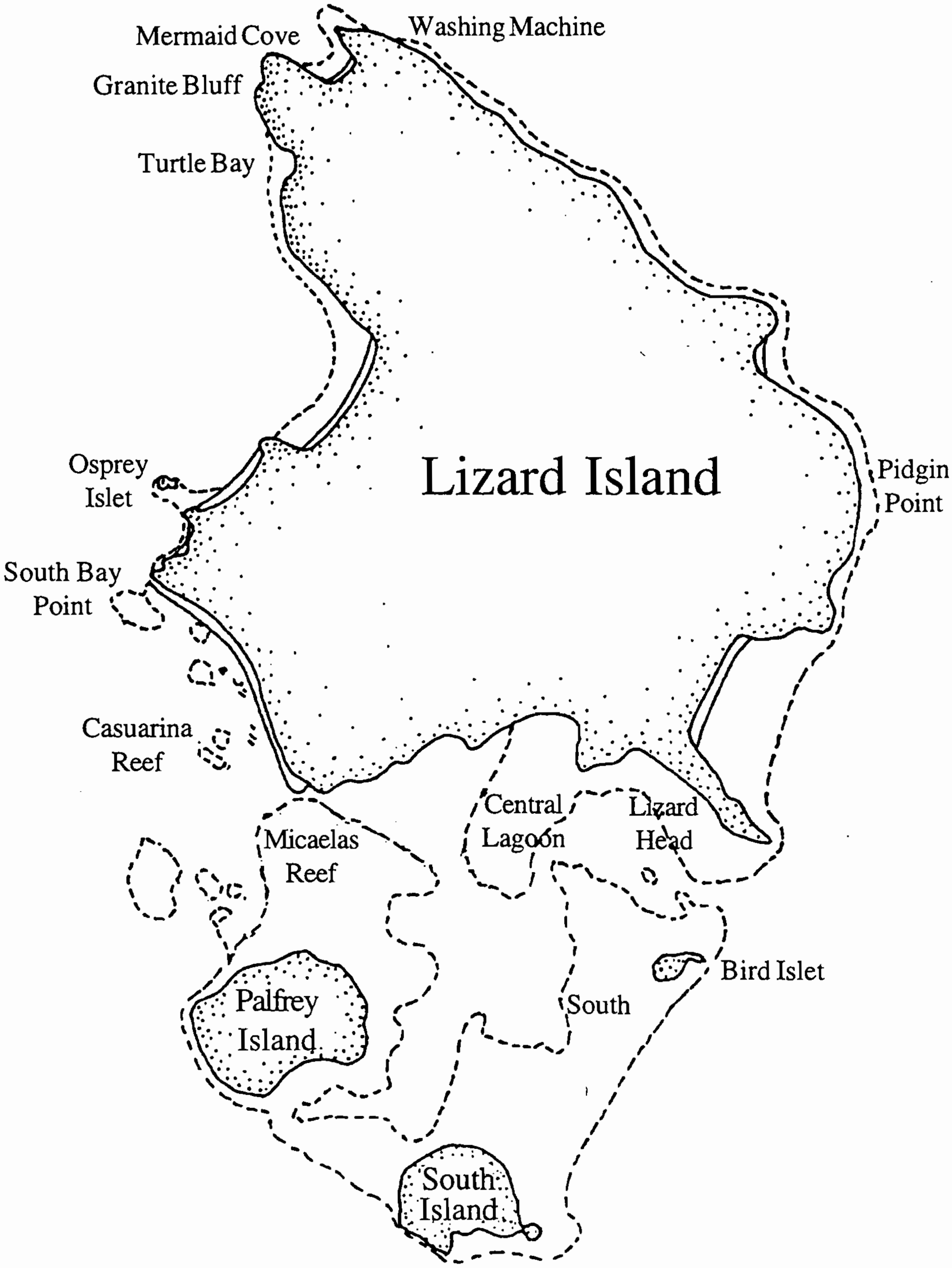


Fig 1 Map of Lizard Island showing study sites

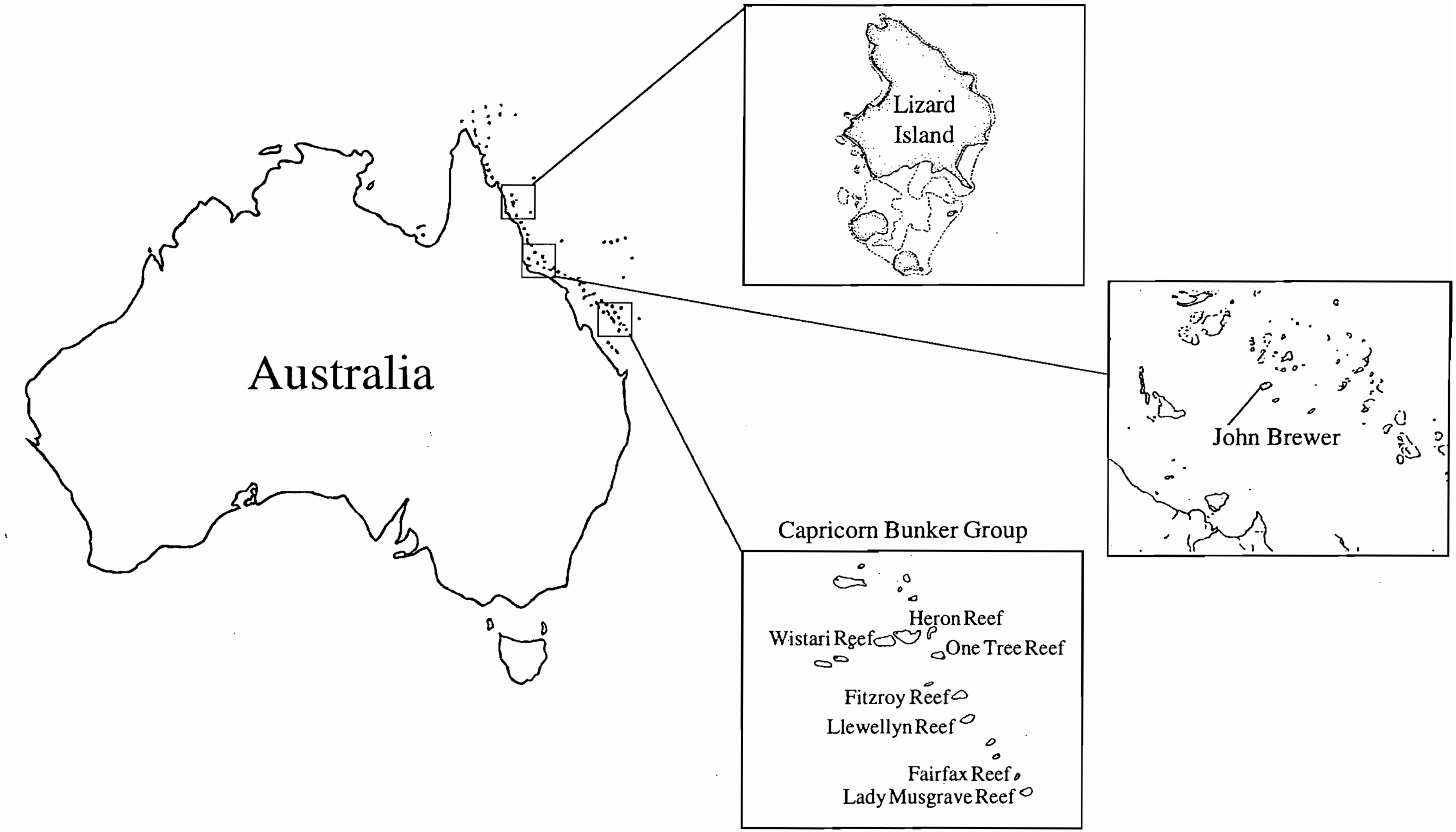


Fig 2 Map of Australia, showing the locations of the reefs that were compared in this thesis

CHAPTER 3

Use of implant microtags for studies on populations of small reef fish

3.1 Abstract

Ecological studies on small reef fish could often be improved by distinguishing among individuals or cohorts within populations, but this has not been possible with conventional tagging methods. Historically, tagging of recently settled juveniles has proven to be particularly necessary and difficult. What is needed is a method for individually recognising small individuals. Here, use of two types of implant microtag are verified for this purpose, visible implant fluorescent tags (VIF) and coded wire tags (CWT). Retention rates of these tags were determined when injected into two size classes of a coral reef damselfish, *Pomacentrus moluccensis* (10 mm - 20 mm juveniles; 25 mm - 40 mm adults). The influence of tagging on growth and survivorship was also measured. Microtag retention rates were high at 100% for new settlers and between 80% and 100% for adults. In addition, survivorship and growth of juveniles and adults were not significantly different for fish with and without microtags. These microtags should provide the means to understand the importance of processes occurring within a few weeks of settlement and throughout the reef associated phase of small fishes.

3.2 Introduction

Population studies often require recognition of either individuals or cohorts. Conventional methods used for tagging marine fishes are not appropriate for use in the majority of coral reef species because the tags are too large in proportion to the fish. They are particularly inadequate for marking recently settled juveniles, and this may be why this is one of the least understood phases in the life history of benthic fishes. Several studies have found that loss of fish is greatest during the first days after settlement (Doherty and Sale, 1985; Aldenhoven, 1986; Victor, 1986; Eckert, 1987; Shulman and Ogden, 1987; Meekan, 1988; Sale and Ferrell, 1988; Warner and Hughes, 1988; Hixon and Beets, 1989) but have not had the means to investigate this further. Without some degree of recognition, for example, it is not possible to look at degree of site attachment, variation in growth, size specific mortality, ontogenetic shifts in microhabitat preferences or to distinguish mortality from migration. Distinguishing between these factors is essential for understanding the population ecology of reef fishes. This can only be fully achieved with recognition of individual fish.

Various methods have been employed to allow recognition of individual fish: intrinsic variables such as size or natural markings (Sale, 1974; Reese, 1975; Aldenhoven, 1986; Connell and Jones, 1991); fin clipping (Sale, 1971); heat branding (Jones, 1987); external tags (Randall, 1961; Emery, 1973; Fricke, 1973); subcutaneous dyes (Kelly, 1967; Hart and Pitcher, 1969; Phinney and Matthews, 1973; Lotrich and Meredith, 1974; Thresher, 1978; Mapstone, 1988); implanted diazo film (Heugel, 1977); internal marks (Brothers, 1985; Volk et al., 1990); parasites (reviewed by Buckley and Blankenship, 1990); liquid latex (Riley, 1966; Forrester, 1990) and internal tags (Bergman et al., 1968; Buckley et al., 1994). However, not all of these techniques are suitable for long term recognition of small fish. Problems include negative effects on the fish, an inability to identify small individuals, the restricted time frame of some techniques (Mapstone, 1988) and mark loss (Buckley et al., 1994). Juvenile fish will be growing fairly rapidly and therefore techniques such as heat branding and dyeing will wear off relatively more quickly than for individuals that are growing more slowly.

Two types of implant microtag have been developed for fisheries research which may overcome these problems. They have been shown to have a low impact on juvenile survival and to have retention rates of > 93% for four temperate reef fish species (Buckley et al., 1994). Histological examination revealed negligible tissue reaction to these microtags (Hargreaves, 1986; Fletcher et al., 1987; Bergman et al., 1972). The Visible Implant Fluorescent filament (VIF) tag (Northwest Marine Technology Inc, Unpublished) and the binary - Coded Wire Tag (CWT - Jefferts et al., 1963) are bio-compatible internal microtags (Buckley et al., 1994). The VIF tags are cylindrical polyester tags, which, when injected into translucent tissue and fluoresced by ultra violet-A light, can be seen in live fish in the field. This attribute means that the fate of each cohort may be followed through time. CWT's are made from stainless steel wire and have unique batch or sequential codes etched onto their surfaces. Thus these microtags allow individual or cohort identification, with codes being deciphered under a binocular microscope. CWT's are magnetised and this feature is used to relocate them. Thus the use of both types of tag would give the ability to identify individuals over long periods of time.

Tagging studies generally assume that the tags have no influence on the variables to be measured, such as growth and survivorship. There is an increasing awareness of the need for verification of these assumptions of tagging (Emery and Wydoski, 1987; Buckley and Blankenship, 1990; McFarlane et al., 1990; Bergman et al., 1992), but to date very few coral reef fish studies have included the empirical evidence required. What is needed is a species specific assessment of the effects of tagging. This study examines the application of microtags to newly settled and adult damselfish of the species *P. moluccensis*. It tests the reliability of microtag retention when injected singly and in combination, and the effects of tagging on fish growth and survivorship.

3.3 Methods

This experiment included two phases, a laboratory phase (the first 45 days) and a field phase (the second 45 days). During the laboratory phase, fish were kept in aquaria because identifying individuals with lost tags was more precise in a confined environment. The field phase used isolated patch reefs to assess retention rates and impact of the microtags on fish on the reef. Censuses were performed after 9 days, 45 days and 90 days to measure microtag retention rates and fish standard length. During the laboratory phase, survivorship was checked daily but during the field phase only once, after 90 days.

3.3.1 Laboratory Phase

As stated in the introduction, the ideal scenario for subsequent studies was to be able to use both types of microtag, the Visible Implant Fluorescent Tag (VIF) and the

Coded Wire Tag (CWT), in combination. However, it was possible that injection of two microtags into an individual may cause more problems than injection of one and each tag type may have unique effects. Hence, the experimental design included three treatments to allow assessment of each type of tag separately and in combination. The treatments were as follows: one coded wire tag, one VIF and both microtags. The tagging process involves two steps, the first to anaesthetise the fish, the second to inject the microtag/s. Fish were immersed until unconscious, approximately 10 seconds, in a solution of quinaldine. The quinaldine solution which was found to be most effective was 1 : 15 : 4500, quinaldine : ethanol : sea water. The microtags were then injected with the aid of a binocular microscope, under the scales and into the dorsal muscle. All tags were implanted at least one-tag length away from the insertion point to allow a healing area behind the tag (Buckley et al., 1994). When two microtags were to be injected, one was placed on each side of the fish. To minimise the damage incurred by the fish, particularly to the scales, each was placed in a click seal polyethylene bag for the injection process. Sterile technique was employed as far as possible, by washing the injector and microtags in an antiseptic solution prior to injection. Injection of a single microtag using this method took no more than 2 minutes, and no longer than 3 minutes for 2 microtags.

Two controls were used in the lab phase to assess the impact of anaesthetising and tagging and to assess the impact of the anaesthetising alone. Control 1 fish were placed in aquaria and were untouched other than for censusing to test the impact of anaesthetising and tagging. Control 2 fish were anaesthetised, placed in a polyethylene bag for 3 minutes and then released into the aquaria to test the impact of the anaesthetising alone. The time period chosen was the maximum time that any fish would be kept in a polyethylene bag.

All fish were kept in aquaria for 45 days. Ten individuals, two from each tagging treatment and two from each control, were placed in each aquarium. Treatments and controls were allocated randomly among individual fish. Adults and new recruits were kept in separately with 5 new recruit aquaria and 6 adult aquaria. For the purpose of this study new recruit refers to an individual of 10 - 20 mm standard length at the start of the experiment and adult refers to fish between 25 - 40 mm standard length at the start.

Previous studies (Buckley et al., 1994) have found that the ratio of muscle size to tag weight and size may be important in terms of the percentage microtags retained. Therefore different sizes of microtag were used according to the size of *P. moluccensis* tested. Standard length microtags 1 mm long were injected into the adults and half length microtags 0.5 mm long were injected into the new settlers.

Approximately 9 days and 45 days after injection, tag status and fish standard length were determined. Tag rejection due to unacceptable location or tagging procedures is usually established by 30 days (Buckley and Blankenship, 1990).

3.3.2 Field Phase

After 45 days all tagged fish were placed onto patch reefs. Patch reefs were 2 m^2 , 20 m apart and consisted of a base of coral rubble above which were placed four hard live coral heads. Species used were *Pocillopora damicornis*, *Stylophora pistillata*, *Acropora nobilis* and *Acropora nasuta.* Six adults and six new settlers, 2 from each tagging treatment, were placed on each reef. A third control group was introduced at this stage to test for any effects of the entire laboratory phase. Approximately 100 m away from the first set of patch reefs, a second set of identical reefs was constructed for control 3 fish. These fish were captured from the nearby contiguous reef and placed on these patch reefs in the same densities as the treatments. The spatial isolation of the two sets of reefs was required to enable separation of individuals that had lost their tags from control individuals. This design was chosen to adequately test microtag retention rates, the issue which the authors consider to be the most important. A consequence of this is that whilst some aspects of mortality were adequately tested in the aquaria, any increased predation pressure that might be encountered when a fish is first released back onto the reef has not been tested here. All reefs were censused after 90 days. Recoveries of tagged fish were made by using UV-A light to fluoresce the VIF tags.

3.4 Results

3.4.1 Retention

Percentage retention rates of microtags were 100% for all new recruits and adults when injected singly (figure 1). They were lower when injected into adults in combination (80%; figure 1). The slightly lower figure for both microtags was due to losses with the larger size standard microtags. This indicates that use of standard microtags increases the likelihood of tag loss in this species and suggests that the half-length microtags would be more appropriate.

3.4.2 Survivorship

The percentage of fish remaining (figures 2 and 3) at 45 days was very high in new recruits and adults from the aquarium control (90%, 100%), CWT (100%, 100%) and both microtag (100%, 90%) treatments. The lower survivorship shown by the VIF and Quinaldine controls (new recruits: 85%, 80%; adults: 75%, 70%) was probably an aquarium specific phenomenon due to conspecific aggression rather than due to any aspect of the tagging procedure. The results indicate that survivorship of individuals with both types of tag is good and it is therefore counter intuitive to consider that single VIF tags could increase mortality. In addition, several individuals that died had fin damage of some description with some severe cases having the entire caudal fin missing. Losses in all groups were greater, but did not exceed 23%, during the field phase of the experiment and were comparable between treatment and control groups.

3.4.3 Growth

There was no significant difference in standard lengths between treatments and controls after 90 days, for either juveniles (figure 3, table 1) or adults (figure 4, table 1). Juveniles grew approximately 10 mm in 90 days in all tagging treatments and controls (figure 3). Average growth in length was considerably less for adults, but, again, there was no negative effect due to implanting single or double tags.

Table 1 ANOVA tables comparing the final standard length/mm of VIF, CWT, Both and Control 3 individuals for A) new settlers and B) adults. Variances homogeneous in both new settlers and adults.

a) New settlers

SOURCE	DF	SS	MS	F	P
BETWEEN	3	65.4705	21.8235	1.22	0.3232
WITHIN	26	466.099	17.9269		
TOTAL	29	531.569			

b) Adults

SOURCE	DF	SS	MS	F	P
BETWEEN	3	237.278	79.0928	2.75	0.0581
WITHIN	33	948.272	28.7355		
TOTAL	36	1185.55			

3.5 Discussion

This study shows that the use of microtags in a small coral reef damselfish *P. moluccensis* can be a useful tool for providing long term individual recognition. It shows that reliability of microtag retention is high for both new recruits and adults when injected singly (100%, 100%) and in combination (100%, 80%), and also shows that there is negligible impact on growth and survivorship. It is a good technique for recognition of individuals of 11 mm standard length or more, and it may be that fish smaller than this could be tagged with practice. There is an indication from this study that size of microtags used can have an important effect on tag retention and for *P. moluccensis* the half length microtags are more reliable when two microtags are to be used in combination. This confirms findings elsewhere that tag size in relation to muscle size was an important factor in determining tag retention rates. It is probable that any microtag losses occurred within 45 days of injection, because all fish remaining on the patch reefs were tagged. If tag loss occurred in the field it was also accompanied by either mortality or dispersal. Previous work has indicated that these fish are extremely site attached rarely moving greater than 2 m (Mapstone, 1988). Mapstone, (1988) marked 99 *P. moluccensis* and found that only one moved further than 2 m over a period of three years. Fish losses in all groups were greater, but did not exceed 23%, during the field phase of the experiment and were comparable between treatment and control groups. Many predators colonised these patch reefs during the experiment and hence when individuals disappeared from the reefs it was more likely to be due to a fatality than to dispersal. Perhaps disorientation when first released onto the reefs increased fish vulnerability to predation.

Using this technique it should now be possible to answer major questions in reef fish ecology. For example, it should now be possible to measure the importance of immigration and emigration from populations or experimental units for individuals of 11 mm standard length or more. This will include new settlers for most reef fish species. Many scarids and acanthurids settle at <6 mm, but with practice these too may be possible to tag.

Some authors have suggested that there is no temporal or spatial variation in mortality rates (Doherty and Fowler, 1994; Victor, 1986). Without well replicated tagging programmes it is impossible to fully ascertain the processes occurring, for example to separate mortality from migration. This inability to distinguish between processes has often been accepted as an assumption of settlement studies (Aldenhoven, 1986; Eckert 1987; Meekan, 1988; Sale and Ferrell, 1988). It is mostly because of these problems that little is known about the mortality rates of new settlers and juvenile coral reef fish (Victor, 1986). Therefore, these microtags should provide a means to understand the importance of processes occurring within a few weeks of settlement and in shaping reef fish populations.

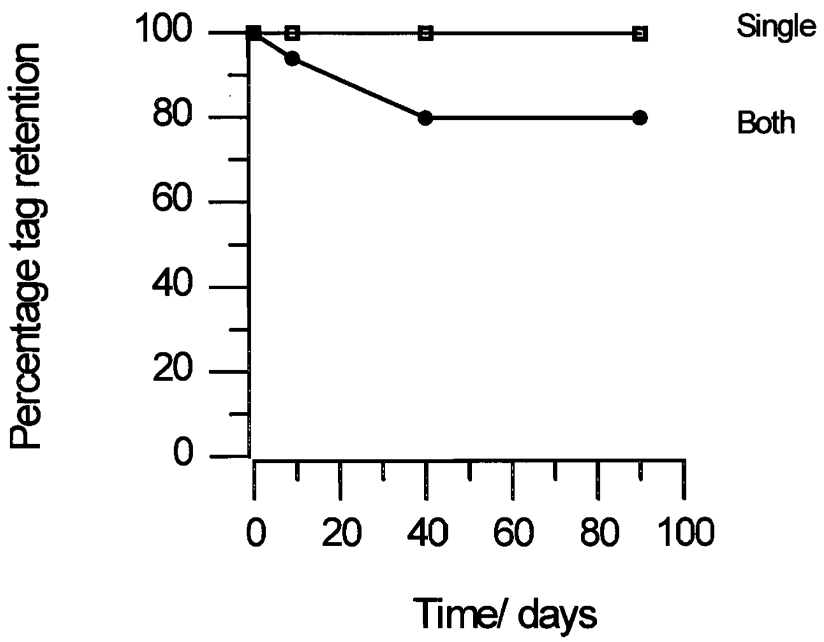


Fig 1 Retention rates for microtags injected singly and in combination into *Pomacentrus moluccensis* adults. n = 36.

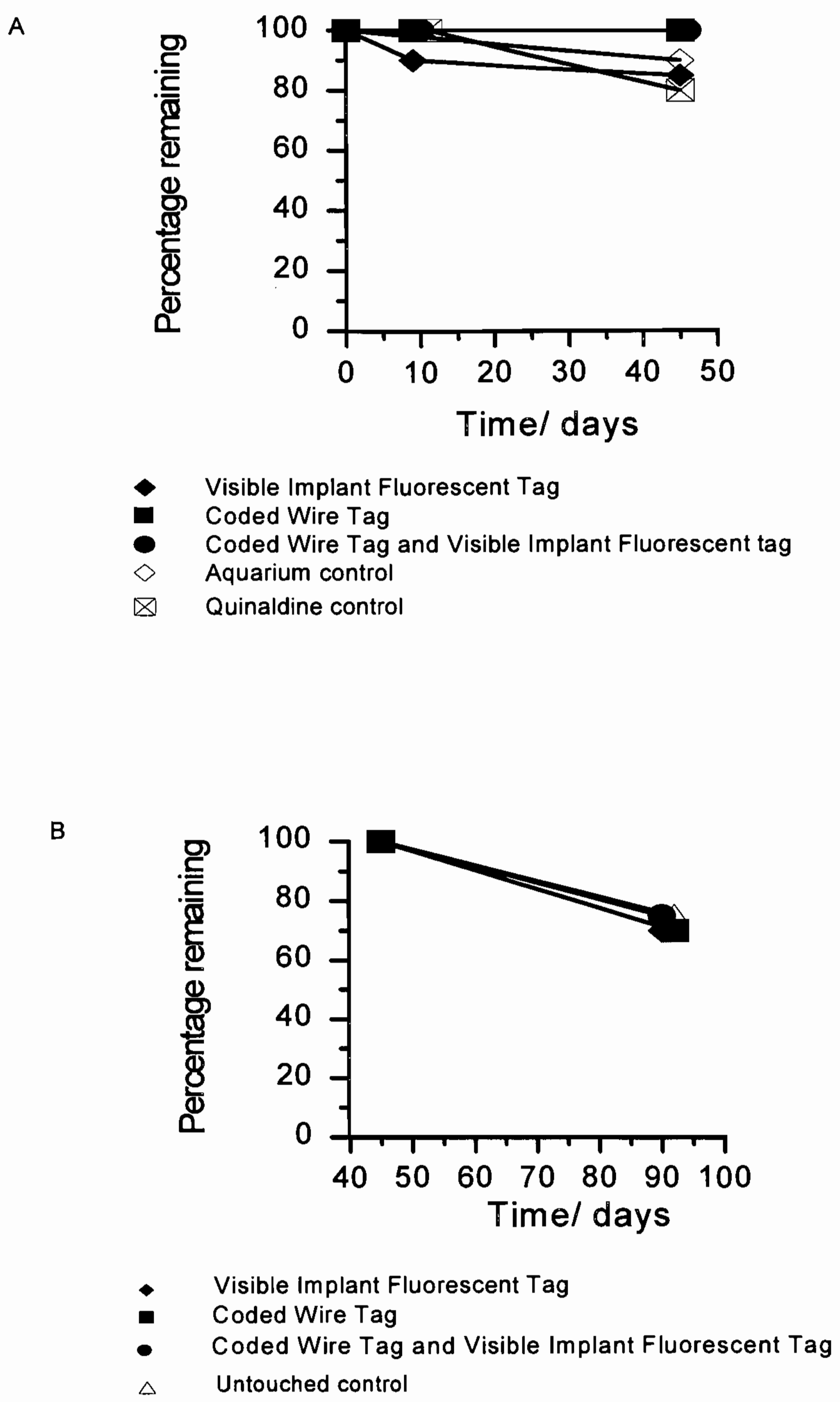


Fig 2 A comparison of percentage survivorship of *Pomacentrus moluccensis* new settlers in (A) the laboratory phase (B) the field phase of the experiment. For each line n = 10.

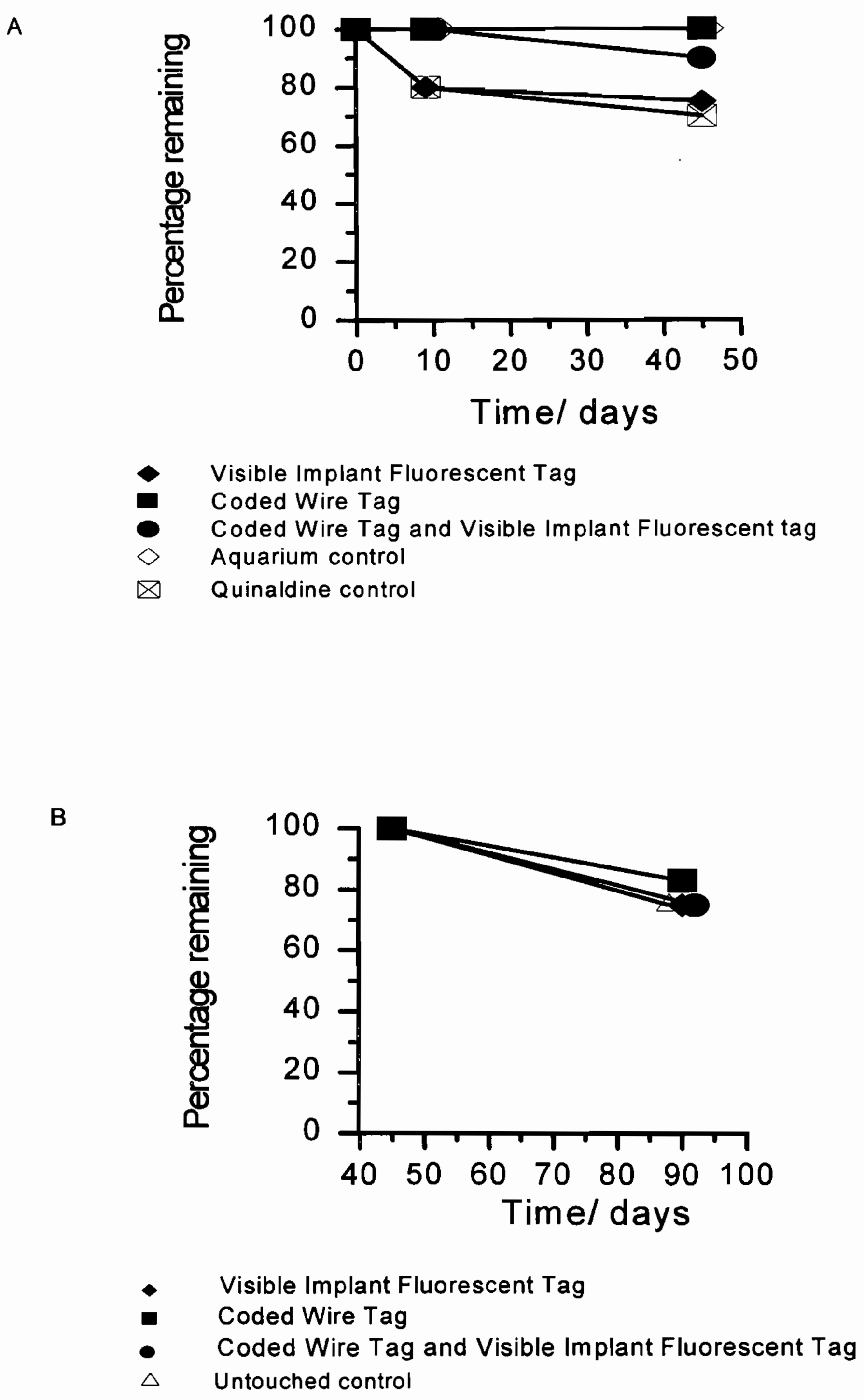


Fig 3 A comparison of percentage survivorship of *Pomacentrus moluccensis* adults in (A) the laboratory phase (B) the field phase of the experiment. For each line n = 12.

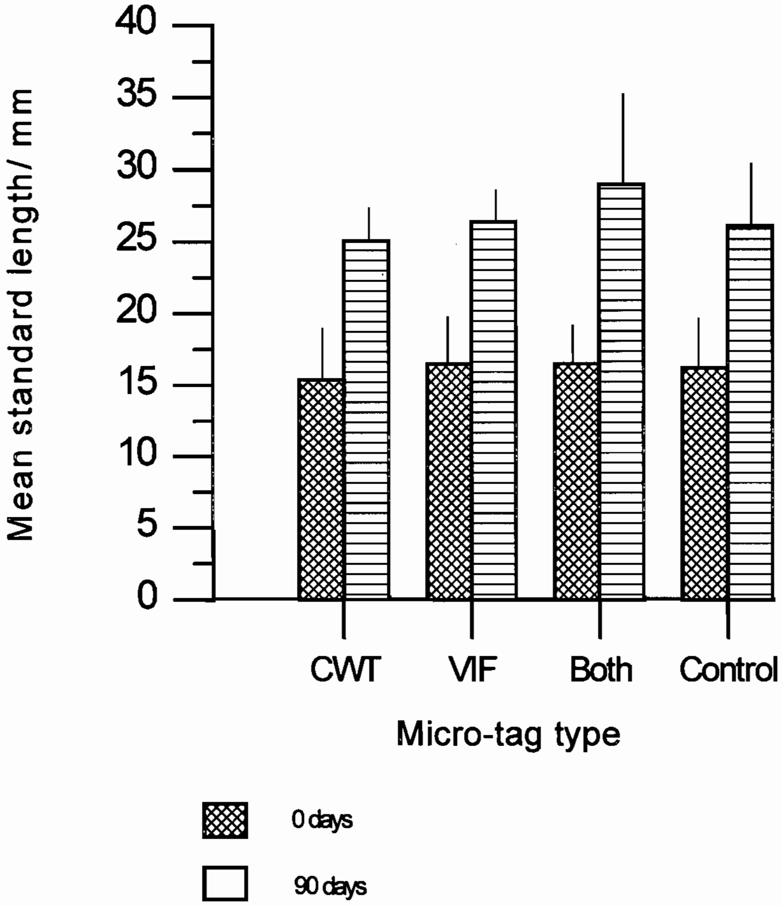


Fig 4 Standard lengths ($\bar{x}$ ± sd) of new settlers of *Pomacentrus moluccensis* at time of tagging and 90 days later. n = 40.

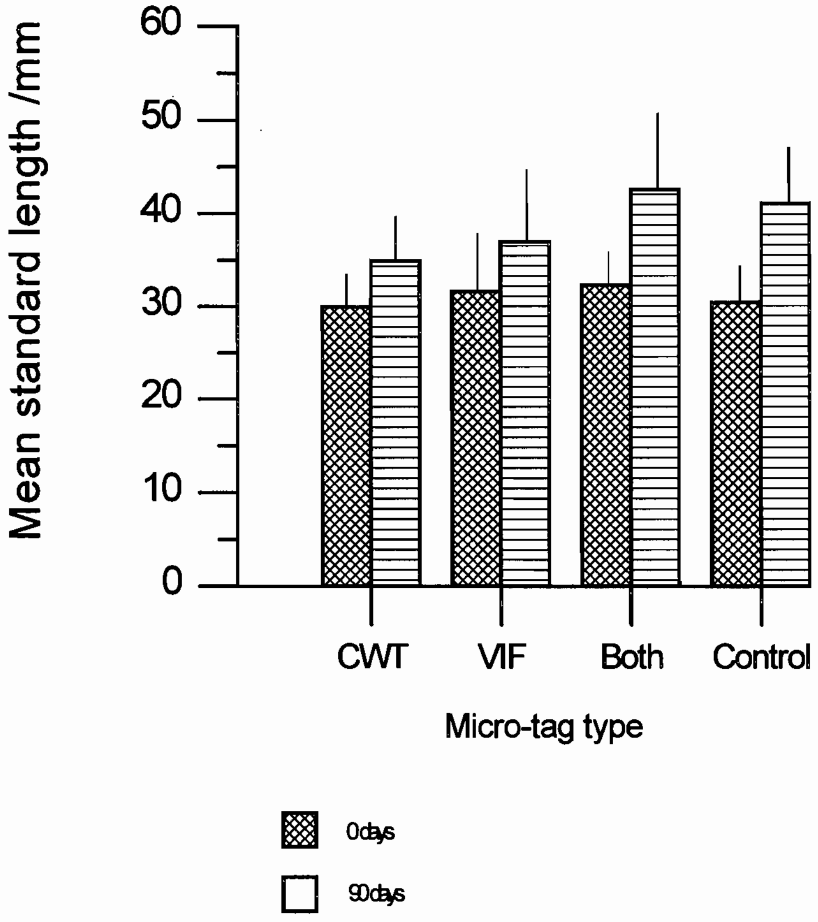


Fig 5 Standard lengths ($\bar{x}$ ± sd) of *Pomacentrus moluccensis* adults at time of tagging and after 90 days. n = 48.

CHAPTER 4

Age and growth of a coral reef damselfish, *Pomacentrus moluccensis*

4.1 Abstract

Age based demographic information, such as size at age and longevity, is necessary for assessing fundamental questions about population dynamics and regulation. If otoliths are to be used for ageing, it is essential to validate that the increments in otoliths are readable and annual for each location. Here, annual ageing was validated using tetracycline and stress markers in the otoliths and growth curves were plotted using a polynomial function for *Pomacentrus moluccensis* populations at Lizard Island, northern GBR. These results were compared to those obtained for this species on Southern reefs of the GBR.

Validation confirmed that otoliths of this species at Lizard Island had regular increments laid down yearly. Longevities were the same at three sites examined with very few individuals living longer than 6 years. This contrasts with southern reefs where other studies show that 10% of individuals were greater than 18 years old. However, growth rates at these sites were remarkably similar and showed no indication that individuals at Lizard Island were growing faster as would be expected by their shorter life-span. This species therefore provides an excellent opportunity to compare processes regulating this damselfish between latitudes and under a range of conditions.

4.2 Introduction

Accurate estimates of growth and longevity are fundamental for addressing questions about the regulation of fish populations (Doherty and Williams, 1988; Cushing, 1988). Many of the models used in fisheries management require such information to determine sustainable levels of exploitation (Shepherd, 1988). There is a long history of using annual increments in otoliths to obtain estimates of fish age and growth. Too often in the past, however, annual increment deposition in otoliths has been assumed without any attempt at validation (Beamish and McFarlane, 1983). Given that inaccuracy in age estimation may profoundly effect our understanding of a species biology, age validation must be seen as essential.

Annual increments in the otoliths of *P. moluccensis*, a common coral reef damselfish, have been validated at two southern reefs and one central reef in the Great Barrier Reef (GBR) (Fowler, 1990; Fowler and Doherty, 1992). However, Beamish & McFarlane (1983) also stress the need for age estimates to be validated for populations at different locations. This is particularly important for coral reef fish, as the ability to obtain age estimates for another species of damselfish, *Pomacentrus wardi*, has been shown to vary with latitude (Fowler and Doherty, 1992). A fairly precise relationship between otolith weight and age has also been found for *P. moluccensis* on southern reefs (Worthington et al., 1995). This suggests that otolith weight may be a useful predictor of age, however, the consistency of this relationship between locations and under different conditions is unknown.

Previous work had found that populations of *P. moluccensis* were recruitment limited on six out of seven reefs in the southern GBR (Doherty and Fowler, 1994). Recruitment limitation is most likely to occur when levels of recruitment are low and a species is short lived. At Lizard Island, in the northern GBR, recruitment is known to be relatively higher than on the southern reefs (Sweatman, 1985), hence recruitment limitation would appear less likely at this location. However, the importance of recruitment fluctuations is also likely to be influenced by the longevity of individuals in the population (Warner and Hughes, 1988). Here, knowledge of life history parameters for *P. moluccensis* at Lizard Island would shed further light on the factors likely to be regulating this population.

The aim of this study was firstly to validate the use of otoliths for annual ageing of *P. moluccensis* at Lizard Island. On the basis of this validation it was then planned to use otolith increments to determine parameters of growth and longevity for the Lizard Island population. The relationship between otolith weight and age was also to be assessed. Finally, results from this study were compared to those from the southern reefs, with a view to how factors regulating populations may differ between the two locations.

4.3 Methods

4.3.1 Age validation

The first annual ring was validated by marking the otoliths of 10 *P. moluccensis* new recruits with tetracycline and leaving fish on the reef for one year. Previously, annual rings were validated for this species at two southern Great Barrier Reef sites, up to nine years old (Fowler, 1990; 1992). Hence, at Lizard Island it was not considered necessary to validate all age classes. Individuals were marked with fluorescent microtags for ease of relocation.

4.3.1.1 Fish tagging

The tagging process involved two steps (sensu Beukers et al., 1995), the first being to anaesthetise the fish, the second to inject the tag. Fish were immersed until unconscious, approximately 10 seconds, in a solution of quinaldine. The quinaldine solution which was found to be most effective was 1 : 15 : 4500 (quinaldine : ethanol : sea water). The microtag was then injected with the aid of a binocular microscope, under the scales and into the dorsal muscle. All tags were implanted at least one tag length away form the insertion point to allow a healing area behind the tag (Buckley et al., 1994). One tag was implanted into each fish. The Visible Implant Fluorescent filament (VIF) tags (Northwest Marine Technology, Inc, Unpublished) are bio-compatible internal microtags. They are cylindrical polyester tags, which, when injected into translucent tissue and fluoresced by ultra violet light, can be seen in live fish in the field.

To minimise the damage incurred by the fish, particularly to the scales, each was placed in a click seal polythene bag for the injection process. Sterile technique was employed to some degree, by washing the injector and microtags in an antiseptic solution prior to injection. Injection of a single tag using this method would take no more than 1 minute.

All tagged fish were placed in a tetracycline solution of 220mg to 1L seawater and kept in the dark for 24 hours. They were all returned to their resident coral head within 30 hours of removal. Individuals were collected after 10 to 12 months on the reef. Tagged fish were found by searching a 5m radius circle around each coral head. Fluorescent tags could be seen with the use of an ultra-violet light to bring out their fluorescence. Individuals were taken back live to the laboratory where they were sacrificed using ice. Sagittal otoliths were removed, cleaned and stored.

4.3.1.2 Otolith preparation

One sagittal otolith from each fish was haphazardly selected and a transverse section prepared. Initially the otolith was adhered to a microscope slide using crystal bond so that the primordium was perpendicular to the slide and level with the edge. The projecting half of the otolith was ground down using wet and dry paper (800 grade followed by 1200 grade) such that the primordium remained intact. The crystal bond was then melted and the otolith relocated so that the primordium was parallel to the slide and the ground end of the otolith faced towards the slide. The otolith was ground down parallel to the slide to produce a thin transverse section approximately 100μm thickness.

4.3.1.3 Otolith examination

Otoliths were viewed under a compound microscope at a magnification of 100x using both incident fluorescent and transmitted light. The position of any fluorescent band was noted using the fluorescent light with excitation bands between 450 and 490nm and barier filters at 510 and 515nm. Age estimates were obtained, using transmitted light, by counting increments along the dorsal lobe of the otolith.

4.3.2 Population age and growth

4.3.2.1 Otolith collection

All *P. moluccensis* on twenty five patch reefs at South Bay Point were removed in October using quinaldine and immediately gut injected with formalin. Standard length was measured and otoliths were removed. Sixty individuals were collected from Bird Islets in the lagoon, and Turtle Bay respectively, in February. Individuals were taken back live to the laboratory where they were sacrificed using ice. Standard length was measured using callipers and sagittal otoliths were removed, cleaned and stored.

