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Recruitment in time and space: the dynamics and distributions of reef fish populations on a low latitude coral reef

Thesis submitted by

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for the degree of Doctor of Philosophy
in the School of Marine and Tropical Biology
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STATEMENT OF CONTRIBUTION OF OTHERS

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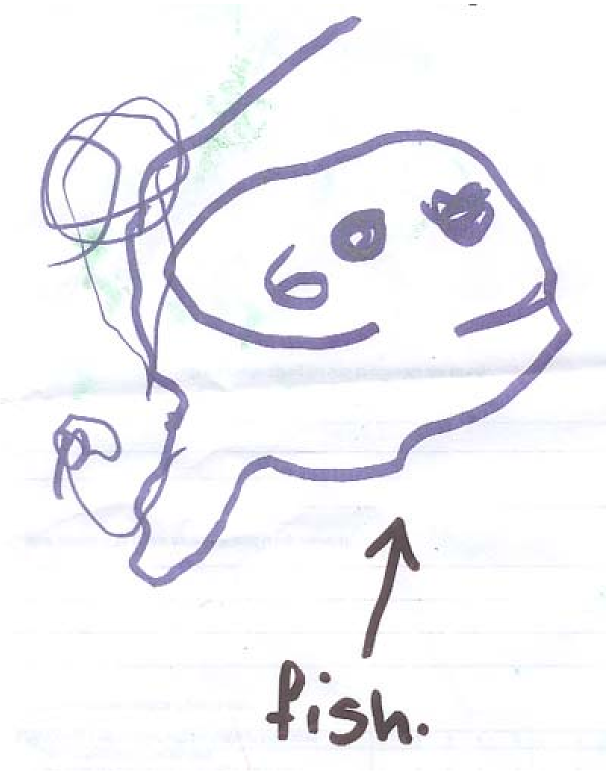

GENERAL ABSTRACT

Most benthic marine fishes have a pelagic larval stage, which after metamorphosis, recruits into adult habitat. Recruitment is known to play a major role in determining the dynamics and spatial distribution of coral reef fish populations. Temporal and spatial patterns in recruitment can arise through variation in larval supply, habitat selection and/or the availability of suitable recruitment habitat. Most of the work demonstrating the importance of recruitment on coral reefs has been carried out at high-latitude, seasonal locations, where reproduction and subsequent recruitment occur over a restricted period. Theory predicts a more continuous larval supply near the equator, and because of greater fish species diversity, a higher level of specialisation and dependence on habitat characteristics. However, very few studies have examined recruitment patterns, habitat degradation and the consequences for reef populations at low latitudes.

The primary goal of this thesis was to extend our knowledge of the causes and consequences of temporal and spatial patterns in reef fish recruitment to a low latitude coral reef in the Indo-Pacific (Kimbe Bay, Papua New Guinea, $5^{o}30'$S; $150^{o}05'$E). Specifically, the chapters set out to examine: (1) temporal patterns in recruitment, with particular emphasis on describing extended recruitment periods and underlying processes affecting recruitment periodicity; (2) spatial patterns in recruitment, with particular emphasis on microhabitat specialisation and the role of microhabitat availability in determining reef-wide patterns in recruitment; (3) the underlying mechanisms responsible for establishing and reinforcing distinct narrow depth distributions in the recruitment of reef fishes in this region; and (4) the influence of recruitment patterns on the temporal dynamics and spatial distributions of adult fish populations against a background of declining coral reef health.

Coral reefs in Kimbe Bay are subject to a monsoon climate, with distinct wet (November-February) and windy (April-June) seasons, and annual temperature deviations of just 1-2^{o}C. Due to the lack of variation in temperature, I predicted that most fish species would reproduce and recruit year-round (Chapter 2). To test this I carried out quantitative surveys of new recruits of all abundant, non-cryptic reef fishes every 1-2 months on inshore reefs over a 2.5-year period (December 1998 to April 2001). For the vast majority of species, new recruits were present during most months of the year, with damselfishes (Pomacentridae) and wrasses (Labridae) accounting for 90% of all new recruits observed. The majority of wrasse species exhibited year-round recruitment with broad peaks from November to May, while most damselfish species had negligible recruitment during the wet season (December-February), followed by one or two broad recruitment peaks between May and November. Species with year-round recruitment exhibited the highest cumulative recruit abundances. The reproductive output of three damselfish species was monitored for just over a year, and it was found that reproduction occurred throughout the year, even during the wet season. Although reproductive output decreased during the wet season, this was not considered sufficient to explain the lower recruitment of these species during this time. I argue that the lack of damselfish recruitment during the wet season is due to both decreased reproductive output and increased mortality of larvae, possibly due to hypo-saline conditions in surface waters. These results indicate that consistent family-wide recruitment strategies that may play a significant role in the dynamics of populations at low latitudes.

As a consequence of high fish diversity and steep reef profiles in Kimbe Bay, I predicted a high level of specialisation on settlement substrata that would be a major determinant of the spatial distribution and abundance of recruits (Chapter 3). Recruitment surveys were carried out using a spatially structured sampling design to determine differences in abundance among reefs located different distances from shore, among depths and reef zones within reefs (macrohabitats), as well as among different recruitment substrata (microhabitats). The microhabitats used by new recruits were recorded and compared with microhabitat availability from annual benthic surveys carried out at the same sites and depths. Over half the common species (23 out of 38) occupied corals in the family Acroporidae in proportions greater than expected based on their availability, and 12 species preferentially occupied non-living substrata (i.e. bare rock, rubble and sand). There were only five species, two damselfishes and three wrasses, which used all 13 microhabitat categories. At both the family-level (for

damselfishes and wrasses) and the species-level, depth explained the greatest percentage of the variance in the spatial recruitment data (just under 50% on average) and microhabitat availability explained the lowest. Therefore, although the level of microhabitat specialisation suggests that microhabitat availability might be an important factor in determining recruitment patterns, in terms of spatial patterns, the region is primarily characterised by a strong depth gradient.

A number of potentially important factors co-vary down a depth gradient. To determine whether the narrow depth range of new recruits was determined by the depth distribution of preferred microhabitats or depth itself, I conducted further surveys at additional depths on two reefs, in combination with a field experiment, using patch reefs composed of identical coral substrata at the same five depths (3, 6, 10, 15 and 20 m). Settlement patterns from the patch reef experiment were compared to those on un-manipulated reef habitat (i.e. patterns from surveys), to determine whether new settlers have preferences for particular depths, independent of microhabitat structure. For all species, settlement on patch reefs differed significantly among depths despite uniform substratum composition, indicating that depth preferences are largely independent of microhabitat structure. For four of the six species tested, depth-related settlement patterns on un-manipulated habitat and on patch reefs did not differ. For the other two species, depth ranges were greater on the patch reefs than on un-manipulated habitat. A second experiment examined whether depth preferences reflected variation in growth and survival when microhabitat was similar. Newly settled individuals of *Chrysiptera parasema* and *Dascyllus melanurus* were placed, separately, on patch reefs at five depths (as above) and their survival and growth monitored. For *D. melanurus*, which is restricted to shallow depths, both survival and growth were highest at the shallowest depth. Depth did not affect either survival or growth of *C. parasema*, which has a broader depth range than *D. melanurus* (between 6 and 15 m). This suggests that the stronger the depth preference, the greater the fitness costs incurred by settling at the extremes of, or outside, a preferred depth range.

The final aim of this project was to determine how temporal and spatial recruitment patterns influence adult fish populations. The temporal surveys of

new recruits were conducted during a time of a dramatic decline in coral cover caused by a series of bleaching events and change in fish communities. Associated with this, 75% of the common reef fish species declined in abundance, with 50% declining to less than half their original numbers. Wrasses exhibited the greatest range of responses, including species that increased, species that declined and others that remained stable. The majority of damselfish species declined and the magnitude of declines were greater than for most wrasses. The magnitude and direction of the long-term change in fish abundance was inversely correlated with the degree of association between recruits and live branching corals. Species that did not recruit into live coral tended to increase in abundance, while the greater the dependence of recruits on live coral, the greater the adult decline. For many species, long-term trends in adult numbers were interrupted by a spike of increased abundance in 2001, which was associated with high recruitment the previous year. Spatial patterns in the abundance of adults across reefs and depths were positively correlated with recruitment levels for 80% of the species examined. For some species, adult distributions tended to be more even than recruit distributions, indicating post-settlement expansion in distributions. A comparison of recruit-adult relationships among species and families established that a given average density of recruits resulted in greater average densities of adult damselfishes, compared with wrasses. Within each family, species with higher recruitment exhibited higher adult densities, but the magnitude of the increase in adult numbers declined as a function of increasing recruitment. I suggest that short-term fluctuations in adult abundance arise through fluctuations in larval supply, while longer-term trends reflect a combination of changes in habitat availability, habitat-limited recruitment and adult survival. In contrast, adult spatial distributions are primarily explained by strong habitat-specific settlement preferences.

This first study of coral reef fish recruitment in Papua New Guinea confirms that recruitment is a major determinant of the dynamics and spatial distribution of adult fishes in this high diversity region. While extended recruitment seasons clearly influence short-term population dynamics, longer-term trends in population size appear to be driven by habitat-limited recruitment and habitat change. Spatial gradients indicate a high level of specialisation with regard to depth and dependence on live coral as recruitment microhabitat. Documenting variation in spatial and temporal dynamics has also revealed a number of previously unknown family-wide and species-specific themes. The family-level differences between damselfish and wrasses may reflect fundamental differences in their life history traits, reliance on living corals and the carrying capacities of their habitats. Greater attention to variation in recruitment dynamics along biodiversity and biogeographic gradients will be required to understand and respond to the impacts of global change on coral reef fish populations.

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CHAPTER 1: GENERAL INTRODUCTION

One of the central goals of ecology is to explain patterns in the abundance of organisms in both time and space (Elton 1966; Andrewartha 1961; Krebs 1994). The processes that determine abundance are often complex, with different suites of processes responsible for temporal and spatial variation, and different patterns evident at different temporal and spatial scales (Wiens 1989; Levin 1992; Chave and Levin 2003). Although the basic demographic processes that can bring about changes in abundance are common to all populations (recruitment, mortality, immigration, emigration), the relative importance of each may vary among areas and over time. Quantifying recruitment is a logical starting point to develop an understanding of the processes that establish patterns in abundance. Recruitment can be defined as the input of juveniles to the population of interest (sensu Krebs 1994) and is therefore the primary means by which populations are replenished and ultimately persist over time. Recruits may be sourced from adults living within the population of interest ("closed" population) or may be dispersed from elsewhere ("open" populations) (Hixon et al. 2002). However, although recruitment may be intrinsically more variable for open populations, it is always a potentially important determinant of either temporal patterns in adult populations, the distribution of individuals along spatial gradients, or both. A comprehensive understanding of the significance and role of recruitment requires a detailed description of patterns and processes occurring in both time and space.

Populations of the majority of marine species are generally considered to be open and primarily linked by larval dispersal rather than adult migration (Palmer et al. 1996; Caley et al. 1996; Hixon et al. 2002; Sale and Kritzer 2003). Spatial and temporal variation in recruitment is often more extreme in open marine populations, and because of this, it can be a critical determinant of the temporal and spatial dynamics of populations and communities (Connell 1985; Gaines and Roughgarden 1985; Roughgarden et al. 1988; Underwood and Fairweather 1989; Booth and Brosnan 1995). For marine species, recruitment is usually equated with the successful transition of juveniles from the pelagic environment to the adult habitat. Numerous studies have shown that temporal and spatial variation in recruitment can be dependent on several factors, including larger scale processes affecting the supply of larvae, the quality and quantity of appropriate settlement habitat, and interactions with conspecifics or other species (Butman 1987; Grosberg and Levitan 1992; Rodriguez et al. 1993; Olafsson et al. 1994). The relative importance of recruitment and post-recruitment processes in determining adult numbers has been an issue subject to ongoing debate (Caley et al. 1996; Hixon and Webster 2002; Halpern et al. 2005). However, it is clear that recruitment to adult habitat is a critical transition that has important consequences for the dynamics of marine populations.

Coral reef fishes have been considered typical of marine species, with open populations characterized by variable recruitment in time and space (Sale 1980; Doherty and Williams 1988; Doherty 2002). They often form discrete populations associated with discontinuous reef habitat, and extensive larval connectivity is considered the norm (Armsworth 2002; Mora and Sale 2002; James et al. 2002). Temporal and spatial variation in recruitment is known to play a major role in determining the dynamics and structure of coral reef fish populations (Sale 1980; Doherty and Fowler 1994; Caley et al. 1996; Doherty 2002; Jones and McCormick 2002). While there is also considerable evidence that post-recruitment ecological interactions can also modify patterns of distribution and abundance (Jones 1991; Hixon 1991; Jones and McCormick 2002), unless density-dependent processes are extreme, variations in the magnitude of recruitment will have some effect on the structure and dynamics of populations (Caley et al. 1996; Hixon and Webster 2002; Osenberg et al. 2002). Recruitment of coral reef fishes can be determined by many processes operating over different spatial scales, including the regional processes affecting larval supply (Doherty 1991) and the local availability of critical recruitment habitat (Holbrook et al. 2000, 2002). There is also increasing evidence that although there is considerable large-scale larval connectivity (Roberts 1997; Mora and Sale 2002; Sale et al. 2005), there can also be significant levels of larval retention that may be influenced by local processes (Jones et al. 1999, 2005; Cowen et al. 2000, 2006). Given this background, reef ecologists must consider a wide range of processes that may determine spatial and temporal patterns of recruitment and their subsequent effects on adult distribution and abundance.