4.3.2.2 Otolith preparation and examination

Otoliths were prepared and aged as previously. A subsample of 60 otoliths were re-examined to look at intra reader variability. The difference was measured as the deviation of the first count from the second count. The variation in estimates per age class could then be calculated and assessed.

4.3.2.3 Growth curves

Polynomial functions were fitted to the size at age data for three sites (sensu Chen et al., 1992), as growth did not appear to reach an asymptote. The growth curve from John Brewer Reef (Fowler, 1990) was plotted, using the Von Bertalanffy equation, onto the same graph as the curves obtained in this study for comparison.

4.4 Results

4.4.1 Age validation

In each otolith examined both a fluorescent band and one increment were visible (Plate 1). In all cases the increment was located outside the fluorescent band indicating that it was formed after the marking process in April. This shows that these increments were annual and therefore could be used to estimate the age of fish in years.

4.4.2 Population age and growth

All otoliths examined had an interpretable internal structure (Plate 2). Increments were formed towards the end of September because all otoliths removed from fish in the October sample showed an increment on the otolith margin. Precision between two counts by one reader was high. All counts were within 1 year or less of each other (Table 1) and were unbiased. They were therefore considered to be precise enough for making the comparisons between sites and locations.

There was a strong linear relationship between otolith weight and fish age ($r^2 = 0.71$), however there was a high degree of overlap in the range of weights for adjacent years, resulting in a relatively shallow slope to the line. The relationship was improved by using a multiple regression of weight and standard length ($r^2 = 0.78$, Table 2).

Longevities at all three sites were the same at 6 years old. As expected growth declined with age (Figs 2 - 4). The polynomial equations for the two sites at February were very similar ($y = -0.7809x^2 + 9.3152x + 20.073$, and $y = -0.9133x^2 + 10.763x + 16.961$ respectively and fitted well ($r^2 = 0.845$ and $r^2 = 0.856$). The third site, collected in October, lacked a year 0 cohort because increments were formed in late September and recruitment for that season had not yet started. Interestingly, the polynomial fit was good ($r^2 = 0.770$) and was virtually a straight line implying uniform growth rates. This could merely be a result of the missing year class because the growth would have been higher during that year, given mean size at settlement of approximately 10mm SL.

Comparison of the two February samples from this study with a February sample from a previous study at John Brewer Reef (central GBR) showed very little difference in the growth, given the variance within age classes at each site. This species at John Brewer reef is much longer lived and size reached an asymptote, so Fowler, (1990) fitted a Von Bertalanfffy curve. Despite the different equations used, the curves are remarkably similar particularly for cohorts 4 - 6.

Table 1 Intra-reader variability in 2 counts of otolith increments. Difference is the deviation of the first count from the second count and Variation is the percentage of otoliths per age class that differed by the amounts indicated.

Second	Difference				Variation	
Count	-1	0	1	Total	0	1
0		6		6	100	0
1	3	10	1	14	71.4	28.6
2	4	9	2	15	60	40
3	1	7	2	10	70	30
4		4	2	6	66.6	33.3
5	1	4	3	8	50	50
6			1	1	0	100
Total	9	40	11	60		
Percent	15	66.7	18.3			

Table 2 Multiple regression of otolith weight and standard length by age of *Pomacentrus moluccensis* at Lizard Island.

PREDICTOR VARIABLES	COEFFICIENT	SE	T	P	VIF
CONSTANT	-3.33912	0.71253	-4.69	0.0000	
WEIGHT	234.07	1306.914	0.76	0.4495	
SL	0.15305	0.03755	4.08	0.0002	

r^2	0.7834	MSE	0.49806
ADJUSTED r^2	0.7742	sd	0.70573

SOURCE	DF	SS	MS	F	P
REGRESSION	2	84.6709	42.3354	85.00	0.0000
RESIDUAL	47	23.4090	0.49806		
TOTAL	49	108.080			

4.5 Discussion

In recent years there has been much discussion about the processes regulating reef fish populations. In order to answer this question adequately detailed information about population demography is needed (Mapstone and Fowler, 1988). Previous studies had confirmed that ageing *P. moluccensis* was possible at seven reefs in the southern GBR and at John Brewer in the central GBR. This study increases the geographical range to include reefs in the northern GBR. Hence, this species would be ideal for making latitudinal comparisons in demography and population regulation.

It has been suggested that otolith weight may provide a good estimate of age (Boehlert, 1985) particularly when interpretation of annuli is ambiguous, and would be much quicker than grinding otoliths and then counting the increments. Coefficients of determination range from 0.95 (Boelhert, 1985) to 0.51 (Beamish, 1979). A previous study on *P. moluccensis* (Worthington et al., 1995) found that 86 - 92.4 % of the variation in age was explained by otolith weight compared with 71 % found in this study. Results could be improved using a multiple regression of weight and standard length to explain age with 78% of the variation explained. The largest error in these estimations would occur due to overlap in weights for adjacent year classes and it would remove the high degree of subjectivity involved in counting otolith increments (Worthington et al., 1995). Findings here concur with those of Worthington et al. (1995) and suggest that this method would be useful for monitoring population age structures and may increase precision by increasing sample sizes due to the relative speed of the process.

Longevities at Lizard Island were substantially lower (6 years) than those observed on the southern GBR at One Tree (>18 years, Mapstone, 1988), and Wistari (14 years, Doherty and Fowler, 1994). Fish at John Brewer Reef (central GBR) were at least 9 years old and may have been older (Fowler, 1990). Thus there may be a gradient of reduced longevity moving in a northern direction. Life history theory predicts that shorter lived species would grow faster, however there was no evidence of differential growth between the Lizard Island and John Brewer populations. At Lizard Island the reduced longevities would suggest that populations are more likely to be recruitment limited. In contrast, it has been suggested (Sweatman, 1985) that recruitment rates may be an order of magnitude higher to northern reefs compared to southern reefs suggesting that populations are more likely to be governed by post-recruitment processes. Which one prevails? In order to answer this quesiton information on mortality rates is needed and that is what the next chapter addresses.

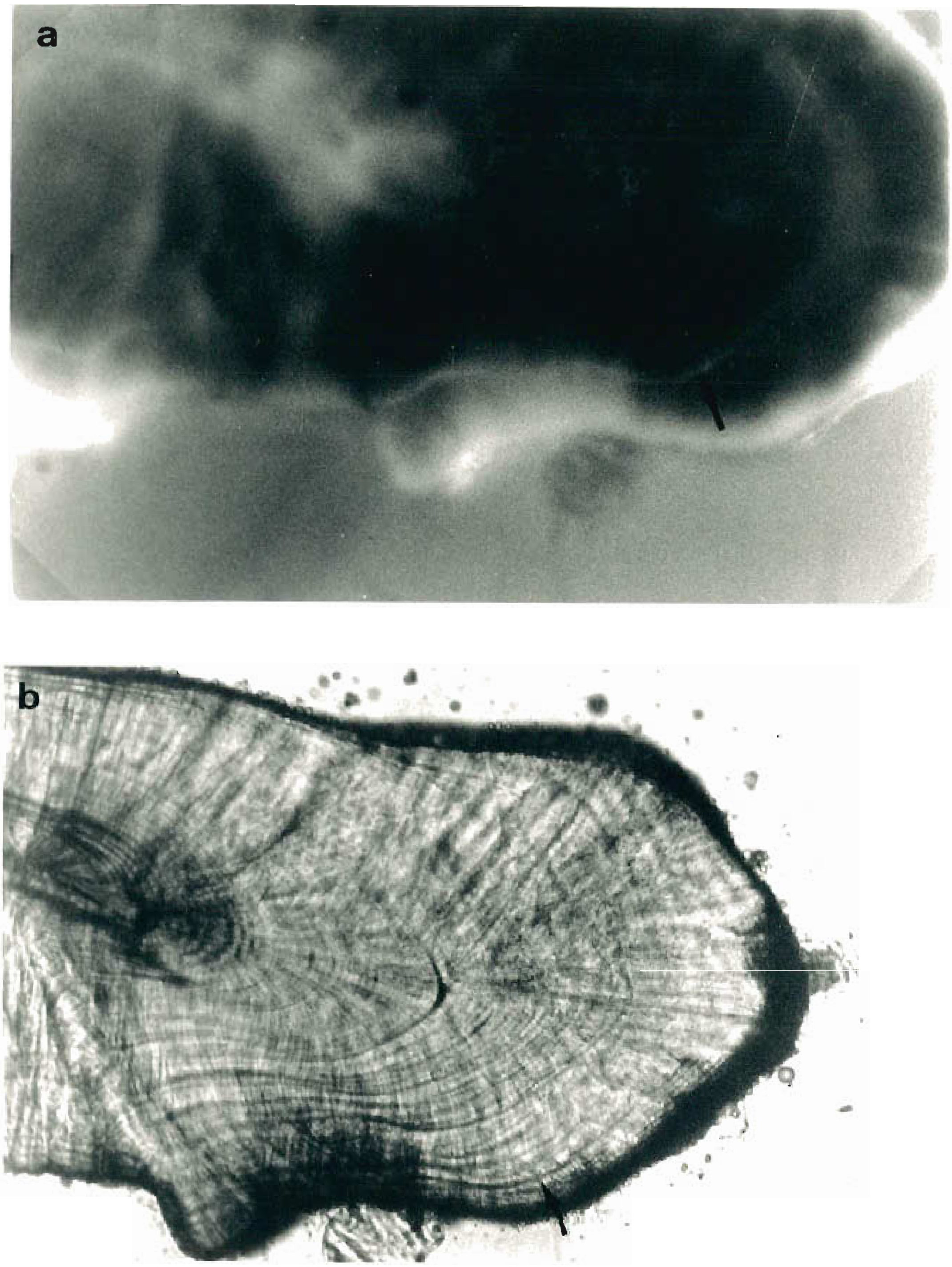


Plate 1. Light micrographs of a sagitta from a one year old *P. moluccensis* treated with tetracycline under a) incident UV light showing the position of the fluorescent tetracycline mark, and b) transmitted light showing the position of the annulus.

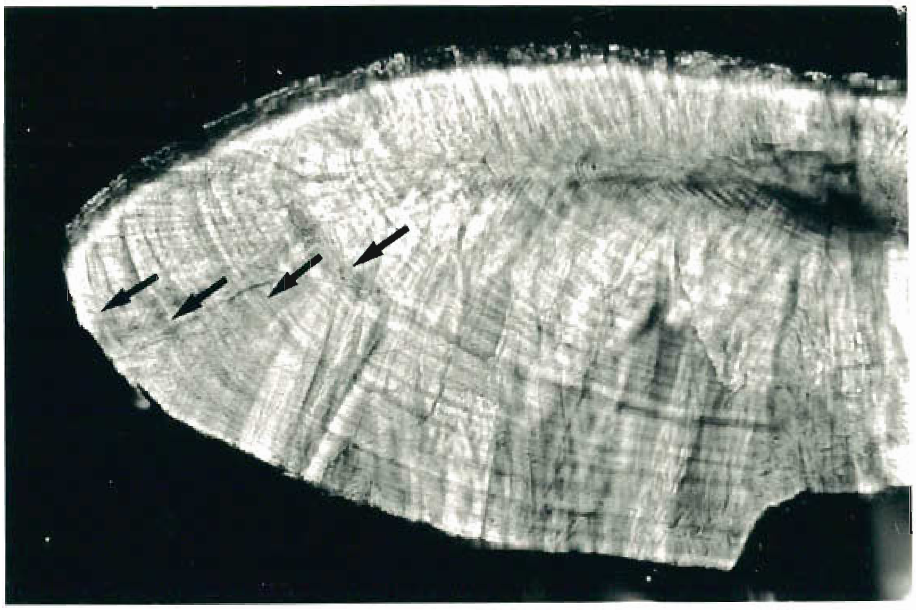


Plate 2. Light micrograph of a sagitta from a 4 year old *P. moluccensis* under transmitted light showing the positions of the annuli.

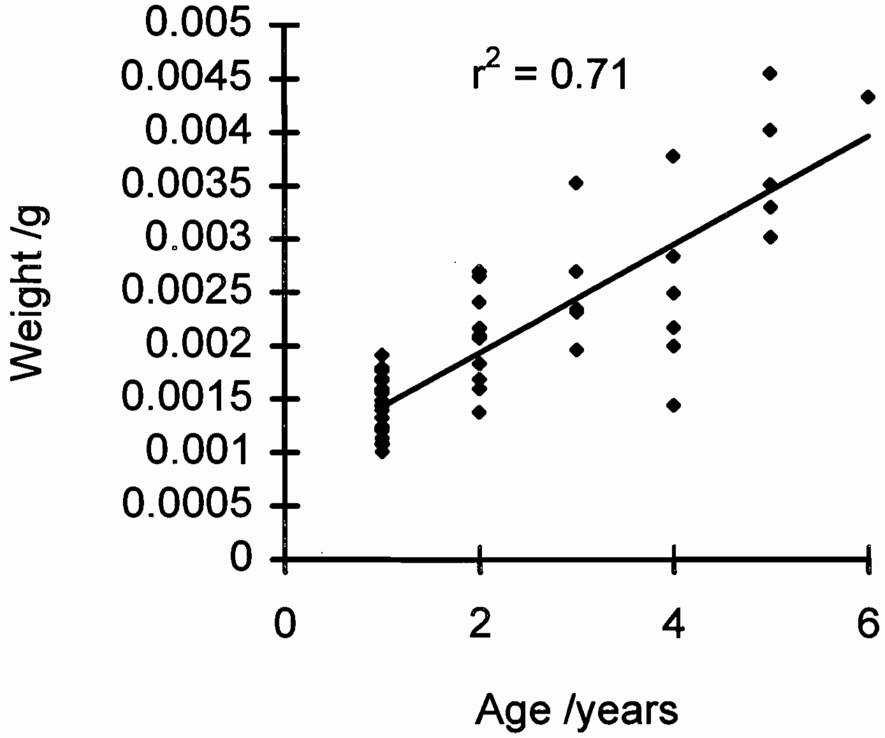


Fig 1 Regression of otolith weight (g) against age (years) for *P. moluccensis* at Lizard Island. n = 50.

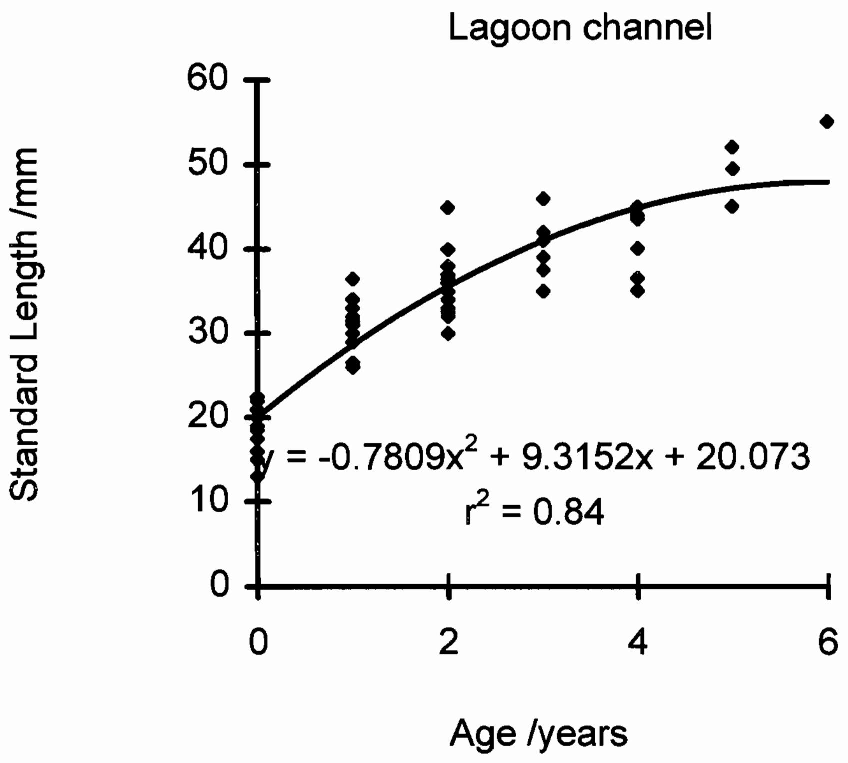


Fig 2 Size at age relationship for *Pomacentrus moluccensis* at Lagoon Channel, Lizard Island. n = 60.

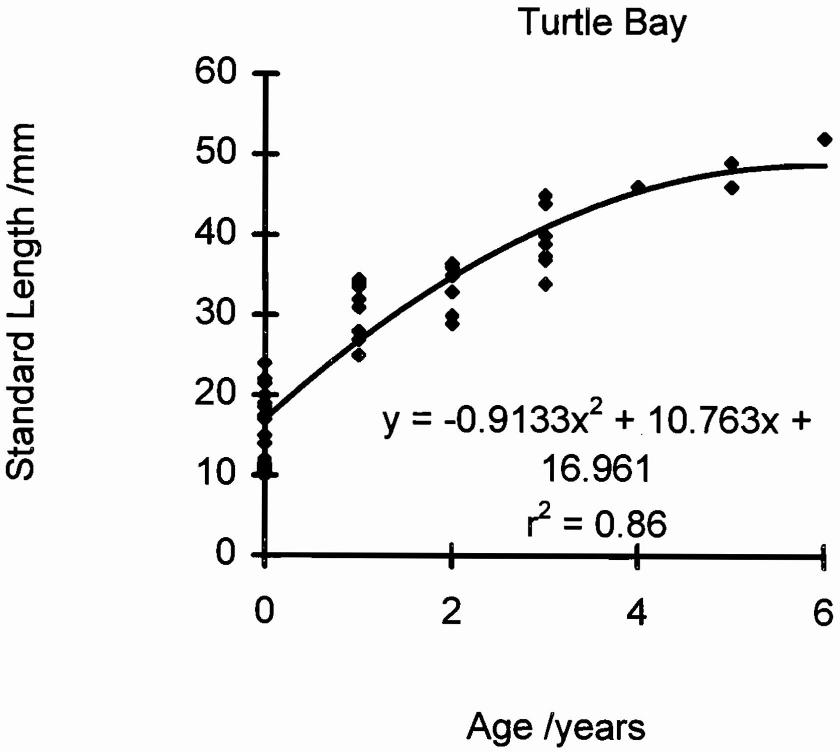


Fig 3 Size at age relationship for *Pomacentrus moluccensis* at Turtle Bay, Lizard Island. n = 60.

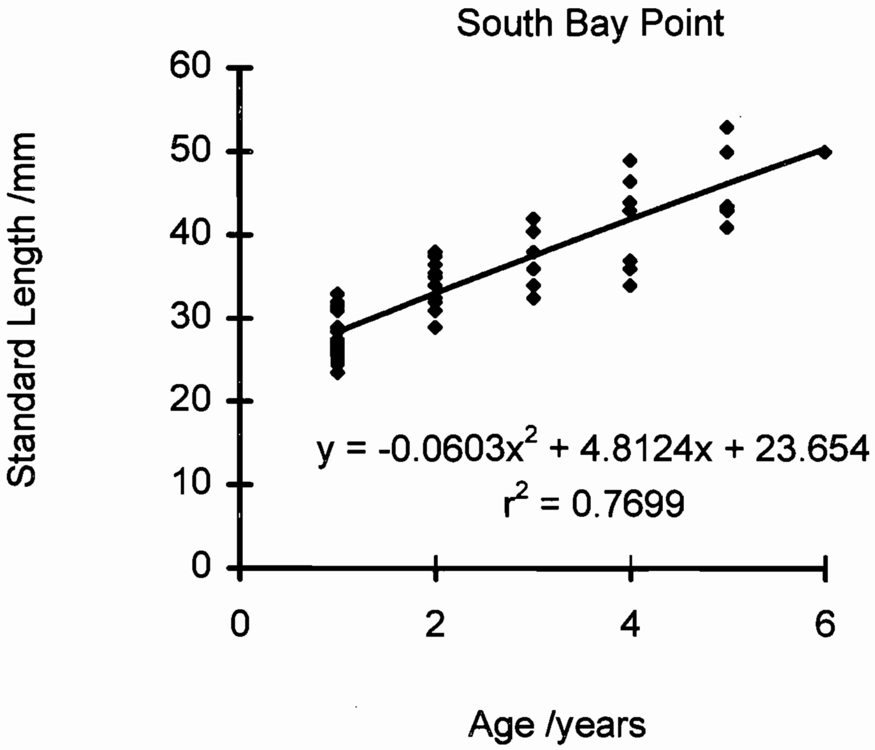


Fig 4 Size at age relationship for *Pomacentrus moluccensis* at South Bay Point, Lizard Island. n = 60.

Fig 5 Comparison of growth curves for *Pomacentrus moluccensis* at Lizard Island, northern GBR and John Brewer Reef, central GBR.

CHAPTER 5

The importance of variation in recruitment and mortality in the dynamics of a reef fish population

5.1 Abstract

In open marine populations, the local dynamics may be determined by variation in recruitment and mortality but the relative importance is seldom estimated. Patterns of recruitment may be modified by density-dependent or independent mortality disrupting any relationship between recruitment and population changes. Here, I measured spatial and temporal patterns, in the recruitment, mortality, adult density and population structure of *Pomacentrus moluccensis*, at two spatial scales. Firstly, populations were measured at a local scale on twelve permanent transects (10m x 1m), one to ten metres apart, monitored at four sites over three years. Secondly, a broad scale study was undertaken of populations in three reef zones classified according to exposure, and at three sites hundreds of metres to a few kilometres apart, in each zone, over two years.

The size structures of populations at the four local scale sites were significantly different with 65% of the population at Osprey under 30mm SL, while at South 84% of the population were greater than 30mm SL. Age structures at sites adjacent to three of the four local sites were also significantly different from each other.

Adult densities were relatively stable at three of the four local sites with the other, Granite, exhibiting a long term decline. This pattern did not correlate with recruitment patterns at transect level, which showed similar fluctuations at the three stable sites and constant recruitment at Granite. At the broad scale there was a significant difference in densities of adults and new recruits between zones and sites over two years and in percent mortality between three zones. The relationship between adults and new recruits at these nine sites was significantly curvilinear implying density-dependent effects ($r^2 = 0.54$).

Densities of several cohorts of new recruits which were widely differing in year 1

showed convergence in year 2. Rank order of abundances in the second year differed markedly from the relative cohort sizes observed at recruitment. This could be explained by density-dependent mortality as observed at both local and broad scales during the first reef associated year. There was considerable variance in this relationship at low recruitment densities in permanent transects at four local scale sites. This variance could be due to either density-dependent or independent processes or perhaps both. It implies that at this level there may be other processes which are of importance in determining mortality rates as well as density.

These results contrast with other studies on *P. moluccensis* on the southern Great Barrier Reef which suggest recruitment limitation of populations. At Lizard Island, sites appear to reach much greater mortality rates. Density-dependent and site specific variation in mortality rates appear to be important at Lizard Island. The local dynamics of this species appears to be fundamentally different between the two areas studied. This could be due to either differences in the scale of sampling or could represent regional differences.

5.2 Introduction

Explaining mechanisms of population regulation is one of the fundamental aims of ecology (Murdoch, 1994). Population size is determined by the combined effects of processes that increase and decrease counts of individuals. Until recently, most models of population dynamics were based on "closed" systems where the progeny contributed to the growth of the same local population (Nicholson, 1933; Haldane, 1953; Andrewartha and Birch, 1960; Varley et al., 1973). These models emphasise the importance of population regulation by density-dependent processes affecting birth or death rates (Haldane, 1953). However, where the life history includes a broadly dispersing phase the local population dynamics may be independent of the production of offspring. Examples of open populations are included in marine invertebrates, marine fish, broadly dispersed plants and stream associated insects. In these open populations numbers arriving at the adult habitat could limit the population below the carrying capacity. Recruitment rates are decoupled from birth rates and this could regulate abundance. This hypothesis is known as recruitment limitation (Doherty, 1983; Hughes, 1984; Underwood and Denley, 1984; Roughgarden et al., 1985; Victor, 1986; Karlson and Levitan, 1989). Open populations could potentially be controlled by either density-dependent or independent processes affecting recruitment and/or mortality, but the relative importance has seldom been measured.

The recruitment limitation model has become arguably the most popular model of marine population regulation. For such populations settlement by larvae is predicted to be insufficient for the population to saturate available resources (Doherty, 1983). Two facets of the recruitment limitation model are firstly, that mortality rates must be density independent and secondly, that adult abundance should vary linearly with abundance of new recruits. Several studies of tropical fish (Victor, 1986, Doherty and Fowler, 1994), temperate fish (Levin, 1994), temperate barnacles (Connell, 1985) and corals (Harriott, 1985) have shown that mortality of new recruits was density independent. This would lead to varying numbers of adults in response to fluctuations in recruitment and these populations must, by definition, be recruitment limited. Mortality rates could only regulate populations if they were density-dependent (Nisbet and Gurney, 1982). Thus it can be seen that testing for density-dependent mortality allows easy discrimination between the importance of these two processes, recruitment versus mortality (Mapstone and Fowler, 1988).

Recent work on a common pacific damselfish *P. moluccensis*, on patch reefs in the southern Great Barrier Reef suggests that this species is recruitment limited (Doherty and Fowler, 1994a,b). However, since these southern reefs are well known to have low levels of recruitment (Sale et al., 1984; Williams, 1991), the results may not be generally applicable. Density-dependent mortality is more likely to occur where recruitment was high. At Lizard Island in the northern section of the Great Barrier Reef, levels of recruitment may be substantially higher than those on southern reefs. Sweatman (1985) has indicated that rates of recruitment of two damselfish species at Lizard Island may be on average 10 - 20 times greater than in similar habitats at One Tree, 1200km to the south. To my knowledge, no published studies have attempted to compare latitudinal variation in recruitment with latitudinal variation in adult distributions. This study measured patterns of new recruit and adult abundance of *P. moluccensis*, and basic demographic parameters such as rates of recruitment, growth and mortality, in order to assess which processes may be influencing this species at Lizard Island. These results were then compared to those obtained in the southern study.

5.3 Materials and methods

5.3.1 Local scale temporal and spatial variation in adult densities and recruitment

Lizard Island was divided into three zones according to exposure - sheltered, lagoon and exposed. Densities of new recruits and adults of *P. moluccensis* were monitored in permanent transects at four contiguous reef sites, two in each of the sheltered and lagoonal zones over three years. These were: Granite bluff, Osprey Islet, Lizard Head and South, (Fig 1). Twelve 10m x 1m transects, usually 1m to 10m apart, were individually marked using nails and garden tags. Fish were counted as either new recruits (10-24.9mm SL) or adults (>25mm SL) in January 1994 and this was repeated along the same transects in January 1995 and 1996. Spatial and temporal variation in densities of adults and new recruits were analysed using repeated measures ANOVA. The univariate test was used because it is more robust than MANOVAR. The analysis included site and time as random factors. In addition, the Greenhouse - Geisser Epsilon correction factors for sphericity were both approaching 1.0, indicating that the assumptions regarding correlation structures would not be violated (Green, 1993). Tests indicated that assumptions of normality and heteroscedasticity were not violated by the data.

5.3.2 Local scale variation in population structure

The size structures of local populations were assessed at the same four sites: Granite bluff, Osprey Islet, Lizard Head and South in January 1994 and 1995. All individuals of *P. moluccensis* were counted along twelve, 10m x 1m transects and assigned into one of five 10mm size classes.

Age structures were assessed at three sites using otolith readings. Sixty individuals were collected from sites adjacent to three of the four local variation sites from section 1. They were adjacent to Granite, Osprey and Lizard Head (Granite A, Osprey A, Lizard Head A). Sixty *P. moluccensis* were collected from Osprey A in October 1994 and from Granite A and Lizard Head A in February 1995 using the fish anaesthetic quinaldine. Individuals were killed by cold shock. Standard length was measured using callipers, sagittal otoliths were removed, cleaned and stored. Transverse sections of one otolith per individual were prepared to obtain age estimates (sensu chapter 4). Age structures were compared using a chi-square analysis. For the purpose of this comparison it was necessary to reconstruct a value for cohort 0+ individuals at Osprey A using the age structures from the other two sites. Recruitment occurs between November and February, and otolith increments were laid down in this species in the Austral Spring (August, September, chapter 4). Hence the October collection from this site had no cohort 0+ individuals.

5.3.3 Broad scale spatial and temporal variation in recruitment and adult density

Spatial and temporal variation in the broad scale distribution and abundance of *P. moluccensis* was investigated at two larger scales. Within each of the three zones around Lizard Island, three random sites (hundreds of metres to a few kilometres apart) were censused (Fig 1). At each site fish were counted along twelve 10m x 1m transects placed haphazardly each sampling time. Fish were counted as either new recruits (10-24.9mm SL) or adults (>25mm SL) in January 1995 and 1996. Spatial and temporal variation in the densities of adults and new recruits of *P. moluccensis* at this broad scale were investigated using a three-way nested ANOVA. The analysis included time and site as random factors and zone as a fixed factor. The analysis was partially heirarchical because sites were nested within zones. Assumptions of normality and heteroscedasticity were met by the data.

5.3.4 Validation of density estimates for survival

Population density was assessed using two base units: area and population (sensu Jones, 1987). When area is used to assess mean density, areas with very few individuals may be censused and given equal weighting to areas with high numbers of individuals. This involves counting the number of individuals along random transects or in random quadrats. However, this approach does not estimate the average local density experienced by individuals in the population. The latter could be estimated by counting the number of conspecifics around random individuals. Sampling in this way would give a greater weighting to areas where there were more fish and therefore a greater percentage of the population. This information is more relevant because it provides an estimate of the density of conspecifics that an average individual of the population is likely to be experiencing. For the purpose of this chapter this mean density calculated from a population base unit is called mean effective density (Jones, 1987).

The mean effective density was calculated from the mean density using the equation:

$$ED = \frac{x \times (x \times y)}{\Sigma\ (x \times y)}$$

Where

x = density classes of *P. moluccensis*

y = frequency of transects for each density

5.3.5 Spatial variation in survival

Mortality was assessed at each of the four local scale sites and for the three zones of the broad scale study. It was calculated according to the following equations:

$$\%M = \frac{(R - C1)}{R}$$

Where

%M = percent mortality during the first reef associated year

R = abundance of cohort 0+ in year 1, new recruits /100m^2

C1 = abundance of cohort 1+ in year 2, /100m^2

The percentage of adults that were 1 year old was calculated using the age structures for Lizard Island in January. This figure was then used to assess the number of adults in cohort 1 (C1) counted on the transects. Because the local scale censuses used the same transects over three years, mortality estimates could be obtained at transect level. Estimates of mortality during the first reef associated year were calculated for new recruits settling in 1994 and 1995. At the broad scale, mortality estimates during the first reef associated year, were calculated for new recruits setting in 1995 at nine sites.

5.3.6 The relationship between recruitment, mortality and adult density

As stated previously, three relationships have often been used to assess the relative importance of recruitment versus mortality in regulating populations (Caley et al., in press). The first is the relationship between adult density and recruitment density (Doherty and Fowler, 1994). A positive linear relationship will indicate recruitment limitation provided there is no spatial variation in mortality. I followed Doherty and Fowler (1994) and used mean recruitment density over several years to overcome problems of fluctuating recruitment. The second relationship that has been used is percent mortality as a function of recruitment density. If populations are not recruitment limited there should be no positive relationship. The third is natural log of density against time for cohorts of different size. If populations are recruitment limited, the lines should not converge. The three relationships were plotted at the transect scale for the local study and at site scale for the broad study. The r^2 value was used to assess whether the relationships were linear or curvilinear. In all cases both linear and log equations were used to see which best described the data, and were only plotted if statistically significant.

5.4 Results

5.4.1 Local scale temporal and spatial variation in adult densities and recruitment

The abundance of adults of *P. moluccensis* varied over time, but the patterns of change differed among the four sites (Fig 2, Table 1). Densities of adults declined at three sites over three years. At the fourth site adult densities decreased between January 1994 and January 1995 and then increased in January 1996. The site with the highest abundance of adults in 1994 was Granite and by 1996 this was the site with the lowest abundance of adults. Overall densities of adults varied from 60 to 175 per $100m^2$.

Table 1 Repeated Measures ANOVA table for adult densities at four sites over three years. G-G is the corrected P-value obtained by applying the Greenhouse-Geisser Epsilon correction factor for sphericity.

Between Transects

Source	DF	SS	MS	F	P
SITE	3	15386.1111	5128.7037	2.07	0.1179
Error	44	109011.1111	2477.5253		

Within Transects

Source	DF	SS	MS	F	G - G
Time	2	64072.2222222	32036.1111111	25.54	0.0001
Time*Site	6	85872.2222222	14312.0370370	11.41	0.0001
Error	88	110388.8888889	1254.4191919		

Table 2 Repeated Measures ANOVA table for new recruit densities at four sites over three years. G-G is the corrected P-value obtained by applying the Greenhouse-Geisser Epsilon correction factor for sphericity.

Between Transects

Source	DF	SS	MS	F	P
SITE	3	42836.1111	14278.70370	5.71	0.0022
Error	44	110027.77778	2500.63131		

Within Transects

Source	DF	SS	MS	F	G - G
Time	2	132776.38889	66388.1944444	34.80	0.0001
Time*Site	6	108434.7222222	18072.4537037	9.47	0.0001
Error	88	167855.5555556	1907.4494949		

Patterns in the densities of new recruits of *P. moluccensis* also varied over time, with concordant patterns at some sites but not others (Fig 2, Table 2). Recruitment was relatively consistent between 1994 and 1995 but increased at three of the four sites in 1996. Again, Granite was atypical, showing a relatively constant recruitment over three years. Overall, Osprey had the highest recruitment, followed by Granite, Lizard Head and South respectively. Densities of new recruits varied from 0 to 160 (per $100m^2$) and there was little relationship between patterns of change in juveniles and adults.

5.4.2 Local scale variation in population structure

There was significant spatial variation in the size structures at the four local scale sites ($p < 0.001$, Table 3).The two extremes were at Osprey and South (Fig 3). Over

Table 3 Chi-square test for spatial variation in size frequency distributions of *P. moluccensis* at four sites (n = 12 transects per site).

SL/mm	Liz Head A		Granite		Osprey		South		Totals
	O	E	O	E	O	E	O	E	
10-19.9	22	18.69	19	18.50	28	18.69	5	18.12	74
20-29.9	28	25.76	25	25.50	37	25.76	12	24.97	102
30-39.9	38	43.70	46	43.25	30	43.70	59	42.36	173
40-49.9	10	9.85	7	9.75	3	9.85	3	9.35	39
Totals	98		97		98		98		388

OVERALL CHI-SQUARE	53.22
P-VALUE	0.0000
DEGREES OF FREEDOM	9

the study period most individuals at Osprey were in the smaller size classes with very few >40mm and none in the largest size class. However, at South there were relatively few individuals in the smaller size classes, recruitment was extremely low relative to the other sites, but the majority of the population there were over 30mm SL and this was the only site with individuals >50mm SL. The high overall losses from Granite Bluff were mostly due to losses from the 10-20mm new recruits and from the 30-40mm size class. All other sizes remained unchanged. At Osprey, between January and April 1994, the 10-20mm class decreased and the 20-30mm increased, suggesting net growth. All other classes remained unchanged. Between April 1994 and January 1995, however, there was a large recruitment pulse yet still there was a net loss from this site due to decreases in the 20-40mm classes. The only size class which increased over the study period at Lizard Head was the smallest due to the recruitment pulse in January 1995. All other sizes either decreased or remained unchanged.

Table 4 Chi-square test for spatial variation in age structures of *P. moluccensis* at three sites (n = 60 individuals per site).

Age	Liz Head A		Granite A		Osprey A		Totals
	O	E	O	E	O	E	
0+	25	34.69	38	34.69	40	33.62	103
1+	21	22.23	20	22.23	25	21.54	66
2+	26	19.20	20	19.20	11	18.60	57
3+	10	10.44	15	10.44	6	10.12	31
4+	10	6.06	1	6.06	7	5.88	18
5+	5	4.38	3	4.38	5	4.24	13
Totals	97		97		94		288

OVERALL CHI-SQUARE	21.98
P-VALUE	0.0152
DEGREES OF FREEDOM	10

Age structures suggested similar longevities at the three sites (Fig 4). The oldest individual at all sites was 6 years old. There was significant spatial variation in the age structures of *P. moluccensis* (p = 0.015, Table 4). The bulk of the population at South Bay Point in October were either 1 or 2 years old. At Lagoon channel 69% of the population were less than 2 years old with equal numbers in cohorts 0, 1 and 2. At Turtle Bay 38% of the population were new recruits, twice the size of the next largest age class, and 93% were less than 3 years old.

5.4.3 Broad scale spatial and temporal variation in adult densities and recruitment

There was considerable broad scale variation in densities of adults (Fig 5, Table 5a) There was a significant interaction between time and zone and between both time and site for adults, indicating a high degree of temporal and spatial variation in their

Table 5. ANOVA table for a) adult densities and b) new recruit densities in three broad scale zones with three sites nested in each zone and at two times.

Source	DF	SS	MS	F	P
a) ADULTS					
Time	1	289.35185	289.35185	0.32	0.5744
Zone	2	58514.81481	29257.40741	31.99	< 0.0001
Site(Zone)	6	34563.88889	5760.64815	6.30	< 0.0001
Time*Zone	2	29159.2592	14579.62963	15.94	< 0.0001
Time*Site(Zone)	6	37763.88889	6293.9814	6.88	< 0.0001
Error	198	181075.0000	914.5202		
b) NEW RECRUITS					
Time	1	246037.5000	246037.5000	103.96	< 0.0001
Zone	2	46977.7778	23488.8889	9.93	< 0.0001
Site(Zone)	6	107622.2222	17937.0370	7.58	< 0.0001
Time*Zone	2	215744.4444	107872.2222	45.58	< 0.0001
Time*Site(Zone)	6	52788.8889	8798.1481	3.72	0.0016
Error	44	49050.00000	1114.77273		

densities. In 1995 the highest densities of adults were at Granite and Mermaid on the sheltered side and at Bird Islet on the Exposed side. But in 1996 those three sites had decreased adult densities while densities at all lagoon sites increased. Patterns of abundance of new recruits of *P. moluccensis* were also significantly variable in space and time (Fig 6, Table 5b). At most sites densities of recruitment were higher in 1996 than in 1995. At three sites, Granite and Mermaid on the Sheltered side and at Bird Islet on the exposed side, new recruit densities were very similar across years. Patterns of relative densities between that zones were not consistent between years. There was also a similar pattern to the adults, because in 1995 there were low numbers of new recruits at all lagoon sites and yet in 1996 these sites had the highest numbers seen.

5.4.4 Validation of density estimates for survival

The mean density of a population varied according to the method used for calculation (Table 6). When area was the base unit mean density was 3.86 individuals per $10m^2$. When the population was the base unit the mean effective density was 7.98 individuals per $10m^2$ indicating that most individuals were at twice

Table 6 Calculation of a) mean density and b) mean effective density of *P. moluccensis* by using a) transects and b) individuals as replicates.

Density ($10m^2$) (x)	Frequency of Transects (y)	Frequency of Individuals (x * y)	x * (x * y)
0	32	0	0
1	8	8	8
2	10	20	40
3	11	33	99
4	3	12	48
5	14	70	350
6	4	24	144
7	7	49	343
8	4	32	256
9	3	27	243
10	1	10	100
11	2	22	242
12	4	48	576
13	1	13	169
14	1	14	196
15	1	15	225
16	1	16	256
Total	107	413	3295

a) Mean density (transects) = 413/107 = 3.86
b) Mean effective density (individuals) = 3295/413 = 7.98

the local density indicated by random transects.

5.4.5 Spatial variation in survival

Using the age structure information, the percentage of adults that were in cohort 1 was found to be 30.5% (Table 7). Mortality over one year of new recruits of *P. moluccensis* was variable at the four local scale sites (Fig 7). In some cases values for mortality were slightly negative, probably due to sampling error. The patterns in mortality between 1994 and 1995 were very different to those between 1995 and 1996. During the first time period, mortality at Lizard Head was the lowest of the four sites, but during the second period it was the joint highest. There was also spatial variation at a broader scale (Fig 8). Mortality rates between island zones were significantly different (Table 8). The highest mortality rates (90% ± 3) were on the exposed side of the island and the lagoon had the lowest mortality (10% ± 7).

5.4.6 The relationship between recruitment, mortality and adult density

There was a poor relationship between relationship adult and new recruit densities of *P. moluccensis* among the permanent transects (averaged over three years) (Fig 9, $r^2 = 0.06$). That is, recruitment was a poor predictor of adult densities. Density of new recruits varied from 0 to 230 individuals per 100m^2. At low densities of recruits, adult numbers varied from 0 to 170 individuals per 100m^2.

When numbers of individuals in cohorts from 1994 and 1995 were followed through time the natural log of mean densities at these four sites converged slightly after one year, and in some cases the absolute sizes of the cohorts reversed (Fig 10). The rank order of cohort size after one year was not the same as they were at the time of recruitment.

There was a significant curvilinear relationship between percent mortality of new recruits over one year and new recruit density on transects at a local scale (Fig 11, $r^2 = 0.57$, $p < 0.001$). The declining curvilinear relationship explained 25% more of the

Table 7 Calculations of percentage of adults in cohort 1 from age frequency data for Lizard Island *P. moluccensis*

Age (years)	Population Frequencies (totals)	Population Frequencies (% of pop))	Adult Frequencies (% of Pop)	Adult Frequencies (% of adults)
0	38	31.67		
1	25	20.83	20.83	30.49
2	28	23.33	23.33	34.15
3	15	12.50	12.50	18.29
4	7	5.83	5.83	8.54
5	5	4.17	4.17	6.10
6	2	1.67	1.67	2.44
Total	180	100.00	68.33	

variation than a linear relationship. At low densities of new recruits the percent mortality varied from 0 to 100%. At higher densities of new recruits the spread of the data was much less.