Most of the work demonstrating the importance of recruitment to coral reef fish populations has been limited to a few well-studied geographic areas and a few well-studied species (see reviews by Sale 1980; Doherty and Williams 1988; Doherty 2002; Hixon and Webster 2002; Jones and McCormick 2002). Patterns of recruitment are best known for the Great Barrier Reef and some areas in the Caribbean (reviewed in Doherty 1991). Contrasting patterns between the two regions highlight the potential importance of geographic variation in recruitment dynamics and that no single coral reef location may be representative of all. Also, debate over the importance of recruitment has often been based on empirical research on one or a few well-known species or case studies (e.g. Doherty 2002; Hixon and Webster 2002; Osenberg et al. 2002). It is not known to what degree the current generalisations apply to coral reef fishes as a whole. As information on reef fish life history strategies accumulate, it is clear that there are major species-specific and family-wide differences in key traits such as growth and longevity (Choat and Robertson 2002; Depczynski and Bellwood 2005). However, it is not known whether these extend to family-wide differences in recruitment strategies or the impact of recruitment on the distribution and abundance of adult fishes.

Although coral reefs are globally centered on the equator, the majority of studies on temporal patterns in recruitment have been conducted at relatively high latitude reefs with seasonal environments. Recruitment periods are typically short, and variation in the magnitude of recruitment pulses can lead to fluctuations in population size (reviewed by Doherty and Williams 1988; Robertson et al. 1993). For example, on the Great Barrier Reef, recruitment of most fish species occurs over several months during the southern hemisphere summer (November-February), with many species having very short recruitment pulses within the season (Russell et al. 1974, 1977; Talbot et al. 1978; Williams and Sale 1981; Milicich et al. 1992; Milicich and Doherty 1994). While it is generally assumed that recruitment will occur year-round in a less seasonal environment, there have been surprisingly few studies that have monitored recruitment of coral reef fishes near the equator. The notable exception is a comprehensive series of studies from the San Blas Archipelago in Panama where broad annual patterns have been documented (Robertson 1990; Robertson et al. 1993, 1999). There have been no comparable studies from the more diverse equatorial populations of the Indo-Pacific. The influence of recruitment on the dynamics of populations in highly seasonal environments is likely to be fundamentally different from locations with year-round recruitment.

Most of the studies examining spatial patterns of recruitment have also been carried out at mid/high latitude coral reefs. Large-scale patterns in recruitment across regional gradients, or differences among reefs, are driven by larval supply (Doherty 1991, Booth 1992; Caselle and Warner 1996; Sponaugle and Cowen 1996a, 1996b). However, on smaller scales, active choice of habitat by settling fishes can influence the distribution of fishes among reef zones (Milicich et al. 1992; Milicich and Doherty 1994; Gutierrez 1998), depths (Eckert 1985) and substratum types (Booth 1992; Wellington 1992; Booth and Wellington 1998; Öhman et al. 1998). Consequently, the structure of recruit assemblages can vary dramatically among reefs different distances from shore, as well as among depths and, on a much finer scale, among patches of different microhabitat types. There is substantial variation among reef fishes and among geographic locations in levels of specialisation on microhabitats and the degree to which the availability of recruitment microhabitats determine the distribution and abundance of recruits (Tolimieri 1995, 1998a, 1998b; Caselle and Warner 1996; Schmitt and Holbrook 2000; Sale et al. 2006). While there is clearly a continuum between highly specialised and generalist species, where most coral reef fish lie between these extremes is unknown. Coral reef fish communities tend to be more diverse nearer the equator and species may be more finely tuned to features of their habitat (Stevens 1996; Willig et al. 2003). However, spatial patterns in recruitment on low latitude reefs are poorly understood. In general, the importance of habitat structure to coral reef fishes at the critical life history transition from pelagic to reef existence requires further investigation.

Coral reef fishes often exhibit distinct spatial gradients in the magnitude of recruitment that broadly coincide with adult distributions (Green 1996; Jones

1997). However, the underlying factors that limit the spatial distribution of new recruits and the consequences of settling beyond these limits are poorly understood. There are often many factors that co-vary along spatial gradients, and determining exactly what juveniles are responding to can be extremely difficult. One of the most obvious patterns on coral reefs is the turnover of fish species along depth gradients, from emergent reef flats to deep reef slopes. While most reef fishes recruit to particular depth strata, it is unknown whether they intrinsically prefer particular depths, select particular microhabitats that are only found at these depths or are responding to resident reef fish assemblages. Experimental studies have clearly demonstrated that settlers can choose among substratum types (Eckert 1985; Booth 1992; Tolimieri 1995; Danilowicz 1996; Öhman et al. 1998) and can respond to the presence of conspecifics and/or other species (Sweatman 1985, 1988; Jones 1987b; Booth 1992; Forrester 1995; Öhman et al. 1998; Tolimieri 1998b; Lecchini, Planes et al. 2005; Lecchini, Shima et al. 2005). However, further experimental work is required to isolate the effects of the critical factor(s) that establish and reinforce key spatial gradients in reef fish recruitment.

The degree to which recruitment and habitat structure explain temporal and spatial patterns in the distribution and abundance of adults becomes evident in the context of disturbance to coral reef habitat (Jones and Syms 1998, Syms and Jones 2000, Wilson et al. 2006). The long-term degradation of coral reefs worldwide due to threats such as coral bleaching, coastal pollution and over-fishing has become evident over the last 2-3 decades (McClanahan 2002, Hughes et al. 2003, Gardner et al. 2003). There is evidence that reef degradation has been associated with a decline in the abundance and diversity of coral reef fishes, as well as changes in species composition (Booth and Beretta 2002; Jones et al. 2004 – Appendix III; Graham et al. 2006; Bellwood et al. 2006; Wilson et al. 2006). Species that depend on live coral for shelter and/or food are particularly vulnerable to declines in coral cover (Munday et al. 1997; Kokita and Nakazono 2001; Cheal et al. 2002; Spalding and Jarvis 2002; Syms and Jones 2002; Munday 2004; Pratchett et al. 2006). Many species have strong preferences for particular substrata at settlement, particularly live branching corals (Danilowicz 1996; Öhman et al. 1998, Jones et al 2004). A decline in the availability of a preferred substratum is likely to influence the magnitude of recruitment and contribute to long-term declines in population size. A complete loss of microhabitats used by specialists may result in local extinction (Munday 2004). However, mechanisms by which habitat change influences reef fish populations, and in particular the role of recruitment, are poorly understood.

The primary goal of this thesis was to extend our knowledge of the causes and consequences of spatial and temporal patterns in reef fish recruitment to a low latitude coral reef in the Indo-Pacific. It focuses on the coastal reefs in Kimbe Bay (5^{o}30' S; 150^{o}05' E), a large, sheltered bay on the northwestern coast of New Britain, Papua New Guinea (Fig. 1.1a). The communities of corals and reef fishes in this region are among the most diverse in the world (Munday and Allen 2000). There have been no prior studies on patterns of reef fish recruitment in Papua New Guinea and there is scant knowledge of the structure of reef fish communities in this region. The climate in Kimbe Bay is monsoonal, with distinct rainy (November - February) and windy (April - June) seasons, and an annual deviation in mean daily temperature of less than 2^o throughout the year. It was predicted that recruitment of most fish species would occur year-round, with a high degree of spatial segregation associated with high diversity and steep environment gradients.

This study coincided with a period of long-term decline in the health of Kimbe Bay's inshore platform and fringing reefs (Jones et al. 2004; Munday 2004). In the study area (Fig. 1.1) there was a decrease in the cover of branching corals from approximately 70% in 1996 to less than 10% in 2002, and a corresponding increase in the cover of turfing algae (Jones et al. 2004). This shift in benthic community structure appeared to have been caused by a combination of coral bleaching (observed in 1997, 1998 and 2000 – Srinivasan 2000; and in 2001 – personal observation), as well as a gradual increase in sedimentation from terrestrial run-off and outbreaks of crown-of-thorns starfish (Jones et al. 2004). Jones et al. (2004) and Munday (2004) documented the corresponding decline in biodiversity, the change in the structure of fish communities, and local extinction over this period. This thesis extends this work by providing an in depth picture of the temporal and spatial variation in reef fish recruitment, the dependence of recruitment on habitat structure, and how recruitment responds to habitat degradation.

This study employs both descriptive and experimental approaches to provide the foundation and build an understanding of patterns, causes and consequences of reef fish recruitment in Kimbe Bay. Common generalisations regarding the determinants of patterns in recruitment and their effects on the distribution and

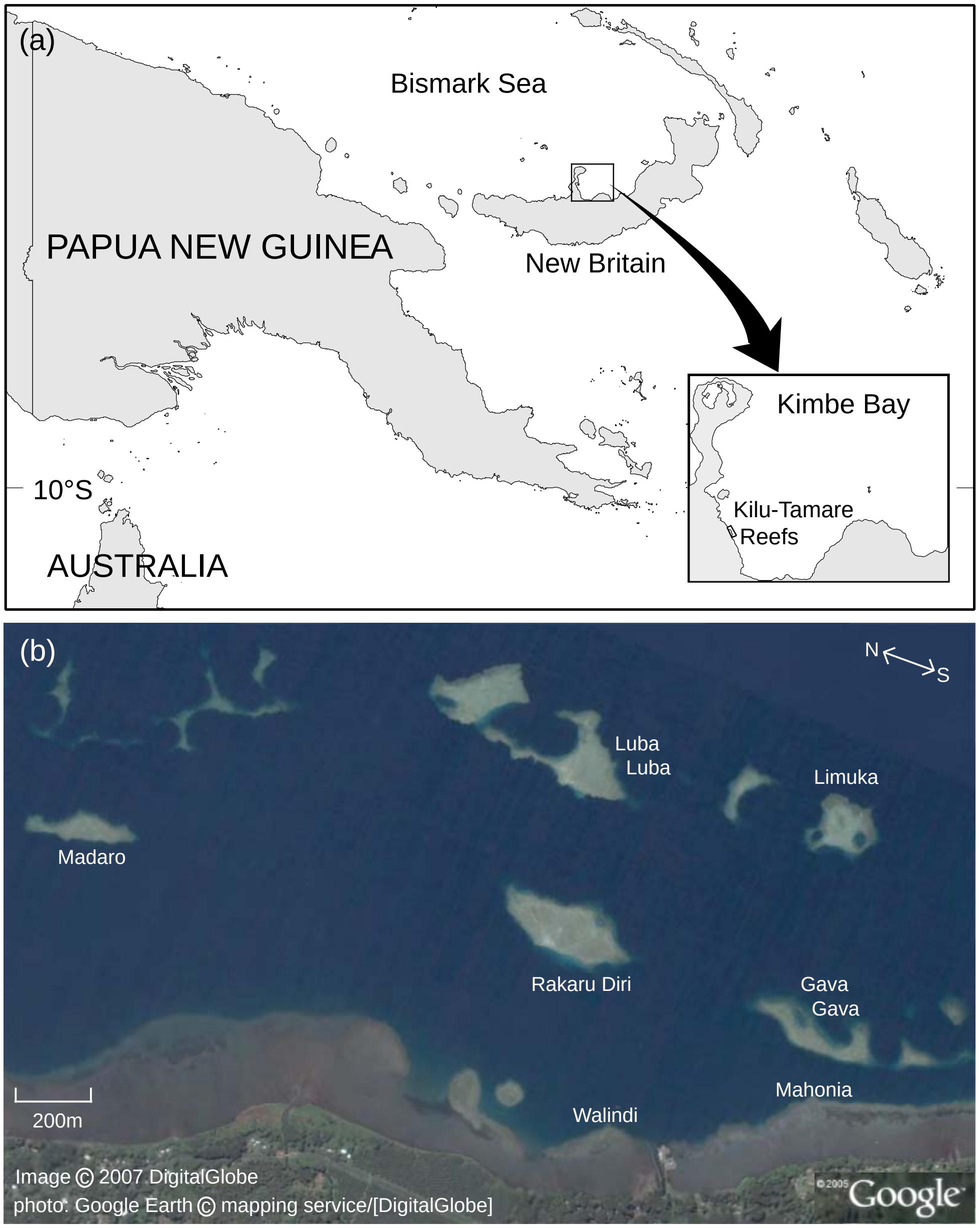

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Figure 1.1 Maps showing (a) the location of Kimbe Bay, and (b) the study sites abundance of adults are examined from a multi-species and multi-family perspective. Primary attention is given to similarities and differences between damselfishes (Pomacentridae) and wrasses (Labridae), because of their numerical dominance among fishes recruiting to coral reef habitat. *The specific objectives were to examine:*

(1) Temporal patterns in recruitment, with a particular emphasis on extended recruitment periods and long-term patterns in the magnitude of recruitment;

(2) Spatial patterns in recruitment, with particular emphasis on microhabitat specialisation and the role of microhabitat availability in determining reef-wide patterns in recruitment;

(3) The underlying mechanisms responsible for establishing and reinforcing distinct narrow depth distributions in the recruitment of reef fishes in this region; and

(4) The influence of recruitment patterns on the temporal dynamics and spatial distributions of adult fish populations against a background of declining reef health.

These 4 objectives provide the basic structure of the thesis.

In Chapter 2, I test the prediction that fishes associated with low latitude coral reefs in the Indo-Pacific are characterized by extended recruitment periods. I describe temporal patterns of recruitment, examine some of the processes that might influence these patterns and the possible consequences for adult populations. As the recruitment periods were previously unknown, recruitment of all conspicuous species was monitored by conducting visual surveys of new recruits on a regular basis over a 2.5-year period. I describe contrasting patterns for damselfishes and wrasses, and compare recruitment seasonality with other geographic locations. Possible causative factors were examined, including sea surface temperatures, rainfall, wind speed and patterns of reproduction.