At a broad scale there was a significant curvilinear relationship between mean adult density and mean new recruit density at the nine sites (Fig. 12, $r^2 = 0.54$, $p = 0.004$). Again, this explained greater variation than the linear relationship indicating that adult numbers were not increasing in direct proportion to recruitment ($r^2 = 0.41$).

When a single cohort from 1995 was followed over one year the log of the densities at seven sites converged while at two sites densities approached zero (Fig 13). The rank order of sites in terms of cohort size in 1996 differed markedly from the relative cohort sizes at recruitment.

There was a significant curvilinear relationship between percent mortality and density of new recruits between nine broad scale sites (Fig. 14, $r^2 = 0.53$, $p < 0.001$, linear relationship $r^2 = 0.41$). At two sites where the mean density of new recruits was between 40 and 50 individuals per $100m^2$ mortality approached 100%. There was a range of mean densities of new recruits from 24 to 98 per $100m^2$. Lowest mortality rates occurred at the two sites with the lowest mean densities of new recruits and were between 20 and 30 %.

Table 8 One way Anova on percent mortality of new recruits of *P. moluccensis* during the first reef associated year, in three broad island zones. (n = 3 sites per zone.)

Source	SS	df	MS	F	P-value
Between	5794	2	2897	11	< 0.00000
Within	1551	6	258		
Total	7345	8			

5.5 Discussion

The most clear result from this study is that knowledge of both recruitment and mortality patterns are necessary to explain patterns abundances of *P. moluccensis* at Lizard Island. Patterns in the distribution and abundance of this species at Lizard Island were not solely driven by patterns of recruitment, as predicted by the recruitment limitation model, but appear to be substantially influenced by density-dependent mortality at at least two sampling scales.

5.5.1 Local scale patterns

Patterns in densities of both adults and new recruits of *P. moluccensis* were variable between four sites across time. There was no clear relationship between adult densities and new recruit densities along transects at the four sites implying that factors other than recruitment must be influencing adult populations of *P. moluccensis* at these sites.

There were consistent extreme differences in the size structures of *P. moluccensis* at four sites which could be due to either differential recruitment, growth, mortality, migration or a mixture of these factors. Differential growth rates can probably be ruled out as growth was shown to be the same between three sites at Lizard Island (Chapter 4) Differential migration is unlikely for this species because there are now two tagging studies (Mapstone, 1988; Beukers et al., 1995) which have shown that individuals are very site attached. Mapstone (1988) showed that they rarely moved more than 1m. These patterns must, therefore, be due to the variability observed in both recruitment and mortality.

It was interesting that despite the extreme spatial variation in these size frequency distributions, indicating potentially differing life history strategies between sites, that there is consistency in longevity at 6 years old between 3 local sites at Lizard Island. However, longevities are not consistent across latitudes. *P. moluccensis* at Lizard Island were much shorter lived than those on southern patch reefs. At Lizard Island 100% of the individuals (n=180) examined were less than or equal to 6 years old. In contrast, approximately 50% (n = 183) at One Tree and nearly 60% (n = 162) from Wistari, were older than 6 years (Doherty and Fowler, 1994). Hence, the likelihood of recruitment limiting the population is increased due to the greatly reduced longevity. Average recruitment to Lizard Island was 40 / 100m^2 compared to 2 / 100m^2 at One Tree and 8 / 100m^2 at Wistari. It follows that if recruitment is greater and longevity is less on Lizard than on southern reefs, that mortality rates at Lizard Island must be higher. This could be for several reasons, firstly due to differences in the ecology of patch and contiguous reefs, secondly due to latitudinal differences, and / or thirdly due to the differences in mean recruitment density. It would be expected that the population at Lizard Island would show characteristics of a rapidly replacing population such as younger age at maturity and higher growth rates. Life history theory predicts that variable recruitment should lead to greater longevity and that reproductive effort should not all be spent on one year but spread over several years (Murphy, 1968). However, the patterns of variable recruitment and reduced longevity observed at Lizard Island do not concur with this theory.

There was a significant curvilinear relationship between percent mortality and density of new recruits of *P. moluccensis*, indicating some density dependence. In addition, this curve shows a high degree of variation at transect level. Variance could be due to either density-dependent or independent variability, it would be extremely difficult to separate the two (Caley et al., in review). Adding to the variation may be any error in the methods for calculating percent mortality. Also, censuses were carried out in February, and some new recruits may have spent up to four months on the reef at that time. This too would add to the variance. This variance was greatest at low abundances of recruitment suggesting that some other factor or factors were over-riding the relationship at these low recruitment densities.

5.5.2 Broad scale patterns

Patterns of densities of adults and new recruits of *P. moluccensis* varied significantly between sites and zones through time, and percent mortality was significantly variable between zones. In addition, the curvilinear relationships observed at nine sites over two years at Lizard Island between both adult density and percent mortality against recruitment indicate density-dependence and hence that post-recruitment processes would modify patterns laid down at settlement at Lizard Island. Various post-recruitment processes have been found to be important in determining the patterns of adult abundance, competition (Sammarco and Williams, 1982), predation (Shulman, 1985), habitat characteristics (Buchheim and Hixon, 1992) and disturbance. In this case a Crown of Thorns (COT) outbreak at Mermaid and Granite certainly contributed to the variability observed. A large percentage of the live coral at these sites died between January 1995 and the beginning of 1996, and abundances of adults of *P. moluccensis* decreased there. While recruitment to most sites was much higher in 1996 compared to 1995, densities of new recruits at COT infested sites remained the same between years.

This study contrasts with other results that showed that there was a strong linear relationship between mean adult densities and mean new recruit densities of *P. moluccensis* on seven reefs in the Capricorn Bunker Group (Doherty and Fowler, 1994a,b). When the two lines are compared it can be seen that reefs in the Capricorn Bunker Group have higher densities of adults compared to sites at Lizard Island with the same densities of new recruits (Fig. 15). This could be due to differences in scale of sampling or could represent regional differences. Doherty and Fowler's (1994) results were based on a larger scale comparison of different reefs. In his review, Williams (1991) suggested that evidence to date shows that recruitment is more likely to be limiting between reefs than within reefs where there is increasing evidence that post-recruitment processes are of importance (Doherty, 1983; Robertson, 1984; Shulman, 1985; Hixon and Beets, 1993).

However, the data collected by Doherty and Fowler (1994) may not be as different from those obtained here as it first appears. They had two main data sets which they used to show recruitment limitation. The first showed a linear relationship between adult abundance and magnitude of recruitment. However, they did find an exception in this relationship. At Lady Musgrave Reef the density of adults was significantly greater than that to all other reefs but the density of new recruits was not significantly different to two other reefs. Although it only occurred at one site out of seven it is evidence of density dependence and it is interesting that it occurred at the site with the highest recruitment. The justification for removal of Lady Musgrave Reef from the analyses was that it was a significant outlier from the rest of the data with lower abundance than expected from the observed level of recruitment. I would argue that such an effect would be exactly why this reef should be included in the analyses. This is key evidence showing density dependence and it directly contradicts the recruitment limitation hypothesis which they are trying to prove. Therefore, it should not have been ignored. Its exclusion leaves the question that if this reef had been included in their analyses would the result have backed the recruitment limitation hypothesis?

They also have data from Lady Musgrave showing that strong age classes were maintained through the duration of the study. This scenario, however, can arise under density-dependent conditions as well as through recruitment limitation (Frogner, 1980; Roughgarden et al., 1985; Warner and Hughes, 1988). It is by no means conclusive evidence for the recruitment limitation hypothesis. Mapstone (1988) found similar results at another reef in the Capricorn Bunker Group, One Tree Island. He found that at the within reef level patterns of recruitment were mostly maintained in the adult population. However, there were exceptions to this and he concluded that the relative importance of recruitment and demersal processes varied considerably. It would appear that these studies all found that natural variation in recruitment success may affect the importance of post-recruitment processes. This type of interaction between processes has been shown in another damselfish *Pomacentrus amboinensis* at One Tree Reef (Jones, 1990).

This study shows clearly that single process theories are inadequate for describing the distribution and abundance of *P. moluccensis* at Lizard Island, where it seems likely that one or more processes were involved. While there is some support for the recruitment limitation theory (Hughes, 1984; Keough, 1984; Doherty and Fowler, 1994) in some times and at some places, there is an ever increasing literature which have empirical evidence that a pluralistic approach to population dynamics is necessary if generalisations are to be made (Warner and Hughes, 1988; Forrester, 1990; Jones, 1990; Menge, 1991). Future models should include both recruitment and post-recruitment mortality and include potential for variation in whether these are density-dependent or independent. The only way to obtain conclusive evidence for the relative importance of these two processes would be to manipulate recruitment and measure mortality rates over time. In addition, any post-recruitment manipulative studies should be aware of the importance of initial recruitment density. These type of manipulations will need to be performed if we are to isolate exactly which processes are most important under a given set of conditions. From this information it would be possible to form theories which are of universal significance.

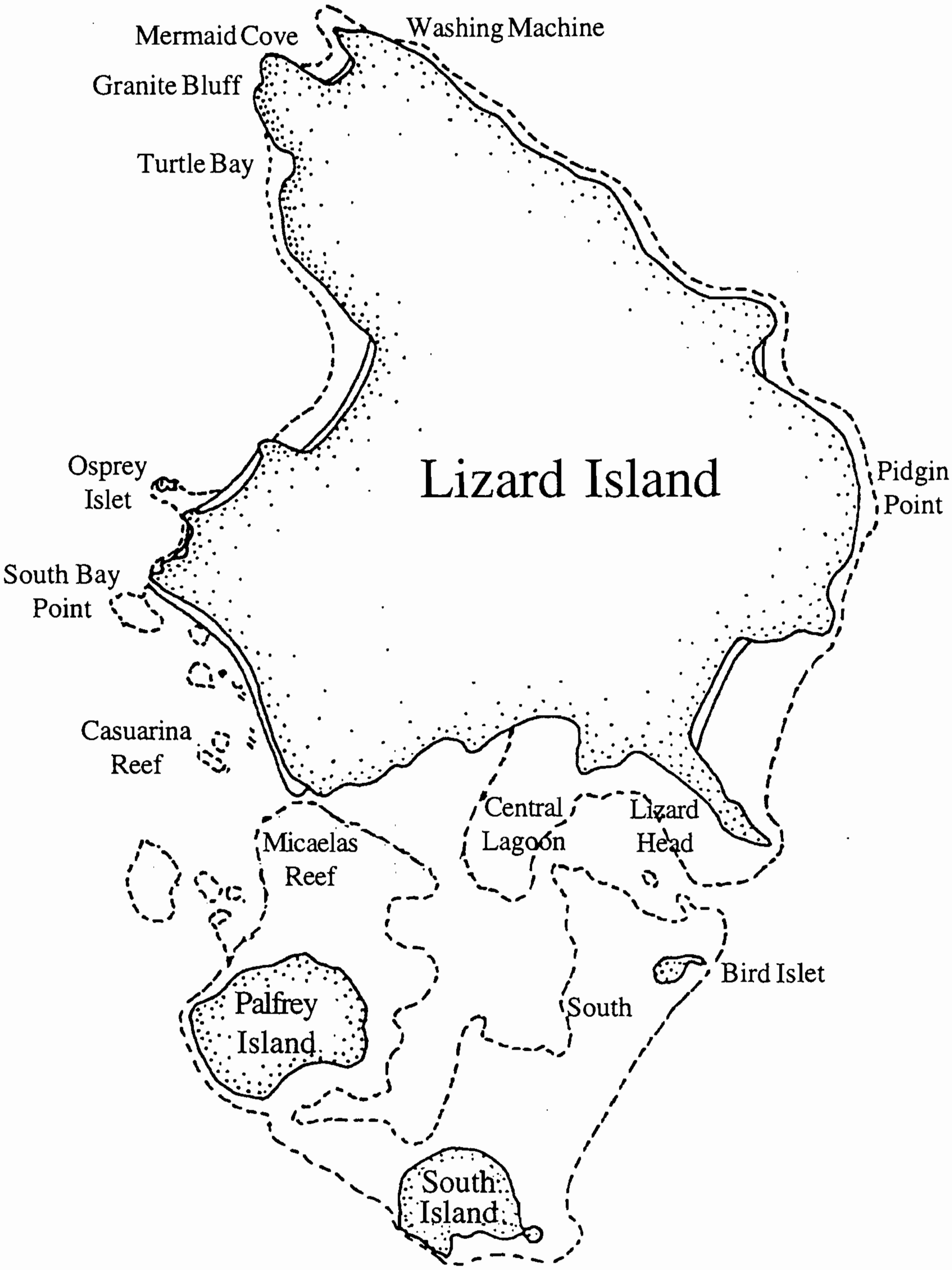


Fig 1 Map of Lizard Island showing study sites

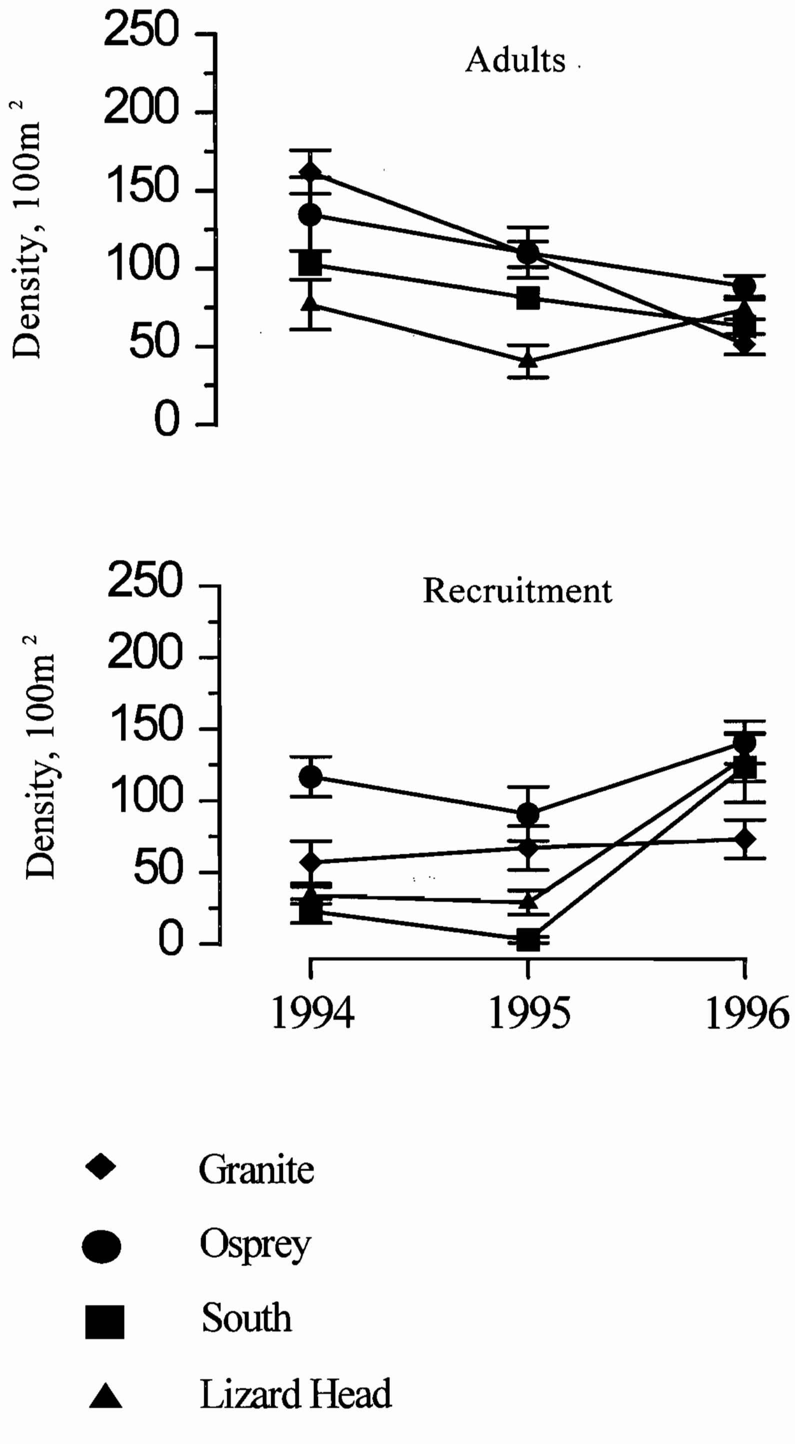


Fig 2 Densities (100m^2) of adults and new recruits ($\bar{x}$ ± SE) of *Pomacentrus moluccensis* in January 1994, 1995 and 1996 at four sites (n = 12 transects per site).

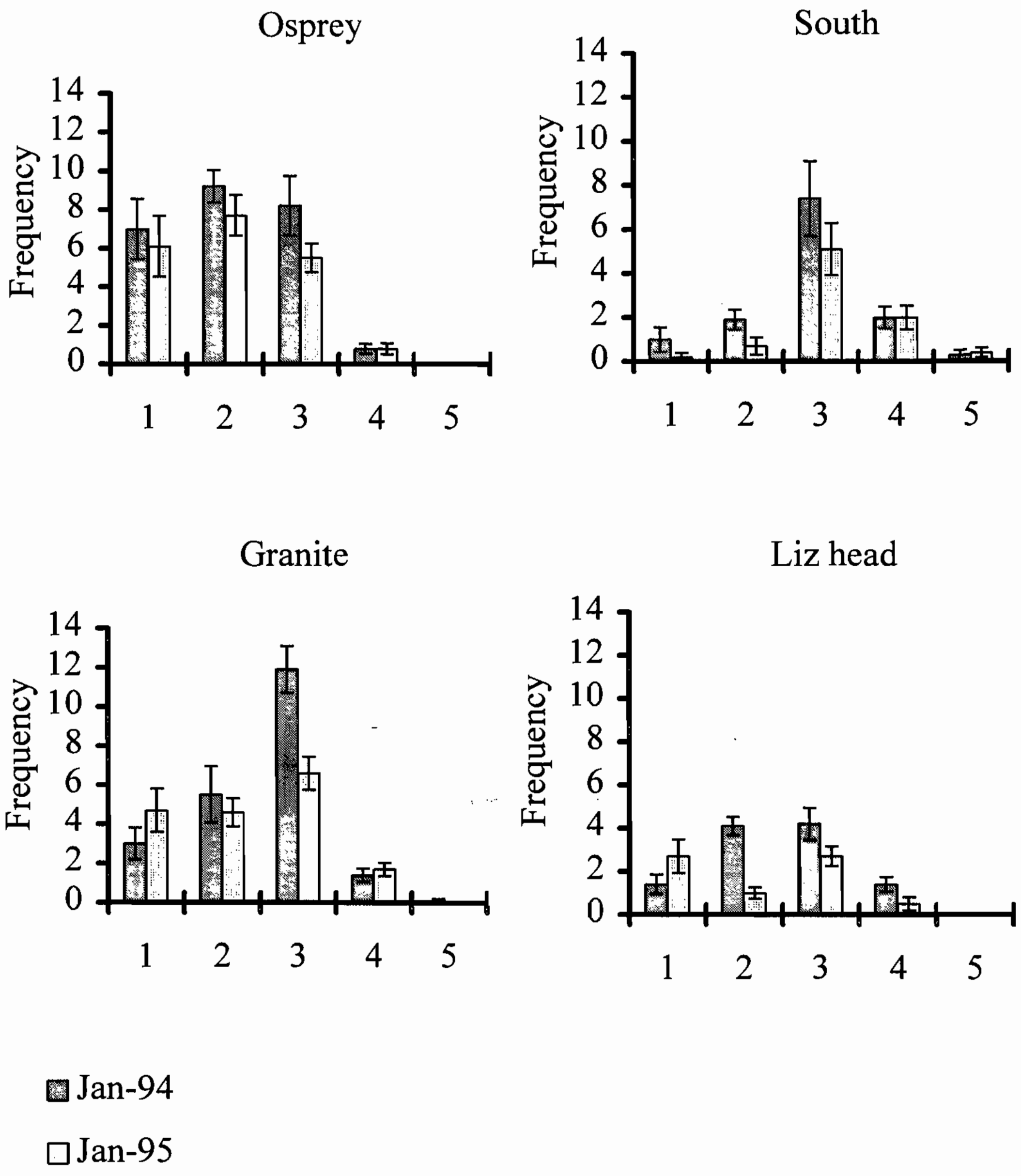


Fig 3 Size frequency distributions ($\bar{x}$ ± SE) of *Pomacentrus moluccensis* in 5 size classes at four sites in January 1994 and 1995 (n = 12 transects per site). The first size class was 10 - 19.9mm SL and they continued in 10mm classes up to > 50mm.

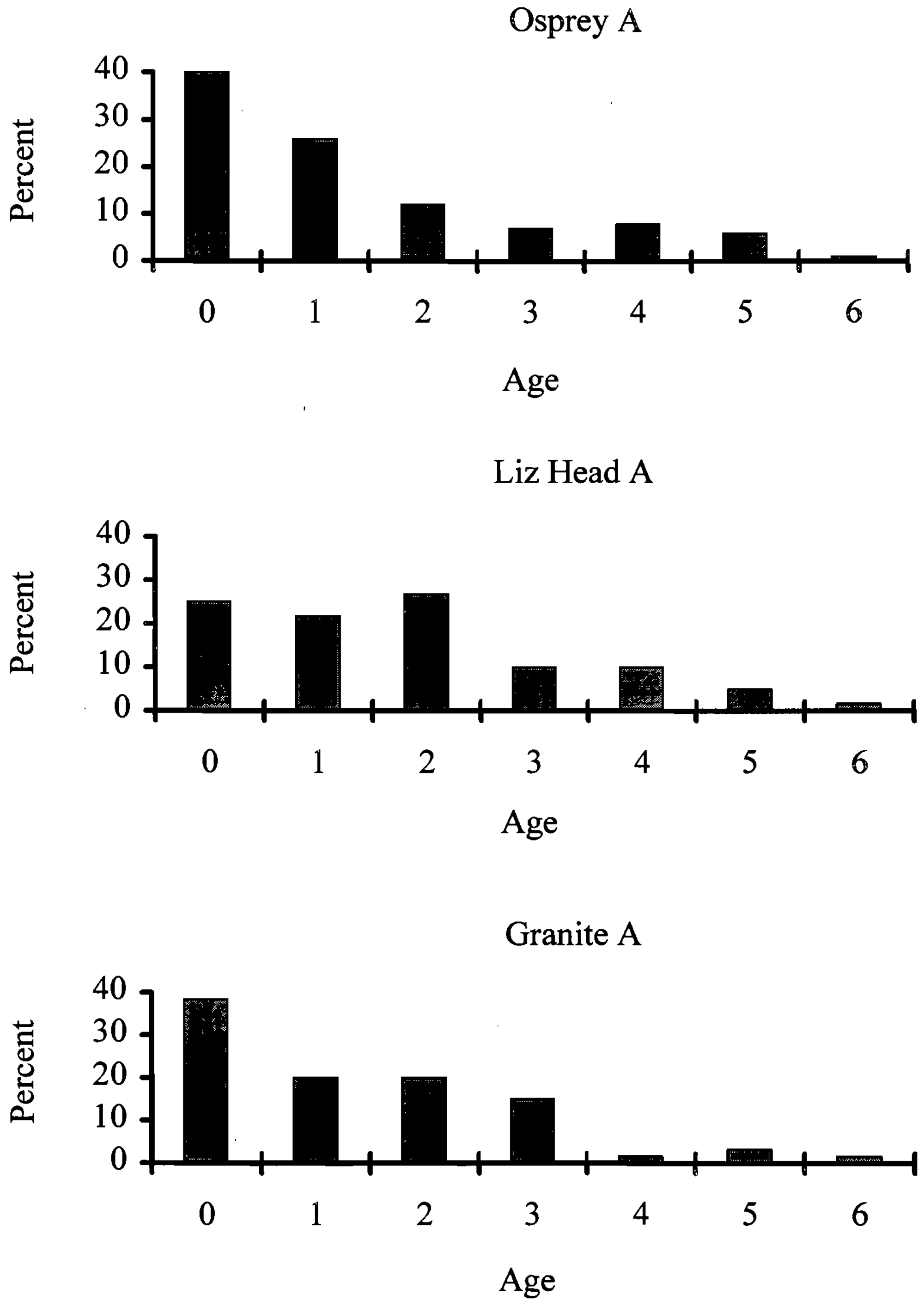


Fig 4 Age structures (percent) of ***Pomacentrus moluccensis*** at Osprey A, Liz Head A and Granite A in January 1995 (n = 60 individuals per site).

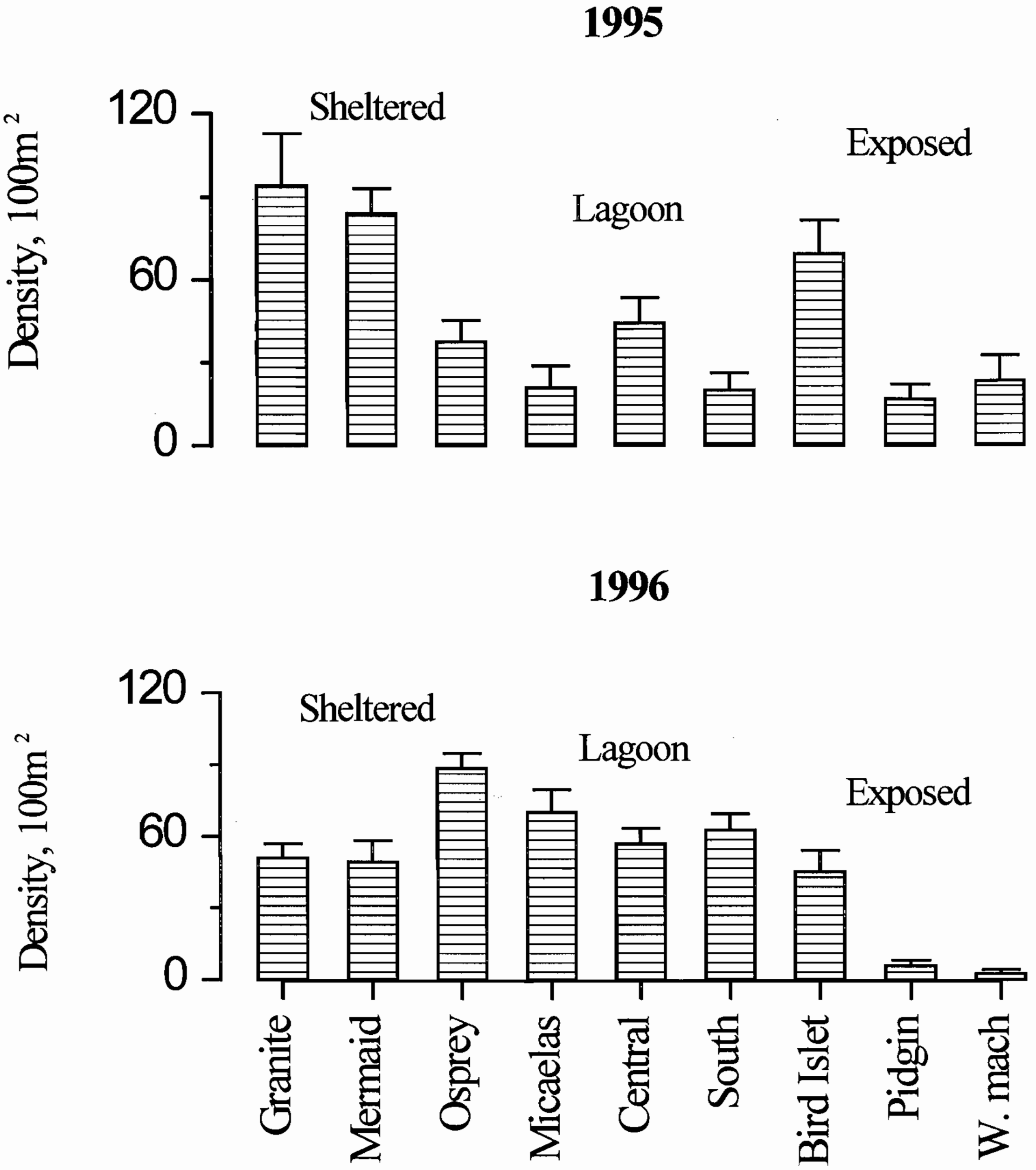


Fig 5 Density of adults (100m^2) of *Pomacentrus moluccensis* at a broad scale ($\bar{x}$ ± SE) , in three zones, and three sites per zone, in January 1995 and 1996 (n = 12 transects per site).

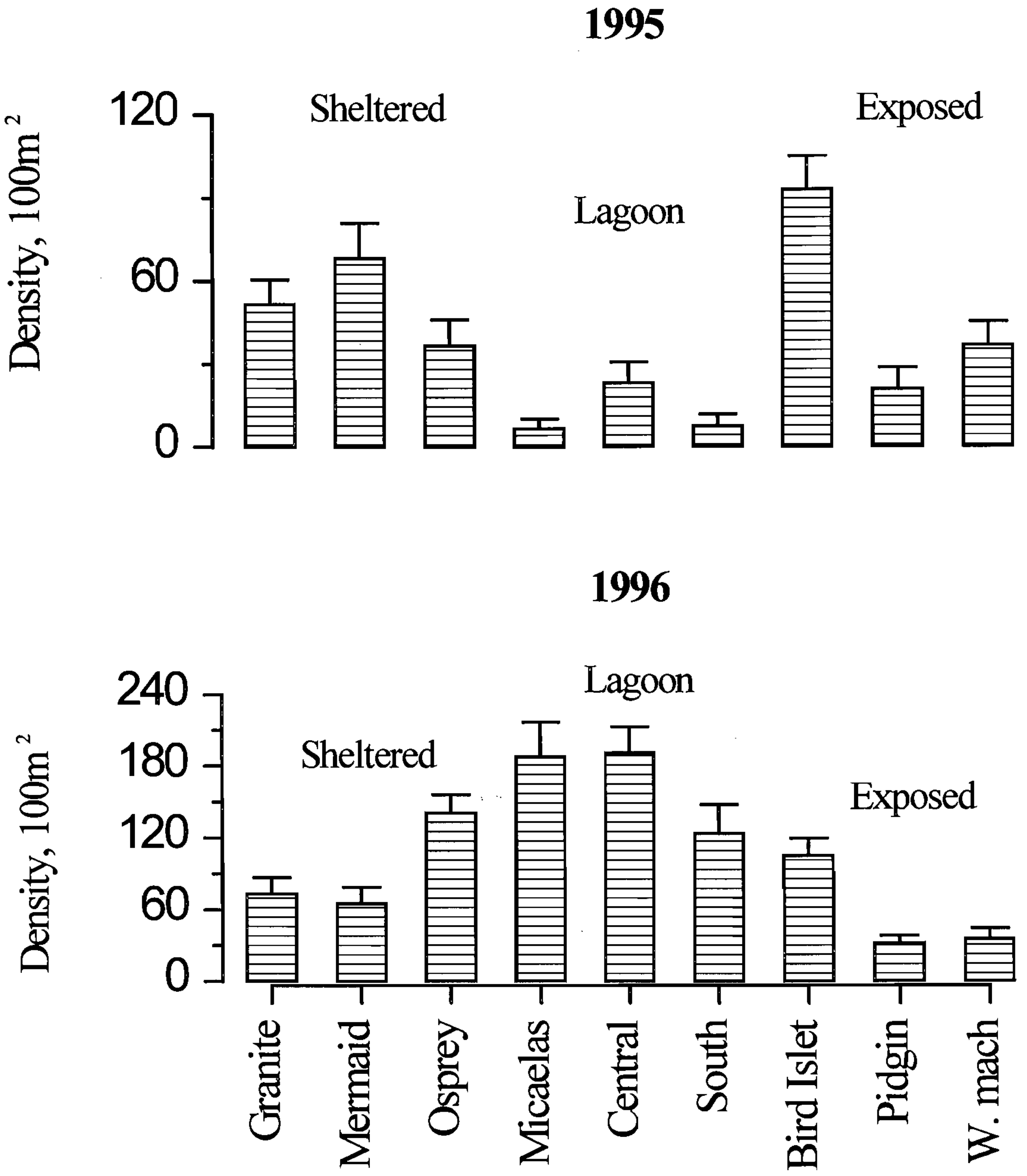
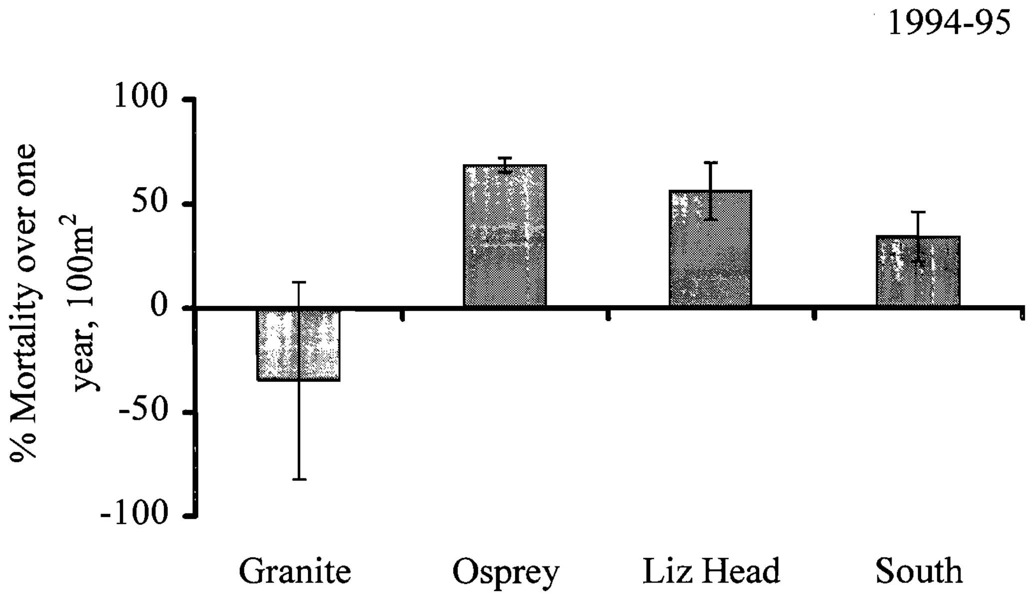


Fig 6 Density of new recruits ($100m^2$) of *Pomacentrus moluccensis* in three zones ($\bar{x}$ ± SE), and three sites per zone, in January 1995 and 1996 (n = 12 transects per site). Note values on y axis for 1996 go to 240 not 120 as for other graphs.



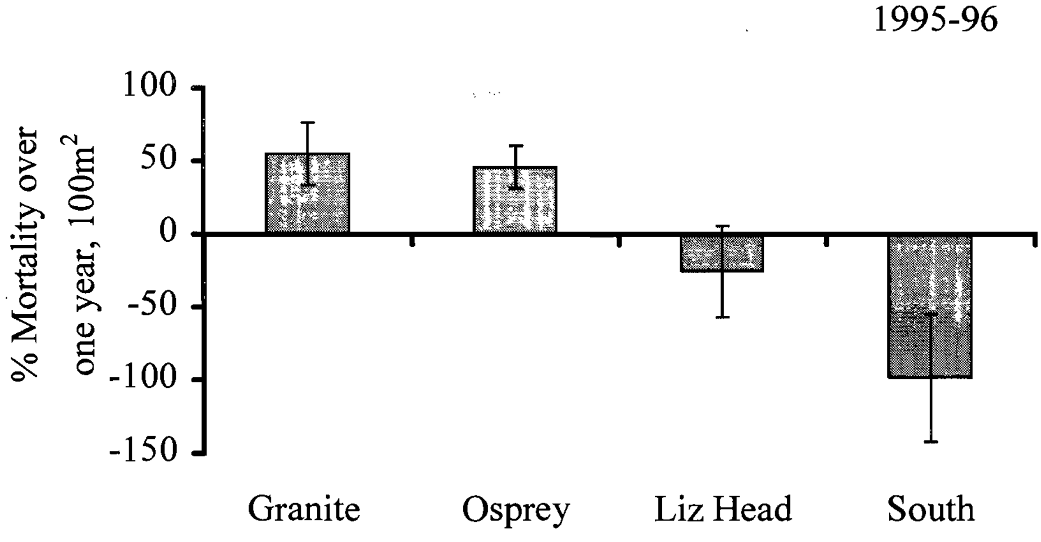


Fig 7 Percent mortality of new recruits of *Pomacentrus moluccensis* ($\bar{x}$ ± SE) at four local scale sites, between 1994 and 1995 and between 1995 and 1996 (n = 12 transects per site).

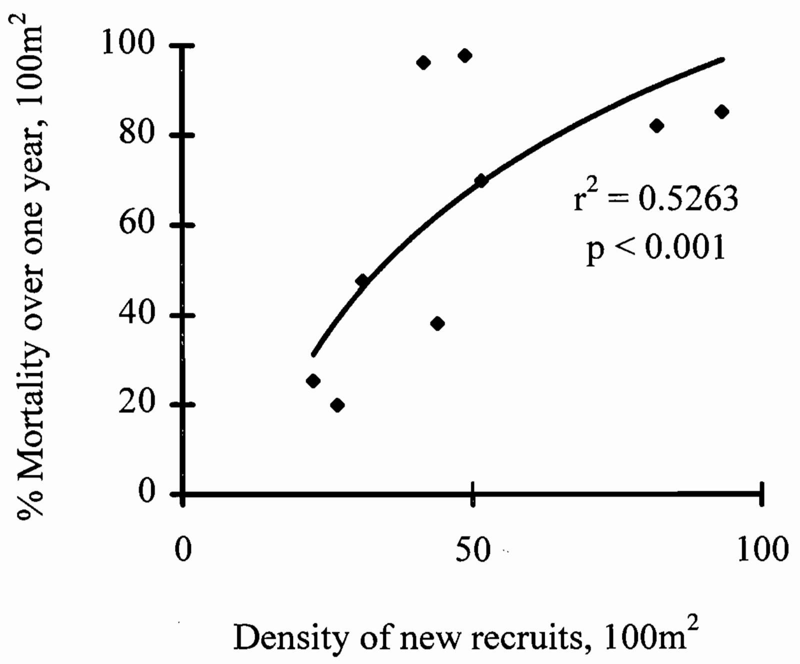


Fig 8 Percent mortality of new recruits of *Pomacentrus moluccensis* (x̄ ± SE) between three broad scale island zones, classified according to exposure (n = 3 sites per zone).

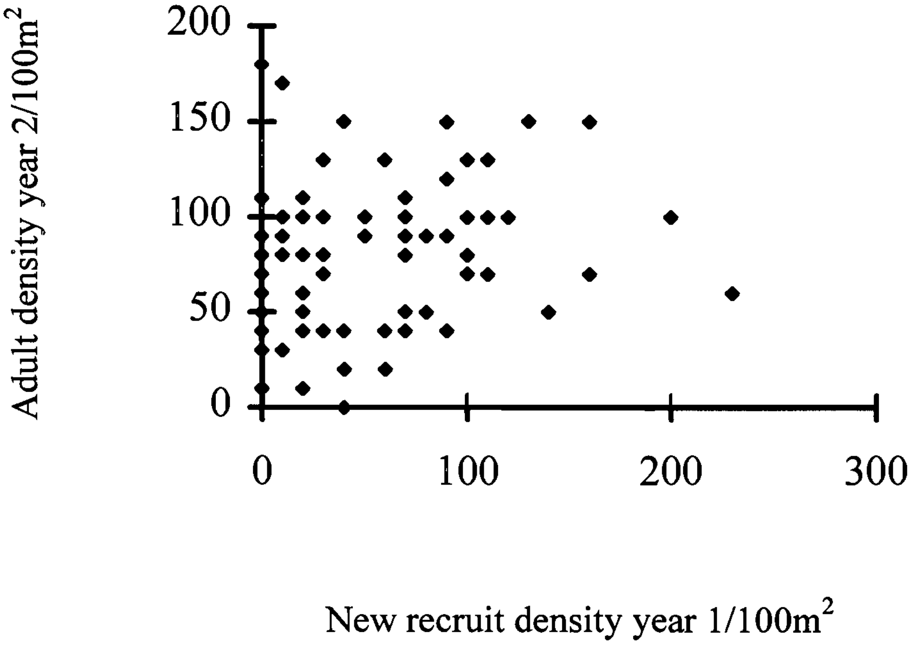


Fig 9 The relationship between densities of adults of *Pomacentrus moluccensis* on transects at four local sites in 1995 and 1996 and new recruit densities on the same transects in the previous year (n = 96 transects).

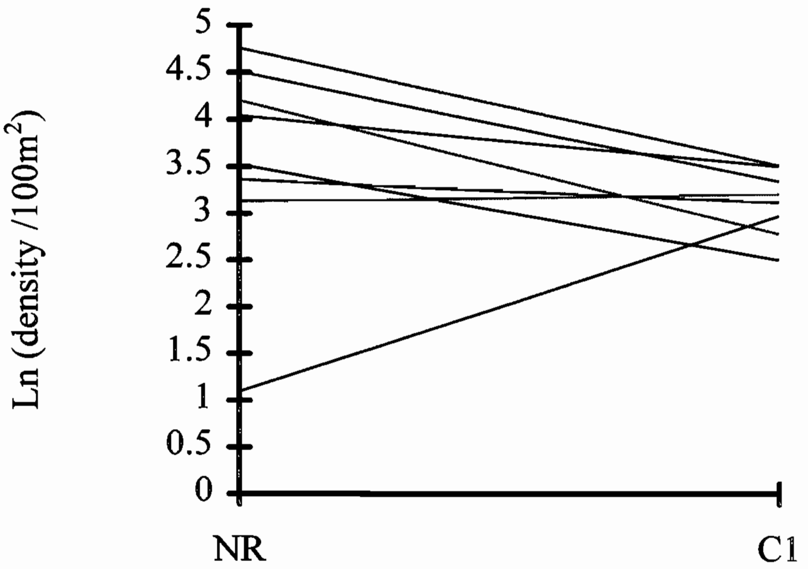


Fig 10 Natural log of the densities of *Pomacentrus moluccensis* as new recruits (NR) in the first year and as cohort 1+ (C1) in the following year. New recruits settling in 1994 and in 1995 were followed at four local scale sites (n = 12 transects per site).