Chapter 3 tests the hypothesis that coral reef fishes in Kimbe Bay have specialised recruitment substrata that are fundamental in determining the spatial distribution and abundance of recruits. Patterns of microhabitat use and specialisation are quantified, and compared with the spatial distributions of new recruits across typical reef gradients. To do this, the regular surveys of new recruits reported in

Chapter 2 included a spatial component, with surveys conducted at several depths, reef zones and distances from shore (Fig. 1.1). The microhabitat types occupied by new recruits of each species were recorded during these surveys, and microhabitat availability was estimated using benthic surveys at the same sites and depths.

In Chapter 4, I examine the potential causes of narrow distributions of new recruits along depth gradients in Kimbe Bay. Contrasting depth distributions of recruits are described for a range of species, along with potential correlates such as the availability of preferred settlement microhabitats. Then, using a field-based experiment in which preferred corals were transplanted to different depths, I explore whether these distributions are independent of microhabitat availability. A second experiment was carried out to assess the fitness costs (i.e. reduced growth and/or increased mortality) associated with settling beyond, or at the extremes of, the normal recruitment depth range.

Chapter 5 examines the role of recruitment and recruit microhabitat requirements in explaining: (1) the temporal changes in adult abundance in response to declining coral cover; (2) the distinct spatial distributions of adults; and (3) the overall relative abundance of fish species. To do this, I first examined whether long-term trends in adult abundance are influenced by the degree of substrate specificity of new recruits, as well as the effect of recruitment on short-term population dynamics. Secondly, I examined whether the distribution and abundance of adult fishes across different reefs and depths could be explained by spatial patterns of recruitment. Finally, I examined the relationships between long-term average recruitments levels and the relative abundance of species.

CHAPTER 2: EXTENDED BREEDING AND RECRUITMENT PERIODS OF FISHES ON A LOW LATITUDE CORAL REEF [1]

2.1 Abstract

The temporal dynamics of fish recruitment to equatorial Indo-Pacific coral reefs are not well known. This chapter documents fish recruitment over a 2.5-year period in Kimbe Bay (PNG) and shows that it is much less seasonal than is typically described for higher latitude coral reefs. Two families, wrasses (Labridae) and damselfishes (Pomacentridae), which accounted for 90% of all non-cryptic reef fish settlers, exhibited contrasting patterns. Most wrasse species had year-round recruitment with irregular peaks in abundance between November and May. Damselfish species showed a wider range of recruitment patterns, but most had negligible recruitment during the wet season (December-February), followed by one or two recruitment peaks between May and November. Species with longer seasonal recruitment periods exhibited higher cumulative levels of recruitment. For three focal damselfish species, reproductive output was reduced during the wet season, but this alone did not account for the low recruitment at this time. I hypothesise that the lack of damselfish recruitment during the wet season is due to a combination of reduced reproductive output and increased larval mortality associated with monsoonal conditions. My results indicate that there are consistent family-wide recruitment strategies that may play a significant role in the dynamics of populations in equatorial waters.

2.2 Introduction

Recruitment can strongly influence the structure and dynamics of open marine populations (Roughgarden et al. 1988; Underwood and Fairweather 1989; Booth and Brosnan 1995; Caley et al. 1996). Most of the work demonstrating the

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importance of recruitment has been done in highly seasonal environments, where variation in small pulses of recruitment often lead to "year-class phenomena" and dramatic fluctuations in population size. Spawning seasons may be timed to coincide with the best conditions for larval growth and survival (Qasim 1956; Cushing 1987). The influence of recruitment on the dynamics of populations is likely to differ closer to the equator where favourable conditions for larval survival might extend throughout the year (Longhurst and Pauly 1987; Winemiller and Rose 1992). Longer breeding seasons are usually associated with lower fecundities in fishes (Winemiller and Rose 1992; Vila-Gispert et al. 2002), which may reduce the potential for strong cohorts and modify the intensity of post-recruitment processes. In general, patterns of recruitment variability in equatorial species are poorly understood, yet are critical to understanding the dynamics of tropical marine populations.

While recruitment of coral reef fishes has been researched extensively at high latitudes in both the Indo-Pacific and the Caribbean, most of the information on recruitment at low latitudes comes from just one location in the Caribbean (the San Blas Archipelago in Panama, 9^{o}34'N). Extensive work here has shown that recruitment occurs throughout the year, although there are seasonal peaks that vary in timing among species (Victor 1986; Robertson 1990, 1991; Robertson et al. 1993, 1999; Wilson 2001) and among locations differing in exposure (Wilson 2001). At higher latitude reefs (>10^{o}N/S), recruitment patterns are typically very seasonal (reviewed by Doherty and Williams 1988; Doherty 1991; Booth and Brosnan 1995). For example, on the Great Barrier Reef, recruitment of most fish species occurs during summer with species-specific pulses of recruitment within the season (Russell et al. 1974, 1977; Talbot et al. 1978; Williams and Sale 1981; Milicich et al. 1992; Milicich and Doherty 1994). While the degree of seasonality in spawning and recruitment of coral reef fishes may decline with decreasing latitude, there have been no studies on temporal patterns of larval supply and recruitment near the equator in the Indo-Pacific to evaluate this hypothesis.

Even in places where there is little annual variation in water temperature, spawning and recruitment patterns might still be influenced by seasonal cues. Equatorial species may respond to smaller absolute changes in temperature than their temperate counterparts (Stevens 1996). Also, tropical locations are subject to seasonal monsoonal conditions, which might have as much influence on reproduction and recruitment as temperature cycles. For example, at San Blas, Panama, strong onshore winds during the dry season can have a negative effect on spawning (Clifton 1995; Robertson 1990; Robertson et al. 1999), larval growth (Bergenius et al. 2005) and settlement (Robertson 1990; Robertson et al. 1999) of shallow water fishes. An understanding of the potential environmental drivers of recruitment must begin with a detailed description of recruitment patterns in conjunction with measures of environmental variation.

While one-off surveys may be reasonable indicators of annual patterns of recruitment of fishes on high latitude coral reefs (Williams et al. 1994), quantifying recruitment in populations with extended spawning periods requires prolonged sampling. In this study, recruitment of common fish species associated with coastal coral reefs in Kimbe Bay (Papua New Guinea) was monitored over a 2.5y period. On the basis of comparative studies of marine and freshwater fishes (Winemiller and Rose 1992; Vila-Gispert et al. 2002), it was predicted that while most fish species would have longer recruitment seasons, there would be taxon-specific variation in the length and timing of recruitment periods. The study also examined whether species with longer recruitment periods exhibited lower average monthly levels of recruitment, which may be expected if extended breeding periods are associated with reduced batch fecundities. Finally, the magnitude and timing of recruitment was examined in relation to potential environmental cues such as temperature, rainfall and wind, and the monthly reproductive rates of three selected damselfish species.

2.3 Methods

2.3.1 Study sites

The abundance of new recruits was monitored on six inshore reefs near the township of Kimbe in Kimbe Bay (Fig. 1.1a), a large sheltered bay on the island of New Britain, Papua New Guinea (5°30' S; 150°05' E) between December 1998 and April 2001. The climate in this area is monsoonal and is characterised by a wet season during December-February and a windy season during June-August. The annual variation in mean monthly temperature is just 2°C with average temperatures of between 29-30°C for most of the year. During the study period, rainfall (measured at Walindi Plantation, very close to the study sites) was relatively constant throughout the year, except for one month during each Southern Hemisphere summer (February 1999, January 2000 and February 2001), when rainfall was over 3 times the monthly average rainfall for the other months of the year (Fig. 2.1). Wind speeds (measured by New Britain Palm Oil at Dami Beach, approx. 30 km away) were highest during June-August each year, and were much higher in 2000 than in 1999 (Fig. 2.1).

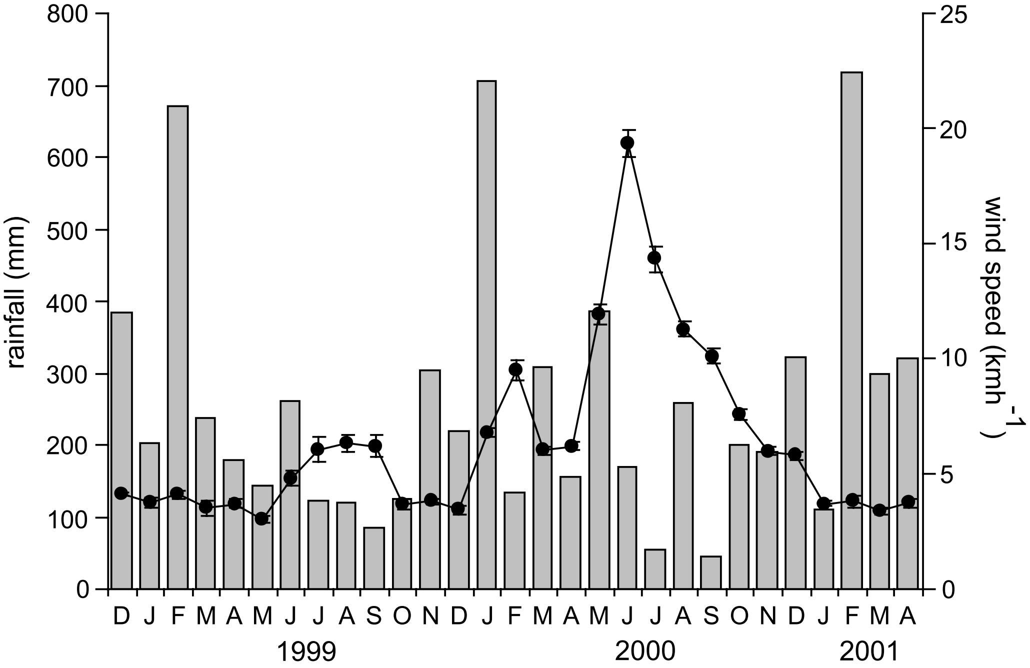


Figure 2.1: Temporal patterns of rainfall and wind speed

The six sites surveyed included two areas of fringing reef (Walindi and Mahonia), and four inshore platform reefs approximately 0.2-1 km from shore (Gava Gava, Limuka, Luba Luba and Madaro, Fig. 1.1b). Each of the two fringing reef sites was a 250 m long section of the fringing reef, which runs parallel to (and 50-100 m from) the shore, and consists of a reef slope extending from the reef flat to 8-10 m. The four platform reefs rose steeply from deep water (80-100 m) and ranged in size from approximately 1.5-3 ha (area of reef flat). They were all separated from adjacent reefs by 0.2-1 km, although some were linked to adjacent reefs by deep (>30 m) saddles. All four reefs had steep reef slopes or walls extending to depths of 40-60 m on the windward side and reef slopes extending to 30-40 m on the leeward side. Coral cover on the leeward reef slopes was not as continuous as on the windward slopes, with numerous areas of sand/rubble and isolated patches of coral. Although the tidal range here is relatively small (1 m), most of the reef flat at all 6 sites was exposed at low tide.

Several depths and reef zones were sampled at each site in order to include as many broad habitat types as possible, thus maximising the number of species surveyed. On the two fringing reef areas, the reef flat, 2 and 6 m depths on the reef slope were sampled, and on the four platform reefs, the reef flat, 2, 6 and 10 m depths on the windward reef slope and 2 m on the leeward reef slope were sampled.

2.3.2 Visual surveys of new recruits

A total of 20 surveys of new recruits were conducted from December 1998 to April 2001, with time periods of 4-8 weeks between surveys. The first survey was in December 1998, and then there were eight surveys carried out in 1999 (January, April, May, June, August, September, October and November), eight in 2000 (February, March, April, June, July, August, September and November) and three in 2001 (February, March and April). During each survey, which took between 5 and 10 days to complete, the six reefs and depths/zones within reefs were sampled in a random order. The time of day that each reef and depth/zone was surveyed also varied, the only restriction being that the reef flats could not be surveyed at low tide. At each depth, four 50 x 2 m belt transects were surveyed by laying out 50 m measuring tapes and swimming one pass of each tape, recording all newly settled individuals within 1 m on either side of the transect line. Roughly the same areas of reef were covered each time, although transect tapes were laid out from a random starting point. On both platform and fringing reefs, reef flat transects were laid out 2-3 m from the reef crest, following the contours of the reef. A total of 2,080 transects were surveyed by the end of the study.

All non-cryptic fishes that could readily be identified to species level in the field were included in these surveys. These included damselfishes (Pomacentridae), wrasses (Labridae), parrotfishes (Scaridae), surgeonfishes (Acanthuridae), butterflyfishes (Chaetodontidae), rabbitfishes (Siganidae), cardinalfishes (Apogonidae) and fairy basslets (Serranidae). Within each transect, all new recruits below a certain threshold size were counted. Only fish that were estimated to have settled within the previous 1-2 weeks were counted in order to avoid re-counting individuals counted during any previous survey. Threshold sizes for each taxon were established from size estimates of fish that had settled on a series of experimental patch reefs that were monitored every 2-3 days during four 6-8 week periods in 1999 and 2000 (Srinivasan 2003 – Appendix II).

2.3.3 Description and analysis of patterns of seasonality

For each of the 40 most abundant species, a one-way ANOVA was used to test for differences in mean abundance among the 16 months surveyed during 1999 and 2000. A planned contrast was used to compare recruit density between the 8 months in 1999 and the 8 months in 2000. The 40 species included 22 damselfish species, 11 wrasse species, 3 surgeonfish species, 2 butterflyfish species, *Cheilodipterus quinquelineatus* (Apogonidae) and *Pseudanthias tuka* (Serranidae). Data from just the depth(s) and distances from shore (positions) at which new recruits of each species were most abundant were used in the ANOVAs. Data for all species were transformed to $(x+0.001)^{0.25}$ to conform to the assumptions of ANOVA. For 27 of the 40 species, within-group variances were heterogeneous (Cochran's test, $P<0.01$) even after transformation. For each of these species, Welch's test was used in the ANOVA as an alternative to the F test as it is more robust to variance heterogeneity (Quinn and Keough 2002).

Patterns of seasonality were examined for the 2 families that included the greatest number of species and individuals in the surveys, the damselfishes and wrasses.

Within these families, recruitment patterns were analysed for all species with a total abundance (summed across all survey periods, sites and depths) of 50 individuals or more. This included 29 damselfishes and 19 wrasses. For each species, a single value of abundance for each month of the year was obtained by averaging across years for months that had been surveyed in more than one year (e.g., surveys were conducted in April 1999, 2000 and 2001, so the total abundance from each of these 3 surveys were summed and divided by 3 to obtain a single abundance value for April). The 12 abundance values were then summed, and each was expressed as a percentage of this total (referred to as the "adjusted total abundance").

For each species, the length of the recruitment period was determined by counting the number of months per year where average recruit abundance was either ≥1% adjusted total abundance for species with adjusted total abundance ≤1000, or ≥10 individuals for species with adjusted total abundance >1000. These cut-off values were arbitrary, and were used to increase the level of recruitment considered significant as total abundance increased. To test the hypothesis that species with shorter recruitment periods exhibit higher average recruitment rates within recruitment periods, separate correlations between mean monthly recruit density (for the months over which recruitment occurs) and the length of the recruitment period were calculated for each of the two families. To test whether total recruitment over the period during which I monitored recruitment was independent of the length of the annual recruitment period (as a result of a potential trade-off between the length of the spawning period and reproductive effort), the relationships between the cumulative total recruitment and the length of the recruitment period of each species were also examined for each of the two families.

2.3.4 Seasonal weather conditions and larval production

To assess whether recruitment was potentially associated with the major climatic factors, the year was divided into four annual periods: the wet (December-February) and windy (June-August) seasons and the two transitional periods between these seasons (March-May and September-November). The number of species of damselfishes and wrasses (the same species used in the analysis of seasonality described above) that had their peak period of recruitment in each of these periods was counted.

To investigate the influence of temporal patterns of larval production on temporal patterns of recruitment, the reproductive condition of females of 3 congeneric damselfishes was monitored every 1-2 months from Feb 2000 to Apr 2001. The 3 species, *Chrysiptera parasema*, *Chrysiptera rollandi* and *Chrysiptera talboti* were chosen because the degree of seasonality in their recruitment patterns varied slightly (at least in the first year of monitoring), and also because they are very abundant and easy to collect. In addition, they usually occur in social groups made up of a mature male (largest individual), mature female and several smaller sub-adults/juveniles, therefore, it was possible to collect just females by targeting the second largest individual in each social group. Monthly collections of 30-40 females of each species were made during 7 months in 2000 (March, April, June, July, September, October and November) and 3 months in 2001 (February, March and April), from a random selection of sites and depths, using clove oil and hand nets. The gonads of each fish were then dissected out and inspected visually. The proportion of females with ripe gonads, or gonads containing ripe eggs, was used as a measure of reproductive condition and was assumed to strongly relate to larval production. The values for monthly reproductive condition and recruit density were then examined qualitatively to determine if zero or low recruitment during the wet season could be the result of zero or low reproduction. A quantitative analysis (e.g. regression), with recruitment data suitably time-lagged, was not possible as there were just 6 months for which reproductive data were available that month, and recruitment data were available the following month.

2.4 Results

2.4.1 Relative abundance of the different families and species

A cumulative total of 115,980 new recruits of 105 species and 8 families were counted in the 20 surveys between December 1998 and April 2001. Of the total number of individuals surveyed, 90% were from just two families, the damselfishes (60%) and the wrasses (30%). The damselfishes had the highest average densities of new recruits (pooled across all sites, depths, survey periods and species), followed by the wrasses. Of the 40 most abundant species, over half were damselfishes and a quarter wrasses (Table 2.1). *Neopomacentrus azysron*, a damselfish, had the highest average density of new recruits across all sites, depths and survey periods, followed by a wrasse, *Halichoeres melanurus*, and another damselfish, *Chrysiptera rollandi* (Table 2.1).

2.4.2 Extent of seasonality and the magnitude of recruitment

In general, most fish species recruited over extended annual periods encompassing 10-12 months of the year. Over half (11 out of 19) of the wrasse species had a recruitment period of 12 months and none had recruitment periods of less than 8 months (Fig 2.2). Temporal periods of recruitment were more restricted in some damselfishes, which had recruitment periods of less than 6 months. However, even for damselfishes, over half (17 out of 29) of the species included in this analysis had recruitment periods of 10 to 12 months of the year (Fig. 2.2).

Although the majority of reef fishes recruited for most of the year, almost all species exhibited marked temporal variation in the abundance of recruits. For all but one of the 40 most abundant species, recruit density differed significantly among the 16 months in 1999 and 2000 (one-way ANOVAs, Table 2.1). *Chromis viridis* (Pomacentridae) was the only species for which recruit density did not differ significantly among months (Table 2.1). For 30 of the 40 most abundant species, there was a significant difference in recruit density between 1999 and 2000 (Table 2.1). For most of these species (25 out of 30, including 17

Table 2.1: Summary of temporal patterns for the 40 most abundant species, showing the total abundance (summed across all survey periods), mean monthly density (per 100m^2, averaged across all survey periods, sites, reef zones and depths), number of months per year that recruits were present at ≥ 1% adjusted total density (or ≥ 10 individuals for species with adjusted total abundance > 1000), and the peak period of recruitment (1=Dec-Feb, 2=Mar-May, 3=Jun-Aug, 4=Sep-Nov). Also shown are the significance values for the one-way ANOVA (Month) and planned comparison (Year) between 1999 and 2000 for each species. For species where within-group variances were homogeneous, the significance value (Month) is for the F-test (denoted with ^{F}), for other species, the significance value is for Welch's test. Data from just the depth(s) shown were used in the one-way ANOVA for each species. All depths are in metres and are on the windward side of each reef except for 2B, which is 2m on the leeward side. Data from all sites were used in the ANOVAs unless indicated by F ('far' platform reefs only), N ('near' platform reefs only) or Fr (fringing reefs only).

	Abundance		Density		Months per yr	Peak period	ANOVA			
Family and Species	Rank	Total	Mean	SE			depth/position	Month	Year	99vs00
Pomacentridae										
Acanthochromis polyacanthus	16	1692	0.94	0.17	6	3	2,2B(F,N)	<0.001^{F}	0.007	00>99
Amblyglyphidodon curacao	8	5735	2.76	0.24	10	4	2,2B	<0.001	0.701	NS
Amblyglyphidodon leucogaster	25	976	0.47	0.07	10	4	10,6	<0.001	0.139	NS
Chromis retrofasciata	26	901	0.43	0.04	10	4	10,6(F)	<0.001^{F}	<0.001	00>99
Chromis ternatensis	9	5284	2.54	0.26	11	3	10,6,2,2B(F)	<0.001	<0.001	00>99
Chromis viridis	23	1232	0.59	0.11	12	3	2	0.153	0.009	00>99
Chrysiptera cyanea	19	1691	0.81	0.17	10	4	0	<0.001	0.001	00>99
Chrysiptera parasema	14	2541	1.22	0.12	12	3	10,6	<0.001	0.862	NS
Chrysiptera rollandi	3	8208	3.95	0.18	12	3	10,6	<0.001	<0.001	00>99
Chrysiptera talboti	15	2143	1.03	0.09	8	3	6,2(F)	<0.001	0.001	00>99
Dascyllus melanurus	31	634	0.30	0.04	11	4	2B(F,N) 2(Fr)	0.001	0.017	99>00
Neoglyphidodon nigroris	30	646	0.31	0.03	7	3	2(F)	<0.001^{F}	0.005	00>99
Neopomacentrus azysron	1	13983	6.72	0.58	12	4	2,2B	<0.001	<0.001	00>99
Plectroglyphidodon lacrymatus	36	346	0.17	0.01	11	4	0	<0.001	0.087	NS
Pomacentrus adelus	13	2760	1.33	0.08	10	2	2,0,2B	<0.001	<0.001	00>99
Pomacentrus aurifrons	4	6946	3.34	0.33	8	3	6,2B	<0.001^{F}	<0.001	00>99
Pomacentrus bankanensis	34	439	0.21	0.02	11	4	0	<0.001	<0.001	00>99
Pomacentrus burroughi	17	1896	0.91	0.07	10	2	10,6,2,2B	<0.001	<0.001	00>99
Pomacentrus lepidogenys	32	512	0.25	0.03	8	4	2(F)	<0.001^{F}	0.006	00>99

Table 2.1 (cont.)	Abundance		Density		Months per yr	Peak period	ANOVA			
Family and Species	Rank	Total	Mean	SE			depth/position	Month	Year	99vs00
Pomacentridae										
Pomacentrus moluccensis	10	4703	2.26	0.16	12	4	2,2B	<0.001	<0.001	00>99
Pomacentrus nigromanus	12	2927	1.42	0.12	9	3	10,6	<0.001^{F}	<0.001	00>99
Pomacentrus simsiang	18	1840	0.88	0.07	10	3	2(Fr)	<0.001^{F}	<0.001	00>99
Labridae										
Diproctacanthus xanthurus	33	444	0.21	0.01	12	2	10,6,2B	<0.001	<0.001	99>00
Halichoeres argus	39	298	0.14	0.02	10	4	0	<0.001^{F}	<0.001	00>99
Halichoeres chloropterus	21	1622	0.78	0.06	11	2	2B(F,N), 0(Fr)	<0.001^{F}	0.011	00>99
Halichoeres melanurus	2	10843	5.22	0.21	12	2	6,2,2B	<0.001	<0.001	00>99
Halichoeres purpurescens	7	6796	3.27	0.16	11	2	10,6,2,2B(N,Fr)	<0.001	<0.001	00>99
Labrichthys unilineatus	24	1210	0.58	0.03	12	4	2(Fr)	<0.001^{F}	0.220	NS
Labroides dimidiatus	29	650	0.31	0.01	12	4	2	<0.001	0.001	00>99
Oxycheilinus celebicus	38	315	0.15	0.01	12	1	10	<0.001^{F}	0.016	99>00
Pseudocheilinus filamentosus	27	871	0.42	0.06	11	3	10	<0.001	<0.001	00>99
Thalassoma hardwicke	11	3231	1.55	0.09	12	1	0	<0.001	0.064	NS
Thalassoma lunare	6	6816	3.28	0.15	12	1	2,2B	<0.001^{F}	<0.001	00>99
Apogonidae										
Cheilodipterus quinquelineatus	5	6842	3.29	0.25	10	3	6,2,2B	<0.001^{F}	<0.001	00>99
Serranidae										
Pseudanthias tuka	20	1680	0.81	0.14	6	3	10	0.001^{F}	0.081	NS
Acanthuridae										
Ctenochaetus binotatus	40	293	0.14	0.01	11	1	6,2,2B	<0.001	<0.001	99>00
Ctenochaetus strigosus	35	408	0.20	0.02	11	4	6,2,2B	<0.001	0.001	99>00
Ctenochaetus tominiensis	22	1304	0.63	0.04	12	4	10,6	<0.001	0.221	NS
Chaetodontidae										
Chaetodon baronessa	37	334	0.16	0.01	12	4	2	0.008	0.890	NS
Chaetodon octofasciatus	28	817	0.39	0.04	12	2	6,2(Fr)	0.001^{F}	0.938	NS

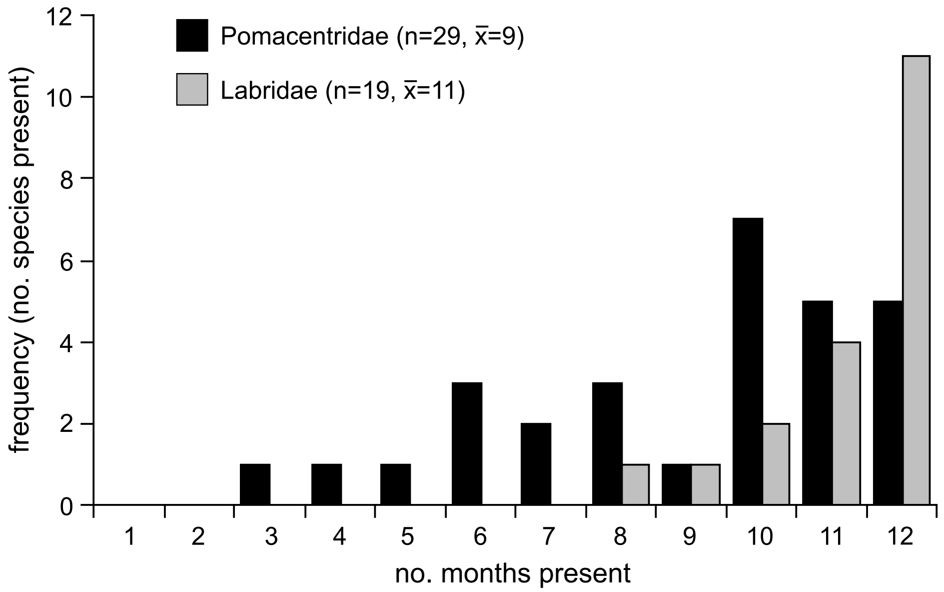


Figure 2.2: The degree of seasonality in recruitment of species in the a) Pomacentridae and b) Labridae, shown as the number of species that have recruits present (at abundance ≥ 1% adjusted total abundance for species where adjusted total abundance ≤ 1000, or at abundance ≥ 10 individuals for species where adjusted total abundance > 1000) for between 0-12 months of the year

damselfish species, 7 wrasse species and *Cheilodipterus quinquelineatus*), recruit densities were higher in 2000 than in 1999 (Table 2.1). For five species (1 damselfish species, 2 wrasse species and 2 surgeonfish species), recruit densities were higher in 1999 than in 2000 (Table 2.1).