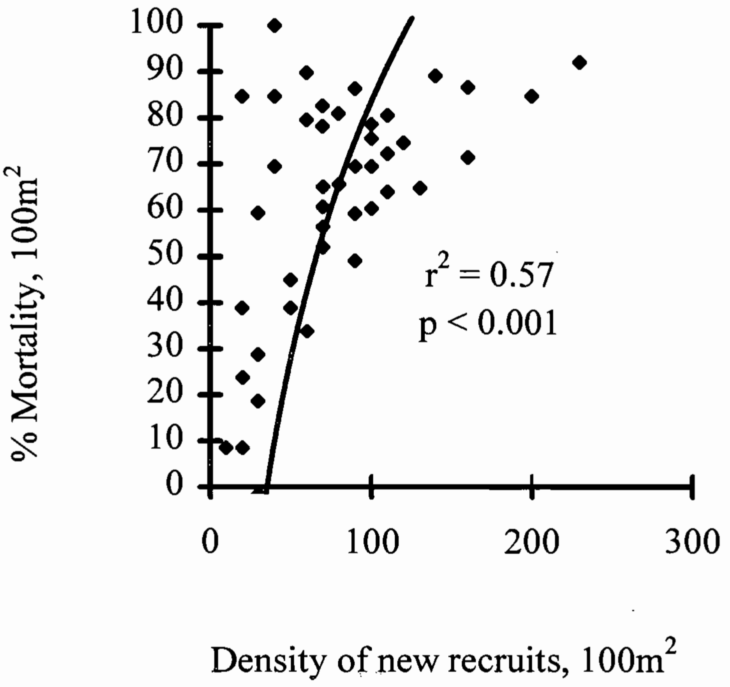


Fig 11 Percent mortality over one year of new recruits of *Pomacentrus moluccensis* against density ($100m^2$) at transect level. Mortality was plotted for new recruits settling in 1994 and 1995 to four local scale sites (n = 12 transects per site).

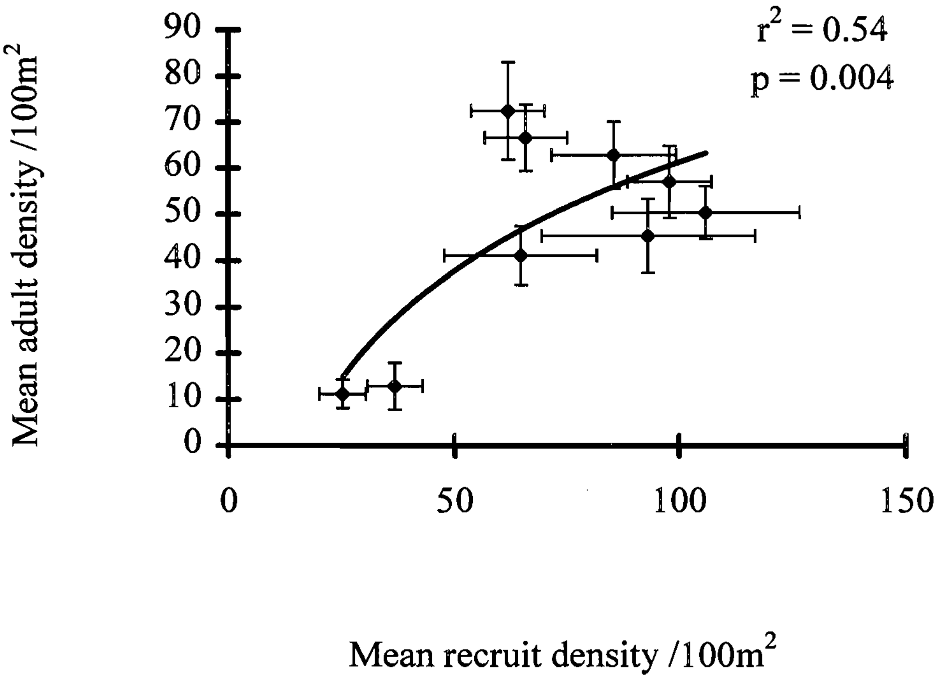


Fig 12 Mean density of adults ($\bar{x}$ ± SE) of *Pomacentrus moluccensis* against mean density of new recruits ($\bar{x}$ ± SE) over two years, 1995 and 1996, at nine broad scale sites at Lizard Island (n = 12 transects per site).

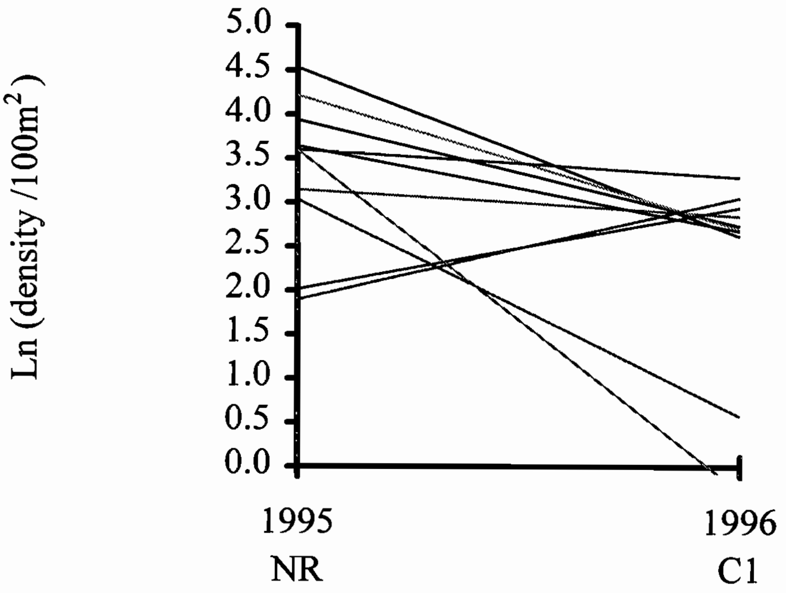


Fig 13 Natural log of the densities of *Pomacentrus moluccensis* as new recruits (NR) in 1995 and as cohort 1+ (C1) in 1996, at nine broad scale sites (n = 12 transects per site).

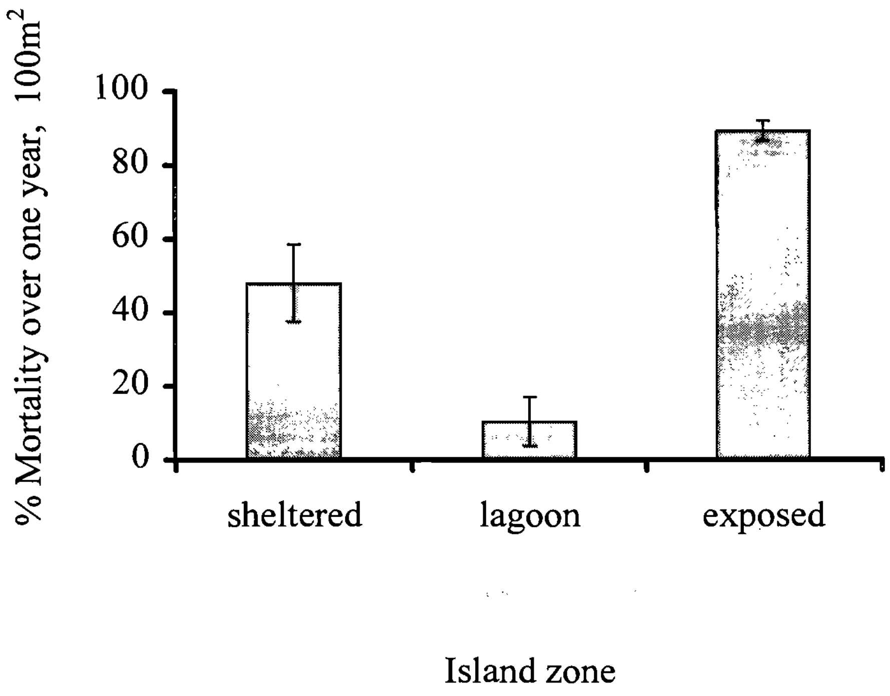


Fig 14 Percent mortality over one year of new recruits of *Pomacentrus moluccensis* against density ($100m^2$). Mortality was plotted for new recruits settling in 1995 to nine broad scale sites (n = 12 transects per site).

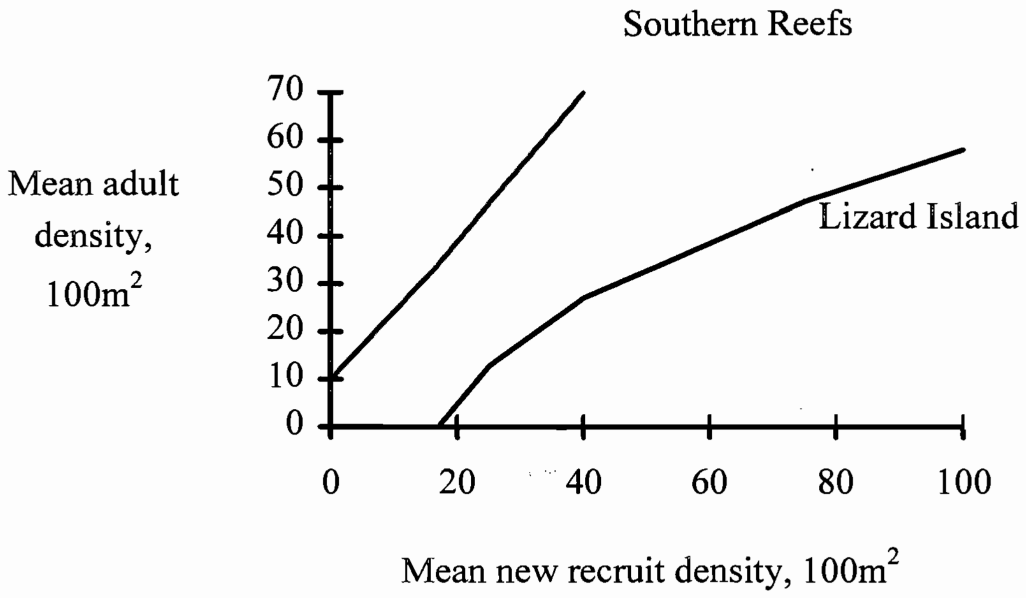


Fig 15 Comparison of the relationship between mean density of adults and mean density of new recruits of Pomacentrus moluccensis on reefs in the Capricorn Bunker group (sensu Doherty and Fowler, 1994) and at nine sites around Lizard Island. All densities over $100m^2$.

CHAPTER 6

Effects of habitat association and complexity on the abundance and mortality of a coral reef fish population

6.1 Abstract

Many reef fish show strong microhabitat associations which may be established at settlement or occur due to post-settlement modification. Several attributes of habitat such as structure have been found to be important in determining an individuals growth and survivorship. Under these circumstances it can have important implications for population regulation. Here, I quantitatively assessed the microhabitats with which a coral reef damselfish, *Pomacentrus moluccensis*, was most commonly associated, at Lizard Island. Recently settled recruits were highly associated with very complex acroporids and pocilloporids, either due to choice, differential mortality or both. All other microhabitats were used less than would be expected given their abundances if fish were using them randomly. Previous studies had found that this species was highly associated with and only settled into live coral habitats. However, at Lizard Island, there was no clear relationship between the abundance of either adults or new recruits and live coral cover. Percentage cover of preferred habitats was a reasonable predictor of density of new recruits ($r^2 = 0.54$), but not adults. These results suggest that not all live corals were used equally by new recruits of *P. moluccensis* and suggests that coral microhabitats may vary in the quality of a needed resource. All the microhabitats with which *P. moluccensis* was highly associated, had a very complex internal structure. To test whether this aspect of coral morphology affected growth and survivorship of *P. moluccensis*, one of the preferred microhabitats (*Acropora diviricata*) was manipulated to produce coral heads of different structural complexity. All juveniles were removed from randomly chosen coral heads, at six random sites. They were tagged and replaced in exactly the same head after coral manipulation. Control coral heads were untouched but juveniles were tagged in exactly the same way. There was no significant difference in either growth or mortality with different coral head structures between April of their first reef associated year and the following February. This could be because the manipulations only modified the peripheral branches and did not modify the internal structure of the coral head. It is the inner core of a coral head which these fish retreat into when alarmed. What was interesting

however, was that mortality rates were so high, even in this highly used coral species, and ranged between 67% and 93% per site. Migration was found to be negligible. It has previously been suggested that mortality of this species may be high during the first few days post-settlement and then settle down to a much reduced figure. However, this study suggests that mortality rates may be extremely high for at least several months post-settlement and they may therefore considerably alter patterns of abundance laid down at settlement.

6.2 Introduction

Many reef fish species are found in quite specific habitats sometimes at a fine scale of 1-100 cm (Shulman, 1984,1985; Eckert, 1985; Shapiro, 1987). These distributions may be due to choices made at settlement (Williams and Sale, 1981; Sale et al., 1984; Eckert, 1985; Booth, 1992; Wellington, 1992) or due to differential rates of mortality post-settlement (Wellington, 1992). Examples of strong microhabitat associations, include species of *Gobiodon* and *Paragobiodon* which are found only within living heads of certain coral species (Colin, 1975). Other species are thought to be wider ranging. *P. moluccensis* is known to show an affinity for live coral (Sale et al., 1984; Eckert, 1985; Mapstone, 1988) but the particular coral species or growth forms which they may use has not been investigated. Other species, such as *Coris variegata*, seemingly show little or no habitat preferences (Eckert, 1985). These habitat associations may change ontogenetically (Lirman, 1994).

Post-settlement mortality and growth have been shown to vary with aspects of habitat such as structure (Eckert, 1987; Jones, 1988; Connell and Jones, 1991; Diehl, 1993), site (Aldenhoven, 1986), availability of shelter (Shulman, 1984, Beherents, 1987) and depth (Doherty, 1980; Jones, 1986). Similarly, adult densities have also been found to correlate with aspects of habitat such as coral cover, habitat complexity and depth (Luckhurst and Luckhurst, 1978; Thresher, 1983; Bell and Galzin, 1984; Roberts and Ormond, 1987; Sano et al., 1987). However, other studies have found that habitat was not important in determining population size (Risk, 1972; Sale and Douglas, 1984; Sale et al., 1994). While some fishes appear to be specialised on certain coral substrata, little is known of the particular attributes of the coral they are responding to.

That is, they may be selecting corals on the basis of their physical attributes (eg. branch spacing) or biological characteristics. If survivorship were to differ in relation to microhabitat characteristics, this would imply that processes such as competition and predation are important for population regulation (Keough and Downes, 1982; Connell, 1985).

Several coral reef fish studies have found that individual loss is greatest during the first days after settlement (Doherty and Sale, 1985; Aldenhoven, 1986; Victor, 1986; Eckert, 1987; Shulman and Ogden, 1987; Meekan, 1988; Sale and Ferrell, 1988; Warner and Hughes, 1988) but have not had the means to investigate this further. When individuals are followed through time, the mortality measurements are usually more reliable than when using other methods such as habitat isolation (Krebs, 1985). Without some degree of recognition it is not possible to look at degree of site attachment, variation in growth, size specific mortality or to distinguish mortality from migration. Conventional methods used for tagging marine fishes are not appropriate for use in the majority of coral reef species, especially newly settled individuals, because the tags are too large in proportion to the fish. However, the use of implant microtags has recently been shown to have a low impact on growth and survivorship of individuals as small as 11mm SL (Beukers et al., 1995), and would enable these factors to be distinguished. A knowledge of these processes is essential for understanding the population ecology of reef fishes.

This study addressed two main questions:
1) What, if any, were the microhabitat associations of *P. moluccensis*?
2) Would attributes of these microhabitats affect the abundance, growth or survivorship of *P. moluccensis*?

6.3 Methods

6.3.1 Microhabitat associations

Here, I used the distribution of *P. moluccensis* individuals to assess which microhabitats they were associated with on the reef. Using the cover estimates of these microhabitats, it was possible to look at whether this species was more closely associated with some microhabitats than others . Note that a non-random distribution with respect to habitat could be brought about by fish preferences and/or variable mortality rates, it would not necessarily be due to habitat preferences.

To assess the microhabitat associations of new recruits, one quadrat, 10 m by 10 m, was set up at six sites with the top edge along the reef crest. Every *P. moluccensis* new recruit (10 - 20mm SL) and the species of coral it inhabited were noted within each quadrat.

The sessile benthic community was assessed within the fish quadrats. Ten line intercept transects were placed perpendicular to the reef crest at 1m intervals along the top edge of the fish quadrats. Along each of these transects, the start and finish of each sessile benthic species directly under the tape was noted. This was subsequently converted to percentage cover data. Acroporids were classified according to Veron's growth forms (Veron, 1986), pocilloporids were all grouped together and remaining hard corals were placed in the other hard corals category. Table 1 shows exactly which species were in each category.

Electivity indices were calculated for each microhabitat category at each site. This gave some indication of the spatial variation in these associations. Habitat association was calculated using an electivity index (Vanderploeg, 1978). This index was devised for calculating dietary preferences but here I used it to look at habitat use relative to its availability on the reef. E* was estimated using r_i , the proportional habitat use and P_i , the proportions of habitat in the environment according to the equations:

$$E* = \frac{[\omega_i - (\frac{1}{n})]}{[\omega_i + (\frac{1}{n})]} \qquad \text{and} \qquad \omega_i = \frac{\frac{r_i}{P_i}}{\Sigma_i \frac{r_i}{P_i}}$$

This index would be biased if categories were rare in the environment (Lechowicz, 1982), and so only a few broad categories were used to minimise this problem.

6.3.2 Relationships between live hard coral cover and preferred habitat cover on distribution and abundance of *P. moluccensis*

The abundance of adult and juvenile *P. moluccensis* and microhabitat availability was assessed along twelve 10m x 1m transects at nine sites. These nine sites were allocated at three random sites within each of three broad scale zones classified according to exposure: sheltered, exposed and lagoon. Transects were placed on the reef slope just below the reef crest. All fish in the range 10 - 24.9mm SL (new recruits) and > 25mm SL (adults) were counted. Percent cover data was collected for benthos by videoing the transect. A sony hi-8 video recorder was held approximately 30cm above the substrate and each transect took roughly 2 minutes to film. The recording was analysed by stopping the video tape 20 times along each transect and noting which substrate was under each of 5 random spots on the screen. Linear regressions were used to assess the relationship between these variables. However, one site, was recovering from recent storm damage and all the coral heads at this site were <10cm diameter. It would be impossible for adult fish (25 - 60mm SL) to get shelter in such coral heads. This site was therefore, very different to the other 8 undisturbed sites and was excluded from the analyses.

6.3.3 Effects of microhabitat complexity on growth and mortality

The results from the first section indicated that *P. moluccensis* was highly associated with caespitose and corymbose acroporids and pocilloporids. The most striking attribute that these species all have is a very complex internal structure. Here, I tested the null hypothesis that microhabitat complexity would have no effect on survivorship of *P. moluccensis* juveniles. I used a single coral species, *Acropora diviricata*, a caespitose acroporid, to eliminate the potentially confounding effect of species when testing for the effects of habitat structure. An individual coral head of this species may be as much as 1.50m diameter.

Table 1 Coral species included within each category for the electivity indices.

Category for electivity index	**Species**
Arborescent acroporids	Acropora micropthalma Acropora nobilis
Bottlebrush acroporids	Acropora elseyi
Caespitose/corymbose acroporids	A. nasuta group A. diviricata A. loripes A. aspera A. sarmentosa A. millepora
Pocilloporids	P. damicornis P. verrucosa Stylophora pistillata Seriatopora hystrix
other hard coral	galaxea goniopora upright echinopora turbinaria fungiidae other unidentifiable hard corals

6.3.3.1 Experimental design

Juveniles of *P. moluccensis* from *Acropora diviricata* coral heads were tagged with microtags in April 1994 and recaptured after 10 months. The experimental design employed one treatment and one control, each performed at three randomly allocated unique sites on the sheltered side of Lizard Island. All coral heads were uniquely labelled using a garden tag attached to a nail in the substrate approximately 20cm away from the head. Control coral heads were untouched and treatment coral heads were manipulated to reduce their complexity. Alternate primary branches were removed using needle-nosed pliers. The broken pieces were removed and discarded at least 100m away from the experimental heads, because they tend to attract fish such as labrids and chaetodonts.

6.3.3.2 Fish tagging

The tagging process involves two steps (sensu Beukers et al. 1995), the first being to anaesthetise the fish, the second to inject the tags. Fish were immersed until unconscious, approximately 10 seconds, in a solution of quinaldine. The quinaldine solution which was found to be most effective was 1 : 15 : 4500 (quinaldine : ethanol : sea water). The microtags were then injected with the aid of a binocular microscope, under the scales and into the dorsal muscle. All tags were implanted at least one-tag length away form the insertion point to allow a healing area behind the tag (Buckley et al., 1994). Two tags were implanted into each fish, one on each side. The Visible Implant Fluorescent filament (VIF) tag (Northwest Marine Technology, Inc, Unpublished) and the binary - Coded Wire Tag (CWT) are bio-compatible internal microtags (Bergman et al., 1968). The VIF tags are cylindrical polyester tags, which, when injected into translucent tissue and fluoresced by ultra violet light, can be seen in live fish in the field. Each CWT is made from stainless steel wire and has a binary code etched onto its surface. Thus they allow individual or cohort identification. CWT's are magnetised and this feature is used to relocate them. The codes can be deciphered under a light microscope.

To minimise the damage incurred by the fish, particularly to the scales, each was placed in a click seal polythene bag for the injection process. Sterile technique was employed to some degree, by washing the injector and micro - tags in an antiseptic solution prior to injection. Injection of a single tag using this method would take no more than 1 minute. All tagged fish were placed in a tetracycline solution of 220mg to 1L seawater and kept in the dark for 24 hours. They were all returned to their resident coral head within 30 hours of removal. Individuals were collected after 10 months on the reef. Tagged fish were found by searching a 5m radius circle around each coral head. Fluorescent tags could be seen with use of an ultra-violet light to bring out their fluorescence.

6.4 Results

6.4.1 Microhabitat associations

The most abundant microhabitat categories were dead hard coral, coral rubble and hard corals other than pocilloporids or acroporids (Fig 1). Arborescent acroporids were the most abundant acroporids on the reefs around Lizard Island. However, new recruits of *P. moluccensis* were found mostly in caespitose and corymbose acroporids. A positive E* indicates that *P. moluccensis* had a higher degree of association with those habitats than would be expected from their percent cover at the six sites. This occurred for three categories: Caespitose and corymbose acroporids, pocilloporids and other acroporids which includes plate and digitate growth forms (Fig 2). However the latter category is relatively rare and has a high variance which extends into negative values. In some cases species within this category were actively avoided. Arborescent acroporids and bottlebrush acroporids were also actively avoided but to a lesser extent than the remaining categories which all had a value of -1. This indicates maximum avoidance.

6.4.2 Relationships between live hard coral cover and preferred habitat cover on distribution and abundance of *P. moluccensis*

Percentage cover of live hard coral varied between 10 and 50 at the eight sites. Neither new recruit density nor adult density were significantly correlated with percent cover of live hard coral (Fig 3). There was a slight positive relationship with new recruits ($r^2 = 0.38$, $p = 0.29$) but not with adults ($r^2 = 0.18$, $p = 0.10$). Preferred habitats were relatively rare, ranging from 0 to 10 percent cover. Despite this small range of cover there was a significant positive correlation between new recruits and percent cover of preferred habitats (Fig 4, $r^2 = 0.53$, $p = 0.039$). However there was only a weak, non significant relationship between adults and percent cover of preferred habitats ($r^2 = 0.37$, $p = 0.11$).

6.4.3 Effects of microhabitat complexity on movement, mortality and growth

All re-located fish were found in the coral heads they were placed in, with one exception. This fish was found in another coral head 2.5m away from the original which was completely crushed and 100% dead in February 1995. It was probably damage from an anchor. Mortality rates of *P. moluccensis* from *Acropora diviricata* at six sites on the sheltered side of Lizard Island were between 67 and 93% between April 1994 and February 1995. Mean loss rates were very similar from both treatments (unmanipulated = 76.8%, manipulated = 79.8%, Fig 5a) Variation in loss rates within each treatment were high. In fact the greatest variation shown was between two sites in the manipulated treatment. There was, therefore, no significant difference in individual loss from manipulated and unmanipulated heads ($F = 0.00$, $p = 0.98$). Because the loss rates were so high there were relatively few recaptures of tagged individuals which lowered the replication for growth comparisons. By chance the design remained balanced with 16 individuals recaptured from each treatment. Growth rates were very similar between treatments ($F = 0.05$, $p = 0.82$). At manipulated sites the mean was 7.2mm over one year, compared with 6.9mm at the unmanipulated sites over the same period of time (Fig 5b).

6.5 Discussion

There is a clear indication from this study that *P. moluccensis* is highly associated with caespitose and corymbose acroporids and pocilloporids. These are the most structurally complex corals on the reefs studied, and therefore, would provide refuges of the closest size to *P. moluccensis* new recruits. (Buchheim and Hixon, 1992) also found that blennies preferentially used holes in coral heads that were most similar to their body diameter. Eckert (1985) showed that *P. moluccensis* at One Tree only settled into live coral substrata. She used both *Pocillopora damicornis* and *Porites cylindrica* and *P. moluccensis* preferred these equally. Similarly, (Ebersole, 1985) found that *Eupomacentrus planifrons* preferred live coral heads with relatively complex internal structure. These microhabitats may provide better protection from storms or from predators.

I cannot determine whether the patterns I observed at Lizard Island were established at recruitment or if there was some post-settlement migration between microhabitats, because settlement sites were not observed directly. Juveniles may have settled several weeks prior to observation. Other studies have found that patterns of fish recruitment are strongly influenced by microhabitat composition (Sale et al., 1984; Eckert, 1985; Carr, 1991; Booth and Beretta, 1994).

There was no evidence that branch spacing within a coral head had an influence on the mortality or growth of *P. moluccensis*. The negative result of this study could be because this aspect of coral morphology is not critical. However then the question arises as to why these fish are so specific in their microhabitat associations? It could be merely coincidental that all coral species they use are highly complex, but it seems unlikely. Jones (1988) showed that two damselfish species survived better in more the complex pocilloporids into which they preferentially settled. However his result may also be partly due to differential migration.

Perhaps a more likely explanation is that altering the outer branches of these coral heads did not change the degree of shelter they provided. When *P. moluccensis* is alarmed it retreats into the inner core of coral heads which it was not possible to manipulate without destroying the entire head. Many of these coral heads were very large sometimes with a diameter of more than 1m. They were also very deep. It was very rare for a branch to break off right down at the base, more often it was further up and it may be that my manipulations were not enough to significantly affect these fish. The aim here was to eliminate the potentially confounding effect of species when testing for the effects of habitat structure. Of course the possibility remains that there is some attribute of these microhabitats other than structural complexity which *P. moluccensis* are utilising, such as feeding on the corals mucous.

It is probable that migration of tagged new recruits was extremely low between April and February of their first year. All relocated fish with one exception were found in the coral head in which they had been placed, despite searching an area of 5m radius around every head. The exception was found 2.5m away from its coral head, which had been completely demolished. If fish did migrate from these coral heads then they must have moved further than 5m. Also some 5m circles around coral heads were adjacent to others but yet I still only found the one individual away from its head. Mapstone (1988) also found that there was little migration of *P. moluccensis* on contiguous reefs at One Tree Reef, in the southern Great Barrier Reef Region.

The observed losses may therefore be attributed to mortality. Effects of the tagging process were considered to be negligible (sensu Beukers et al. 1995). The high mortality rates (67% - 93%) observed in this study are a little surprising given that all fish were associated with one of the microhabitats in which this species is most commonly observed, *Acropora diviricata*. For this reason it would seem likely that *P. moluccensis* mortality would be lowest in these microhabitats. At One Tree Reef, Mapstone (1988) found that mortality of this species was 56% during the first year and Sale and Ferrell (1988) found 52% mortality during the first 18 days post-settlement with no mortality between 19 and 42 days post-settlement. These other studies looked at mortality from a range of microhabitats not just the most highly associated ones. It would appear that there is considerable spatial variation in mortality at the between reefs scale. Thus post-recruitment processes may modify spatial patterns laid down at recruitment.

While it is clear from this study that new recruits of *P. moluccensis* show strong microhabitat preferences it remains uncertain which attributes of these microhabitats are important. This species appears to be very site attached to a single coral head in this case, with very little post-settlement movement during the first reef associated year. The high mortality rates could considerably modify patterns of abundance laid down at settlement and imply that post-settlement processes such as competition and predation may be important in regulating this species.

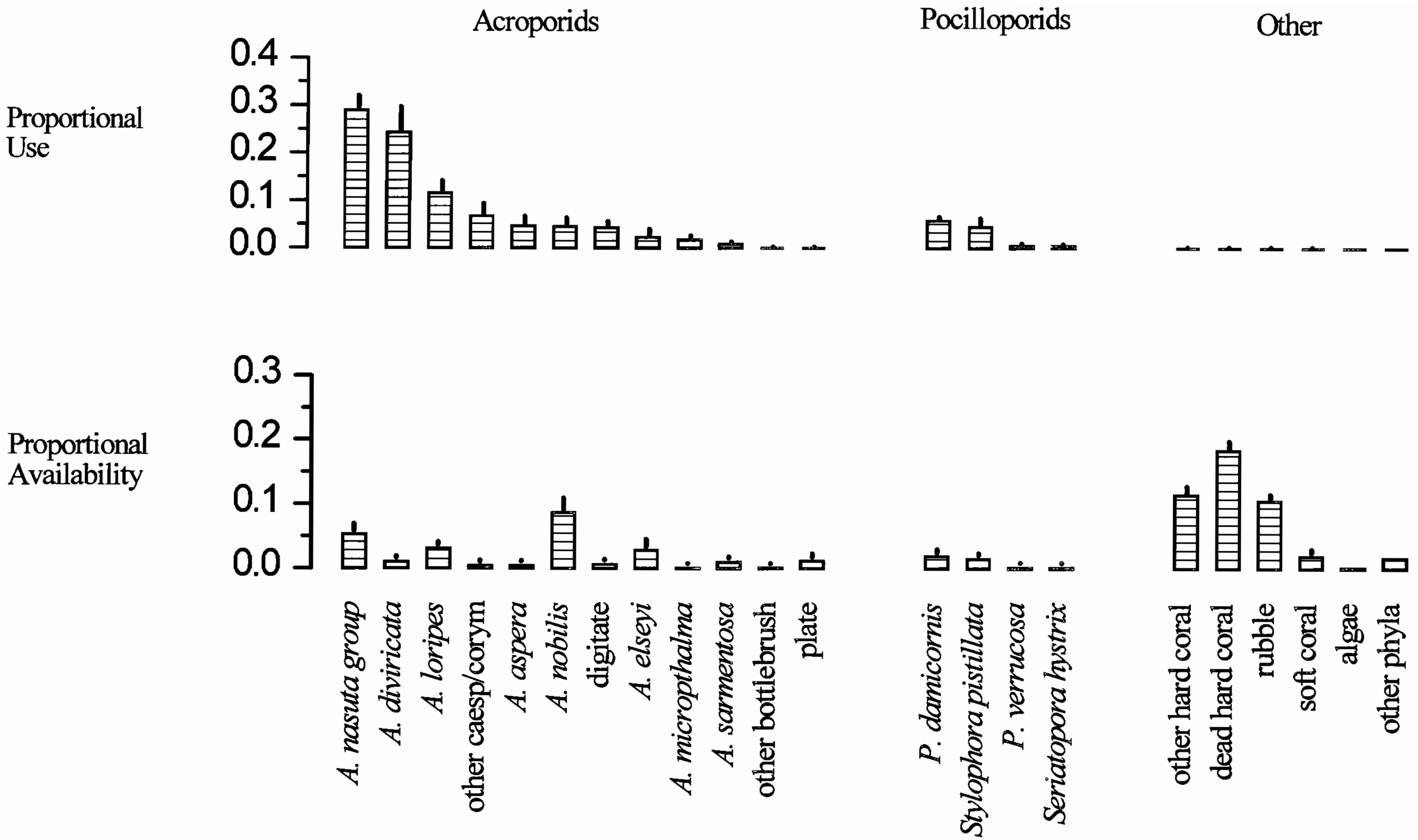


Fig 1a Proportional use (x̄ ± SE) by *Pomacentrus moluccensis* new recruits, and **b)** proportional availability (x̄ ± SE), of microhabitats at six sites at Lizard Island (n = one, 10m x 10m quadrat for *P. moluccensis* and n = 10 habitat transects per site).

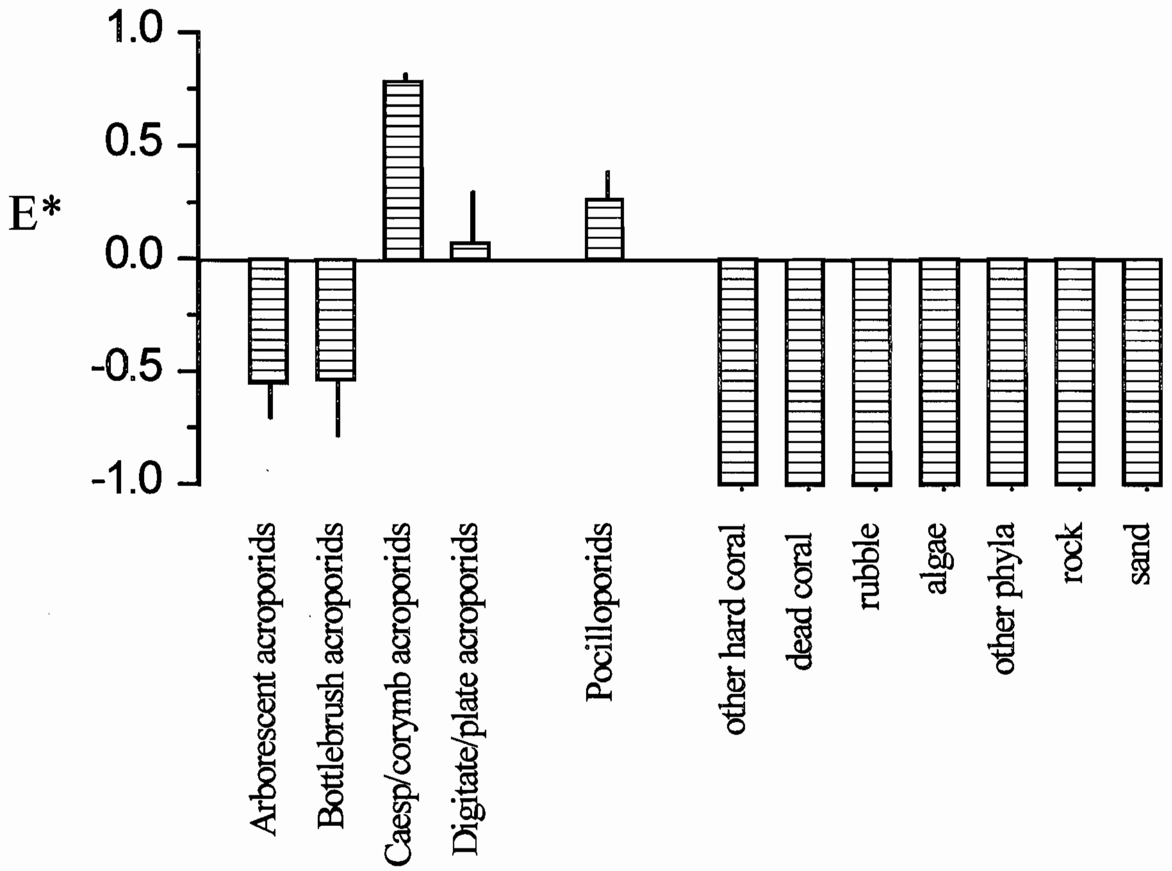


Fig 2 Microhabitat preferences (Vanderploeg and Scavia's electivity index E*, x̄ ± SE) of *Pomacentrus moluccensis* new recruits (n = 6 sites).

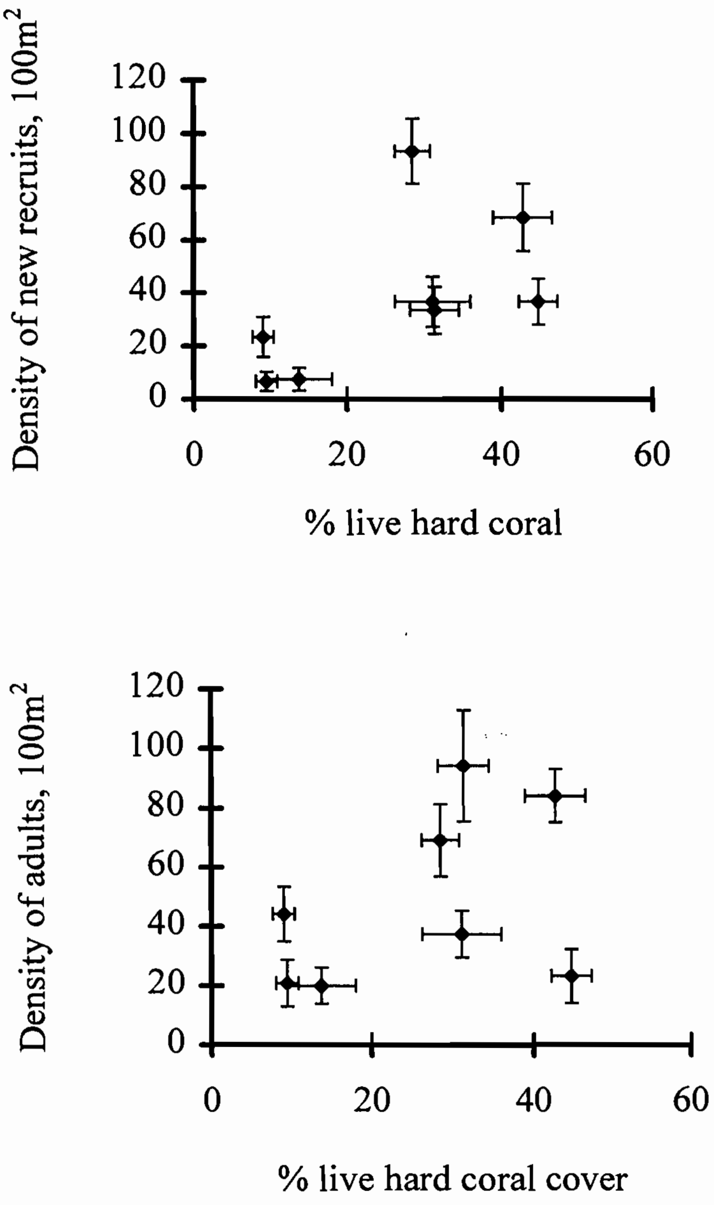
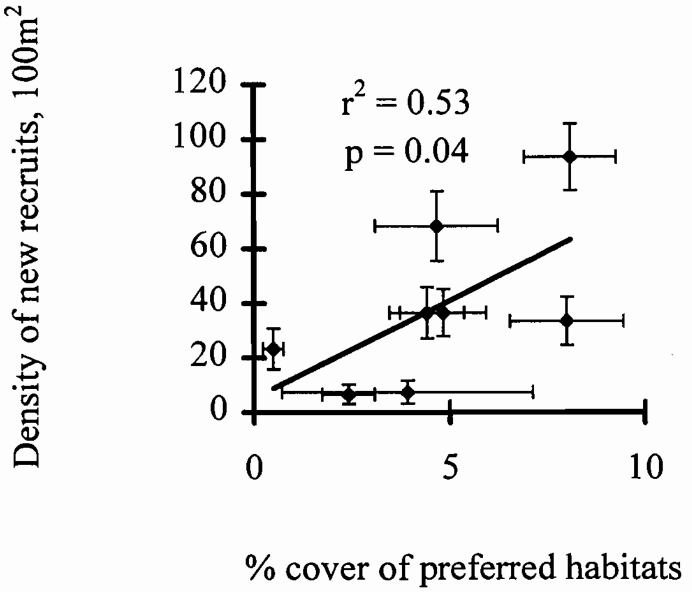


Fig 3 Relationship between both new recruits and adults of *Pomacentrus moluccensis* ($\bar{x}$ ± SE) and percentage cover of live hard coral at nine sites around Lizard Island (n = 12 transects per site).



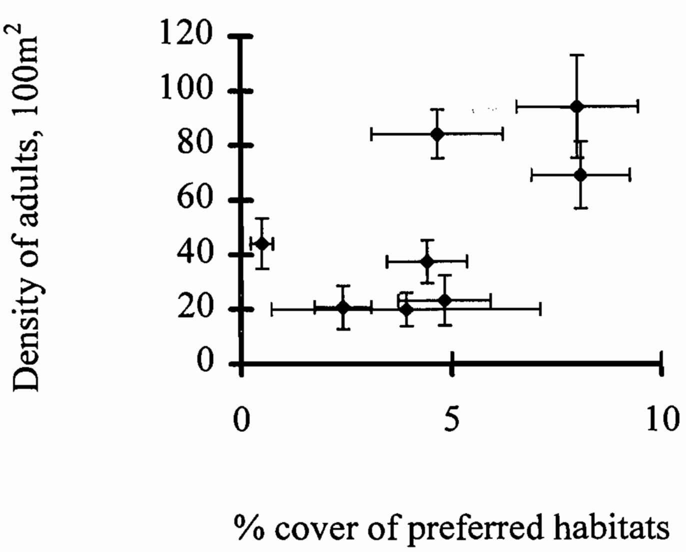


Fig 4 Relationship between both new recruits and adults of *Pomacentrus moluccensis* ($\bar{x}$ ± SE) and percentage cover of preferred coral types at nine sites around Lizard Island (n = 12 transects per site).