Among the 40 most abundant species, there were consistent differences between the damselfishes and wrasses in the timing of peaks in abundance, as illustrated by the three most abundant species in each family (Figs. 2.3 and 2.4). For the three most abundant damselfishes, *Neopomacentrus azysron*, *Chrysiptera rollandi* and *Pomacentrus aurifrons*, there were very few or no recruits present between December and March (during and just after the wet season), and recruit densities peaked between April/May and October/ November each year (Fig. 2.3a-c). Most of the other damselfish species exhibited similar patterns of recruitment. The recruit densities of *P. aurifrons* peaked twice in 1999, but only once in 2000 (Fig. 2.3b). In all 3 species, recruit densities were higher in 2000 than in 1999 (Fig. 2.3, Table 2.1). The three most abundant wrasse species, *Halichoeres melanurus, Thalassoma lunare* and *H. purpurescens*, exhibited patterns of recruitment typical for most

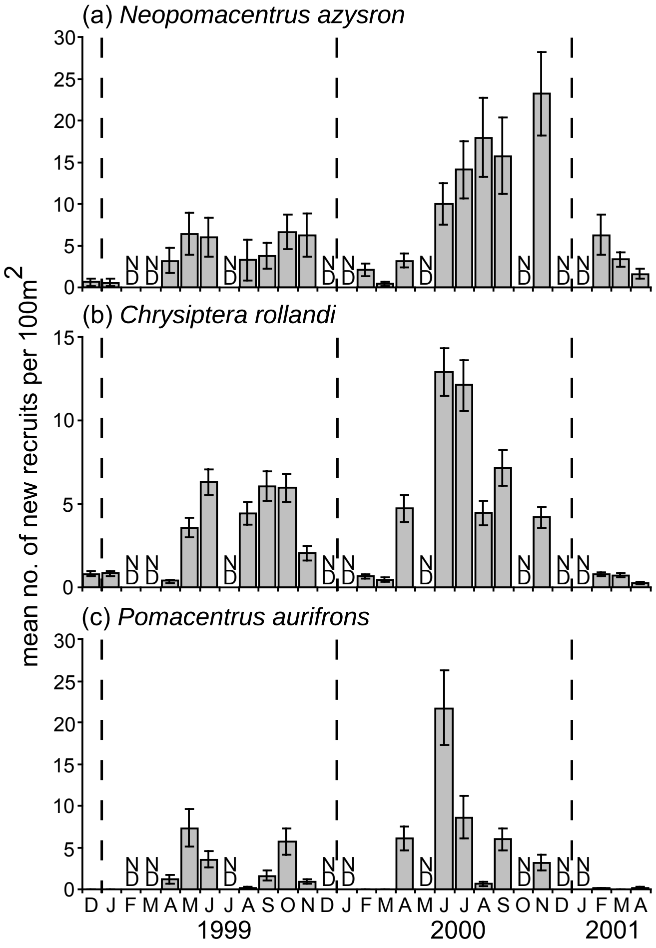


Figure 2.3: Temporal patterns of recruitment of the three most abundant damselfish species. Months not surveyed are indicated by "ND" (no data). Error bars are +/-1SE.

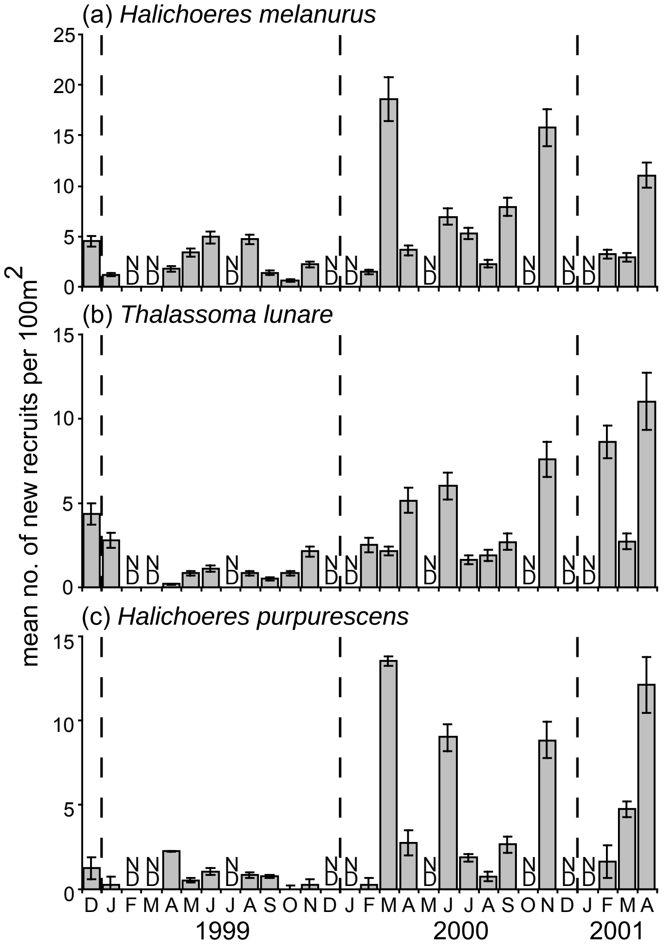


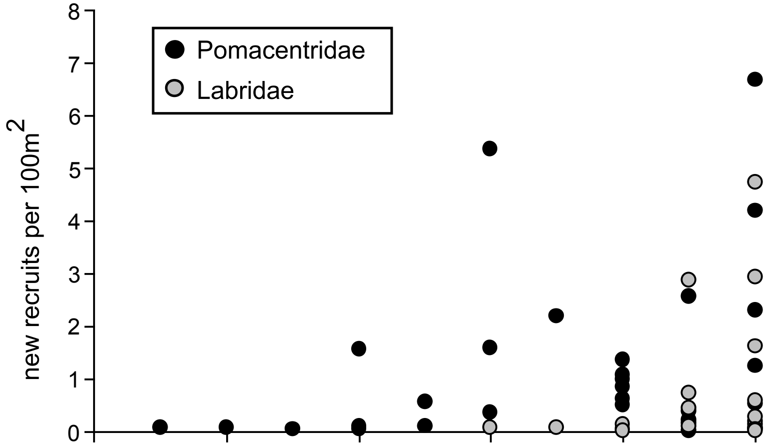
Figure 2.4: Temporal patterns of recruitment of the three most abundant wrasse species. Months not surveyed are indicated by "ND" (no data). Error bars are +/-1SE.

wrasses. Each had recruits present during all months surveyed, with recruit densities peaking at the beginning and end of each year (Fig. 2.4a-c). Recruit densities were higher in 2000 compared to 1999 (Table 2.1), with most of the recruitment occurring in 2-3 months of this year (Fig. 2.4). In March and November in 2000, densities of *H. melanurus* were 2-3 times higher than in other months of the same year (Fig. 2.4a). Similarly, in 2000, recruitment of *Halichoeres purpurescens* was much higher in March, June and November than in other months that year (Fig. 2.4c).

Mean monthly recruit density was not significantly correlated with the length of the recruitment period, for either damselfishes or the wrasses (Fig. 2.5a). That is, species with shorter recruitment periods did not recruit in greater densities than those with longer recruitment periods during the months in which recruitment occurs. However, there was a significant positive correlation between log total cumulative recruit abundance and the length of the recruitment period for the damselfishes ($r = 0.645$, $P < 0.001$), but not for the wrasses (Fig. 2.5b). This indicates that, among the damselfishes, longer recruitment periods are associated with a greater cumulative level of recruitment. Also, the total cumulative recruitment of damselfishes was consistently higher than that for wrasses, for those recruiting over similar time periods (Fig. 2.5b).

2.4.3 Seasonal weather conditions and larval production

When the year was divided into the wet (December-February) and windy (June-August) seasons, and the 2 transitional periods between these seasons, the peak period of recruitment for most of the damselfish species (26 out of 29 species) was either the windy season (June-August) or the period after the windy season (September-November, Fig. 2.6). Recruitment of most species was negligible during the wet season. Among the wrasses, the windy season was the peak recruitment period for just one of the 19 species, and the number of species with peak recruitment in each of the other 3 periods was roughly equal (Fig. 2.6).


(a) density vs. level of seasonality

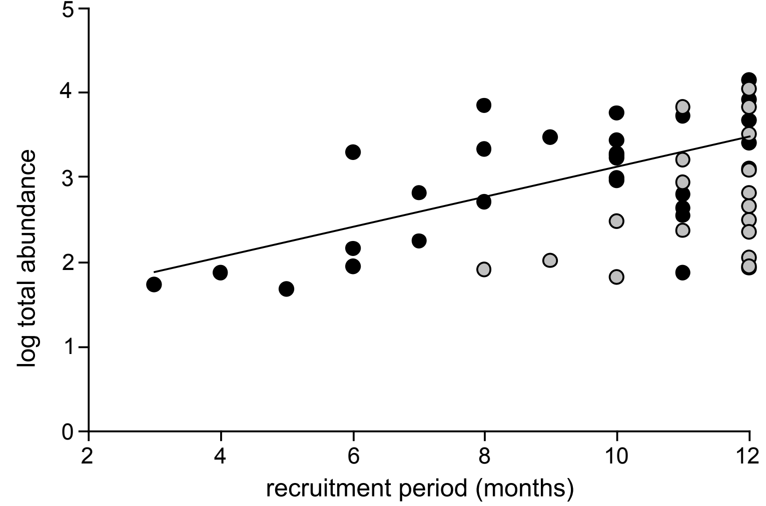

(b) total abundance vs. level of seasonality

Figure 2.5: Relationships between: a) Mean monthly recruit density for months when recruits are present; and b) Log total abundance, and the degree of seasonality in recruitment (i.e. number of months of the year that recruits are present at abundance ≥ 1% adjusted total abundance for species where adjusted total abundance ≤ 1000, or at abundance ≥ 10 individuals for species where adjusted total abundance > 1000) for the 2 focal families (Pomacentridae and Labridae)

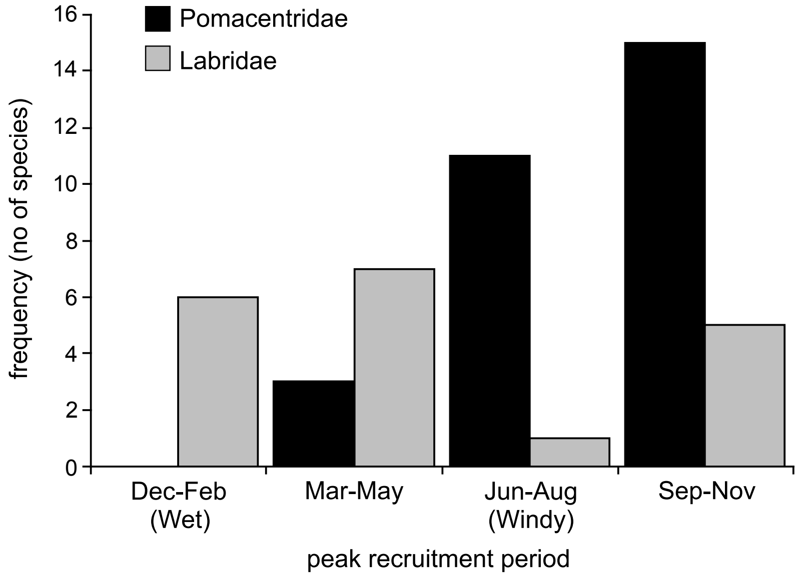


Figure 2.6: The number of species in the two focal fish families (Pomacentridae and Labridae) with the greatest number of new recruits in each of 4 periods (averaged across years): the wet and windy seasons, and the periods between these seasons

All three *Chrysiptera* species selected to monitor reproductive condition had few or no recruits present during and just after the wet season, and peak recruitment between June and September. For all three species, at least 50% or more of the females were in breeding condition during most months sampled (Fig. 2.7). Percentages were low early in the year when recruit densities were very low, i.e. in March 2000, February/March 2001 (with the exception of February 2001 for *C. parasema*), however there were still at least 30% of the females in breeding condition during these months (Fig. 2.7). In February 2001, over 80% of *C. parasema* females, and almost 40% of *C. rollandi* and *C. talboti* females, were in breeding condition, but recruitment levels that month, and in the following month, were low (Fig 2.7).

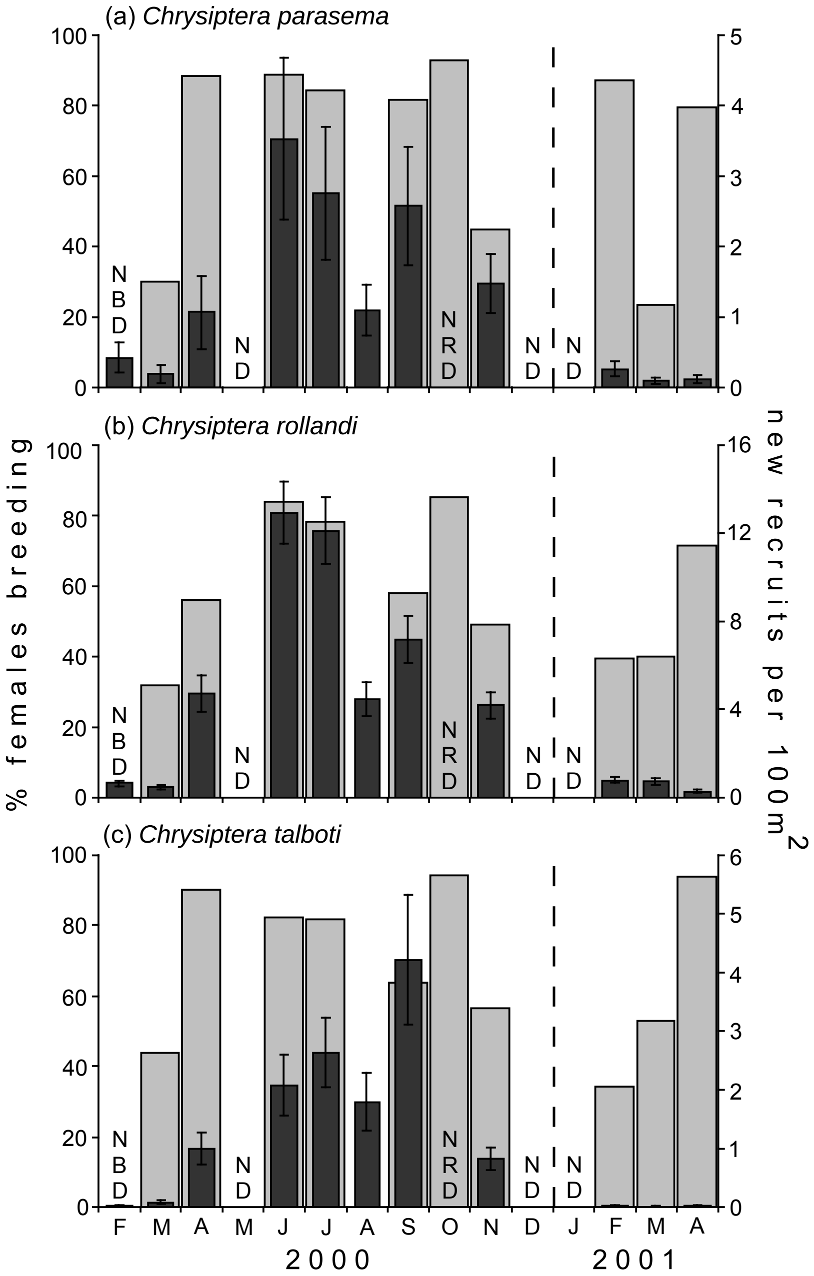


Figure 2.7: Temporal patterns of recruitment (dark grey bars) and reproduction (light grey bars) for the three *Chrysiptera* species. ND = no data (both recruitment and reproduction), NBD = no breeding data (only recruitment estimated), NRD = no recruitment data (only reproduction estimated).

2.5 Discussion

This study confirmed the expectation of extended recruitment seasons, and in many cases year-round recruitment, of coral reef fishes at a low latitude location in the Indo-West Pacific. However, although many of the species surveyed recruited in all months of the year, recruitment did not occur at a constant rate. Distinct annual patterns in the magnitude of recruitment were observed for most species, with broad periods of peak recruitment over the same periods each year. An inter-annual difference in the magnitude of recruitment was also observed. These patterns are similar to those described for the San Blas Archipelago on the Caribbean coast of Panama (Robertson 1990, 1992; Robertson et al. 1993, 1999). This comprehensive series of publications provides the only long-term comparative data for coral reef fishes at low latitude. It appears likely that extended spawning periods and seasonal maxima are typical of coral reef fishes in equatorial waters.

Few studies have examined temporal variation in the taxonomic composition of recruitment to reef fish communities. In our study, the length of the recruitment periods and timing of peak recruitment differed between two families (Pomacentridae and Labridae), which together accounted for 90% of all recruitment recorded over 2.5 years. Recruitment of wrasses was typically less seasonal than most damselfishes, with most recruiting for a greater number of months each year. In over half of the wrasse species, recruitment occurred during all months of the year, while the damselfishes included a small number of species for which recruitment occurred for just 6 months of the year or less. The difference in the seasonality of damselfishes and wrasses observed here was not apparent for the Caribbean (Robertson 1990; Robertson et al. 1999). Other studies have stressed a high degree of variation in patterns of seasonality within the same reef fish families (Russell et al. 1977; Robertson 1991; Robertson et al. 1993).

The recruitment patterns described here, particularly those of the damselfishes, are very different to those at higher latitude reefs in the Indo-West Pacific. For example, at both Lizard Island and One Tree Island, at opposite ends of the Great Barrier Reef, recruitment of the majority of reef fish species usually occurs during the southern hemisphere summer, typically between November and February (Russell et al. 1974, 1977; Talbot et al. 1978; Williams and Sale 1981; Williams 1983; Milicich and Doherty 1994). This restricted period coincides with low (or zero) recruitment of most damselfishes in Kimbe Bay.

Of the 40 species for which recruitment seasonality is described here for Kimbe Bay, surprisingly few have comparable data published for the Great Barrier Reef. One of the most abundant species in the present study, *Cheilodipterus quinquelineatus* (Apogonidae) had 10 or more new recruits present for 10 months of the year, while Williams and Sale (1981) found that recruitment of this species was primarily restricted to between November and May, with just 1-2 recruits counted during the months of August and October. *Acanthochromis polyacanthus* (Pomacentridae) recruited for 6 months of the year (with zero recruitment in December and January) in Kimbe Bay, and for just 3 months of the year (November to January) at One Tree Island (Russell et al. 1977). At the family level, both damselfish and wrasse species recruited for an average of 3 months of the year at One Tree Reef (averaged among species with annual recruitment periods ranging from 1 to 6 months, Russell et al. 1977). This compares with average recruitment periods of 9 months for damselfishes and 11 months for wrasses in Kimbe Bay. Hence there is ample evidence that species in these families have extended recruitment periods nearer the equator.

It has been argued that the strong seasonality on the Great Barrier Reef is associated with spawning at a time that is best for larval growth and survival (Doherty 1983). Even at the northern end of the reef there is a 5^{o}C annual variation in water temperature that is associated with seasonal planktonic production cycles. In contrast, mean monthly temperatures vary by less than 1-2^{o}C in Kimbe Bay. Instead, there are distinct seasonal conditions associated with the monsoon climate, with peaks in rainfall and wind speed occurring at different times of the year. One or more factors associated with monsoonal conditions clearly have the potential to influence seasonal patterns of spawning and recruitment in this region.

The damselfishes consistently exhibited little or no recruitment during, and in the months following periods of heavy rain. In contrast, the peak period of recruitment for many of the wrasse species was during the period of low damselfish recruitment. Temporal patterns in the timing and magnitude of recruitment may be explained by either variation in larval production, factors affecting larval survival or recruitment success, or a combination of these factors. While patterns of reproduction and larval supply have been shown to be good predictors of the timing of recruitment on higher latitude coral reefs (Milicich et al. 1992; Meekan et al. 1993), it is not clear to what extent variation in larval production explains variation in the magnitude of recruitment. One hypothesis that could explain reduced damselfish recruitment over the wet season is that there is a decrease in reproductive activity over this period. However, for the three *Chrysiptera* species studied here, females were found to be reproductive year-round, although there was a decrease in the proportion of females in reproductive condition during the wet season. This decrease was not large enough to explain the low numbers (and in some months a total absence) of recruits of these species at this time. The lack of recruitment during the wet season is likely to be caused by a combination of both reduced larval production and extrinsic factors affecting larval mortality.

There are other data supporting the potential importance of monsoonal conditions in determining coral reef fish recruitment at low latitudes. The studies on temporal patterns of settlement at San Blas in Panama, which also has a wet season (May-November) and a dry/windy season (January-March), have shown that peak settlement of several damselfish species (Robertson 1990), and a wrasse species (*Thalassoma bifasciatum,* Robertson et al. 1999) occurs during the wet season. The strength of onshore winds is believed to be the main factor influencing seasonal patterns of both spawning and settlement at this location. During the dry season, strong onshore winds result in high wave action that is thought to have a negative impact on spawning and the survival of larvae (Robertson 1990; Robertson et al. 1999). Although spawning occurs all year, the gonadosomatic index (GSI) of parrotfish on exposed reefs was highest during the wet season (Clifton 1995).

One possible explanation for the contrasting seasonal patterns of damselfishes and wrasses in Kimbe Bay is that larvae may differ in their susceptibility to extreme fluctuations in salinity in shallow water. In this region, prolonged periods of intensive rain may last for many weeks. Freshwater accumulates in a persistent layer of cooler, low-salinity water to depths of 1-2m. Larval damselfishes tend to be found close to the surface (Doherty and Carleton 1997; Leis 1991a, b; Fisher 2004). The low-salinity water at the surface during and after periods of high rainfall could potentially have a negative impact on the survival of damselfish larvae or limit their ability to find suitable habitat. In contrast, wrasse larvae are often found in deeper water (Leis 1991a, b; Hendriks et al. 2001), which may render them less susceptible to the fluctuating environmental conditions at the surface.

Monsoon climates are complex and clearly many factors may ultimately explain seasonal peaks in recruitment in species with extended spawning periods. Johannes (1978) argued that reef fish might spawn at times of reduced water movement to restrict advection away from reef habitat. Little is known of annual variation in the direction of wind driven and sub-surface currents in Kimbe Bay. One larval tagging study at this location has shown that there is a high degree of local retention of larvae of a damselfish species between March and November (Jones et al. 2005), however seasonal differences in the degree of retention or advection of larvae are unknown. If further work shows that annual variation in the magnitude and direction of water currents varies with depth, this could potentially account for the contrast in recruitment patterns between the damselfishes and wrasses.

Most of the current theory on the role of recruitment in population dynamics has been derived from studies conducted in seasonal environments, where strong pulses in recruitment occur over a relatively short period each year. Published examples of recruitment limitation, recruitment failure and year class phenomena are much more prevalent for species with restricted recruitment seasons (Caley et al. 1996). In less seasonal environments, where recruitment occurs either all year or for a much longer period of the year, the role of recruitment is likely to be quite different and difficult to assess. We found no evidence for the hypothesis that species with shorter recruitment seasons exhibit higher average levels of recruitment from spawning episodes. Such a pattern may result from a life history trade-off, where individuals in seasonal environments increase batch fecundity to compress the same reproductive effort into a shorter period of the year (Winemiller and Rose 1992; Vila-Gispert et al. 2002). There is, however, a suggestion that species with longer recruitment periods accumulate higher annual rates of recruitment, which may result in a greater abundance of such species. Thus, the extent of spawning seasonality may directly contribute to determining the structure of the reef fish community as a whole. The length of the spawning period may also influence the importance of ecological interactions among recruits, with stronger interactions among individuals recruiting over restricted time periods.

Assessing the importance of recruitment rates on low latitude populations with extended recruitment seasons remains problematic. Typical one-off surveys of recruitment (e.g., Sale et al. 1984; Fowler et al. 1992; Williams et al. 1994) would undoubtedly provide a poor indicator of annual patterns in these environments. In this study, even though recruitment was monitored approximately monthly over an extended period, the new recruits counted were estimated to have settled up to 1-2 weeks prior to each survey. Since coral reef fish mortality can be extremely high during the first week after settlement (e.g., Doherty and Sale 1985; Steele and Forrester 2002; Almany and Webster 2006), seasonal differences in post-settlement mortality could also have contributed to the observed temporal patterns in recruitment.

Further studies are needed to document seasonal and annual patterns of recruitment in other low latitude locations, and to investigate the influence of extended recruitment seasons on annual recruitment rates and population dynamics. While common latitudinal trends in the growth, fecundity and body size of fishes appear to be well known, the links between these life history parameters and important demographic rates such as recruitment and mortality remain poorly understood. Our data indicate that intensive sampling of recruitment over a long period can expose patterns that are consistent at the family level, and may be fundamental to the demography of their constituent species. Such data are also critical to developing an understanding of the physical features of tropical environments that are most critical to the reproduction and survival of the great diversity of fish species whose distributions encompass equatorial waters.

CHAPTER 3: HABITAT SPECIALISATION, AVAILABILITY AND SPATIAL RECRUITMENT PATTERNS OF FISHES ON A LOW LATITUDE CORAL REEF

3.1 Abstract

The degree of habitat specialisation and spatial gradients in recruitment success can be critical determinants of the distribution and abundance of marine organisms. For coral reef fishes, the degree of microhabitat specialisation and the influence of microhabitat availability on the spatial distribution and magnitude of recruitment within and among reef zones are poorly understood. This is particularly true for low-latitude, high diversity coral reefs in the Indo-Pacific, where theory predicts a high level of specialisation, and therefore, spatial segregation among species. Here I examine patterns of microhabitat specialisation and associated spatial distributions of new recruits for 40 of the most abundant species at a location close to the equator (Kimbe Bay, PNG). The majority of these species, mostly damselfishes and wrasses, were strongly associated with a narrow range of microhabitats. Both live branching corals (particularly *Acropora* and *Pocillopora* spp.) and dead substrata were preferred recruitment microhabitats for different species. Regression tree analyses revealed strong family-wide patterns of recruit assemblages across depths, reef zones and, to a lesser extent, distances from shore. These spatial distributions were largely independent of the availability of preferred microhabitats. In addition, differences among species in the magnitude of recruitment appeared to be independent of the degree of specialisation with respect to both microhabitat (i.e. substratum) and macrohabitat (i.e. distance from shore, reef zone and depth). Within preferred depth ranges or reef zones, recruit densities were positively correlated with the availability of preferred microhabitats for only 10 of the common species. Our results reveal a high level of microhabitat specialisation and a strong spatial structure that are to a large degree independent of one another. The causes and consequences of strong microhabitat associations and narrow depth distributions require further investigation.

3.2 Introduction

Much current ecological theory seeks to explain recurring patterns in the spatial distribution and turnover of species in natural assemblages. For relatively sedentary marine organisms, most of which have a pelagic larval phase, the spatial distributions of adults can often be traced back to patterns established at recruitment into the adult habitat (Roughgarden et al. 1988; Olafsson et al. 1994; Booth and Brosnan 1995; Caley et al. 1996; Hughes et al. 1999). Indeed, while spatial differences in post-recruitment mortality can modify spatial patterns established at settlement (Gaines and Roughgarden 1985; Gaines et al. 1985; Caley 1993; Levin 1993; Eggleston and Armstrong 1995), very often a strong recruitment signal still remains evident in adult distributions (Jones 1997). Such spatial variation in recruitment can be attributed to spatial variation in larval supply (Grosberg 1982; Gaines et al. 1985; Hurlbut 1991) and/or habitat selection at settlement (Levin 1991; Eggleston and Armstrong 1995; Andrews and Anderson 2004). Therefore, in order to understand the spatial structure of marine assemblages it is necessary to understand the underlying determinants of this spatial variation in recruitment.