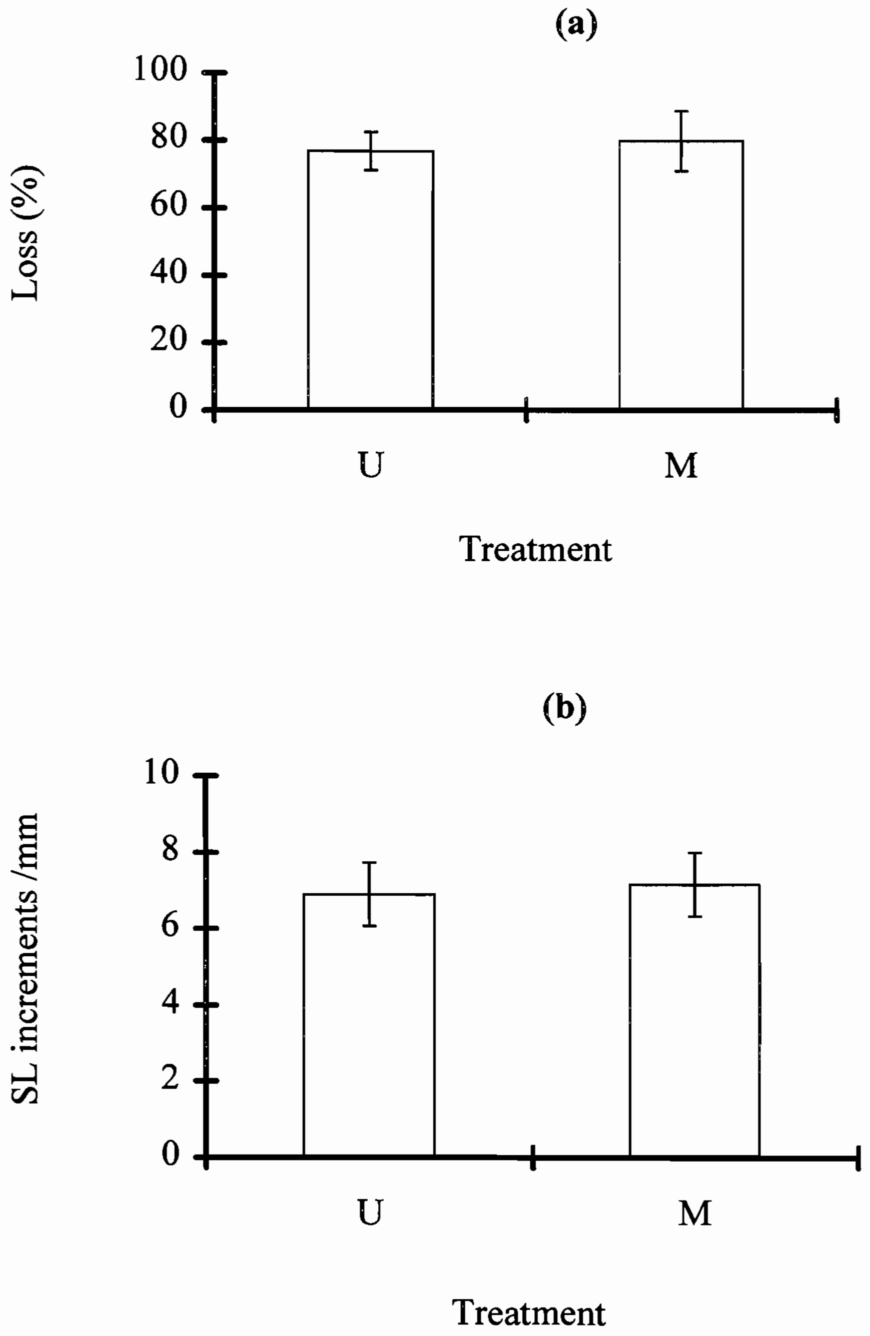


Fig 5a Percent loss (x̄ ± SE) and **b)** growth increments (x̄ ± SE) of individuals of *Pomacentrus moluccensis* after 10 months in manipulated and unmanipulated coral heads (n = 3 sites per treatment for % loss and n = 16 individuals per treatment for growth increments).

CHAPTER 7

Predators, their abundance and resulting predation pressure on new recruits of a reef fish population

7.1 Abstract

Spatial and temporal patterns in the abundance of predators and predation pressure (the likelihood of an individual being consumed), may have an important effect on the distribution and abundance of prey. However, for coral reef fishes, there remains a lack of basic information on these patterns. In this study at Lizard Island, on the Great Barrier Reef, densities of predators on *Pomacentrus moluccensis* were highly variable among locations. Overall predator densities were highly correlated with the densities of recruit *P. moluccensis* suggesting that predators actually recruit or aggregate at sites of high prey abundance. In addition, there was a weak correlation between adult *P. moluccensis* and predators at these sites suggesting that initial patterns of recruitment had been modified.

To measure relative differences in predation pressure newly settled damselfish were captured and then released (using a standard protocol) at nine sites around Lizard Island and their fate was monitored. The main predators of released *P. moluccensis* were *Pseudochromis fuscus* and *Thalassoma lunare*. The other main predators were also small species from the families Labridae (wrasses), Synodontidae (lizardfish), and Parapercidae (sandperches). Released new recruits preferred the same coral microhabitats as undisturbed recruits at these sites. Mortality rates from each of the microhabitats relative to numbers of recruits using them varied considerably with lowest mortalities in the preferred coral habitats. In addition, there was spatial variation in percentage cover of preferred microhabitats.

Forty three percent of new recruits that were released were attacked by non predatory individuals. However, the percentage that were eaten was the same for those that were and were not attacked and so these aggressive interactions may not be important in determining the predation pressure acting on *P. moluccensis* at Lizard Island.

This study suggests that at Lizard Island spatial variation in predator densities and in percentage cover of preferred coral habitats may lead to spatial variation in susceptibility to predation and mortality rates. Hence, it would seem that predation mediated by habitat structure may be altering the patterns of abundance formed at recruitment.

7.2 Introduction

Spatial and temporal patterns in mortality rates caused by predation may have a major influence on the distribution and abundance of a species (Paine, 1966; Murdoch and Oaten, 1975; Sih et al., 1985). In marine organisms patterns of abundance are initially determined at recruitment (Doherty, 1983; Keough, 1984). However, predator induced mortality, whether density-dependent or independent, may be sufficiently strong to disrupt patterns established at the time of recruitment (Hixon, 1991; Caley et al, in press). This cannot be determined without basic information on the distribution and abundance of predators. Also, the likelihood of an individual falling prey to a predator will depend not only on predator abundance but on the availability and quality of suitable refuges.

The effects of predatory fish on the behaviour and survival of their prey have been well documented in freshwater communities (Werner et al., 1983a; Sih et al., 1992) and in some marine habitats such as seagrass beds (Orth, 1977; Summerston and Peterson, 1984; Virnstein et al., 1984) and kelp forests (Holbrook and Schmitt, 1988). In the coral reef literature, however, there has only been sparse interest in the role of predation compared with other potentially structuring factors such as recruitment and competition (Hixon, 1991). A combination of high numbers of predators (Goldman and Talbot, 1976; Williams and Hatcher, 1983) and high mortality rates when fish are newly settled on the reef (Doherty and Sale, 1985; Shulman and Ogden, 1987; Meekan, 1988; Sale and Ferrell, 1988) implies that predation may be an important factor in structuring populations of coral reef fish (Hixon, 1991). The few studies of predation support this argument (Talbot et al., 1978; Shulman et al., 1983; Doherty and Williams, 1988; Sale and Ferrell, 1988;

Warner and Hughes, 1988; Jones, 1991). If predation is to change the patterns of new recruits settling onto the reef through mortality then rates must vary either temporally or spatially. However, there is still a lack of basic information about which predators consume which prey and if there is spatial and/or temporal variation in predation intensities (Choat, 1982; Jones, 1991; Kingsford, 1992).

The high structural complexity of coral reefs, the high species richness of coral reef communities and the open nature of coral reef fish populations have made the study of predation in this ecosystem especially difficult (Hixon and Beets, 1993). For these reasons there have been few quantitative studies on predation by coral reef fish (Sweatman, 1984) or invertebrates. Gut contents analyses have provided estimates of numbers and types of prey eaten. However, this method suffers from several problems such as lack of information on digestion rates and the requirement of large sample sizes due to high temporal and spatial variation (Harmelin-Vivien and Bouchon, 1976; Norris and Parrish, 1988; Kingsford, 1992; Hood et al., 1994). Sweatman (1984), in a particularly informative study, followed individual fish to record predatory behaviour, attack rates and success rates. He showed that predatory fishes have the potential to consume large proportions of prey populations. However, following individual fish is a time consuming exercise which would not be practical for most predatory species that often are either cryptic or highly mobile and consume prey at low rates. Coral trout, for example, are larger predators which roam over substantial areas at relatively high speeds. They have also been estimated to only spend between 0.02 and 0.05% of their time engaged in predatory behaviour (Samoilys, 1986) so the chance of observing a predation event would be extremely low.

Predation pressure here is used to mean the relative likelihood or probability of an individual being consumed. There is very little known about the spatial variation in predation pressure. Shulman (1985) used tethered fish, and the model bottle method (where a prey fish is placed inside a bottle) was used by both Myrberg and Thresher (1974) and Sweatman and Robertson (1994). However, a tethered fish may struggle more than it would under normal conditions and so attract predators from a much greater distance (Sweatman and Robertson, 1994). In order for a prey species to avoid predation it can either use a refuge where the predator cannot reach it, decrease encounter rates with predators or escape following a predation attempt. Keeping fish in a bottle does not allow them the possibility of moving to decrease encounter rates and therefore the results may be inflated. Recently, however, Martin (1994) and then Doherty et al. (1995) trialled an alternative method where they released new recruits onto the reef and followed their fate during a ten minute period. Hence, this method includes a measure of both the numbers of predators at a given site and also a measure of the degree of protection afforded by the microhabitat at that site. While it may not serve to estimate actual predation rates, it represents a useful measure of relative differences in predation pressure in different locations and habitats provided they are released in a standardised manner.

Intuitively, increased predator abundance and/or biomass should lead to higher levels of predation. However, various other factors may also be important in determining the predation pressure exerted on a given prey species. Examples include microhabitat structure, abundance of competitors, diseases and environmental stress. Habitat structure and complexity may have an important bearing on the effects of predation and on predator/prey behaviour. Habitat may provide prey with either total refuges from predation or may decrease encounter rates between predators and their prey (Murdoch and Oaten, 1975). The effect of predation on fishes has been shown to be mediated by habitat (Brock, 1979; Crowder and Cooper, 1982; Werner et al., 1983b; Shulman, 1984,1985; Carr, 1991; Connell and Jones, 1991; Buchheim and Hixon, 1992) but results of coral reef studies have been contradictory (Robertson and Sheldon, 1979; Robertson et al., 1981; Sale et al., 1994), possibly due to experimental problems (Hixon and Beets, 1993). However, there is a growing awareness that knowledge of which habitats new recruits use and how mortality varies with location and structural aspects of the habitat are important for understanding the population ecology of reef fishes (Levin, 1994).

Presence of aggressors could also influence predation pressure. The interactions between competitors and predators have rarely been empirically tested probably due to practical constraints (Sih et al., 1985). The role of predators in mediating the effects of competition have been documented but rarely in marine systems has the reverse been considered. Aggressive interactions between potential prey species may increase their chances of being preyed upon in two ways: Firstly by simple distraction of attention and secondly by leading to a potential prey individual being chased away from shelter such that a predator is able to take it (Robertson et al., 1976; Shpigel, 1980; Diamant and Shpigel, 1985; Sweatman and Robertson, 1994).

In this study I determined the main potential predators of newly recruited *P. moluccensis*, a common damselfish on the Great Barrier Reef, and measured their densities at nine sites around the Island. I also assayed predation pressure exerted on *P. moluccensis* at these sites, using the juvenile release method. I examined the relationship between predator abundance, and the distribution and abundance of juvenile and adult *P. moluccensis*. I also examined the relationship between predator abundance and mortality of experimentally released new recruits. This species is almost exclusively found in live coral (Eckert, 1985; Mapstone, 1988). The structures of these coral species can vary quite considerably and therefore may vary in the degree of protection they provide to the fish that colonise them. Chapter 6 showed that *P. moluccensis* new recruits were very specific in their habitat preferences, preferring caespitose and corymbose acroporids (categories sensu Veron, 1986) and pocilloporids. Here, I investigated the microhabitats in which released *P. moluccensis* new recruits most commonly sought refuge, measured predator success rates when attempting to capture this species from different microhabitats and finally, looked at the consequences of aggressive interactions occurring between *P. moluccensis* new recruits and other reef residents.

7.3 Methods

Spatial patterns in predator and prey densities, predation pressure and refuge availability were assessed at Lizard Island. Three zones were distinguished, according to exposure - sheltered, lagoon and exposed. Within each of these zones three random sites were selected for study.

7.3.1 Predator and prey densities and habitat structure

Data was collected to give information on abundances of predator species, *P. moluccensis* and microhabitats. For the purpose of this paper microhabitat was taken to mean the coral head in which an individual was residing. A census of predators of new recruits was carried out twice at each of the sites. Censuses were in the order of a few days to a couple of weeks apart according to weather conditions. Two methods were used; one for cryptic species and the other for non cryptic species (sensu Stewart and Beukers, in prep). Firstly, a baited point census was used to increase the likelihood of observing cryptic species. Ten points around the circumference of a 5m radius circle were marked out on the reef using fluorescent tape. At the start of the observation period four pilchards were placed in a mesh bag in the centre of the circle and pulverised. All cryptic predatory piscivores seen within this area were counted during a 15 minute period. At the end of the census the mesh bag was placed in a sealed bag and removed from the reef. On each of two separate occasions three spatially separate circles were counted so that a total of six circles were counted for each site.

For non cryptic species the traditional visual census method was used. At each location fish were counted within 18 m by 30 m quadrats. Each quadrat was divided into 6 belt transects 3 m wide, 30 m long and fish were counted by swimming along each of these in turn. All abundances were converted to densities per 100m^2.

The abundance of adult and juvenile *P. moluccensis* and microhabitat availability at these sites was assessed along twelve 10m x 1m transects. All fish in the range 10 - 25mm SL (new recruits) were counted. Percent cover data was collected for benthos by videoing the transect. A sony hi-8 video recorder was held approximately 30cm above the substrate and each transect took roughly 2 minutes to film. The video was analysed by stopping the tape 20 times along each transect and noting which substratum was under each of 5 random spots on the screen. Habitat availability was converted to proportions (see Bellwood 1995).

7.3.2 New recruit releases

New recruit releases were performed to provide four pieces of information. First, to identify the potential predators of *P. moluccensis* new recruits, second, to look at spatial variation in predation pressure, third, the importance of microhabitat for survivorship of new recruits and finally, the effects of aggressive interactions on survivorship of recruits. An aggressive species was defined as any species which did not consume new recruits but nevertheless showed antagonistic behaviour towards released recruits and resulted in that recruit being eaten by another species.

Newly recruited fish were captured just after settlement, released onto the reef and the fate of each was observed. At each of the nine sites, ten *P. moluccensis* new recruits of similar size were released, one at a time, on the reef slope in a haphazard location. The release technique was designed to reduce the degree of dis-orientation. Each recruit was held in a click-seal polythene bag above the point of release for two minutes and then the click-seals were gently opened so that the fish could swim away from the bag. The recruit was watched for ten minutes from a distance of at least 1.5m, and the following data were recorded: time spent in each microhabitat type and all aggressive interactions and the attacking species. If a recruit was eaten the following additional data were recorded: the predator species and the coral species or microhabitat type from which it was eaten. This was repeated at every site, so that 180 new recruits were released in total. Habitat preferences of released new recruits were calculated using Vanderploeg and Scavia's electivity index (E*) as suggested by Lechowicz (1982). This index was devised for calculating dietary preferences but here I used it to look at habitat use relative to its availability on the reef. E* was estimated using r_i, the proportional habitat use and P_i, the proportions of habitat in the environment according to the equations:

$$E* = \frac{[\tilde{\omega}_i - (\frac{1}{n})]}{[\tilde{\omega}_i + (\frac{1}{n})]} \quad \text{and} \quad \tilde{\omega}_i = \frac{\frac{r_i}{P_i}}{\Sigma_i \frac{r_i}{P_i}}$$

This index would be biased if categories were rare in the environment (Lechowicz, 1982), and so only a few broad categories were used to minimise this problem.

7.4 Results

7.4.1 Spatial variation in predator abundance

Spatial variation in predator density was evident at species level for the two most abundant predators *Pseudochromis fuscus* and *Thalassoma lunare*, and also when the densities of all other small predators were pooled (Fig 1). This spatial variation was significant, when all predator species were pooled, between sites but not between zones (Table 1). *Pseudochromis fuscus* was most abundant at Mermaid and Granite, two sites on the sheltered side of the Island, where as *Thalassoma lunare* was most abundant at an exposed site, Bird Islets. In addition, *Thalassoma lunare* was present at most sites in greater abundance than *Pseudochromis fuscus.*

7.4.2 Relationship between *P. moluccensis* and predator abundance

There was a strong positive relationship between new recruits of *P. moluccensis* and total small predator density at nine sites ($r^2 = 0.84$, $p < 0.001$, Fig 2) but there was only a very weak relationship between adults of *P. moluccensis* and total small predator density ($r^2 = 0.16$, Fig 3). There was greater variation in the adult density and predator density relationship at the site level. Adult density was also more variable within sites than new recruit density.

Table 1. Analysis of variance table for densities of predators in three zones classified according to exposure and at three sites per zone at Lizard Island(n= 12 transects per site).

Source	D of F	SS	F	P
TOTAL	53	3816.279035		
ZONE	2	1772.870244	4.89720	0.054821
SITE (ZONES)	6	1086.052319	8.50821	0.000003
ERROR	45	957.356472		

7.4.3 Spatial variation in predation pressure

The main species which consumed experimentally released *P. moluccensis* were *Thalassoma lunare* and *Pseudochromis fuscus* (Fig 4a). Other predators were from a range of families including: Labridae, Parapercidae, Synodontidae and small Serranidae. *Thalassoma lunare* and *Pseudochromis fuscus* were also the most abundant small predatory species (Fig 4b). Some species appeared to be more predatory than others, because they ate more in relation to their abundance. It was interesting that although *Thalassoma lunare* was more than twice as abundant as *Pseudochromis fuscus* on the reefs around Lizard Island, they both consumed the same number of experimentally released new recruits of *P. moluccensis*. It was not possible to identify all predators because some were hidden in the substrate and in other cases the event took place so quickly it was impossible to know which individual was the successful predator.

Forty seven new recruits out of one hundred and eighty (26%) were eaten within 10 minutes of releasing. There was considerable spatial variation in numbers of new recruits eaten (Fig 5). There was also high variation within some sites and no variation within others. The greatest within site variance was observed at the Central site in the lagoon. There was no within site variation at any of the exposed sites. There was no correlation between predator density and number of new recruits eaten (Fig 6, $r = 0.39$, $p = 0.30$).

7.4.4 Coral substratum and predation pressure

Despite the fact that availability of microhabitats was variable between sites, patterns of habitat choice, by experimentally released juveniles were relatively consistent between sites and zones (Figs 7a-c). At all sites, juveniles took refuge in caespitose and corymbose acroporids (categories sensu Veron 1986) and pocilloporids more often than predicted on the basis of their availability (Fig 8). This indicates that coral species in these two habitat categories were used more than expected by the new recruits whereas species in the remaining eleven categories were either under utilised or never used. The other habitat which was frequently used was soft coral, but this was very abundant and hence the electivity indices for this group are negative. The greatest use of soft coral was at sites in the lagoon where it was the most abundant habitat.

There was a strong indication from this study that there was lower consumption of *P. moluccensis* from preferred habitats, relative to the numbers of individuals using these microhabitats (Fig 9). The highest numbers eaten were from soft coral, bare rock and open-water, and the lowest from bottlebrush acroporids and caespitose and corymbose acroporids. Mortality rates from each habitat, relative to the use of that habitat were lowest from caespitose and corymbose acroporids, and pocilloporid corals. They were highest from open-water and other acroporid corals such as plate and digitate growth forms (Fig 10). There was spatial variation in the abundance of both categories of preferred microhabitats (Fig 11). Abundances of both pocilloporids and caespitose/corymbose acroporids were relatively low at the lagoonal sites. The abundance of pocilloporids was highest at Washing machine on the exposed side, and the abundance of preferred acroporids was highest at Bird and Pidgin, also on the exposed side. There was only a slight relationship ($r^2 = 0.24$) between the percent cover of preferred coral habitats and numbers of new recruits eaten (Fig 12).

7.4.5 Aggressive interactions and predation pressure

Forty three percent of released recruits were attacked by non predatory individuals, mostly other *P. moluccensis* or other damselfish. In 8 percent of cases, predation on a new recruit was preceded by an aggressive encounter. The relative numbers of new recruits eaten following a non predatory attack were no greater than the numbers eaten when no attacks occurred (Fig 13).

7.5 Discussion

These results indicate that predation pressure may be influenced by predator abundance, predator motivation and habitat structure. Spatial variation in the mortality of juvenile *P. moluccensis* mortality rates may be due to differences in this predation pressure. Firstly there was spatial variation in densities of key predators. Secondly, there was a strong correlation between densities of new recruits of *P. moluccensis* and densities of predators. This relationship was greatly reduced when adults of *P. moluccensis* rather than new recruits were considered. Thirdly, *P. moluccensis* new recruits showed clear microhabitat preferences and percent mortality from preferred microhabitats was a very low 4%. Percent mortality in other microhabitats was as high as 88%. The experimentally released new recruits, showed identical microhabitat preferences to natural new recruits observed at Lizard Island (Chapter 6). Abundances of these preferred microhabitats were spatially variable, suggesting that predator induced mortality would also vary. In addition, the new recruit releases also showed variability between sites in numbers of recruits eaten, but this could not be statistically tested because at one site the variance was extremely large. With greater replication this technique for measuring predation pressure would work well.

The most successful predators of experimentally released *P. moluccensis* new recruits were *Pseudochromis fuscus* and *Thalassoma lunare*, with lizardfish and sandperches also showing a very high percent success rate. This is surprising given that these are relatively small predators. These small predators are very abundant on the reefs around Lizard Island (Stewart and Beukers, in prep) compared to other locations on the Great Barrier Reef (Connell, 1994). *Pseudochromis fuscus* (Martin, 1994) and *Synodus variegatus* (Sweatman, 1984) have been shown to take fish of half their standard length. Other work at Lizard Island suggests that larger predators rarely eat new recruits (St John, 1995) but to date, with two notable exceptions (Sweatman, 1984; Martin, 1994), the role of these small predators has been largely overlooked. The high predation rate by *Thalassoma lunare* may be exaggerated because they are attracted to divers irrespective of the divers' activities (Martin, 1994). Thus its relative success may be over estimated. *Pseudochromis fuscus* on the other hand is diver neutral (Martin, 1994) so results for this species should not be inflated. Several species that were seen to take new recruits are cryptic and diver negative, for example the cephalopholids, and consequently this method may have underestimated their contribution. Additionally this experiment was conducted during daylight hours. Several predators including the cephalopholids are thought to be crepuscular and nocturnal feeders, and therefore may play a greater role during these times.

This result has important implications for the effectiveness of microhabitats in providing new recruits with shelter. Because predators of new recruits were not that much larger than their prey, refuges would need to closely match prey individuals sizes. This study supports that theory because it was only the highly complex corymbose and caespitose acroporids and pocilloporids that provided a good degree of protection against predation. Buchheim and Hixon (1992) also found that fish needed refuges which were just slightly larger than their bodies diameter. Given that mortality varied from 4% to 88% depending on microhabitat type it would seem that microhabitat has the potential to considerably change patterns of distribution and abundance of coral reef fish.

It is also interesting that densities of small predatory species correlated so highly with densities of new recruits of *P. moluccensis*. This could be due to an aggregative response in which predators aggregate where prey densities are high (Murdoch, 1971;

Hassell and May, 1974). When this occurs, sites of low prey density could provide prey populations with a refuge from predation and may, over time, lead to sites showing similar prey densities (Fretwell and Lucas, 1970; Milinski, 1979). Thus, the aggregative response may have a stabilising effect on predator prey interactions (Hassell and May, 1974; Vanbalen and Sabelis, 1993). This could explain the relationship observed here between densities of adults of *P. moluccensis* and predators where the slope of the line is approaching the horizontal.

On several occasions aggressive interactions culminated to a predation event. However, the proportion of aggressive interactions that lead to a predation event was no greater than the proportions of those that were not attacked. Rarely have aggressors been considered in predation research. Kingsford (1992) has highlighted the need for more consideration to be given to predator and prey community structure when studying predation because predation rates and predator success may vary according to the presence or absence of other species. There is some anecdotal evidence of this occurring in reef fish communities (Sweatman and Robertson, 1994; Diamant and Shpigel, 1985; Shpigel, 1980; Robertson et al., 1976). Shpigel (1980) observed that when damselfish were chased away from their resident coral colonies they were more vulnerable to predation by serranid predators. However, he had no quantitative data about frequency of occurrence of aggressive interactions and how often they lead to a predation event. This study suggests that species which aggressively interact with prey may not be important in determining prey survivorship.

The effectiveness of different types of coral as refuges needs to be tested experimentally. Preliminary data suggests that microhabitat may mediate the affects of predator abundance. Unfortunately the sites used here do not provide a fully orthogonal test but there was some evidence that increasing percent cover of preferred coral species lowered the mortality rates at intermediate predator abundances. This would explain the poor correlations observed for each single factor. The best way to test for an interaction would be a well replicated fully orthogonal experiment in which both microhabitat and predator density were varied. If there was evidence of an interaction then spatial variation in mortality would be highly likely given that both of these factors were spatially variable.

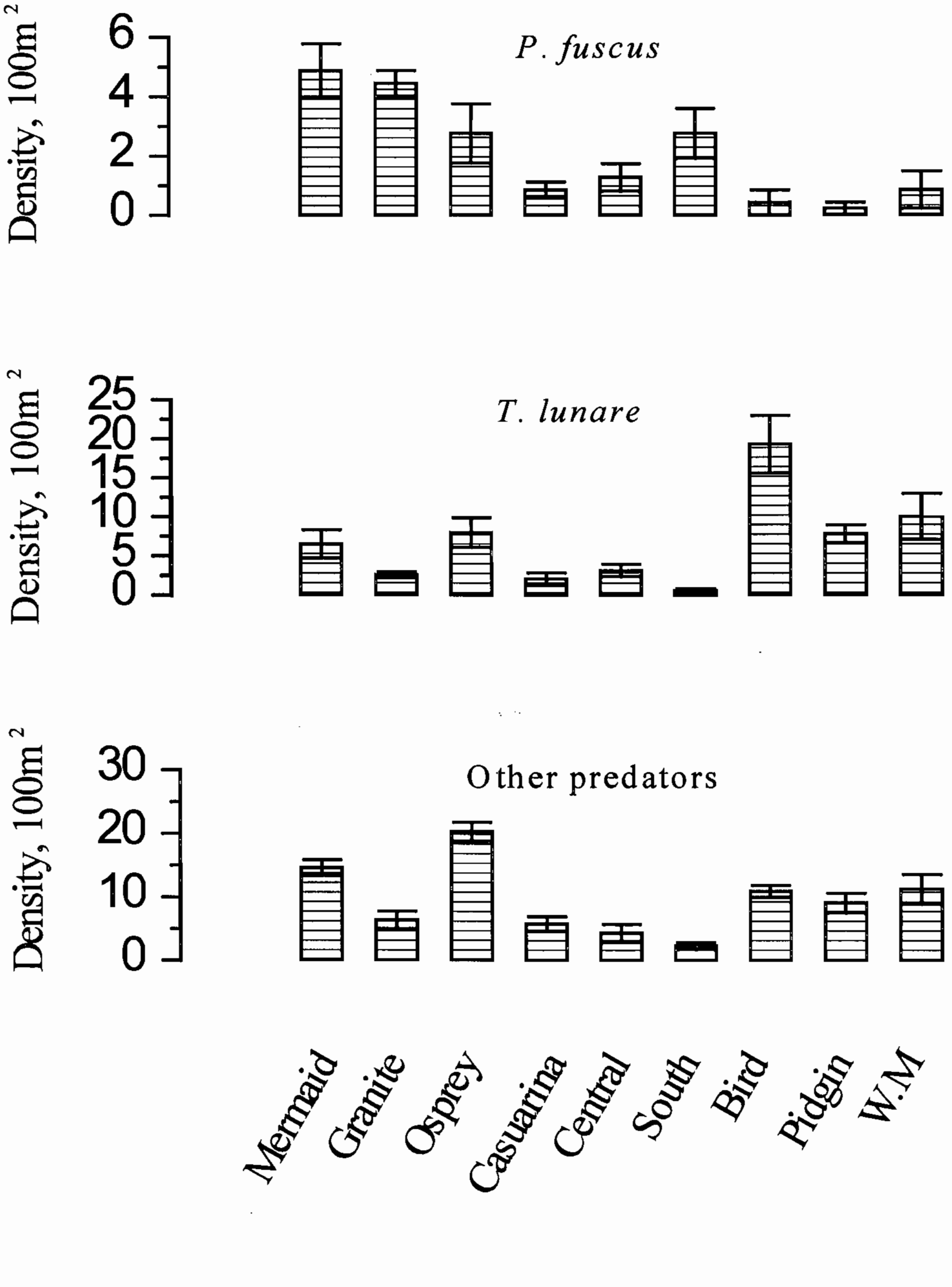


Fig 1 Densities (100 m^2) of *Pseudochromis fuscus* ($\bar{x}$ ± SE), *Thalassoma lunare* and other predator species at 9 sites, n = 6.

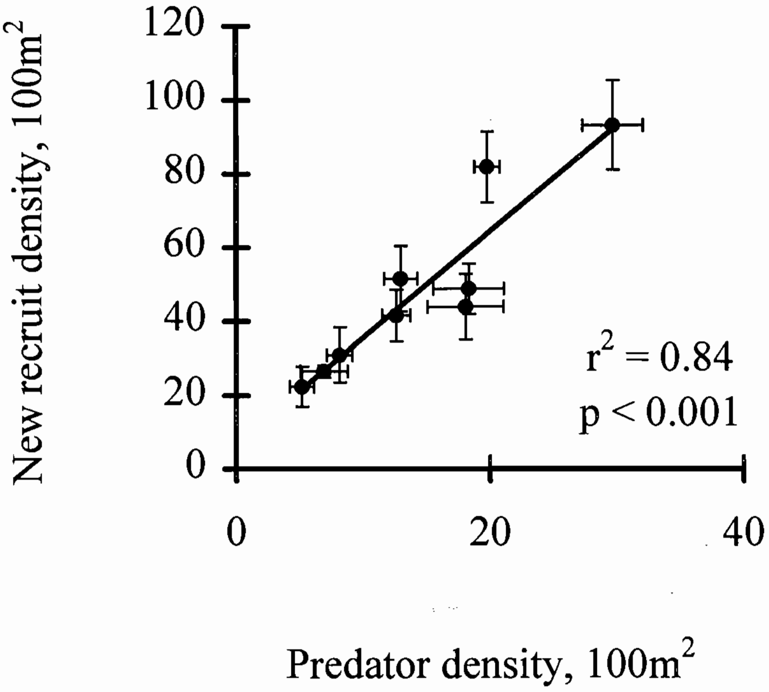


Fig 2 Regression of the density (10m²) of *Pomacentrus moluccensis* new recruits ($\bar{x}$ ± SE) against total predator density (10m²) at 9 sites, n = 12.

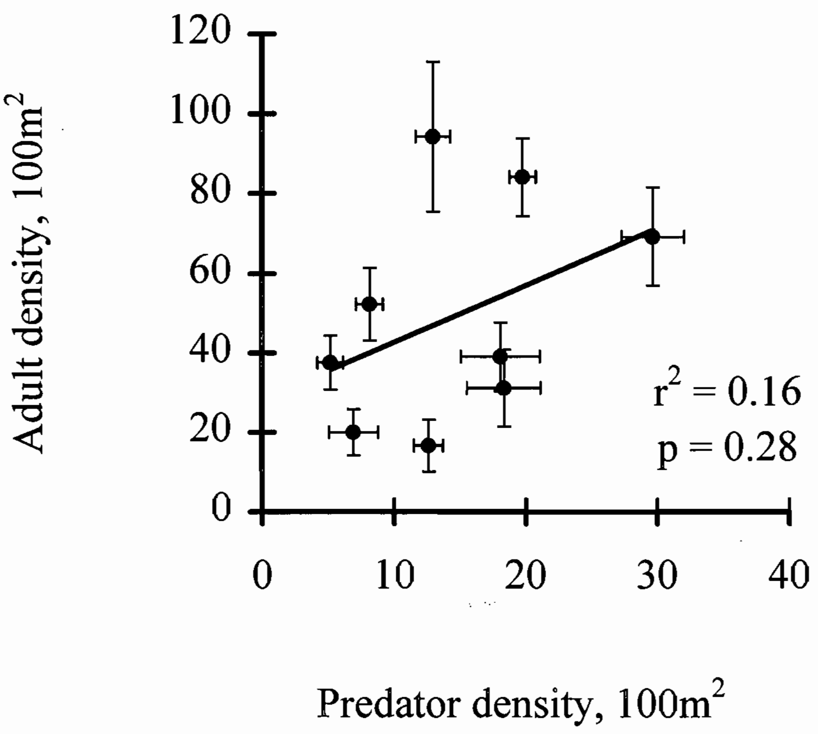


Fig 3 Regression of the density (10m^2) of *Pomacentrus moluccensis* ($\bar{x}$ ± SE) adults against total predator density (per 10m^2) at 9 sites, n = 12.

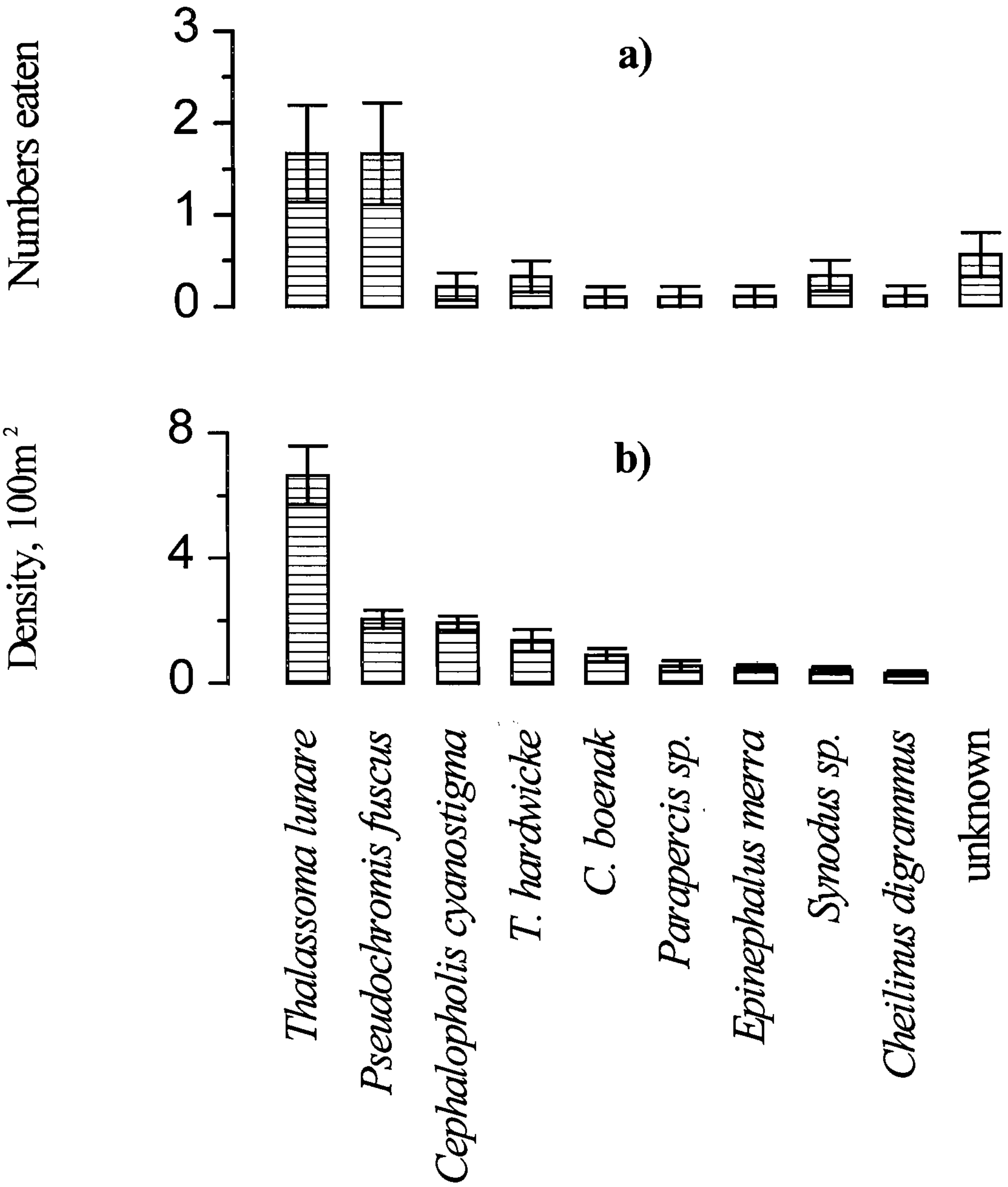


Fig 4a) Numbers (x̄ ± SE) of new recruits eaten, per predator species, when *Pomacentrus moluccensis* were released at 9 sites, n = 18, and **b)** Densities (100 m^2) of each predator species (x̄ ± SE) in rank order of abundance, n = 54.

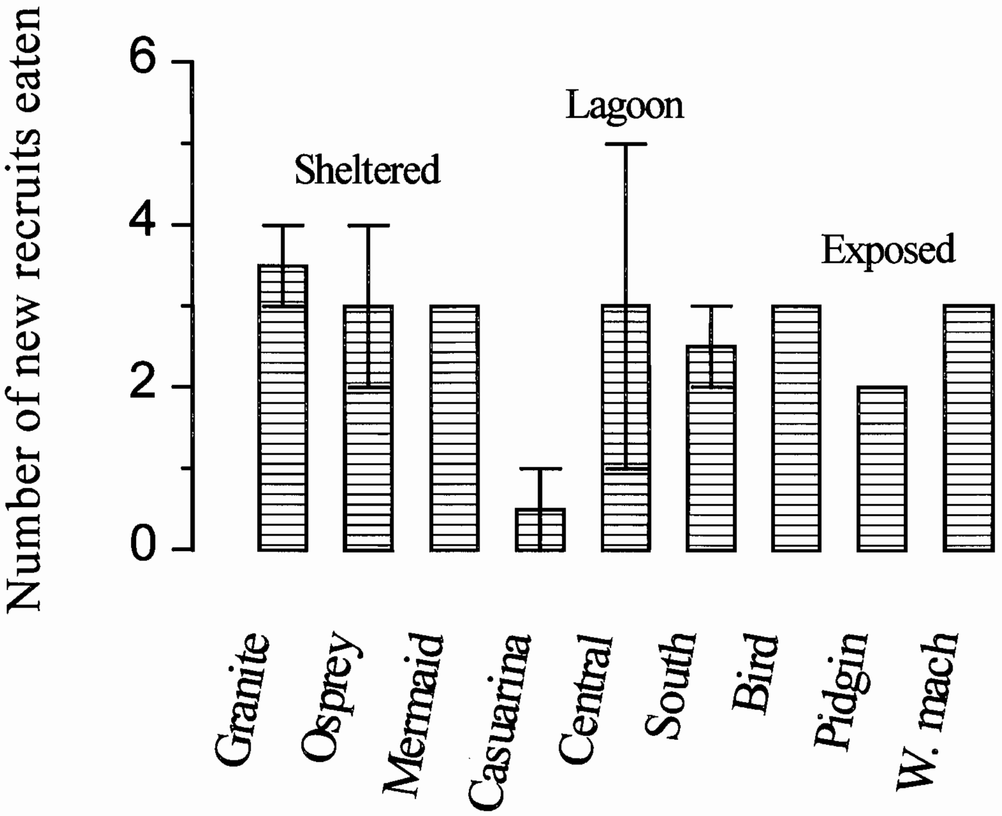


Fig 5 Number of new recruits eaten (x̄ ± SE) of *Pomacentrus moluccensis* released at 9 sites, with 3 sites in each island zone, n = 2.

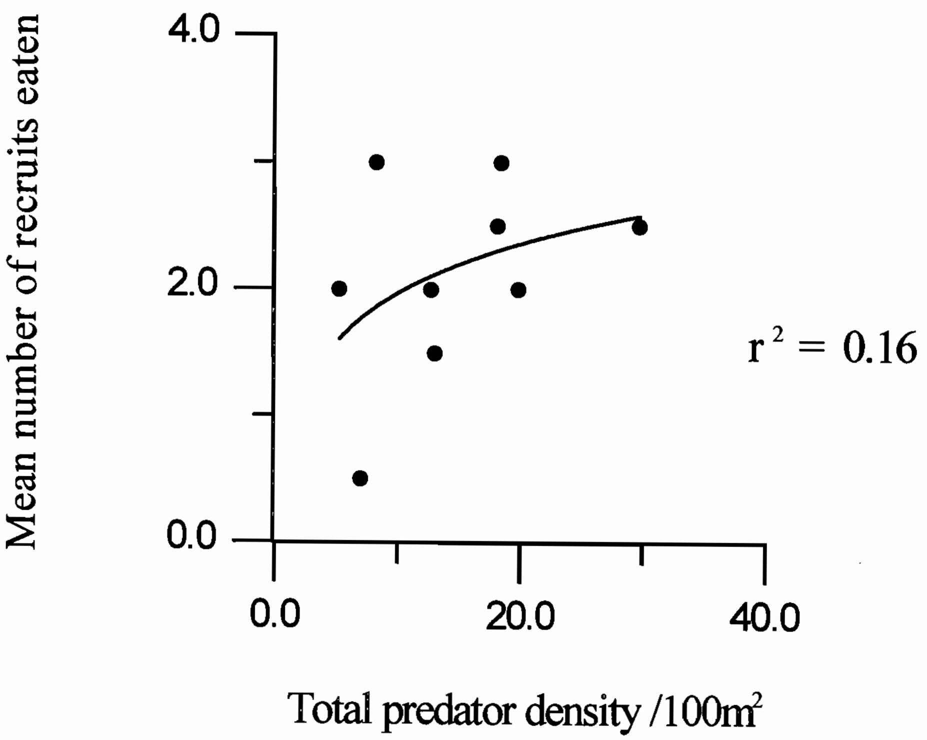


Fig 6 Regression of the number of new recruits eaten of *Pomacentrus moluccensis* released at 9 sites with total predator density, n = 9.