Recruitment sites can be considered a resource that may vary in quantity and quality, and species may differ in the degree to which they become specialised on particular substrata. While the general factors affecting the degree of specialisation and the consequences of differing levels of ecological versatility have received considerable theoretical attention (Fox and Morrow 1981; Futuyma and Moreno 1988; McNally 1995; Robinson and Wilson 1998), little of this theory has been applied to understanding the magnitude and spatial extent of recruitment. Because generalists, by definition, have access to more potential recruitment sites than specialists, they might be expected to achieve a greater local abundance and/or a wider distribution among local habitats (Brown 1984; McNally 1995; Morris 1996; Hughes 2000). Specialists, on the other hand, may be able to use the resources on which they are specialised more efficiently than can generalists, and may therefore, out-compete them in the acquisition of these resources (Futuyma and Moreno 1988). If so, average abundances of generalists and specialists summed across habitats may not vary to any great extent. It has been a long-standing belief that in high diversity communities, species will be more specialised and have narrower niches (MacArthur 1972; Vazquez and Stevens 2004). However, for most high diversity marine assemblages, the levels of recruitment site specialisation, and the spatial turnover in recruitment sites among species have seldom been quantified.

Coral reef fish communities are characterized by high local species diversity, and there is considerable evidence that the spatial distribution and abundance of the adults of the species making up these communities can be strongly influenced by recruitment (Sale 1980; Doherty 1991; Williams 1991). However, the role of habitat specialisation in explaining spatial patterns of recruitment in these species has not been fully investigated. Reef fishes vary in their choice of substrata as recruitment sites (Eckert 1985; Booth 1992; Tolimieri 1995, 1998b; Danilowicz 1996; Öhman et al. 1998; Jones et al. 2004 – Appendix III). Therefore, the degree of microhabitat specialisation at settlement may be an important determinant of their spatial distribution among habitats. Indeed, there is some evidence that more specialised species have narrower distributions across typical reef habitats (Munday et al. 1997; Bean et al. 2002; Munday 2002; Gardiner and Jones 2005), but whether these patterns of habitat occupation reflect recruitment patterns is uncertain. For more specialised species, one would predict a greater influence of the availability of preferred microhabitats on spatial patterns in the abundance of recruits (Munday et al. 1997; Munday 2004). However, while this may be true for microhabitat specialists, where most reef fishes are positioned along a continuum of microhabitat versatility is poorly understood. In addition, which coral reef substrata are most commonly preferred as recruitment sites by most of these species is unknown. An understanding of the roles of habitat specialisation and habitat availability is essential, therefore, for interpreting the spatial structure in reef fish assemblages and their responses to habitat change.

Patterns of larval supply and settlement of coral reef fishes can vary across a range of spatial gradients. For example, the abundance of larvae and new recruits can vary considerably among sites around islands (Milicich et al. 1992; Milicich and Doherty 1994; Caselle and Warner 1996; Sponaugle and Cowen 1996a, 1996b; Schmitt and Holbrook 1999; Shima 2001; Hamilton et al. 2006), different distances from shore (Schmitt and Holbrook 1999; Shima 1999), reef zones (Doherty et al. 1996; Green 1996; Jones 1997; Wilson 2001) and depths (Wellington 1992; Jones 1997; Gutierrez 1998; Leis and Carson-Ewart 2000). The degree to which these different spatial gradients and their interactions contribute to the spatial turnover in species composition on coral reefs has not been evaluated. Combinations of these factors, plus the availability of preferred recruitment microhabitats, may help predict these spatial gradients at a variety of spatial scales.

Although the causes and consequences of spatial recruitment patterns in coral reef fishes have received much attention in recent years, few geographically robust, community-wide generalisations have emerged. Studies vary in terms of geographic location and the extent of coverage of typical coral reef taxa. Much of the work in the high diversity Indo-Pacific region has been carried out at mid- or high-latitude locations, particularly the Great Barrier Reef (see Doherty & Williams 1988, Doherty 1991, Williams 1991). The degree of microhabitat specialisation and the spatial turnover among species at higher diversity locations closer to the equator remain largely undescribed. As diversity generally increases with decreasing latitude (Hillebrand 2004) and because higher diversity is predicted to be associated with a higher degree of specialisation and resource partitioning (MacArthur 1972; Vasquez and Stevens 2004), a much finer degree of spatial segregation might be expected to occur near the equator.

Here I examine the degree of microhabitat specialisation and microhabitat availability as potential determinants of spatial patterns in the recruitment of coral reef fishes at a low-latitude, high diversity location in the western Pacific (Kimbe Bay, Papua New Guinea). I compare recruitment patterns among the most commonly recruiting fish species from eight typical reef fish families. In addition, I examine family-wide patterns for the Pomacentridae and Labridae, the two families that account for the majority of juveniles that recruit to hard reef substrata (<10m depth) at this location. Four main questions are addressed: (1) Are most reef fish recruits associated with, or apparently specialised on, particular reef substrata (microhabitats) shortly after settlement, and if so, which microhabitats are these species specialised on?; (2) To what extent are recruit assemblages structured along typical reef spatial gradients (e.g. distance from shore, reef zone and depth); (3) What are the relationships between microhabitat specialisation, and the local distribution and abundance of these species? That is, is specialisation on a narrow range of microhabitats associated with reduced recruit abundance and/or narrower recruit distributions along broader habitat gradients?; (4) Finally, can the abundances of recruits of the most common species within their preferred depths and reef zones be explained by the availability of their preferred microhabitats?

3.3 Methods

3.3.1 Study sites

This study was conducted on several inshore reefs in Kimbe Bay (5°30'S, 150 °05'E), on the north coast of west New Britain, Papua New Guinea (Fig. 1.1a). Visual surveys of new recruits were carried out at six reefs, with two replicate reefs at each of three distances from shore: (1) fringing reefs (Mahonia and Walindi); (2) platform reefs 0.2-0.5 km from shore (Gava Gava and Madaro); and (3) platform reefs 0.8-1 km from shore (Limuka and Luba Luba) (Fig. 1.1b). Platform reefs were surveyed at depths of 10, 6, and 2 m on the windward reef slope, on the reef flat near the windward edge, and at a depth of 2 m on the leeward side. At the two fringing reef sites, the cover of hard substrata did not extend beyond a depth of 8 m in most places, therefore only 6 and 2 m depths, and the reef flat, were surveyed.

3.3.2 Visual surveys

Four 50 x 2 m replicate belt transects were surveyed at each depth. As these surveys were carried out to examine temporal patterns of recruitment (Srinivasan and Jones 2006 – Appendix II), as well as spatial patterns, a total of 20 surveys were carried out, spaced every 4-8 weeks from December 1998 to April 2001.

During each survey, transect tapes were laid out from a random starting point, however, due to the small sizes of these reefs, roughly the same areas were covered each time. On both platform and fringing reefs, reef flat transects were laid out roughly 2 m from the reef crest. Within each transect, new recruits of all non-cryptic species from a number of families were counted. These included damselfishes (Pomacentridae), wrasses (Labridae), butterflyfishes (Chaetodontidae), surgeonfishes (Acanthuridae), parrotfishes (Scaridae), cardinalfishes (Apogonidae), rabbitfishes (Siganidae), fairy basslets (Serranidae). Within each transect, all new recruits below a certain threshold size were counted. Only fish that were estimated to have settled within the previous 1-2 weeks were counted in order to avoid re-counting individuals from previous surveys. Threshold sizes for each taxon were established from size estimates of fish that had settled on a series of experimental patch reefs (i.e. Srinivasan 2003 – Appendix II) that were monitored every 2-3 days during four 6-8 week periods in 1999 and 2000.

During each survey, the substratum or microhabitat type that each new recruit occupied was recorded. To estimate the availability of these microhabitats, surveys of benthic substrata were conducted at the same sites and depths in March/April 1999, November 1999 and November 2000. Substratum surveys were conducted just once for the leeward sides of the platform reefs, and the fringing reef sites (March 1999 and November 2000 respectively). Four 50 m line-intercept transects were used to estimate the percent cover of benthic substrata at each depth. The type of substratum under each of 100 random points along each transect was recorded and the number of points for each substratum type was then summed to obtain the percentage cover estimate. Substratum and fish recruit surveys were conducted simultaneously on each transect.

Spatial patterns of recruitment were examined qualitatively for all but the rarest of the reef fish species that were observed to recruit into coral reef habitats during this study. These included 70 species for which total recruit abundance ≥ 24 individuals: 33 damselfish species, 23 wrasse species, 6 surgeonfish species, 3 butterflyfish species, 2 rabbitfish species, 1 cardinalfish (*Cheilodipterus quinquelineatus*), 1 parrotfish (*Scarus niger*) and 1 fairy basslet (*Pseudanthias* *tuka*). Data were pooled across all censuses and, for each species, the position (i.e. distance from shore: far, near or fringing), and the depth/zone, with the greatest proportion of recruits was determined. Because the densities of many of these species were too low to adequately examine microhabitat specialisation and spatial distributions, the 40 most abundant species were selected for quantitative analyses of microhabitat selectivity and spatial recruitment patterns (see below).

3.3.3 Analysis of recruitment microhabitats and selectivity

Substratum types were grouped into 13 microhabitat categories for analysis (Table 3.1). Patterns of microhabitat-use were examined for 38 of the 40 most abundant species, each with a total abundance (pooled across all 20 survey periods) of greater than 250 individuals (Table 3.1). These included 21 damselfish species, 11 wrasse species, 3 surgeonfish species, 2 butterflyfish species and *Pseudanthias tuka* (Serranidae). Recruits of 2 of the 40 most abundant species, *Acanthochromis polyacanthus* (Pomacentridae) and *Cheilodipterus quinquelineatus* (Apogonidae), hovered too far above the substratum to score their association with any particular substratum types. Therefore, these species, the 5th and 16th most abundant species respectively, were excluded from analyses of microhabitat selection.

Levels of microhabitat specialisation were compared among species (and families) by estimating the number of microhabitat categories occupied by most of the individuals ($\geq$95%) of each of the 38 species. The percentages of individuals occupying the most frequently occupied categories were summed until a total of at least 95% was reached. This cut-off was used to exclude microhabitat types that were used by a minority of the population.

Resource selection ratios (Manly et al. 2002) were used to determine whether species used certain microhabitats more or less frequently than expected based on their availability. For each of the 38 species, the forage ratio ($\hat{w}_i$) was calculated for each of the 13 substratum types using the formula $\hat{w}_i = o_i/\pi_i$, where o_i is the proportion of recruits occupying substratum type i, and π_i is the proportion of substratum type i available (percent cover/100). For each selection ratio, a Bonferroni-corrected 95% confidence interval was calculated using the formula

$z_{\alpha/2I}\sqrt{\{ o_i(1- o_i)/(u_+\pi_i^2)\}}$, where $z_{\alpha/2I}$ is the critical value of the standard normal distribution, $\alpha = 0.05$, I = number of substratum types, and u_+ = total number of recruits for which microhabitat-use was recorded (Manly et al. 2002). A 95% confidence interval containing the value 1 indicates that a substratum type is used in proportion to its availability. A 95% confidence interval that spans values greater, or less, than 1, but that does not include 1, indicates that a substratum type is used more, or less, frequently than expected based on its availability (Manly et al. 2002). As microhabitat availability differed among depths, reef zones and reef types (fringing or platform), resource selection ratios were based on microhabitat-use and availability data from the combination of depth/zone and reef position at which each species was most abundant (Table 3.1). Microhabitat availability data for each combination of depth and reef position were pooled across the 3 censuses.

3.3.4 Spatial patterns in recruitment among reef zones

Multivariate and univariate regression trees were used to partition variation in recruitment with respect to position (distance from shore), depth/reef zone (treated as a single factor) and microhabitat availability on spatial patterns of recruitment, at the family level for 2 families (damselfishes and wrasses) as well as at species level for the same 38 species for which microhabitat use was examined above. Regression trees were chosen for analyses as they can be used with unbalanced sampling designs, and both continuous and category explanatory variables can be included in the same analysis (De'Ath and Fabricius 2000; De'Ath 2002). Regression trees were constructed using the statistical package TreesPlus (De'Ath 2002). For each tree, 50 sets of 10-fold cross-validations were carried out, and the modal tree size was selected using the 1SE rule (De'Ath and Fabricius 2000; De'Ath 2002).

To describe family level patterns of habitat use for the damselfishes and wrasses, a multivariate regression tree was constructed for each family, with the densities of the 10 most abundant species in the family as response variables, and position, site, depth/reef zone, and the availability of 11 microhabitat categories as explanatory variables. The 10 most abundant species in each of these families was used to avoid an overly complicated regression tree. Two microhabitat categories (crustose coralline algae and macroalgae) were not commonly used by new recruits of most species. Therefore, these two categories were not included in these analyses. Species densities were averaged across the 20 survey periods, and converted to the proportion of individuals out of the total in each transect. This was done to standardize abundances among the 10 species in each family. Doing so reduces the influence of the most abundant species on the outcome of the analysis. The percent cover estimates for each microhabitat category were averaged across the 3 survey periods and converted to estimates of proportion cover.