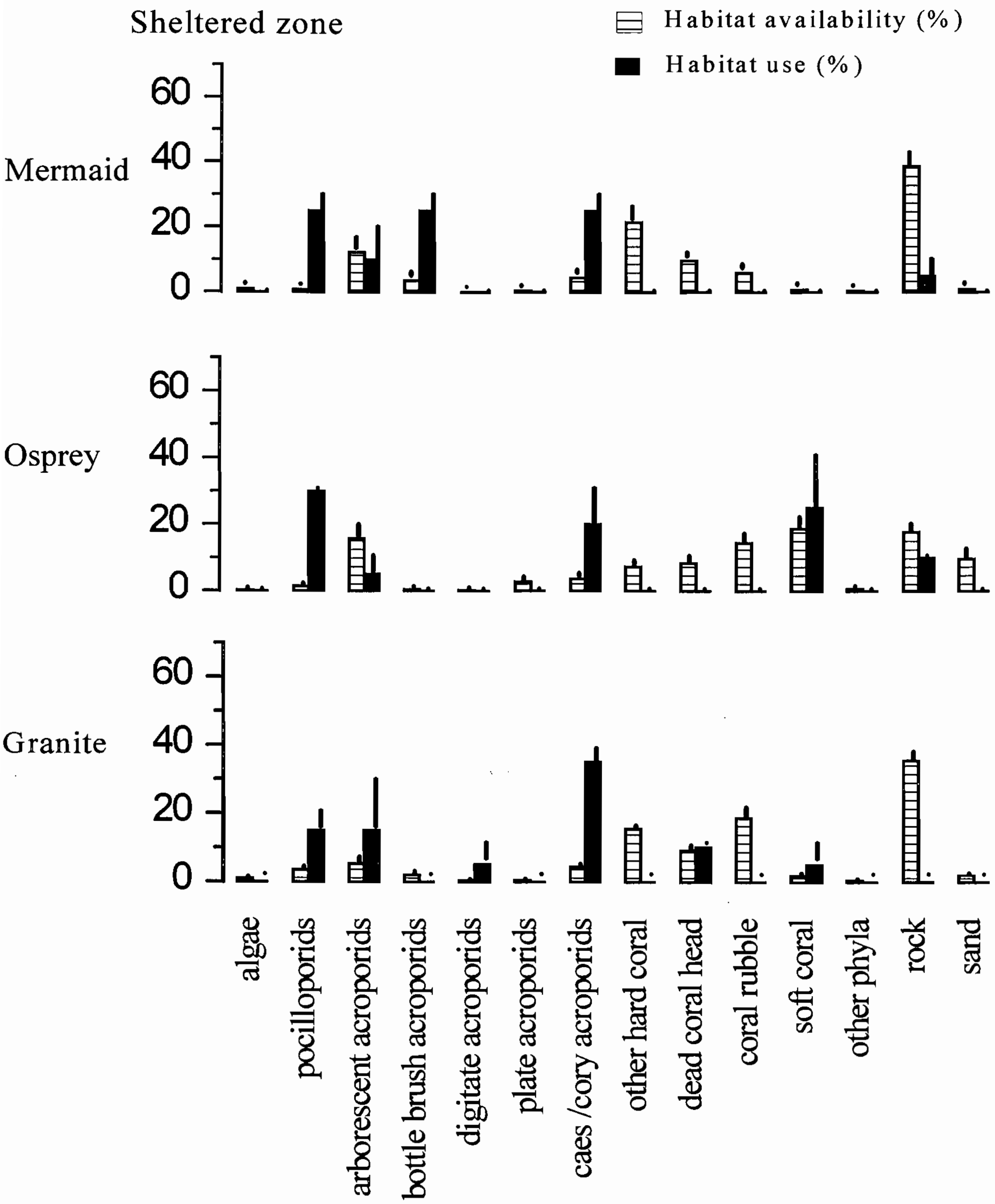


Fig 7a) Percentage availability and use of microhabitats by released *P. moluccensis* ($\bar{x}$ ± SE) new recruits, at three sites inthe sheltered zone, for availability n = 6, for use n = 2.

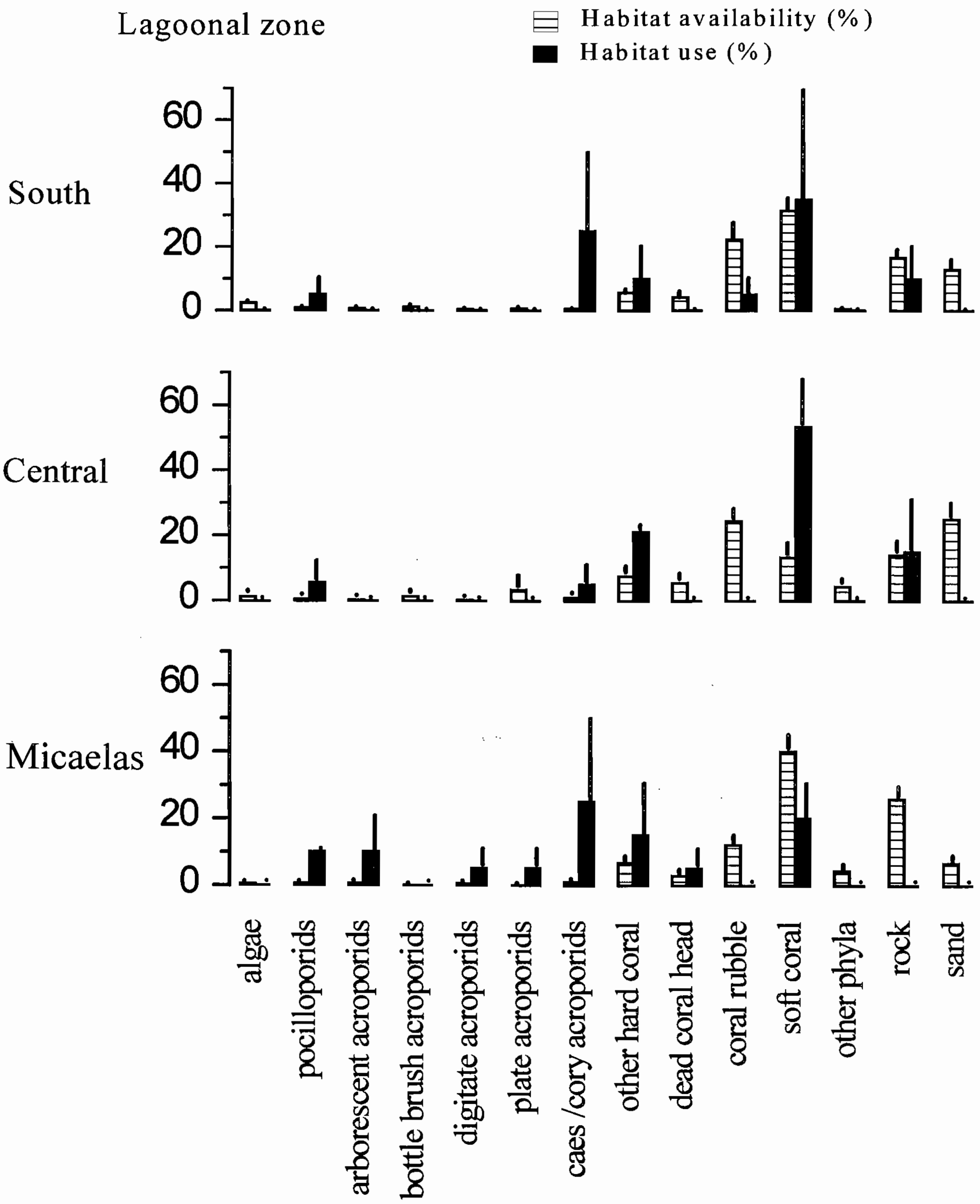


Fig 7b) Percentage availability and use of microhabitats by released *P. moluccensis* (x̄ ± SE) new recruits, at three sites in the lagoonal zone, for availability n = 6, for use n = 2.

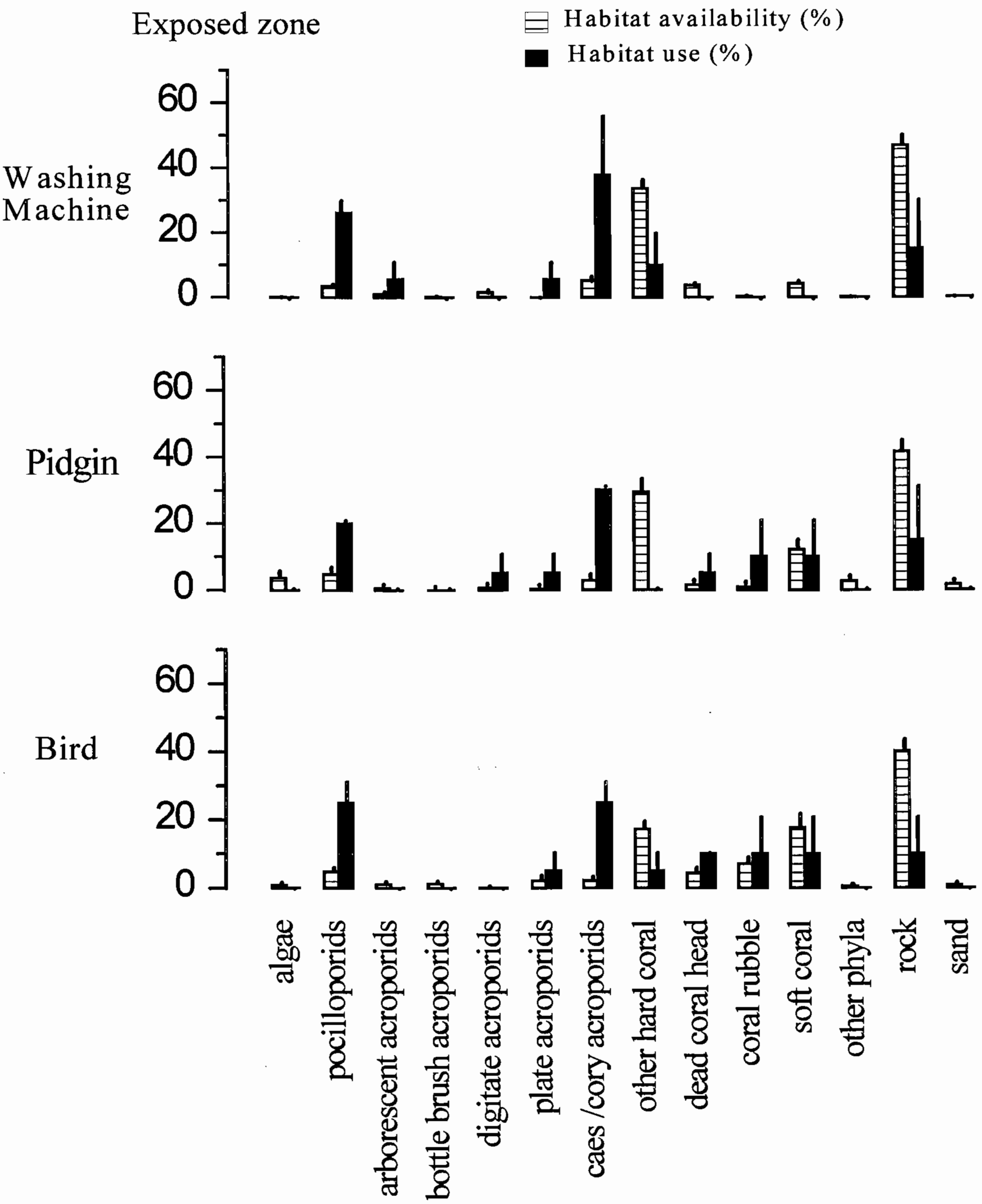


Fig 7c) Percentage availability and use of microhabitats by released *P. moluccensis* (x̄ ± SE) new recruits, at three sites in the exposed zone, for availability n = 6, for use n = 2.

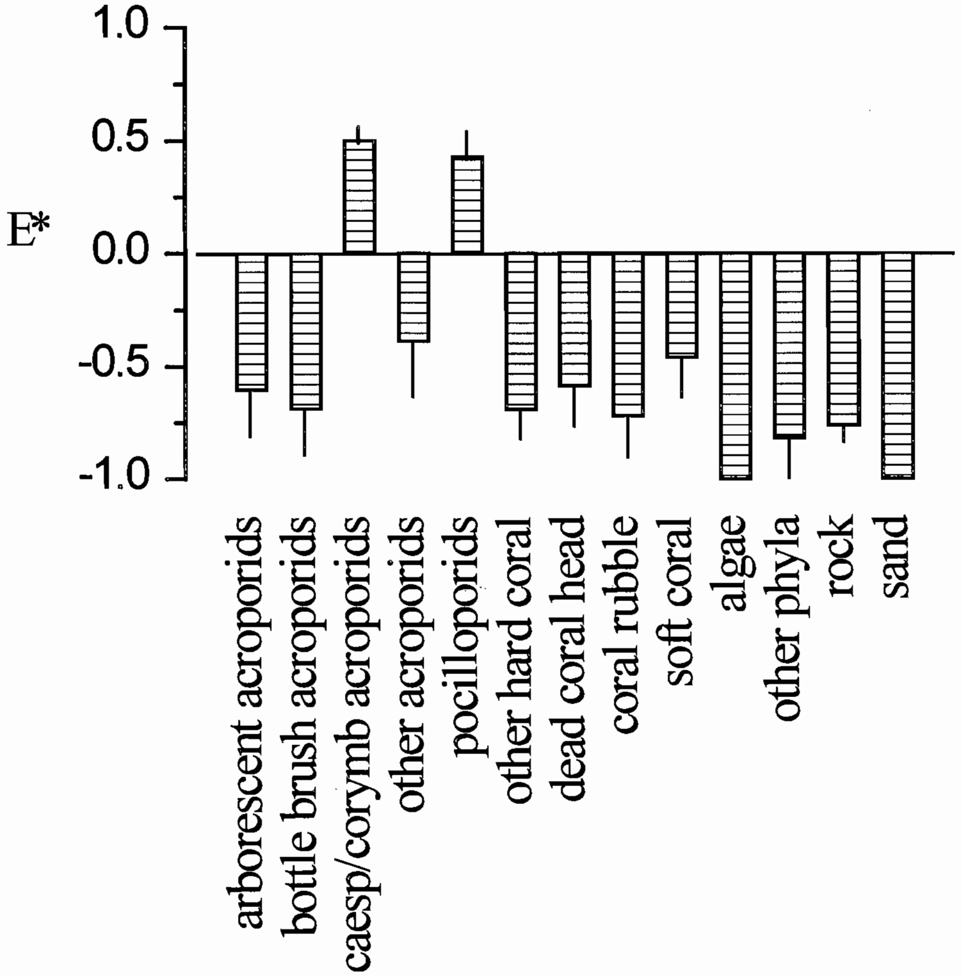


Fig 8 Microhabitat preferences (E*) of experimentally released *P. moluccensis* ($\bar{x}$ ± SE) new recruits at nine sites, n = 9.

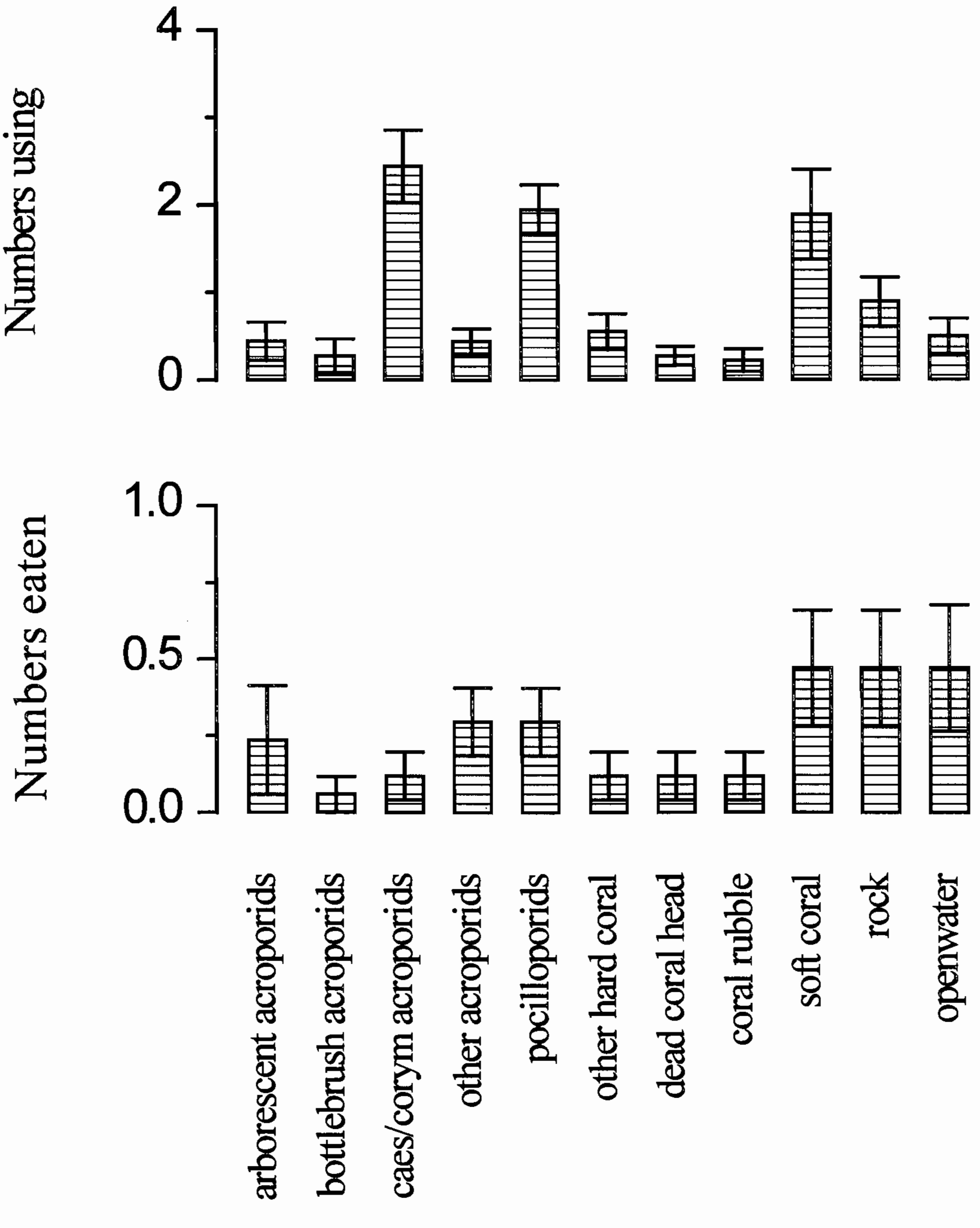


Fig 9 Number of experimentally released *Pomacentrus moluccensis* new recruits using and being eaten from (x̄ ± SE) each microhabitat at nine sites, n = 2.

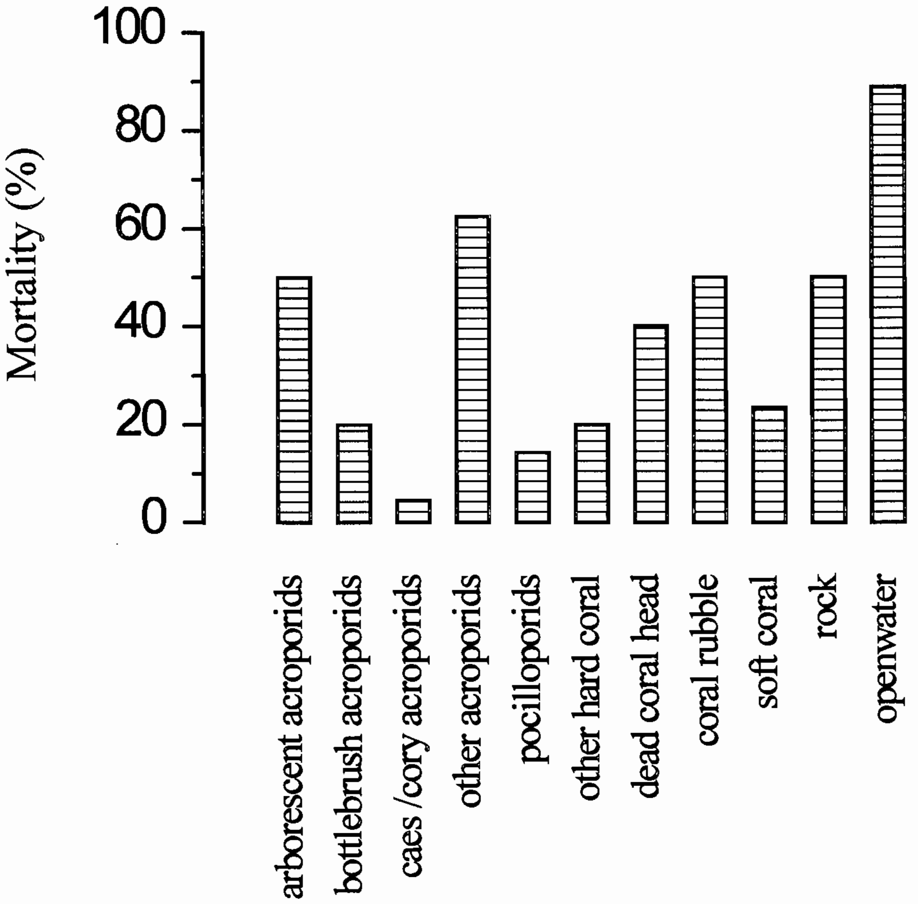


Fig 10 Percentage mortality ({number eaten / number using} x 100) of experimentally released *Pomacentrus moluccensis* new recruits from each microhabitat, n = 2.

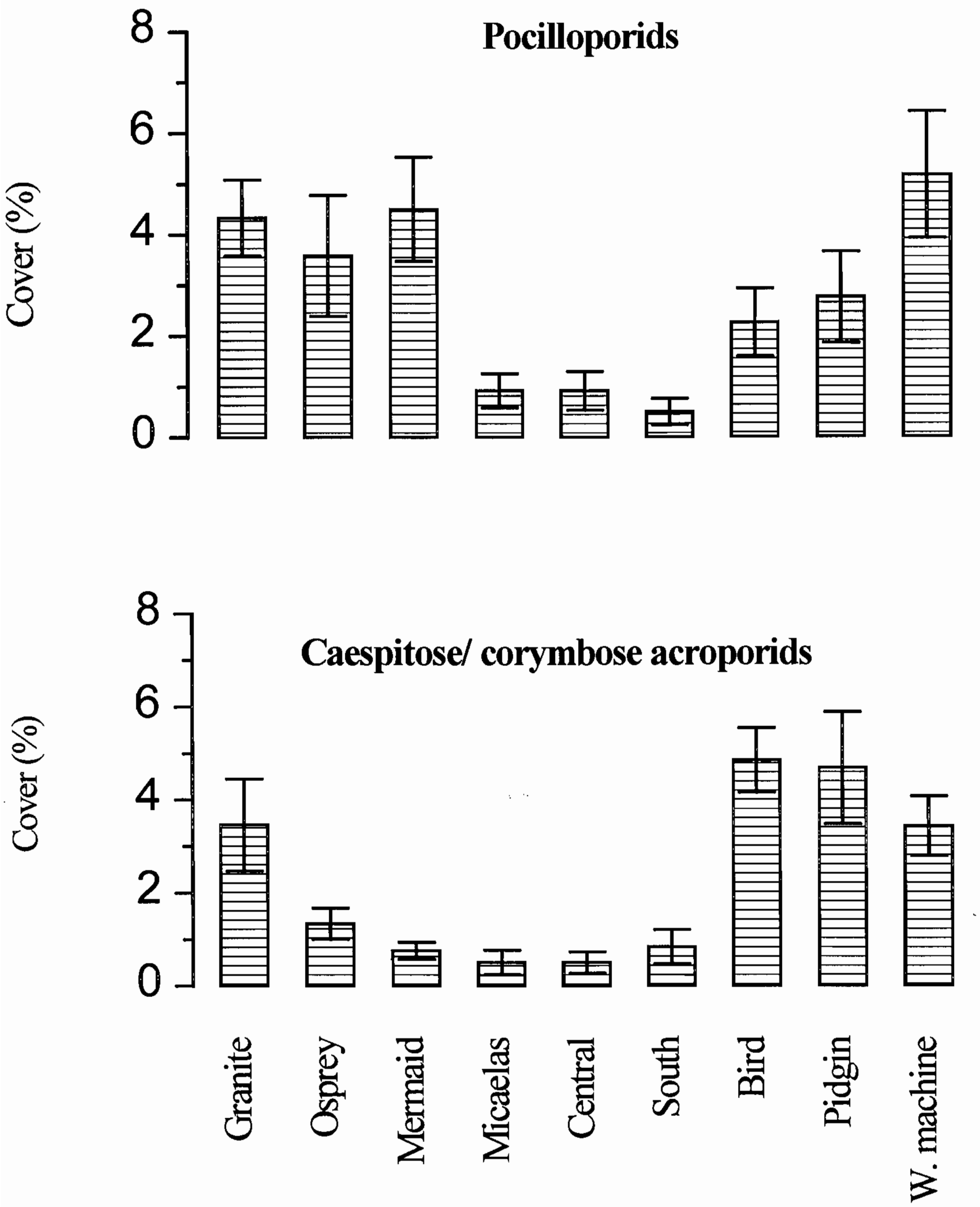


Fig 11 Percentage cover of the preferred coral types of *Pomacentrus moluccensis* new recruits (x̄ ± SE), caespitose and corymbose acroporids and pocilloporids, at each site. n = 12.

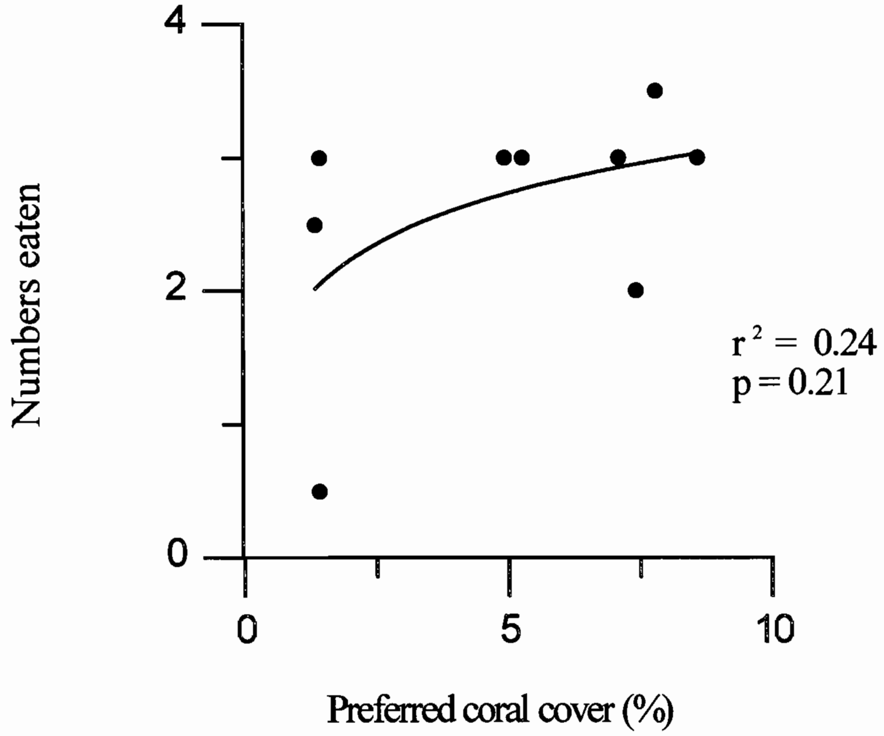


Fig 12 Regression of numbers of experimentally released new recruits that were eaten against mean percentage cover of preferred coral types at nine sites, n = 9.

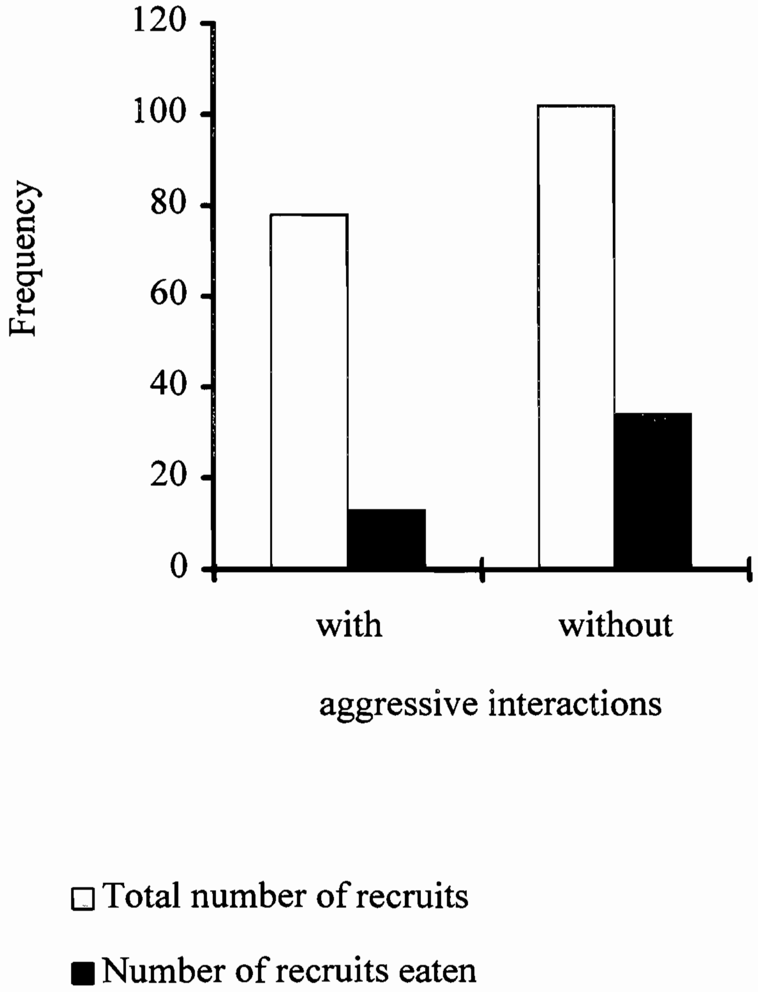


Fig 13 Number of experimentally released *Pomacentrus moluccensis* new recruits ($\bar{x}$ ± SE) that were attacked versus not attacked by aggressors, and the numbers of each that were subsequently eaten, n = 180.

CHAPTER 8

Habitat complexity modifies the impact of piscivores on a coral reef fish population

8.1 Abstract

Patterns in juvenile mortality rates can have a profound affect on the distribution and abundance of adult individuals, and may be the result of a number of interacting factors. Field observations at Lizard Is (Great Barrier Reef, Australia) showed that for a coral reef damselfish, *Pomacentrus moluccensis*, juvenile mortality (over 1 yr) varied between 20 and almost 100% among sites. Correlative data showed that juvenile mortality increased as a function of initial densities (recruitment), predator densities and the availability of preferred coral substrata. A multiple regression showed that these three variables together did not explain significantly more variation in mortality than the single factor showing the strongest relationship. This appeared to be because recruitment, predator densities and preferred coral substrata were all highly correlated, suggesting that one, two or all of these factors may be influencing juvenile mortality rates. One hypothesis is that density-dependent mortality in juveniles was the result of an interaction between predators (which appear to aggregate at high recruitment sites) and the availability of preferred substrata (predator refuges). Here I tested in both laboratory and field experiments, whether fish predation could significantly alter survivorship of this damselfish, and whether this impact was dependent upon the coral substratum.

The laboratory experiment was designed to test the effects of three common predators (*Pseudochromis fuscus*, *Cephalopholis boenak* and *Thalassoma lunare*) and three different coral substrata that varied in their complexity (*Pocillopora damicornis*, *Acropora nasuta* and *Acropora nobilis*) on the survival of juvenile *P. moluccensis*. There was a significant interaction between predator species and microhabitat in determining survival. *Pseudochromis fuscus* and *Cephalopholis boenak* were both significantly better at capturing juvenile damselfish than *Thalassoma lunare*. The survival of juveniles given the more complex corals as shelter, *Pocillopora damicornis* and *A.. nasuta*, was significantly better than those

given *Acropora nobilis*, a pattern which reflects habitat selection in the field. Predators differed in their strike rates and the proportion of strikes that were successful, but all exhibited greater success at prey capture where *Acropora nobilis* was provided as shelter.

The interaction between the effect of predators and microhabitat was tested in the field for a cohort of juvenile *P. moluccensis.* Juvenile survival in the presence and absence of two predators that co-occur on natural patch reefs (*Cephalopholis boenak* and *Pseudochromis fuscus*) was examined on experimental patch reefs constructed from both high complexity (*Pocillopora damicornis*) and low complexity (*Acropora nobilis*) coral substrata. Both juveniles and predators were translocated to reefs at natural densities. The effects of predation were clearly dependent upon the microhabitat. Reefs of the high complexity coral with predators supported the same high numbers of *P. moluccensis* as the reefs with no resident predators. However, damselfish abundance was significantly lowered on low complexity reefs with resident predators, relative to the other treatments. Background rates of loss were high, even on preferred coral in the absence of the manipulated predator, suggesting transient predators may be even more important than the residents. We suggest that adult abundances in this species will be strongly influenced by the densities of different predators and the availability of preferred refuges.

8.2 Introduction

Predation is one of the major processes influencing the size of populations and the structure of ecological communities (Paine, 1966; Murdoch and Oaten, 1975; Hassell, 1978; Talbot et al., 1978; Taylor, 1984; Sih et al., 1985). However, the importance of predation must be evaluated against the magnitude of other processes such as competition and recruitment (Hairston et al., 1960; Menge and Sutherland, 1987; Power, 1992). These processes may interact to determine the distribution and abundances of organisms. By consuming prey, predators can control prey populations by altering the relative and absolute abundances and species diversity of prey (Sih, 1987). The importance of any one factor will be influenced not only by the strength of the process, but by other factors which modulate its effect (Hunter and Pric, 1992). It is these modulating factors that can determine when and where each process will dominate in regulating populations. One of the factors that may modulate the effects of predation is habitat complexity (Crowder and Cooper, 1982; Werner et al., 1983; Menge and Sutherland, 1987; Hixon and Menge, 1990; Caley and St John, 1996). Complex habitats may provide refuges to prey, thus reducing the importance of predation relative to other processes.

Prey can reduce the risk of predation in two ways: by avoiding encounters with predators or by escaping after an encounter (Sih, 1987). Structurally complex habitats may reduce predation rates by providing absolute prey refuges where predators cannot physically reach prey individuals or by decreasing encounter rates between predators and prey (Murdoch and Oaten, 1975; Anderson, 1984; Savino and Stein, 1989; Christensen and Persson, 1993). Prey have often been observed to use more complex habitats in the presence of predators (Stein and Magnuson, 1976; Dill and Fraser, 1984; Shulman, 1984; Holbrook and Schmitt, 1988a; Sih et al., 1992), and predators have been found to be less efficient foragers in more complex habitats (Savino and Stein, 1982; Anderson, 1984; Cook and Streams, 1984; Persson and Eklov, 1995). Furthermore, increasing the number of refuges or habitat complexity has been shown in some ecosystems to increase either species diversity or survivorship (Behrents, 1987; Hixon and Beets, 1989,1993; Connell and Jones, 1991; Diehl, 1993; Caley and St John, 1996). There is a growing awareness that knowledge of how demographic processes vary with structural aspects of the habitat is important for understanding the population ecology of reef fishes (Levin, 1994).

8.2.1 Coral reef studies

The high structural complexity of coral reefs, the high species richness of coral reef communities and the open nature of coral reef fish populations have made the study of predation in this ecosystem especially difficult (Hixon and Beets, 1993). Hence, relatively few coral reef fish studies have attempted to look at predation compared with other potentially important processes such as competition or recruitment.

Because of this, the importance of predation in controlling populations of coral reef fish remains uncertain. In a recent review, Hixon (1991) highlighted the need to use experimental manipulation to test for a causal relationship between predators and their prey. To date none of the studies that have attempted predator manipulations have examined the effect of predators in relation to habitat structure (i.e. Bohnsack, 1982; Stimson et al., 1982; Thresher, 1983b; Doherty and Sale, 1985). Much correlative evidence suggests that several aspects of habitat including coral cover and topographic complexity may be important in determining adult densities (Luckhurst and Luckhurst, 1978; Thresher, 1983a; Bell and Galzin, 1984; Roberts and Ormond, 1987; Sano et al., 1987). However, some studies found that habitat was not important (Risk, 1972; Sale and Douglas, 1984; Sale et al., 1994). Hence, without further experimental work, few generalizations are likely to emerge.

Other experimental manipulations of habitat have been performed to directly assess the importance of shelter in determining abundance (Robertson and Sheldon, 1979; Fricke, 1980; Robertson et al., 1981; Shulman, 1984; Hixon and Beets, 1989,1993; Buchheim and Hixon, 1992), but many of these used artificial structures and none have included manipulations of predators. Fricke (1980), Shulman (1984), Hixon and Beets (1989,1993) and Buchheim and Hixon (1992) all showed that an increase in the number of shelter sites lead to an increase in the number of study species, however, the other two studies found that habitat had little effect. In addition, (Jones, 1988) tested the effects on fish survival of two coral species and found survivorship was significantly higher in the most complex coral species. Although a significant effect of habitat may be due to the effects of predation, it was not demonstrated by these experiments because habitat could be important for other reasons such as shelter from storms.

8.2.2 Natural history of the damselfish, *Pomacentrus moluccensis*

The lemon damselfish (*Pomacentrus moluccensis*), is one of the most abundant damselfish on the reefs around Lizard Island. After approximately 20 days in the plankton (Wellington and Victor, 1989), and at about 10 mm standard length, larvae recruit onto the reef and are almost always associated with live coral (Sale et al., 1984; Eckert, 1985; Mapstone, 1988). This damselfish is planktivorous and new recruits of this species are preyed upon by several small carnivorous reef fish, including the pseudochromid, *Pseudochromis fuscus,* the small serranid, *Cephalopholis boenak*, and the abundant wrasse, *Thalassoma lunare* (Martin and Jones, in prep., Chapter 7). In chapter 6, I showed that the abundance of juvenile *P. moluccensis* was correlated with the cover of preferred coral substrata (corals with corymbose or caespitose growth forms). In chapter 7, I showed that the abundance of predators was correlated with juvenile densities. Here I examine the consequences of these patterns for juvenile mortality, and ultimately the distribution and abundance of adult fishes.

The aim of this study was, therefore, to examine whether the predators have an impact on the survival of juvenile *P. moluccensis*, and determine whether the magnitude of the effect is modified by the microhabitat or coral substratum used as shelter. The study proceeded in three phases. Firstly, spatial patterns in juvenile mortality (see Chapter 5) were examined to determine the relative strengths of correlations with initial juvenile density (recruitment), predator densities and the availability of preferred coral substrata. Secondly, an experiment was performed in aquaria to look at success rates of three predator species in capturing *P. moluccensis* given three different corals that varied in complexity as shelter. Lastly, a field experiment was performed to test the hypothesis that predators and microhabitat interact to determine the survival of juvenile *P. moluccensis.*

8.3 Methods

This study was carried out at Lizard Island which is located in the northern section of the Great Barrier Reef Marine Park, Australia (14°42’ S, 145°28’ E). Lizard Island is surrounded by shallow fringing reefs, the primary habitat of *P. moluccensis.* The main island is connected to two smaller granite islands by reefs which form protected lagoonal areas. Individual study sites were located on the upper reef slope areas of reef on the exposed (eastern) and sheltered (western) sides of the island, and also in the lagoon. The study was carried out between December 1994 and January 1996.

8.3.1 Spatial variation in the mortality of juvenile *Pomacentrus moluccensis*

Spatial variation in juvenile mortality was examined at eight locations distributed around the exposed and sheltered sides of the island, and in the lagoon (see Chapter 5). Here I examined the relative strengths of correlations between juvenile mortality and (1) initial juvenile densities, (2) cover of preferred coral substrata, and (3) predator densities. Relationships among these variables were also examined to determine their degree of independence, and multiple regression was used to provide the best predictor of mortality rates.

Patterns of juvenile density (recruitment) were assessed along twelve haphazard transects (10m x 1m), at eight random sites (hundreds of metres to a few kilometres apart), in January 1995 and 1996. All fish between 10mm and 24.9mm SL were counted as juveniles. Any individual >25mm SL was counted as an adult (sensu Mapstone, 1988). Juvenile mortality over one year was calculated according to the following equation:

$$\%M = \frac{(R - C1)}{R}$$

Where

%M = percent mortality during the first reef associated year

R = abundance of cohort 0+ in year 1, new recruits $/100\text{m}^2$

C1 = abundance of cohort 1+ in year 2, $/100\text{m}^2$

The percentage of adults that were 1 year old was calculated using age structures for Lizard Island in January (Chapter 5). This figure was then used to assess the number of adults in cohort 1 (C1) on each transect. Mortality estimates during the first reef associated year, were calculated for new recruits settling in 1995 at eight sites.

Along the same transects, patterns in the abundance of preferred coral substrata were assessed. A sony hi-8 camera was used to video each transect (see Chapter 6). The camera was held approximately 25cm away from the reef and 2 minutes was taken to film each 10m transect. The video tape was analysed by stopping at twenty places along each transect. The substrate at five random places on the monitor screen were noted at each of the twenty stops.

Patterns in the abundance of small predators of juvenile reef fish were were censused twice at every site (see Chapter 7). Two methods were used, one developed for cryptic species and the other for non cryptic species (Stewart and Beukers, in prep). For cryptic species (e.g. *Pseudochromis fuscus* and *Cephalopholis boenak*), a baited point census was used to increase the likelihood of observing individuals of these species. Ten points around the circumference of a 5m circle were marked using fluorescent tape. All cryptic predatory piscivores seen within this area were counted during a 15 minute period. At the start of the observation period four pilchards were placed in a mesh bag and pulverised. At the end of the census the mesh bag was placed in a sealed bag and removed from the reef. On each of two separate occasions three spatially separate circles were counted so that a total of six circles were counted for each site.

For diurnally active, non-cryptic species (e.g. *Thalassoma lunare*) the traditional visual census method was used. At each location fish were counted within 18 m by 30 m quadrats. Each quadrat was divided into 6 belt transects 3 m wide, 18 m long and fish were counted by swimming along each of these in turn. Abundances were converted to densities per 100m^2.

8.3.2 Effects of predator species and coral substratum on juvenile survival: an aquarium experiment

An orthogonal experiment was set up in December 1994, to test the effects of three small predators (*Pseudochromis fuscus*, *Cephalopholis boenak*, and *Thalassoma lunare*) on the survival of juveniles given three different coral species as shelter (*Acropora nasuta, Acropora nobilis* and *Pocillopora damicornis*). Thirty-six tanks (each 100cm by 50cm) were set up with 5cm of sand covering the bottom. Two coral heads of the each species to be used as shelter were placed in the centre of each tank. Every treatment tank contained one predator and one coral species, and additional control tanks contained the same coral species without predators. Five juvenile *P. moluccensis* (10 - 20mm SL) were placed in each tank. There were three replicates of each treatment and control. Predators were placed in the aquaria for three days before juvenile *P. moluccensis* were added, to become accustomed to their surroundings. During this time they were not fed. When *P. moluccensis* were released into the aquaria, care was taken to reduce disorientation. Five new recruits were floated in a click-seal polythene bag for 2 minutes above one of the coral heads. Then the bag was gently opened so that the fish could swim away from the bag. There were no cases of new recruits being eaten before they reached the coral head. Recruit survivorship in all aquaria was recorded continuously for the first hour after release and then every 24 hours for 7 days. The number of successful and unsuccessful predatory strikes made by the predator, were also counted during the first hour. Final recruit density was analysed with a two-way ANOVA followed by a Tukey's Studentised Range test.

8.3.3 Does habitat complexity modulate the effect of predators? A field experiment.

An experiment was set to test the effect of two predators normally resident on small patch reefs on the survival of juvenile *P. moluccensis* on patch reefs contructed from two different types of coral, one of high complexity (*Pocillopora damicornis*) and one of low complexity (*Acropora nobilis*). To determine densities of juvenile *P. moluccensis* and predators to be used in the experiment, their densities on natural patch reefs were surveyed. The numbers of *P. moluccensis* in the range 10 - 25 mm SL inhabiting each coral head of the two coral species were counted on natural reefs during January 1995. The volume of coral was approximated by measuring the greatest length, its perpendicular width and the depth of the coral head. Abundances were converted to densities per $0.315m^3$of coral for use in setting up the field experiment. Numbers of *Pseudochromis fuscus* and *Cephalopholis boenak* were counted on 28 patch reefs at each of two patch reef sites. Reefs were selected of approximately the same size to be constructed for the field experiment reefs.

The experiment was carried out on a large flat sandy area in the lagoon of Lizard Island. A fully balanced, orthogonal experiment was set up with two factors: predator density and habitat complexity. Each factor had two levels. Predators were either present or absent at approximately natural density (1 individual of each species per reef). Patch reefs were constructed from two coral substrata, ten made out of *Pocillopora damicornis* and ten of *Acropora nobilis*. The dimension of each reef was approximately 90 cm x 70 cm x 50 cm giving each a volume of $0.315m^3$ and surface area of $0.223m^2$. They were placed on sand 30 m apart at 5m depth on the highest tides. Treatments were assigned to reefs using a randomised block design with 5 replicates. To examine migration rates from each of these corals without resident predators, twenty *P. moluccensis* new recruits (10-20mm SL) were released on each reef and their numbers were monitored for one week. Before the experiment started a density of 15 individuals per reef was required to reflect natural densities. After some initial migration, numbers were adjusted downward to establish densities of 15 per reef, before predators were added to the reefs. Reefs were checked daily for one week to monitor any emigration of predators, but this did not occur. Pelagic predators were able to access all reefs equally and therefore did not influence treatment effects. Censuses of all fish on the reefs were carried out after two months. The numbers of *P. moluccensis* remaining in each treatment were analysed using a log transformation to normalise data, a two-way ANOVA followed by a Tukey's Studentised Range test.

8.4 Results

8.4.1 Spatial variation in the mortality of juvenile *Pomacentrus moluccensis*

The mortality of juvenile *P. moluccensis* varied between 20% and almost 100% among the eight sites examined. This variation was potentially explained by initial juveniles densities, predator densities and/or the availability of preferred coral substrata (Fig 1a-c). Mortality increased as a function of recruiment levels, but the rate of increase in mortality decelerated with increasing recruitment (the natural log of initial densities explained 67.6% of the variation - Fig 1a). There was a significant linear relationship between mortality and predator densities that explained 56% of the variation (Fig 1b) and an almost significant linear relationship between mortality and the cover of preferred coral substrata (Fig 1c) that explained 46% of the variation. A multiple regression using all three variables to predict mortality rates was not significant ($F_{[3, 4]} = 1.98$, $p = 0.26$), and explained no more variation than recruitment or predators alone (multiple $r^2 = 0.60$). A more detailed analysis of the relationships between recruitment, predators and % cover of preferred corals indicated that these were unlikely to be independent variables. Pairwise comparisons showed significant positive correlations between recruitment (ln) and predators ($r = 0.93$), recruitment and cover of preferred corals ($r = 0.68$), and between predators and coral cover ($r = 0.66$), thus obscuring any potential cause-effect relationships.

8.4.2 Effects of predator species and coral substratum of juvenile survival: an aquarium experiment

Both predators and coral substratum had a significant effect on the survivorship of juvenile *P. moluccensis* (Fig 2, Table 1a). The magnitude of the effects of different predators was dependent upon the coral substratum (Table 1a). Overall, the mean survivorship was significantly lower for two of the predators, *Cephalopholis boenak* and *Pseudochromis fuscus,* compared to the controls with no predator present (Table 1b). Survivorship was approximately 20% in the presence of these two predators and almost 100% in controls. The effect of predation by *Thalassoma lunare* was much lower, with almost 80% survival in this treatment (Fig 2).

The survival of *P. moluccensis* in treatments with predators differed significantly among the three coral types (Fig 3). For the two most important predators, *Pseudochromis fuscus* and *Cephalopholis boenak*, survivorship was significantly better for *Pocillopora damicornis* and *Acropora nasuta*, compared *Acropora nobilis*, where 100% mortality occurred. The effects of the two predators were slightly different, with *Pseudochromis fuscus* being more successful than *Cephalopholis boenak* at capturing prey in *Pocillopora damicornis* (Table 1b). Survivorship (± SE) was the same for all coral types when no predator was present (4.5 ± 0.41).

The two most successful predators, *Pseudochromis fuscus* and *Cephalopholis boenak* made the highest percentage of successful predatory strikes in *Acropora nobilis* (Fig's 4 and 5). However, the frequency of predatory strikes differed between the two predator species and also for individuals of the same species attacking prey given different corals as shelter. *Pseudochromis fuscus* made large numbers of predatory strikes with a very low success rate in the most complex coral *Acropora nasuta* (Fig 4), while *Cephalopholis boenak* made relatively few strikes regardless of the coral species (Fig 5). Qualitative aspects of the behaviour of *Cephalopholis boenak* also varied according to microhabitat type. In the most open coral they would continuously chase prey until a successful capture, which in most cases was no more than a few seconds. In the higher complexity habitats, *Cephalopholis boenak* stalked their prey, moving gradually closer and closer, and sitting motionless for long periods. The final strike was extremely quick and was more likely to be successful in all three coral species when compared to_*Pseudochromis fuscus*.

8.4.3 Does habitat complexity modulate the effect of predators? A field experiment.

For the two coral types to be used in the field experiment, the densities of juvenile *P. moluccensis* were consistently higher in the more complex coral species (Fig. 6). These juveniles may have spent up to 3 months on the reef and this was therefore a measure of numbers recruiting plus any post-settlement modification that may have

Table 1a) Analysis of variance table (variances homogeneous) and **b)** Tukey's studentised range test on for number of new recruits present in aquaria after 2 months. Groups with the same category do not have significantly different means. Low = low numbers remaining, high = high numbers remaining.

a)

Source	DF	SS	MS	F Value	**P**
PRED	3	2.55702034	0.85234011	30.14	0.0001
CORAL	2	0.28164475	0.14082238	4.98	0.0155
PRED*CORAL	6	0.42658760	0.07109793	2.51	0.0496

b)

habitat / predator	*A. nasuta*	*P.damicornis*	*A. nobilis*
P. fuscus	Low, Med, High	Low	Low
C. boenak	Low, Med	Med, High	Low
T. lunare	Med, High	High	Med, High
No predator	High	High	High

occurred. Mean densities per $0.315m^3$ for *Acropora nobilis* were in the range 3 - 10 individuals, in *Pocillopora damicornis* they were 13 - 30 individuals. An overall average of 15 was used for the experiment.

The mean densities of *Pseudochromis fuscus* and *Cephalopholis boenak* on natural patch reefs were in all cases less than one (Fig 7). The densities of *C.boenak* varied from 0 to 3 individuals per reef, and of *Pseudochromis fuscus* varied between 0 and 2 individuals per reef. In each case, the two most common situations were densities of 0 or 1 per reef, so these were chosen as the two levels in the experiment. The two predators frequently co-occured on the same reefs.

There was a significant interaction between predator density (presence, absence) and microhabitat type (Fig 8, Table 2a). On the low complexity reefs with predators *P. moluccensis* recruits showed significantly lower final abundance than on all of the other reefs (Fig 8, Table 2b). The high complexity *Pocillopora damicornis* reefs with predators supported the same high numbers of *P. moluccensis* as the reefs with no predators. Loss rates were high, even on reefs without resident predators. There was no significant difference in loss rates from the two reef types in the week prior to predators being added ($p = 0.1570$, Table 3), and the experiment was started with juveniles which had been resident for one week.

Table 2a) Analysis of variance table (variances homogeneous) and **b)** Tukey's studentised range test on number of new recruits remaining on patch reefs after 2 months. Groups with the same category do not have significantly different means. Low = low numbers remaining, high = high numbers remaining.for number of new recruits present on patch reefs after 2 months.

a)

Source	DF	SS	MS	F	P
CORAL	1	0.30524806	0.30524806	4.25	0.0559
PRED	1	0.40854025	0.40854025	5.69	0.0298
CORAL*PRED	1	0.36391717	0.36391717	5.06	0.0388

b)

Predators/habitat	P. damicornis	A. nobilis
Present	High	Low
Absent	High	High

Table 3 Analysis of variance table (variances are homogeneous) for number of new recruits present on patch reefs after 1 week without predators present.

Source	DF	SS	MS	F	P
Model	1	0.25911392	0.25911392	2.18	0.1570
Error	18	2.13813575	0.11878532		
Corrected Total	19	2.39724967			

8.5 Discussion

Correlative data implicated the importance of both recruitment levels, predators and the availability of preferred coral substrata in determining patterns in the mortality of juvenile *Pomacentrus moluccensis*. However, since all these factors appear to be interrelated, the potential cause-effect relationships were obscure. The strong correlation between recruitment levels and predator densities suggested that predators may be involved in determining the apparent density-dependent mortality. Predators aggregating at high recruitment sites would lead to increased mortality rates as a function of density (see Chapter 7). However, if predators are important, the patterns suggest that their effects decline with increasing density. This may be due to an interaction between the effects of predators and the availability of preferred shelter for the prey species. Juveniles exhibit a strong association with particular coral substrata (Chapter 6), and recruitment and mortality increased with the availability of preferred coral cover. In this chapter, the hypotheses that predators do have an impact, and that their impact is modulated by the availability of preferred substata were tested on both aquarium and field experiments. Both hypotheses were supported by the results.

Coral substrata clearly differ in the degree of shelter they provide to species such as *P. moluccensis*. The degree of protection afforded appears to depend not only on attributes of the microhabitat itself, but also on the attributes of particular predators. In aquaria, there was a significant interaction between the effects of predator species and microhabitat on the survivorship of *P. moluccensis*. Predator success in each microhabitat varied according to species. Both *Pseudochromis fuscus* and *Cephalopholis boenak* were most successful in the structurally least complex coral species (*Acropora nobilis*). However, there were differences among predators. *Pseudochromis fuscus* had a higher percentage of successful strikes in *Pocillopora damicornis* than *Acropora nasuta,* while *Cephalopholis boenak* exhibited the opposite pattern. It seems likely that this was due to the differences in their predatory behaviour. Unfortunately, it was not possible from this experiment to show which attributes of microhabitat were important for increased damselfish survival. It would seem that more complex coral head structures provided better refuges from predation as has previously been shown in freshwater communities (Werner et al., 1983; Holbrook and Schmitt, 1988b; Persson and Eklov, 1995). It must be borne in mind that under conditions with several predators using different search modes and predatory behaviour, the ability of prey to avoid predation may differ substantially (Kingsford, 1992).

Survivorship of *P. moluccensis* in the aquaria with *Thalassoma lunare* was not significantly different to the controls. *Thalassoma lunare* is a mobile predator and individuals often forage in a group. In aquaria individuals spent most of their time swimming up and down the glass. It is most likely that the aquaria significantly altered their behaviour, but it could also be that *Thalassoma lunare* is not a particularly important predator of *P. moluccensis*.

In the field, microhabitat modified the effects of resident predators on *P. moluccensis*. The reefs constructed from the higher complexity coral, *Pocillopora damicornis,* with predators present, supported the same high numbers of the damselfish as those with no resident predators. This is consistent with the study by Jones (1988), who found that damselfish survivorship at One Tree Reef was higher in *Pocillopora damicornis* than in a less complex coral. However, the question remains as to whether this difference was due to mortality or migration. One of the main problems that most mortality studies have, is that they cannot avoid the potentially confounding effects of immigration and emigration. My field experiment was no exception to this, however, there is some evidence against and no evidence for, differential migration. Firstly there was no significant difference in losses from reefs prior to adding the resident predators. The result is therefore definitely a direct result of the addition of resident predators. Although there was some initial emigration, the experiment was started with juveniles that had remained resident for a week. Evidence for migration occurring would come from reefs that showed a net increase in numbers of *P. moluccensis* but all reefs showed net losses. In addition, previous work in this thesis has shown that *P. moluccensis* is extremely site attached (see Chapter 6). Also, Mapstone (1988), marked ninety nine *P. moluccensis* and found that only one moved further than 2 m over a period of three years.

Patterns of predator and microhabitat abundance could explain the distribution of adult *P. moluccensis*. While patterns in the distribution of juveniles may be explained by variation in larval supply (Doherty, 1987; Milicich and Doherty, 1994), patterns of the relative abundance of juveniles and adults were consistently different over the three years of this study (Chapter 5). Both site-specific and density dependent patterns in mortality may be due to predators, but the absolute magnitude of the effect may be dependent on the magnitude of recruitment relative to the local availability of preferred coral. These experiments show that resident predators could alter patterns of distribution of *P. moluccensis* between microhabitats. Resident predators have been shown to significantly alter population abundance and size structure on natural patch reefs in the Caribbean (Carr and Hixon, 1995). These effects were prey species specific and so could lead to changes in the relative abundance of species in the community . However, high background mortality on reefs in the absence of resident predators also implicates the role of transient predators in this and other studies.

Spatial variation in mortality rates have been observed in other studies on *P. moluccensis* (Doherty and Fowler, 1994) and many other coral reef fish species (DeMartini and Anderson, 1980; Jones, 1984,1986; Aldenhoven, 1986; Eckert, 1987; Sale and Ferrell, 1988; Connell and Kingsford, 1992; Booth and Beretta, 1994). Doherty and Fowler (1994) observed lower abundances of adults and reduced life expectancies of *P. moluccensis* at a site with relatively high recruitment when compared to One Tree Island, and suggested that this was due to differential predation. Unfortunately they only had one high recruitment site and several low to intermediate reefs, so this result remains tentative. Spatial variation in the availability of microhabitats (Done, 1982; Nelson, 1994) and predator community structures have been documented at Lizard Island (Chapter 7; Stewart and Beukers, in prep.). These factors could account for the observed spatial variation in mortality rates of *P. moluccensis*.

Spatial variation in mortality would modify recruitment patterns and alter numbers subsequently reaching maturity. Doherty and Fowler (1994) and Mapstone (1988) concluded that the most important factor determining *P. moluccensis* in the Southern Great Barrier Reef was recruitment. Thus it could be that while at some sites, for example where habitat is complex, recruitment rates may be the most important factor determining abundance, at others it could be a complex interaction of settlement patterns and the degree of protection provided by habitat components against the suite of predators present. The variability in the results of previous habitat studies on coral reefs would support a pluralistic theory whereby several processes were important in structuring populations of reef fish and whose importance varied temporally and/or spatially (Jones 1991, Hixon 1991 and others).

In this predator-prey system, variation in microhabitat and predators had significant effects on mortality rates, and could potentially account for much of the observed spatial and temporal variation in adult numbers. Given that mortality appears to be density-dependent, there is some evidence that the prey population is being regulated. Hence it would seem that post-settlement processes are playing a significant role in shaping populations of this coral reef damselfish.

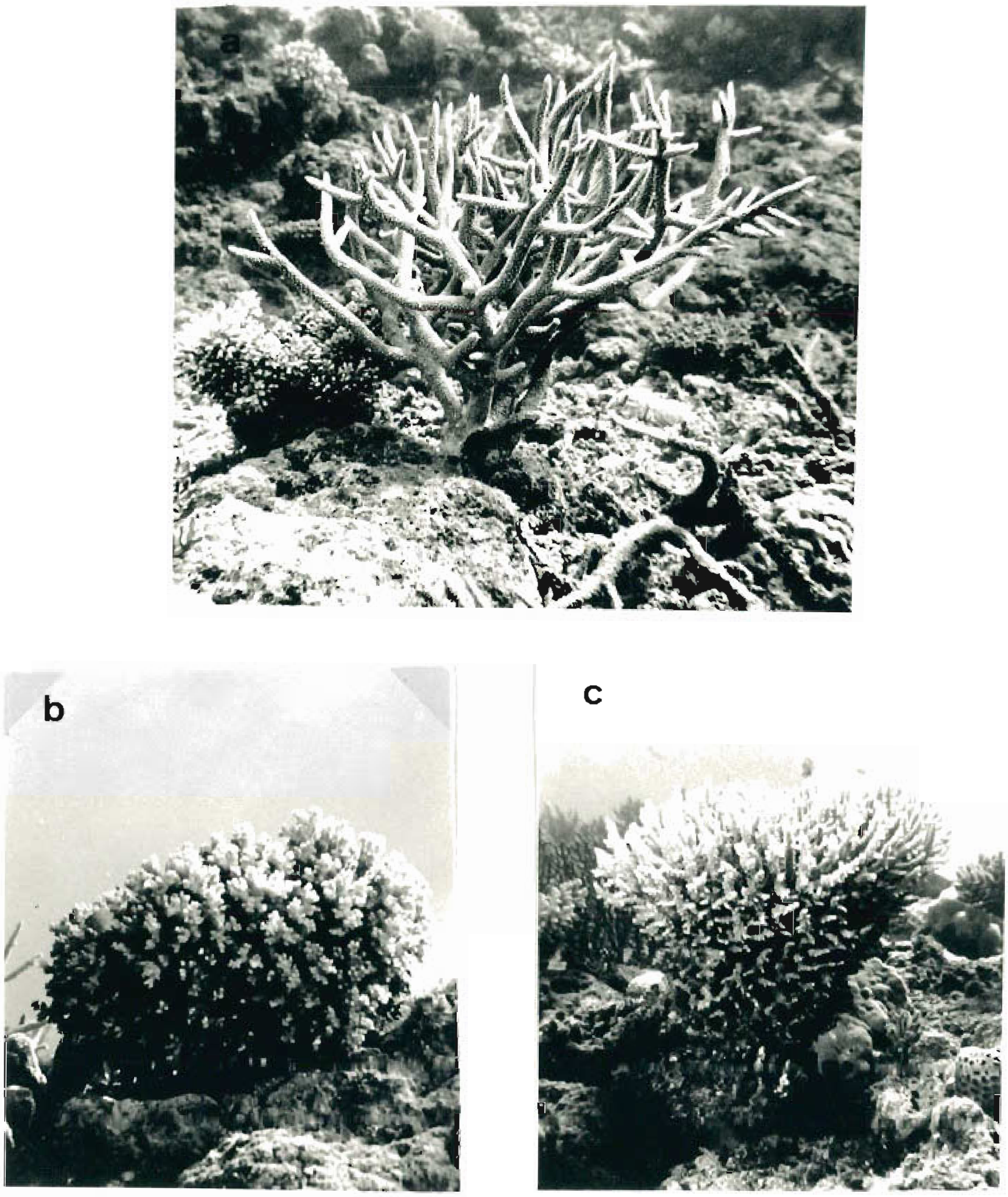


Plate 1) A typical stand of a) *Acropora nobilis* showing its low complexity and large inter - branch distances b) *Pocillopora damicornis* showing its high complexity and c) *Acropora nasuta* showing its high complexity and small inter - branch distances.

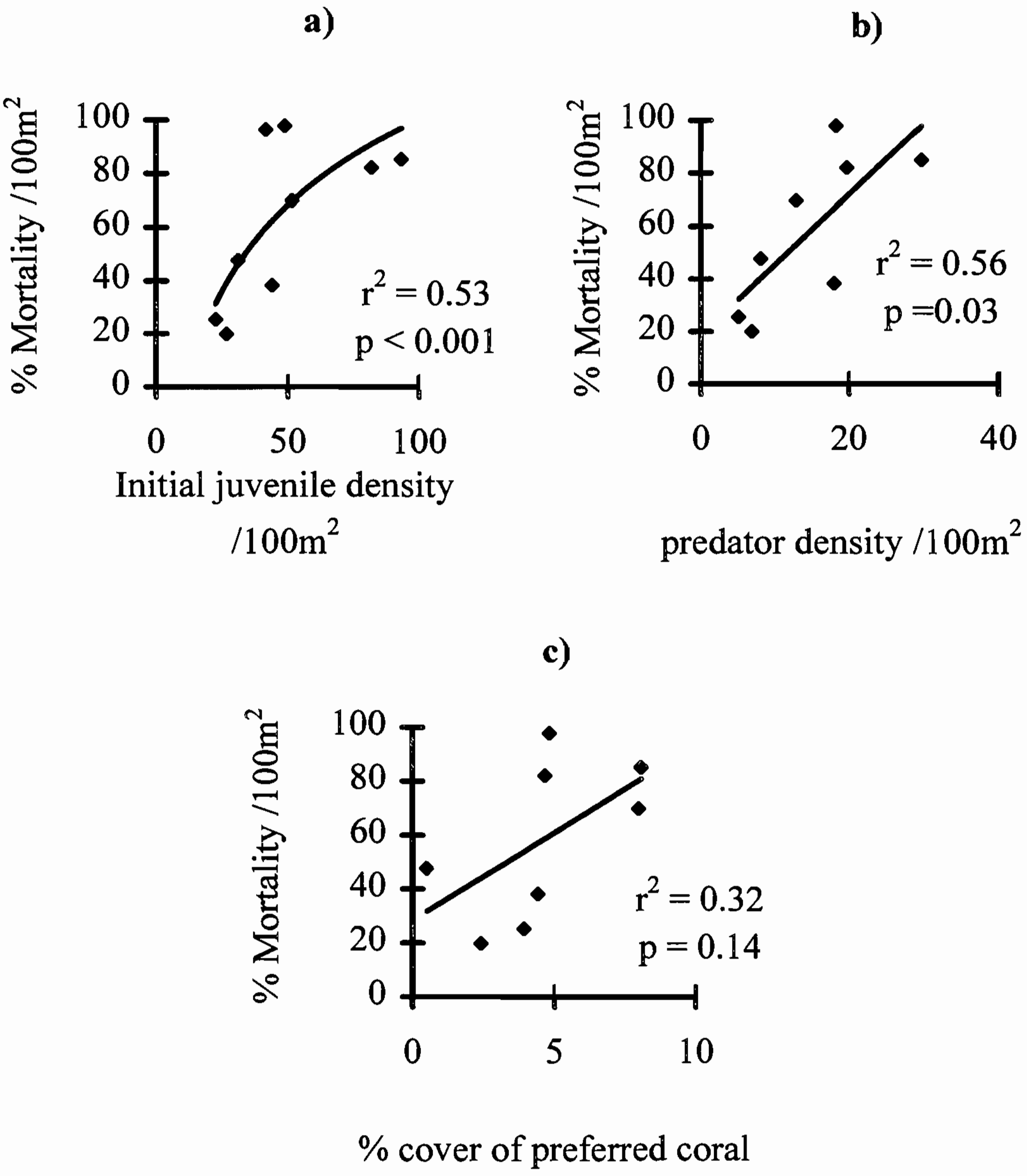


Fig 1 Relationships between the mortality (% mortality over one year) of juvenile *P. moluccensis*, and (a) initial juveniles densities, (b) predator densities, and (c) the cover of preferred coral substrata, from a comparison of 8 sites at Lizard Island.

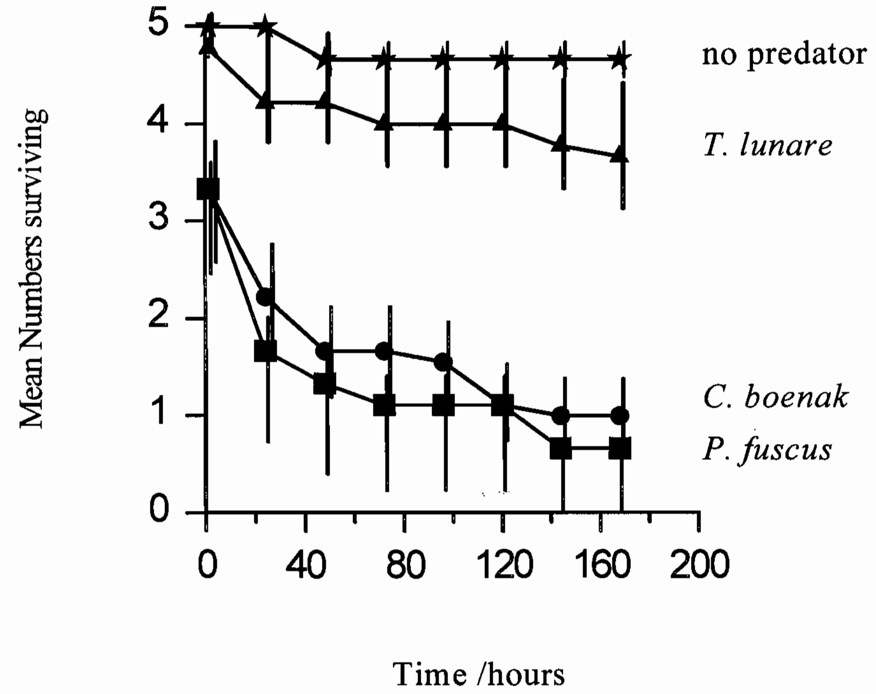


Fig 2 Survivorship curves for *Pomacentrus moluccensis* ($\bar{x}$ ± SE) in aquaria under different predator regimes and pooled across three habitat treatments. For each data point, n = 15.

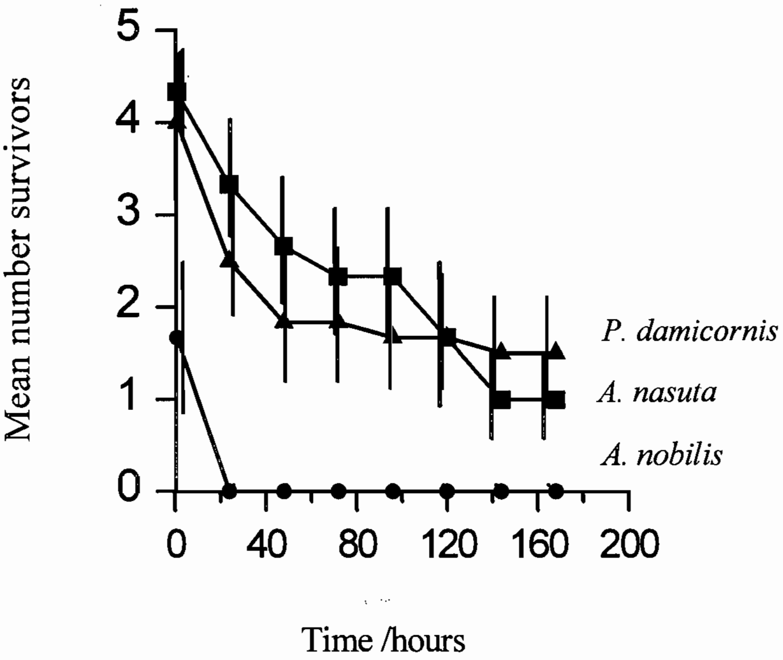


Fig 3 Survivorship curves for *Pomacentrus moluccensis* (x̄ ± SE) in aquaria under different habitat regimes and pooled across the two predator treatments, where predation occurred (*Pseudochromis fuscus* and *Cephalopholis boenak*).

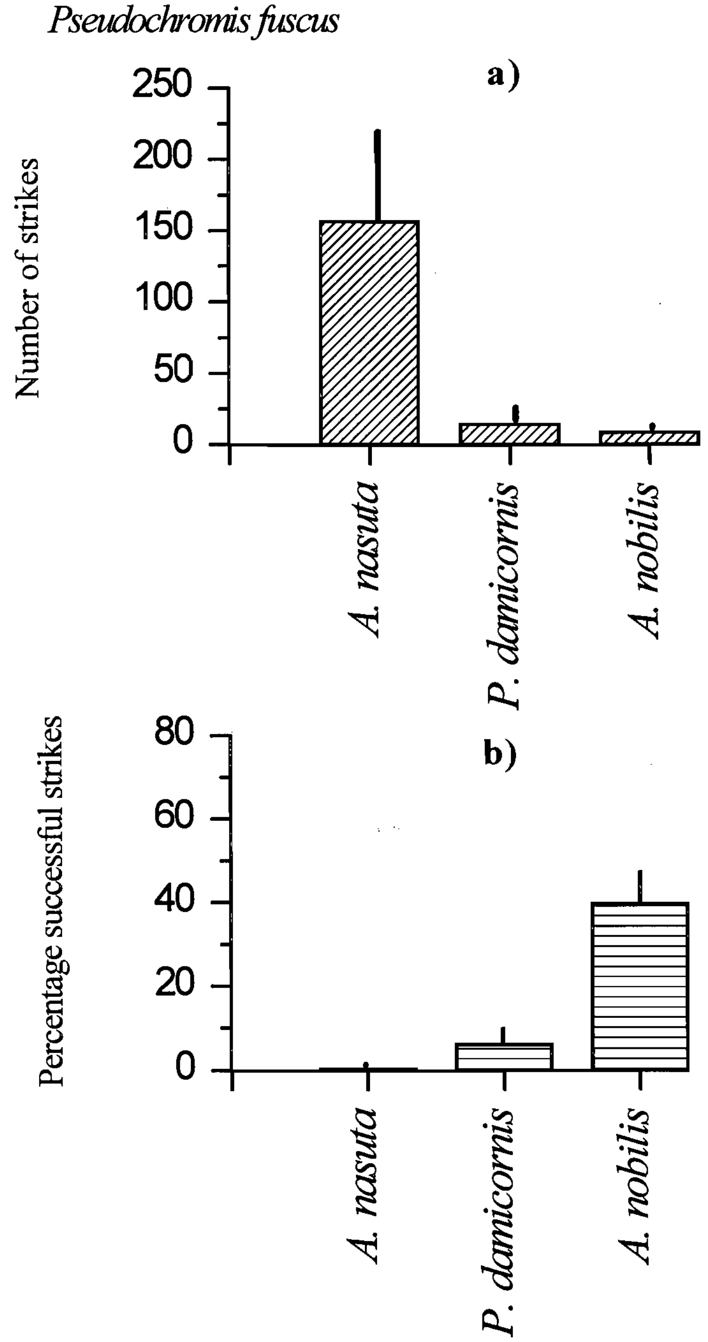


Fig 4 Predatory strike rates for *Pseudochromis fuscus* (x̄ ± SE) from three microhabitat types. A) Number of predatory strikes made during the first hour and B) the percentage of those strikes that resulted in successful capture of a *Pomacentrus moluccensis* juvenile.

Cephalopholis boenak

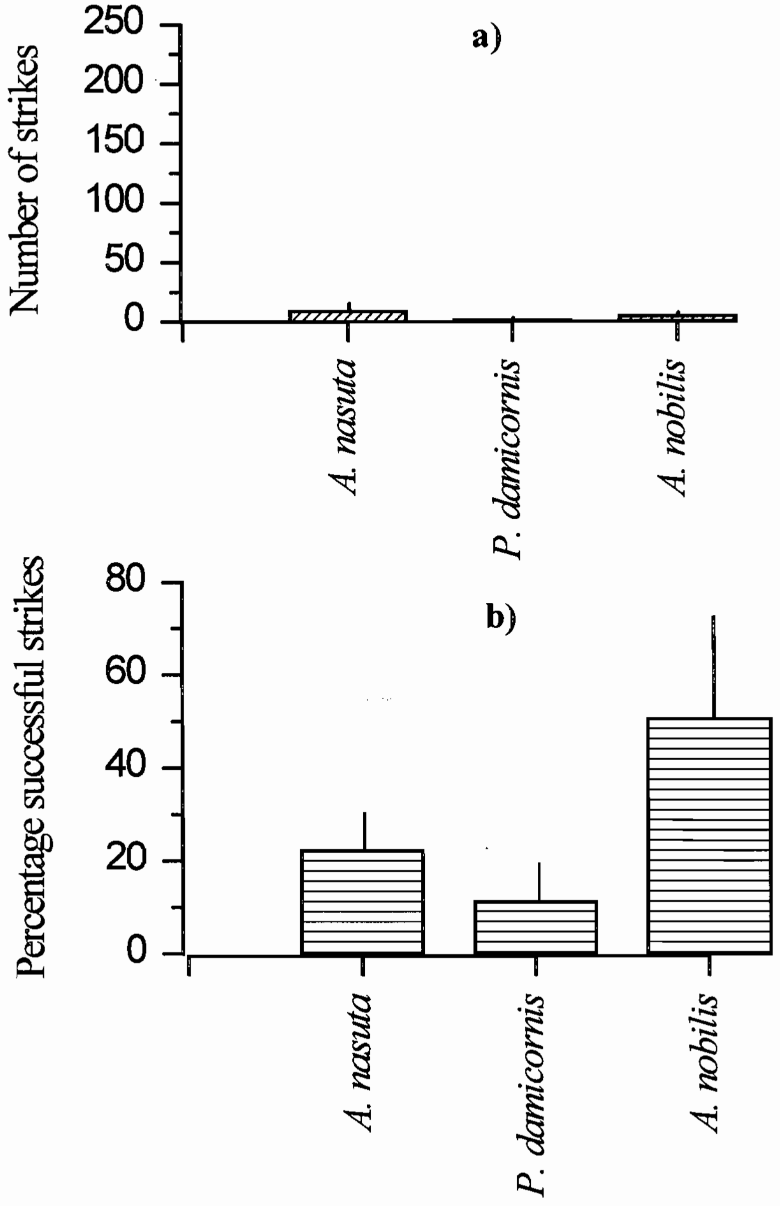


Fig 5 Predatory strike rates for *Cephalopholis boenak* (x̄ ± SE) from three microhabitat types. A) Number of predatory strikes made during the first hour and B) the percentage of those strikes that resulted in successful capture of a *Pomacentrus moluccensis* juvenile.

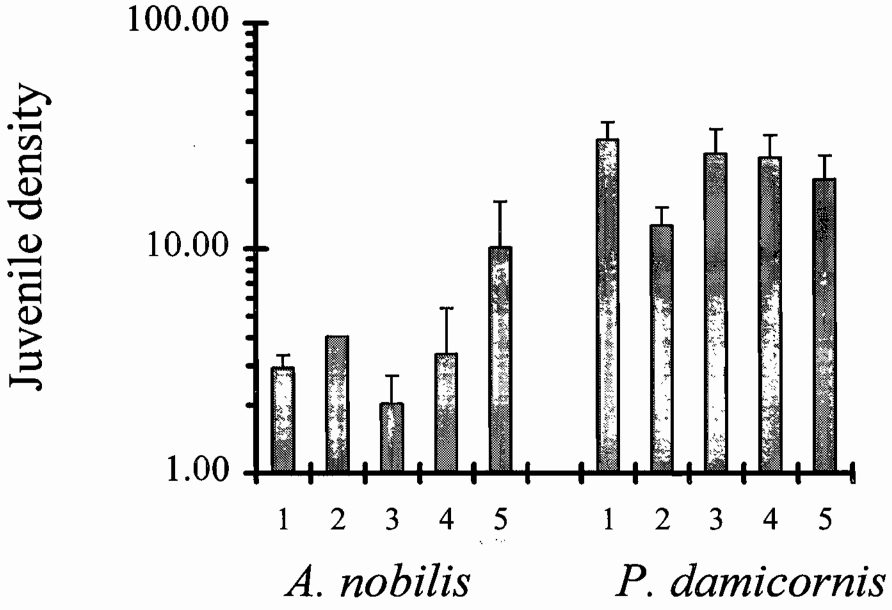


Fig 6 Densities (0.315m^3 of coral) of *Pomacentrus moluccensis* ($\bar{x}$ ± SE) on natural reefs at Lizard Island in *Acropora nobilis* and *Pocillopora damicornis*, the coral species used for the field experiment.

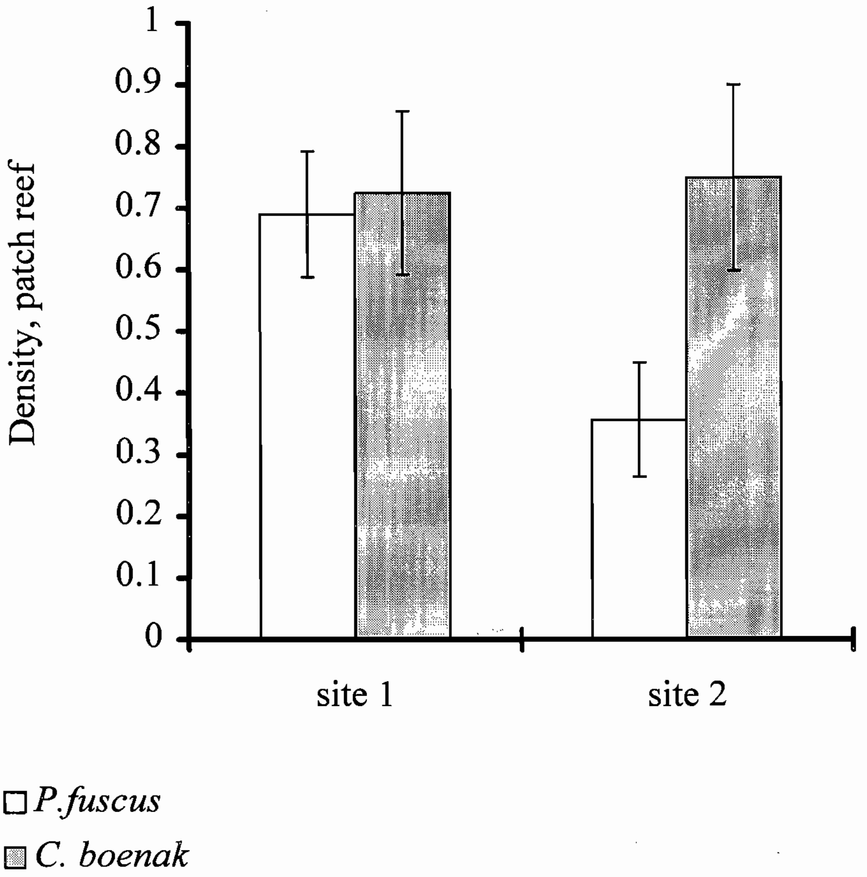


Fig 7 Densities (patch reef) of the two predator species (x̄ ± SE) used for the experiments *Pseudochromis fuscus* and *Cephalopholis boenak*.

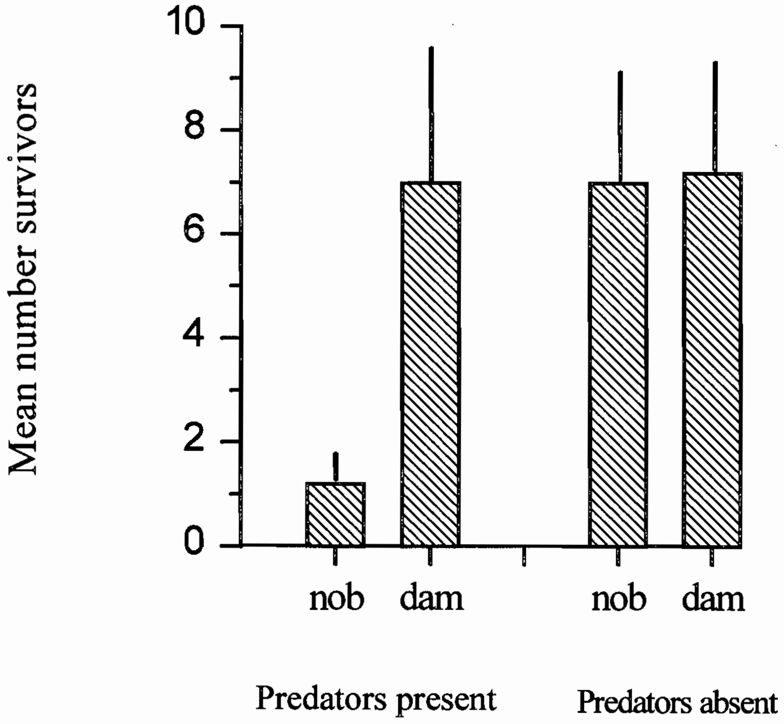


Fig 8 Number of *Pomacentrus moluccensis* (x̄ ± SE) that survived for two months, when placed on patch reefs. There were two patch reef types, *Acropora nobilis* and *Pocillopora damicornis*, and predators were either present (2 individuals) or absent. For each bar, n = 75.

CHAPTER 9:

General Discussion

This study has expanded our understanding of the population biology of *Pomacentrus moluccensis*, and represents another important step in our understanding of the dynamics of coral reef fish in general. In addition, it has provided biologists working on small fish, with a new tagging technique which will be of fundamental use in future studies of growth, movement and survivorship. The results of this work show clearly that both mortality and recruitment are important and interact to regulate the abundances of populations of adults of this reef fish at Lizard Island. It showed that at least two post-recruitment processes, predation and the availability of preferred shelter sites, were capable of significantly modifying patterns of mortality. It also identified major regional differences in the population dynamics and life history of *P. moluccensis*. The significance will be discussed.

9.1 Recruitment versus post-settlement mortality

The relative importance of recruitment versus post-recruitment processes has been a major topic of debate in the coral reef fish literature (Sale, 1974, 1977, 1978; Doherty, 1983; Doherty and Fowler, 1994;) and marine ecology generally (Keough, 1984; Connell, 1985; Roughgarden, 1985; Karlson, 1989, Forrester, 1995). This study joins an increasing number that have detected density-dependent mortality (Jones, 1984, 1987; 1988; Behrents, 1987; Anderson, 1993; Forrester, 1995). Here, density-dependent mortality modified patterns of recruitment at two scales, in transects (metres to tens of metres apart) and at sites (hundreds of metres to a few kilometres apart). However, there was considerable variation in this correlation at transect level. The variation was related to recruitment density and it therefore seemed possible that natural variation in recruitment success may affect the importance of post-recruitment processes(see also Jones, 1990, 1991). Thus, recruitment, density-dependent mortality and density-independent mortality interacted to form patterns in population size. These results support recent views that both recruitment and mortality must be considered in future work if generalisations are to be made (Warner and Hughes, 1988; Forrester, 1990; 1995; Jones, 1990; Menge, 1991, Caley et al., in press).

9.2 A mechanism of density-dependent regulation : Predator aggregation

The only reasonable explanation for the strong correlation observed between predator abundance and the density of juvenile *P. moluccensis* (Chapter 7) is that predators were aggregating at sites of high prey abundance. This provides the most likely explanation of density-dependent juvenile mortality (Chapter 5). The correlation between predators and new recruits was probably not due to the recruitment of predators unless patterns of recruitment were consistent over several years, because the majority of predators counted were not new recruits. Predator aggregation has frequently been cited as a mechanism of population regulation for terrestrial populations but there have only been sparse observations in coral reef studies (Connell, 1994, Hixon, unpubl. data, Forrester, unpubl. data). All other observations made in this thesis would concur with the predator aggregation hypothesis: Firstly, predator densities were significantly variable between nine broad scale sites (Chapter 7). Secondly, densities of *P. moluccensis* also were significantly different between those nine sites (Chapter 5) and thirdly, predator aggregation could account for the density-dependence observed both in mortality rates and in the correlation between adult and new recruit densities (Chapter 5). In addition, other studies have also found variability in predator community composition and/or abundance at several scales both within reefs (Connell, 1994, Robertson and Lassig, 1980, Wright et al., 1986, Harmelin-Vivien, 1989), among reefs (Munro and Williams, 1984, Russ, 1984a,b) and on a cross-shelf scale (Anderson et al., 1991, Williams, 1992).

It is likely that where prey densities are patchily distributed the densities of their predators will also be heterogeneous. It has been proposed that "if a consumer were to forage in an optimal manner, the process of redistribution would continue until the profitabilities of all patches were equal" (Fretwell and Lucas, 1970, Parker, 1970, in Begon et al, 1990). This has been called the "ideal free distribution" (Fretwell and Lucas, 1970). Here, densities of cohorts at nine sites converged over time (Ch 5). Patch choice by both predators and prey has been found to be a complex amalgam of factors including relative profitability, distance between patches, predator abundance and shelter availability (Parker and Stuart, 1976, Chesson, 1983, Holbrook and Schmitt, 1988). This is clearly a complex issue which appears to be of fundamental importance, particularly to populations at Lizard Island, but it is also potentially of broader significance. Future studies should consider which predator species show aggregative effects, the temporal and spatial scale of the movement of each species, which predators consume which prey and the factors leading to patch choice.

9.3 Mediation of predation by habitat

There was much evidence in this thesis that microhabitat had an important effect on the distribution and abundance of *P. moluccensis* at Lizard Island. Juveniles exhibited strong microhabitat associations implying that some attribute of microhabitat was important either at settlement or early afterwards. In addition, experimentally released new recruits survived better in the highly associated microhabitats implying that these microhabitats offer varying degrees of shelter (Chapter 7). This could be due to the availability of either total or partial refuges. Chapter 8 clearly showed that both resident predators and habitat were important in determining the survivorship of *P. moluccensis*. It also showed that there was inter-species variability in predatory capabilities according to microhabitat. The differences observed could be due to either the different structures of the coral species that were compared or due to some species specific factor. Structural differences would be the most intuitive explanation but the one experiment performed to test this directly, failed to show a difference (Chapter 6). In that experiment peripheral branch structure was manipulated. There are three possible explanations for these results: Firstly, the important factor was species specific and unrelated to peripheral branch structure. Secondly, shelter was not provided by the peripheral branches or thirdly, the peripheral branches do provide shelter but removing 50% of them is not sufficient to effect survivorship. Further work is clearly needed to separate the effects of coral species from coral head structure.

These observations and those showing patchiness in predator community structure and abundance, would account for the observed increase in mortality rates in relation to density. Where shelter is limiting the predation and competition hypotheses overlap (Hixon, 1991) and thus further work is needed to evaluate the role of competition. Competition may be important and may interact with the effects of other processes. What seems most likely to date is that coral head structure mediated the effects of predation and hence, altered patterns of mortality. Several studies have shown that increasing the number of available refuges can lead to an increase in either survivorship or species diversity (Werner et al., 1983; Beherents, 1987; Holbrook and Schmitt, 1988; Diehl, 1993; Persson and Eklov, 1995), but evidence within coral reef fish communities has been sparse (but see Shulman, 1984; Hixon and Beets, 1989; 1993; Buchheim and Hixon, 1992).

9.4 Regional variation in the biology of *P. moluccensis*

Comparison of populations of *P. moluccensis* from three locations on the Great Barrier Reef GBR has shown considerable intra-species variation. Recruitment to Lizard Island has been demonstrated to be up to an order of magnitude higher than recruitment to the Southern Reefs. This concurs with findings for other species between these two locations (Caley, 1991, Sweatman, 1985). Mortality rates were generally much higher at Lizard Island, leading to a much shorter life span compared to One Tree Reef on the southern GBR and John Brewer on the central GBR. Recruitment is more likely to be a limiting factor when populations show reduced longevities (Warner and Hughes, 1988). However, in populations at Lizard Island localised effects in mortality rates seemed to over-ride the effects of a reduced life-span. This study has shown that both recruitment and density-dependent mortality are important in the regulation of *P. moluccensis* at Lizard Island but between Southern Reefs regulation was primarily by recruitment (Doherty and Fowler, 1994).

Differences in population regulation may be due to: the higher recruitment, and/or differences in either predators or habitat or both between these locations. Predator community structure seems to be very different between locations (Caley, 1991; Connell, 1994). Small predators such as Pseudochromids, Synodontids, Parapercids and Cephalopholids seem to be more abundant at Lizard Island and more important in causing mortality of new recruits (Caley, 1991; Chapter 7, Martin and Jones, in prep). In contrast, Connell (1994) found that the most important predators of new recruits of the damselfish, *Acanthochromis polyacanthus*, at One Tree Reef were larger than 20cm. Predation has received relatively little attention within the coral reef fish literature, despite the fact that it has been shown to be an extremely important process in many other systems (Paine, 1966; Murdoch and Oaten, 1975; Hassell, 1978; Sih et al., 1985), and information is therefore limited for making these comparisons. This study joins a growing literature which implicates predation as an important structuring force in coral reef fish communities (Shulman, 1984; Hixon and Beets, 1989; 1993; Carr and Hixon, 1995)

9.5 Conclusion

As pointed out by Hixon (1991), unproductive debates have been escalated by over generalising from the study of a species, at one place, at one scale, over one period. What is needed is to consider several species over a range of scales, times and places. *P. moluccensis* is the first species for which different locations, spatial scales and time scales can be compared. This study has enabled comparisons to be made between three locations on the Great Barrier Reef and has revealed a high degree of plasticity in both life history traits and mechanisms of population regulation. It demonstrates empirically the dangers of both single process theories and making generalisations from small scale studies. At the same time it provides a template for the development of a model that can be tested on other species. Intra and inter-species comparisons will allow the construction of models with predictive power and hence, realistic generalisations will be possible.

These conclusions are of some importance to fisheries management because they mean that it is not sufficient to only consider recruitment when generating models for determining sustainable catch. Mortality rates and the factors affecting mortality must also be included.

References

Aldenhoven, J. M., (1986). Local variation in mortality rates and life-expectancy estimates of the coral-reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). Marine Biology 92: 237-244.

Anderson, G. R. V., Ehrlich, A. H., Ehrlich, P. R., Roughgarden, J. D., Russell, B. C., Talbot, F. H., (1981). The community structure of coral reef fishes. American Naturalist 117: 476-495.

Anderson, O., (1984). Optimal foraging by largemouth bass in structured environments. Ecology 65: 851-861.

Andrew, N. L., Mapstone, B. D. (1987). Sampling and the description of spatial pattern in marine ecology. Oceanography and Marine Biology Annual Review 25: 39-89.

Andrewartha, H. G., Birch, L. C. 1960. The distribution and abundance of animals. Univ. of Chicago Press, Chicago.

Beamish, R. J., (1979). Differences in the age of Pacific Hake (*Merluccius productus*) using whole otoliths and sections of otoliths. Journal of Fisheries Research Board of Canada 36: 141-151.

Beamish, R. J., McFarlane, G. A., (1983). The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112: 735-743.

Behrents, K. C., (1987). The influence of shelter availability on recruitment and early juvenile survivorship of *Lythrypnus dalli* Gilbert (Pisces: Gobiidae). Journal of Experimental Marine Biology and Ecology 107: 45-59.

Bell, J. D., Galzin, R., (1984). Influence of live coral cover on coral reef fish communities. Marine Ecology Progress Series 15: 265-274.

Bergman, P. K., Jefferts, H. F., Fiscus, H. F., Hager, R. L., (1968). A preliminary evaluation of an implanted coded wire fish tag. Washington Department of Fisheries, Fisheries Research Paper 3: 63-84.

Bergman, P. K., Haw, F., Blankenship, H. L., Buckley, R. M., (1992). Perspectives on the design, use and misuse of fish tags. Fisheries 17: 20-25.

Beukers, J. S., Jones, G. P., Buckley, R. M., (1995). Use of implant micro-tags for studies on populations of small reef fish. Marine Ecology Progress Series 125: 61-66.

Beverton, R. J. H., Holt, S. J., (1957). On the dynamics of exploited fish populations. UK Ministery of Agriculture, Fisheries and Food, Fishery Investigations ser. 2, 19: 533pp.

Bodenheimer, F. S., (1928). Welche Faktoren regulieren die individuenzhal einer insektenart in der natur? Biol. Zentralbl. 48: 714-739.

Boehlert, G. W., (1985). Using objective criteria and multiple regression models for age determination in fishes. Fishery Bulletin 83: 103-117.

Bohnsack, J. A. 1982. Effects of piscivorous predator removal on coral reef fish community structure. In: Gutshop '81: Fish Food Habits Studies. (Cailliet, G. M., Simenstad, C. A., editors.) Sea Grant Publ., Seattle, Washington, pp. 258-267.

Booth, D. J., (1992). Larval settlement patterns and preferences by domino damselfish, *Dascyllus albisella* Gill. Journal of Experimental Marine Biology and Ecology 155: 85-104.

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

Brock, R. E., (1979). An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. Marine Biology 51: 381-388.

Buchheim, J. R., Hixon, M. A., (1992). Competition for shelter holes in the coral reef fish *Acanthemblmaria spinosa* Metzelaar. Journal of Experimental Marine Biology and Ecology 164: 45-54.

Buckley, R. M., Blankenship, H. L. (1990). Internal extrinsic identification systems: overview of implanted wire tags, otolith marks and parasites. American Fisheries Society Symposium 7: 173-182.

Buckley, R. M., West, J. E., Doty, D. C., (1994). Internal micro-tag systems for marking juvenile reef fishes. Bulletin of Marine Science 55: 850-859.

Caley, M. J., Carr, M. H., Hixon, M. A., Jones, G. P., Hughes, T. P., (in press). Recruitment and the local dynamics of open marine populations.

Carr, M. H., (1991). Habitat selection and recruitment of an assemblage of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 146: 113-137.

Carr, M. H., Hixon, M. A., (1995). Predation effects on early post-settlement survivorship of coral reef fishes. Marine Ecology Progress Series 124: 31-42.

Carruthers, J. N., Lawfors, L. A., Veley, V. F. C., Parrish, B. B., (1951). Variations in brood-strength in North Sea haddock, in the light of relevant wind conditions. Nature 168: 317-319.

Chen, Y., Jackson, D. A., Harvey, H. H., (1992). A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. Canadian Journal of Fisheries and Aquatic Sciences 49: 1228-1235.

Choat, J. H., (1982). Fish feeding and the structure of benthic communities in temperate waters. Annual Review of Ecological Systematics 13: 423-449.

Christensen, B., Persson, L., (1993). Species-specific anti-predator behaviours: effects on prey choice in different habitats. Behavioural Ecology and Sociobiology 32: 1-9.

Colin, P. L. 1975. Neon gobies. TFH Publications, Neptune City, New Jersey.

Connell, J. H., (1985). The consequences of variation in initial settlement versus post-settlement mortality in rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 93: 11-45.

Connell, S. D., Jones, G. P., (1991). The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. Journal of Experimental Marine Biology and Ecology 151: 271-194.

Connell, S. D., Kingsford, M. J., (1992). Interactions between predators and their prey. Proceedings of the Seventh International Coral Reef Symposium 2: 952.

Cook, W. L., Streams, F. A., (1984). Fish predation on *Notonecta* (Hemiptera): relationship between prey risk and habitat utilisation. Oecologia 64: 177-183.

Crowder, L. B., Cooper, W. E., (1982). Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802-1813.

Cushing, D. H., Harris, J. G. K., (1973). stock and recruitment and the problem of density-dependence. Rapports et Proces-verbaux des reunions, conseil international pour L'exploration de la mer 104: 142-155.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge Univ. Press, London.

Cushing, D. H. 1988. The study of stock and recruitment. In: Fish population dynamics. (Gulland, J. A., editor.) Wiley, Chichester, .

DeMartini, E. E., Anderson, M. E., (1980). Comparative survivorship and life history of painted greenling. Environmental Biology of Fishes 5: 33-47.

Diamant, A., Shpigel, M., (1985). Interspecific feeding associations of groupers with octopuses and moray eels in the Gulf of Eilat. Environmental Biology of Fishes 13: 153-159.

Diehl, S., (1993). Effects of habitat structure on resource availability, diet and growth of benthivorous perch, *Perca fluviatilis*. Oikos 1993 SEP, 67: 403-414.

Dill, L. M., Fraser, A. H. G., (1984). Risk of predation and the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*). Behavioural Ecology and Sociobiology 16: 65-71.

Doherty, P. J. (1980). Biological and physical constraints on populations of two sympatric territorial damselfishes on the southern Great Barrier Reef. Ph.D. Dissertation, University of Sydney, Sydney.

Doherty, P. J., (1983). Tropical territorial damselfishes: Is density limited by aggression or recruitment? Ecology 64: 176-190.

Doherty, P. J., Sale, P. F., (1985). Predation on juvenile coral reef fishes: An exclusion experiment. Coral Reefs 4: 225-234.

Doherty, P. J., (1987). The replenishment of coral reef fishes, recruitment surveys amd the problems of variability manifest on multiple scales. Bulletin of Marine Science 41: 411-422.

Doherty, P.J., Williams, D. McB., (1988). The replenishment of coral reef fish populations. Oceanography and Marine Biology Annual Review 26: 487-551.

Doherty, P. J. 1991. Spatial and temporal patterns in recruitment. In: The Ecology of Fishes on Coral Reefs. (Sale, P. F., editor.) Academic Press, London, pp. 261-293.

Doherty, P. J., Fowler, A., (1994). An empirical test of recruitment-limitation in a coral reef fish. Science 263: 935-939.

Doherty, P. J., Fowler, A., (1994b). Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. Bulletin of Marine Science 54: 297-313.

Doherty, P. J., Dufour, V., Planes, S., (1995). Untitled Comment. Coral Reefs 14: 26.

Done, T. J., (1982). Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1: 95-107.

Ebersole, J. P., (1985). Niche separation of two damselfish species by aggression and differential microhabitat utilization. Ecology 66: 14-20.

Eckert, G. J., (1984). Annual and spatial variation in recruitment of labroid fishes among seven reefs in the Capricorn/Bunker Group, Great Barrier Reef. Marine Biology 78: 123-127.

Eckert, G. J., (1985). Settlement of coral reef fishes to different substrata and at different depths. Proceedings of the Fifth International Coral Reef Congress 5: 385-

390.

Eckert, G. J. (1987). Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. Marine Biology. 95: 167-171.

Emery, A. E. (1973). Comparative ecology and functional osteology of fourteen species of damselfish at Alligator reef, Florida Keys. Bulletin of Marine Science. 23: 649-770.

Emery, L., Wydoski, R. (1987). Marking and tagging of aquatic animals: an indexed bibliography. US Fish and Wildlife Service Resource Publication 165.

Fletcher, D. H., Haw, F., Bergman, P. K. (1987). Retention of coded wire tags implanted into cheek musculature of largemouth bass. North American Journal of Fisheries Management 7: 436-439.

Feltmate, B. W., Williams, D. D., (1991). Evaluation of predator-induced stress on field populations of stone flies. Ecology 72: 1800-1806.

Forrester, G. E. (1990). Factors influencing the juvenile demography of a coral reef fish population. Ecology 71: 1666-1681.

Forrester, G. E., (1995). Strong density dependent survival and recruitment regulate the abundance of a coral reef fish. Oecologia 103: 275-282.

Fowler, A. J., (1990). Validation of annual growth increments in the otoliths of a small tropical coral reef fish. Marine Ecology Progress Series 64: 25-38.

Fowler, A. J., Doherty, P. J., (1992). Validation of annual growth increments in the otoliths of two species of damselfish from the southern Great Barrier Reef. Australian Journal of Marine and Freshwater Resources 43: 000.

Fraser, D. F., Gilliam, J. F., (1992). Non-lethal impacts of predator invasion facultative suppression of growth and reproduction. Ecology 73: 959-970.

Fricke, H. W. (1973). Behaviour as part of ecological adaptation. Helgoländer. Wissenschaftliche Meeresuntersuchungen 24: 120-144.

Fricke, H. W., (1980). Control of different mating systems in a coral reef fish by one environmental factor. Animal Behaviour 28: 561-569.

Frogner, K. J., (1980). Variable developmental period: intraspecific competition models with conditional age-specific maturity and mortality schedules. Ecology 61: 1099-1106.

Goldman, B., Talbot, F. H. 1976. Aspects of the ecology of coral reef fishes. In: Biology and Geology of Coral Reefs. (Jones, O. A., Endean, R., editors.) Academic Press, New York 125-154.

Green, R. H., (1993). Application of repeated measures designs in environmental impact and monitoring studies. Journal of Australian Ecology 18: 81-98.

Gulland, J. A., (1982). Why do fish numbers vary? Journal of Theoretical Biology 97: 69-75.

Hairston, N. G., Smith, F. E., Slobodkin, L. B., (1960). Community structure, population control, and competition. American Naturalist 94: 421-424.

Haldane, J. B. S., (1953). Animal populations and their regulation. New Biology 15: 9-24.

Hargreaves, N. B., LeBrasseur, R. J. (1986). Size selectivity of coho preying on juvenile chum salmon. Canadian Journal of Fisheries and Aquatic Sciences. 43: 581-

586.

Harmelin-Vivien, M. L., Bouchon, C., (1976). Feeding behaviour of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). Marine Biology 37: 329-340.

Harriott, V. J., (1985). Recruitment patterns of scelaractinian corals at Lizard Island, Great Barrier Reef. Proceedings of the Fifth International Coral Reef Congress 4: 367-372.

Hart, P.J.B., Pitcher, T.J. (1969). Field trials of fish marking using a jet inoculator. Journal of Fish Biology 1: 383-385.

Hassell, M. P. (1978). The dynamics of arthropod predator-prey systems. Princeton University Press., Princeton, NJ.

Hassell, M. P., (1985). Insect natural enemies as regulating factors. Journal of Animal Ecology 54: 323-334.

Heincke, F. 1898. Naturgeschichte des herrings I. Die loklformen und die wanderungen des herings in den europaischen meeren. In: Abhandlungen der deutschen Seefishereivereins. (Salle, O. editor.) Berlin, .

Heugel, B. R., Joswiak, G. R., Moore, W.S. (1977). Subcutaneous diazo film tag for small fishes. Progressive Fish-Culturist 39: 98-99.

Hixon, M. A., Beets, J. P. (1989). Shelter characteristics and Caribbean fish assemblages: Experiments with artificial reefs. Bulletin of Marine Science 44: 666-680.

Hixon, M. A., Menge., (1990). Species diversity: Prey refuges modify the interactive effects of predation and competition. Journal of Theoretical Biology 39: 178-200.

Hixon, M. A. 1991. Predation as a process structuring coral reef fish communities. In: The Ecology of Fishes on Coral Reefs. (Sale, P. F., editor) Academic Press, New York, 475-507.

Hixon, M. A., Beets, J. P., (1993). Predation, prey refuges and the structure of coral reef fish assemblages. Ecological monographs 63: 77-101.

Hjort, J., (1914). Fluctuations in the great fisheries of northern Europe. Rapports et Proces-verbaux des reunions, conseil international pour L'exploration de la mer 20: 1-228.

Hjort, J., (1926). Fluctuation in the year classes of important food fishes. Journal du Conseil 1: 1-38.

Holbrook, S. J., Schmitt, R. J., (1988a). The combined effects of predation risk and food reward on patch selection. Ecology 69: 125-134.

Holbrook, S. J., Schmitt, R. J., (1988b). Effects of predation risk on foraging behaviour: mechanisms altering patch choice. Journal of Experimental Marine Biology and Ecology 121: 151-163.

Holm, E. R., (1990). Effects of density-dependent mortality on the relationship between recruitment and larval settlement. Marine Ecology Progress Series 60: 141-146.

Hood, P. B., Godcharles, M. F., Barco, R. S., (1994). Age, growth, reproduction and the feeding ecology of black sea bass, *Centropristis striata*, in the Eastern Gulf of Mexico. Bulletin of Marine Science 54: 24-37.

Huffaker, C. B., Messenger, P. S. 1964. The concept and significance of natural control. In: Biological control of insect pests and weeds. (DeBach, P., editor.) Chapman & Hall, London, pp. 74-117.

Hughes, T. P., (1984). Population dynamics based on individual size rather than age: a general model with a coral reef example. American Naturalist 123: 778-795.

Hughes, T. P., (1990). Recruitment limitation, mortality, and population regulation in open systems : a case study. Ecology 71: 12-20.

Hunter, M. D., Price, P. W., (1992). Playing chutes and ladders: bottom-up and top-down forces in natural communities. Ecology 73: 724-732.

Iles, T. D., (1973). Interaction of environment and parent stock in determining recruitment in the Pacific sardine as revealed by anaysis of density-dependent O-group growth. Rapports et Proces-verbaux des reunions, conseil international pour L'exploration de la mer 164: 228-240.

Jefferts, K. B., Bergman, P. K., Fiscus, H. F. (1963). A coded wire identification system for macro-organisms. Nature 198: 460-462.

Jones, G. P., (1984). The influence of habitat and behavioural interactions on the local distribution of the wrasse, *Pseudolabrus celidotus*. Environmental Biology of Fishes 10: 43-58.

Jones, G. P., (1986). Food availability affects growth in a coral reef fish. Oecologia 70: 136-139.

Jones, G. P. (1987). Competitive interactions among adults and juveniles in a coral reef fish. Ecology 68: 1534-1547.

Jones, G. P., (1988). Experimental evaluation of the effects of habitat structure and competitive interactions of the juveniles of two coral reef fishes. Journal of Experimental Marine Biology and Ecology 123: 115-126.

Jones, G. P., (1990). The importance of recruitment to the dynamics of a coral reef fish population. Ecology 71: 1691-1698.

Jones, G. P., (1991). Postrecruitment processes in the ecology of coral reef fish populations: A multifactorial perspective. In: The Ecology of Fishes on Coral Reefs. (Sale, P. F., editor.) Academic Press, New York, 294-328.

Karlson, R. H., Levitan, D. R., (1989). Recruitment-limitation in open populations of Diadema antilarum: an evaluation. Oecologia 82: 40-44.

Kelly, W. H. (1967). Marking freshwater and a marine fish by injected dyes. Transactions of the American Fisheries Society 96: 163-175.

Keough, M. J., Downes, B. J., (1982). Recruitment of marine invertebrates: the role of active larval choice and early mortality. Oecologia 54: 348-352.

Keough, M. J., (1984). Dynamics of the epifauna of the bivalve *Pinna bicolor*: Interactions among recruitment, predation and competition. Ecology 65: 677-688.

Kingsford, M. J., (1992). Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). Coral Reefs 11: 193-198.

Krebs, C. J. 1985. Ecology: the experimental analysis of distribution and abundance. Harper and Row, New York, 694pp.

Lasker, R., (1978). Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fishery

Bulletin 73: 453-462.

Lechowicz, M. J., (1982). The sampling characteristics of electivity indices. Oecologia 52: 22-30.

Levin, P. S., (1994). Fine-scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement versus post-settlement loss. Oecologia 97: 124-133.

Lirman, D., (1994). Ontogenetic shifts in habitat preferences in the three spot damselfish, *Stegastes planifrons*, in Roatan Island, Honduras. Journal of Experimental Marine Biology and Ecology 180: 71-81.

Lotrich, V. A., Meredith, W. H., (1974). A technique and the effectiveness of various acrylic colors for subcutaneous marking of fish. Transactions of the American Fisheries Society 103: 140-142.

Luckhurst, B. E., Luckhurst, K., (1978). Diurnal space utilisation in coral reef fish communities. Marine Biology 49: 325-332.

MacArthur, R. H., Wilson, E. O. 1967. The Theory of Island Biogeography. Princeton Univ. Press, Princeton,NJ.

Mapstone, B. D. 1988. Patterns in the abundance of *Pomacentrus moluccensis* (Bleeker). Ph.D. Unpublished PhD thesis, University of Sydney, Sydney.

Mapstone, B. D., Fowler, A. J., (1988). Recruitment and the structure of assemblages of fish on coral reefs. Trends in Evolution and Ecology 3: 72 - 77.

Martin, J. 1994. Predation on juvenile coral-reef fish at Lizard Island, Northern Great Barrier Reef: and ecological and behavioural study. BSc(Hons) Thesis, James Cook

University of North Queensland, Townsville. 65pp.

Martin, J. M., Jones, G. P., (in prep). Approaches to detecting the predators of juvenile reef fishes. Journal of Fish Biology.

McFarlane, G. A., Wydoski, R. S., Prince, E. D. (1990). Historical review of the development of external tags and marks. American Fisheries Society Symposium 7: 9-29.

Meekan, M. G., (1988). Settlement and mortality patterns of juvenile reef fishes at Lizard Island northern Great Barrier Reef. Proceedings of the Sixth International Coral Reef Symposium 2: 779-784.

Menge, B. A., Sutherland, J. P., (1987). Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130: 730-757.

Menge, B. A., (1991). Relative importance of recruitment and other causees of variation in rocky intertidal community structure. Journal of experimental marine biology and ecology 146: 69-100.

Milicich, M. J., Doherty, P. J., (1994). Larval supply of coral reef fish populations: magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef. Marine Ecology Progress Series 110: 121-134.

Murdoch, W. W., Oaten, A., (1975). Predation and population stability. Advanced Ecological Research 9: 1-131.

Murdoch, W. W., (1994). Population regulation in theory and practice. Ecology 75: 271-497.

Murphy., (1968). Patterns in life history and the environment. American Naturalist 102: 139.

Nelson, V. M., (1994). Demographic processes and spatial heterogeneity in community structure and dynamics of corals on the reef crest. Doctoratal Thesis, James Cook University of North Queensland, Townsville, Australia.

Nicholson, A. J., (1933). The balance of animal populations. Journal of Animal Ecology 2: 131-178.

Nisbet, R. M., Gurney, W. S., (1982). Modelling fluctuating populations. John Wiley & Sons, London.

Norris, J. E., Parrish, J. D., (1988). Predator-prey relationships among fishes in pristine coral reef communities. Proceedings of the Sixth International Coral Reef Symposium 2: 107-113.

Orth, R. J., (1977). The importance of sediment stability in seagrass communities. In: Ecology of marine benthos. (Coull, B. C., editor.) University of South Carolina Press, Columbia, USA, 281-300.

Paine, R. T., (1966). Food web complexity and species diversity. American Naturalist 100: 65-75.

Persson, L., Eklov, P., (1995). Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 76: 70-81.

Phillips, B. F., (1986). Prediction of commercial catches of the Western rock lobster. Canadian Journal of Fisheries and Aquatic Sciences 43: 2126-2130.

Phinney, D. E., Matthews, S. B., (1973). Retention of fluorescent pigment by coho salmon after two years. Progress in Fish-Culture 35: 161-163.

Power, M. E., (1992). Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73: 733-746.

Pringle, JD., (1984). Efficiency estimates for various quadrat sizes used in benthic sampling. Canadian Journal of Fisheries and Aquatic Sciences 41, 1485-1489.

Randall, J. E., (1961) Tagging reef fishes in the Virgin Islands. Proceedings of the Gulf and Caribbean Fisheries Institute 14: 201-241.

Reese, E. S., (1975). A comparative field study of the social behaviour and related ecology of reef fishes of the family Chaetodontidae. Zeitschrift für Tierpsychologie 37: 37-61.

Ricker, W. E., (1954). Stock and recruitment. Journal of Fisheries Research Board of Canada 11: 559-623.

Riley, J. D., (1966). Liquid latex marking technique for small fish. Journal du Conseil 30: 354-357.

Riley, G. A., (1946). Factors controlling phytoplankton populations on Georges Bank. Journal of Marine Research 6: 49-68.

Risk, M. J., (1972). Fish diversity on a coral reef in the Virgin Islands. Atoll Research Bulletin 153: 1-6.

Roberts, C. M., Ormond, R. F. G., (1987). Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Marine Ecology Progress Series 41: 1-8.

Robertson, D. R., Sweatman, H. P. A., Fletcher, E. A., Cleland, M. G., (1976). Schooling as a mechanism for circumventing the territoriality of competitors. Ecology 57: 1208-1220.

Robertson, D. R., Sheldon, J. M., (1979). Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. Journal of Experimental Marine Biology and Ecology 40: 285-298.

Robertson, D. R., Hoffman, S. G., Sheldon, J. M., (1981). Availability of space for the territorial Caribbean damselfish *Eupomacentrus planifrons*. Ecology 62: 1162-1169.

Robertson, D. R., (1984). Cohabitation of competing territorial damselfishes on a Caribbean coral reef. Ecology 65: 1121-1135.

Robertson, D. R., (1988). Abundances of surgeonfishes on patch-reefs in Caribbean Panama: due to settlement, or post-settlement events? Marine Biology 97: 495-501.

Roughgarden, J., Iwasa, Y., Baxter, C., (1985). Demographic theory for an open marine population with space-limited recruitment. Ecology 66: 54-67.

Sale, P. F., (1971). Apparent effect of prior experience in habitat preference exhibited by the reef fish, *Dascyllus aruanus*. Animal Behaviour 19: 251-256.

Sale, P. F., (1974). Mechanisms of co-existence in a guild of territorial fishes at Heron Island. Proceedings of the Second International Coral Reef Symposium 1: 193-206.

Sale, P. F., (1977). Maintenance of high diversity in coral reef fish communities. American Naturalist 111: 337-359.

Sale, P. F., (1978). Coexistence of coral reef fishes - A lottery for living space. Environmental Biology of Fishes 3: 85-102.

Sale, P. F., Doherty, P. J., Eckert, G. J., Douglas, W. A., Ferrell, D. J., (1984). Large - scale spatial and temporal variation in recruitment to fish populations on coral reefs. Oecologia 64: 191-198.

Sale, P. F., Douglas, W. A., (1984). Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecology 65: 409-422.

Sale, P. F., Douglas, W. A., Doherty, P. J., (1984). Choice of microhabitats by coral reef fishes at settlement. Coral Reefs 1984: 91-99.

Sale, P. F., Ferrell, D. J., (1988). Early survivorship of juvenile coral reef fishes. Coral Reefs 7: 117-124.

Sale, P. F., Guy, J. A., Steel, W. J., (1994). Ecological structure of assemblages of coral reef fishes on isolated patch reefs. Oecologia 98: 83-99.

Sammarco, P. W., Williams, A. H., (1982). Damselfish territory: Influences on *Diadema* distribution and implications for coral community structure. Marine Ecology Progress Series 8: 53-59.

Samoilys, M. A. 1986. Aspects of the behaviour, movements and population density of *Plectropomus leopardus* at Heron Island Reef, Southern Great Barrier Reef, Australia. Master of Science Thesis, Department of Zoology, University of Brisbane, Brisbane, Queensland, Australia.

Sano, M., Shimizu, M., Nose, Y., (1987). Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at

Iriomote Island, Japan. Marine Ecology Progress Series 35: 267-275.

Savino, J. F., Stein, R. A., (1982). Predator - prey interactions between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 11: 255-266.

Savino, J. F., Stein, R. A., (1989). Behavioural interactions between fish predators and their prey: effects of plant density. Animal Behaviour 37: 311-321.

Schmidt, J., (1930). Racial investigations. X. The Atlantic Cod (*Gadus callarias* L.) and local races of the same. Comptes-renus des travaux du laboratoire Carlsberg 18: 1-71.

Shapiro, D. Y., (1987). Inferring larval recruitment strategies from the distributional ecology of settled individuals of a coral reef fish. Bulletin of Marine Science 41: 289-295.

Shepherd, J. G., (1988). Fish Stock Assessments and their data requirements. In: Fish Population Dynamics. (Gulland, J. A., editor.) John Wiley & Sons, New York 35-62.

Shpigel, M., (1980). The relationship between the spatial structure of branched corals and the species diversity of inquiline fishes. Israeli Journal of Zoology 29: 205.

Shulman, M. J., Ogden, J. C., Ebersole, J. P., McFarland, W. N., Miller, S. L., and Wolf, N. G., (1983). Priority effects in the recruitment of juvenile coral reef fishes. Ecology 64: 1508-1513.

Shulman, M. J., (1984). Resource limitation and recruitment patterns in a coral reef fish assemblage. Journal of Experimental Marine Biology and Ecology 74: 85-109.

Shulman, M. J., (1985). Recruitment of coral reef fishes: Effects of distribution of predators and shelter. Ecology 66: 1056-1066.

Shulman, M. J., Ogden, J. C., (1987). What controls tropical reef fish populations, recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Marine Ecology Progress Series 39: 233-242.

Sih, A., Crowley, P., McPeek, M., Petranka, J., and Strohmeier, K., (1985). Predation, competition and prey communities: A review of field experiments. Annual Review of Ecological Systematics 16: 269-311.

Sih, A., (1987). Predators and prey lifestyles: An evolutionary and ecological overview. In: Predation. Direct and indirect impacts on aquatic comunities. (Kerfoot, W., Sih, A., editors.) University press of New England, Hanover 203-224.

Sih, A., Kats, L. B., Moore, R. D., (1992). Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. Ecology 73: 1418-1430.

Sinclair, M., Bugden, G. L., Tang, C. L., Therriault, J.-C., Yeats, P. A., (1986). Assessment of effects of freshwater runoff variability on fisheries production in coastal waters. In: The Role of Freshwater Outflow in Coastal Marine Ecosystems. (Skreslet, S. editor.) NATO ASI Series G: Ecological Sciences 7 Springer- Verlag, Berlin, pp. 139-160.

Sinclair, M. 1988. Marine Populations. An essay on population regulation and speciation. Univ. Washington Press, Seattle, London.

Sinclair, M., (1991). Keynote Address: Population structure and recruitment variability in North Atlantic fish species. Bureau of Rural Resources 16: 3-19.

Slobodkin, L. B., Smith, F. E., Hairston, N. G., (1967). Regulation in terrestrial ecosystems, and the implied balance of nature. American Naturalist 101: 109-124.

Smith, H. S., (1935). The role of biotic factors in determination of population densities. Journal of Ecology and Entomology. 28: 873-898.

Stein, R. A., Magnuson, J. J., (1976). Behavioural response of crayfish to a fish predator. Ecology 57: 751-61.

Stewart, B. D., Beukers, J. S., (in prep). Community structure of predators at Lizard Island, GBR: development of a new technique for censusing cryptic species. Marine Ecology Progress Series.

Stimson, J., Blum, S., Brock, R., (1982). An experimental study of the influence of muraenid eels on reef fish sizes and abundance. Hawaii Sea Grant Q 4: 1-6.

Summerston, H. C., Peterson, C. H., (1984). Role of predation in organising benthic communities of a temperate zone seagrass bed. Marine Ecology Progress Series 15: 63-77.

Sund, O., (1924). Snow and the survival of cod fry. Nature 113: 163.

Sweatman, H. P. A., (1984). A field study of the predatory behaviour and feeding rate of a piscivorous coral reef fish, the Lizardfish *Synodus englemani.* Copeia 198: 187-194.

Sweatman, H. P. A., (1985). The influence of adults of some coral reef fishes on larval recruitment. Ecological monographs 55: 469-485.

Sweatman, H. P. A., (1988). Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. Journal of Experimental Marine Biology and Ecology 124: 163-174.

Sweatman, H. P. A., Robertson, D. R., (1994). Grazing halos and predation on juvenile Caribbean surgeonfishes. Marine Ecology Progress Series 111: 1-6.

Tabor, R. A., Wurtsbaugh, W. A., (1991). Predation risk and the importance of cover for juvenile rainbow trout in benthic systems. Transactions of the American Fisheries Society 120: 728-738.

Talbot, F. H., Russell, B. C., Anderson, G. R. V., (1978). Coral reef fish communities: unstable high-diversity systems? Ecological monographs 48: 425-440.

Taylor, R. J. 1984. Predation. Chapman and Hall, London.

Thresher, R. E., Gronell, A. M. (1978). Subcutaneous tagging of small reef fishes. Copeia 2: 352-353.

Thresher, R. E., (1983a). Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef Lagoon. Marine Ecology Progress Series 10: 137-145.

Thresher, R. E., (1983b). Habitat effects on reproduction success in the coral reef fish, *Acanthochromis polyacanthus*. Ecology 64: 1184-1199.

Underwood, A. J., Denley, E. J., (1984). Paradigms, explanations and generalisations in models for the structure of intertidal communities on rocky shores. In: (Strong D. R. Jr, Simberloff, D., Abele, L. G., and Thistle, A. B. editors.), 151-180.

Uvarov, B. P., (1931). Insects and climate. Transactions of the Entomological Society London 79: 1-247.

Vanderploeg., (1978). Two electivity indices with special reference to zooplankton grazing. Journal of Fisheries Research Board of Canada 36: 362-365.

Varley, G. C., Gradwell, G. R., Hassell, M. P. 1973. Insect population ecology. Blackwell Scientific Publications, Oxford.

Veron, J. E. N., (1986). Corals of Australia and the Indo-Pacific. Angus and Robertson, Sydney, Australia.

Victor, B. C., (1983). Recruitment and population dynamics of a coral reef fish. Science 219: 419-420.

Victor, B. C., (1986). Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecological monographs 56: 145-160.

Virnstein, R. W., Nelson, W. G., Lewis, F. G. I. I. I., Howard, R. K., (1984). Latitudinal patterns in seagrass epifauna: do patterns exist, and can they be explained? Estuaries 7: 310-330.

Volk, E. C., Schroder, S. L., Fresh, K. L., (1990). Inducement of unique otolith banding patterns as a practical means to mass-mark juvenile Pacific salmon. American Fisheries Society Symposium 7: 203-215.

Warner, R. R., Hughes, T. P., (1988). The population dynamics of reef fishes. Proceedings of the Sixth International Coral Reef Symposium 1: 149-155.

Wellington, G. M., Victor, B. C., (1989). Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Marine Biology 101: 557-567.

Wellington, G. M., (1992). Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. Oecologia 90: 500-508.

Werner, E. E., Mittelbach, G. G., Hall, D. J., Gilliam, J. F., (1983a). Experimental test of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64: 1525-1539

Werner, E. E., Gilliam, J. F., Hall, D. J., Mittelbach, G. G., (1983b). An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

Williams, D. McB., Sale, P. F., (1981). Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within One Tree Lagoon, Great Barrier Reef. Marine Biology 65: 245-253.

Williams, D. McB., Hatcher, A. I., (1983). Structure of fish communities on outer slopes of inshore, midshelf and outer shelf reefs of the Great Barrier Reef. Marine Ecology Progress Series 10: 239-250.

Williams, D. McB. 1991. Patterns and processes in the distribution of coral reef fishes. In: The Ecology of Fishes on Coral Reefs. (Sale, P. F., editor) Academic Press, London, 437-473.

Worthington, D. G., Doherty, P. J., Fowler, A. J., (1995). Variation in the relationship between otolith weight and age: implications for the estimation of age of two tropical damselfish (*Pomacentrus moluccensis* and *P. wardi*). Canadian Journal of Fisheries and Aquatic Sciences 52: 233-242.