To describe species level patterns of microhabitat use, separate univariate regression trees were constructed for each of the 38 species. For each species, the number of recruits per transect was averaged across the 20 survey periods and transformed to $\log(x+1)$. Regression trees do not require that the usual assumptions of parametric tests are valid. However, as many of the species in this study had patchy distributions, log transformations were used to improve the explanatory power of the regression trees. The explanatory variables included in the regression tree model for each species were Position (distance from shore), Depth (depth and reef zone), Site (reef) and the microhabitat category, or categories, utilised most frequently (i.e. the highest ranked habitats were added until at least 75% of the individuals of that species were accounted for). In preliminary analyses using all microhabitat categories, a non-preferred microhabitat explained a large proportion of the spatial variation of several species. These results are probably due to that microhabitat type being a surrogate for some other factor that was not measured. Therefore, only microhabitat types considered likely to have an influence on spatial patterns of recruitment were included in the regression trees. Although 75% was used as the cut-off, this percentage was considerably higher for most of the species. For example, regression trees for 14 of the 38 species included microhabitat categories occupied by ~90% or more individuals.

3.3.5 Specialisation, the availability of preferred microhabitats, and the distribution and abundance of recruits

For each species, the Shannon-Weiner index was used to calculate an index of specialisation with respect to microhabitat (as per Munday 2004). This index was considered suitable to characterise levels of microhabitat specialisation as it takes into account the number of microhabitat categories that each species uses as well as the frequency at which each category is used. It is calculated as $W = \Sigma\ (-\log P * P)$, where P is the proportion of individuals in each microhabitat category. A highly specialised species, using just one microhabitat, will have a microhabitat index of one, and this value increases as more microhabitat categories are used.

To examine if microhabitat specialists (i.e. species using just 1 or 2 microhabitat types) tended to be more rare than generalists, I tested for a correlation between total abundance (pooled across all transects and censuses, and log transformed), and the index of microhabitat specialisation. The Shannon Weiner index was also used to characterise specialisation with regard to the broader habitat categories, or 'macrohabitats' (i.e. distance from shore, reef zone and depth). In this case, P was the proportion of individuals in each of 13 combinations of position (3), and reef zone/depth (5 on platform reefs, 3 on fringing reefs). I examined whether microhabitat specialists tended to have narrower distributions across these broader habitat categories by examining the correlation between the microhabitat and macrohabitat indices. Finally, I examined the correlation between total recruit abundance (log transformed) and the index of macrohabitat specialisation, to determine if species that were restricted to certain macrohabitats were less abundant than generalists.

To determine if the local abundance of recruits was explained by microhabitat availability within preferred depths/zones and/or positions, I examined correlations between density and microhabitat availability at selected depths/reef zones for the same 38 species used in the analysis of microhabitat use. Recruit density data averaged across the time periods from December 1998 to April 2000 were correlated with microhabitat availability data from 1999 (averaged between the March and November censuses) and recruit density data averaged across the time periods from June 2000 to April 2001 were correlated with microhabitat availability data from November 2000. Recruit densities were transformed to log(x+1), to achieve normality, and microhabitat data were converted from percentages to proportions. For each species, the percent cover estimates of the microhabitat categories that the majority of individuals occupied were summed to obtain a single value of percent cover per transect. As with the univariate regression trees, highest ranked habitats were added until at least 75% of the individuals of that species were accounted for, in order to include only the microhabitat types likely to influence spatial patterns of recruitment. As mentioned above, for many species, the actual percentage of individuals that occupied the microhabitats included was close to 90% or more. For each species, the combinations of depth/zone and position used in the analysis were determined by the splits in the univariate regression tree.

3.4 Results

3.4.1 Recruitment microhabitats and selectivity

The mean number of microhabitats used by the majority of individuals (≥95%) was 5.2 ± 0.4 for the 38 common species associated with the substratum (Fig. 3.1a). Fourteen species were extreme specialists occupying ≤ 4 out of the recognized 13 substrata. Twelve species could be considered more generalist (occupying ≥ 7 substrata, but no species was associated with > 10 of the 13 substrata (Fig. 3.1a). Damselfish and wrasses exhibited a similar range of substrata occupied, with both having species at the extremes of microhabitat versatility. Even though many species frequently used 5-6 substratum types (Fig. 3.1a), most of the individuals of all species used a smaller subset of microhabitat categories (Fig. 3.1b). That is, for over half (23 out of 38) of the species, the most frequently used microhabitat categories (between 1 and 4) were occupied by between 91-100% of the individuals (Fig. 3.1b).

Seven species could be considered extreme microhabitat specialists based on the fact that most of the individuals (≥95%) occupied just one or two microhabitat categories. These species could be divided into 3 groups based on microhabitat use: (1) only corals in the family Acroporidae (3 species: a damselfish species, *Chromis viridis*, and two butterflyfish species, *Chaetodon baronessa* and *Chaetodon octofasciatus*); (2) corals in the family Acroporidae and one other coral type, either Pocilloporidae or branching and foliose corals of the genera *Porites* or *Montipora* (3 species: 2 damselfish species, *Chromis ternatensis* and *Dascyllus melanurus*, and a wrasse species, *Labrichthys unilineatus*); or (3) non-living substrata (bare-rock, rubble or sand) as well as turf covered flat surfaces (1 wrasse species, *Halichoeres chloropterus*).

At the other extreme, six species were characterized as microhabitat generalists on the basis that ≥95% of the individuals occupied 9-10 microhabitat categories, and the 4 most frequently used microhabitat categories were occupied by ≤75% of the individuals. These six species included two damselfish species (*Neoglyphidodon nigroris* and *Pomacentrus nigromanus*) and four wrasse species (*Halichoeres melanurus*, *Halichoeres purpurescens*, *Oxycheilinus celebicus* and *Labroides dimidiatus*). The microhabitat types occupied by the specialists were a subset of the microhabitat types occupied by the generalists.

Over half (25 out of 38) of the species occupied just 1 or 2 microhabitat types in greater proportions than expected based on their availability (Table 3.1). Corals of the family Acroporidae were used disproportionately by 23 species, and non-living substrata were used disproportionately by 15 species (Table 3.1, Fig. 3.2). The next most commonly used microhabitat categories included corals of the family Pocilloporidae (used disproportionately by 9 species), turfing algae on flat surfaces, soft coral, and branching/foliose corals of the genera *Porites* and *Montipora* (each used disproportionately by 8 species, Table 3.1, Fig. 3.2). There were no major differences among damselfish, wrasses and the combined other families in terms of the differential use of particular microhabitat types (Fig. 3.2). All families had representative species in which recruits were primarily associated with Acroporids, non-living substrata, Pocilloporids and a range of other substrata. None of the species favoured the microhabitat categories MA and OCF (Fig 3.2).

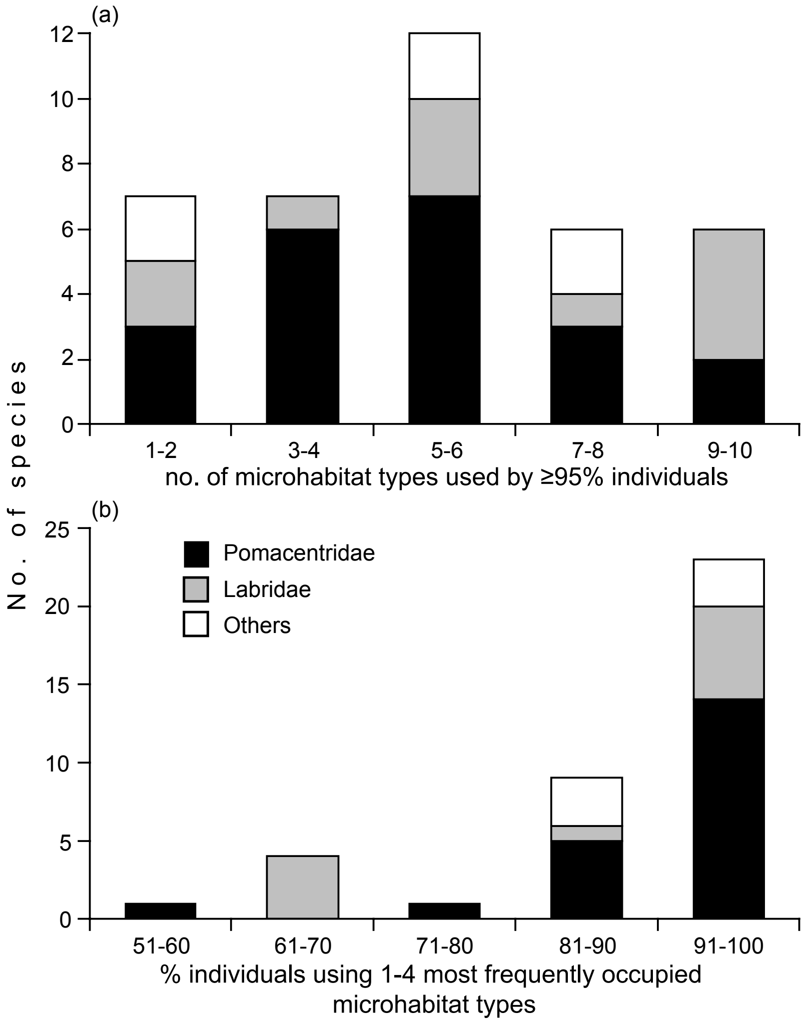


Figure 3.1: The level of microhabitat specialisation of 38 species shown as the frequency (number of species) at which: (a) different numbers of microhabitat categories are used by ≥95% of individuals; and (b) different percentages of individuals occupy the most commonly used microhabitat categories (maximum = 4).

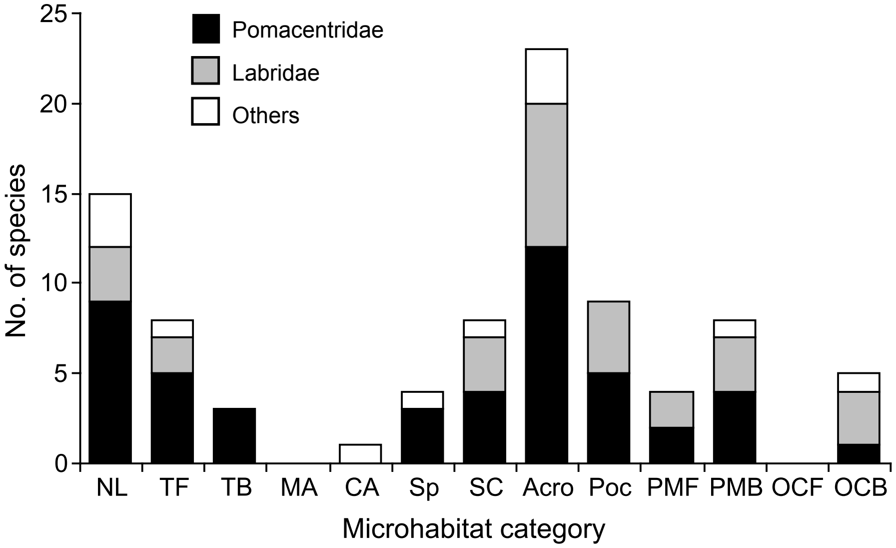


Figure 3.2: The number of species (out of 38) that used each microhabitat category more than expected based on the availability of those microhabitats. Microhabitat categories: NL = non-living substrata (bare rock, rubble and sand), TF = flat surfaces covered in algal turf, TB = branching structures (including dead branching coral) covered in algal turf, MA = macro-algae, CA = crustose coralline algae, Sp = sponges, SC = soft corals, Acro = live corals of the family Acroporidae, Poc = live corals of the family Pocilloporidae, PMF = live corals of the genera *Porites* and *Montipora* with massive or encrusting growth forms, PMB = live corals of the genera *Porites* and *Montipora* with branching, plating or foliose growth forms, OCF = other live corals with massive or encrusting growth forms, OCB = other live corals with branching, plating or foliose growth forms.

Table 3.1: Summary of microhabitat specialisation and preference for 38 species, showing the total number of individuals surveyed (N), the total number of microhabitat categories used (NM), the index of specialisation (SI), the combination of depth/zone and reef position used in resource selection ratio calculations (depth, reef position is platform unless indicated by 'Fr' for fringing reef, and reef zone is windward unless indicated by 'B' for back/leeward), and whether each microhabitat category was used more (+) or less (-) frequently than expected based on its availability, or used in proportion to its availability (NS). 0 = microhabitat not used. Microhabitat categories: NL = non-living substrata (bare rock, rubble and sand), TF = flat surfaces covered in algal turf, TB = branching structures (including dead branching coral) covered in algal turf, MA = macro-algae, CA = crustose coralline algae, Sp = sponges, SC = soft corals, Acro = live corals of the family Acroporidae, Poc = live corals of the family Pocilloporidae, PMF =, live corals of the genera *Porites* and *Montipora* with massive or encrusting growth forms, PMB = live corals of the genera *Porites* and *Montipora* with branching, plating or foliose growth forms, OCF = other live corals with massive or encrusting growth forms, OCB = other live corals with branching, plating or foliose growth forms.

Family/Species	N	NM	SI	depth	NL	TF	TB	MA	CA	Sp	SC	Acro	Poc	PMF	PMB	OCF	OCB
Pomacentridae																	
Amblyglyphidodon curacao	919	8	0.53	2	-	0	-	0	0	NS	+	+	0	-	NS	NS	0
Amblyglyphidodon leucogaster	440	5	0.48	10	0	0	0	0	0	+	NS	+	NS	0	0	0	NS
Chromis retrofasciata	382	11	0.60	10	-	-	-	-	0	-	-	+	+	-	NS	0	NS
Chromis ternatensis	394	4	0.35	6	0	0	-	0	0	0	-	+	0	0	+	0	0
Chromis viridis	683	5	0.06	2	0	0	-	0	0	0	-	+	0	0	-	-	0
Chrysiptera cyanea	1239	10	0.46	0	+	+	-	-	0	0	NS	-	-	-	+	0	NS
Chrysiptera parasema	1588	11	0.23	10	-	-	-	-	0	-	-	+	+	-	-	0	-
Chrysiptera rollandi	3102	13	0.25	6	+	-	-	-	-	-	-	-	-	-	-	-	-
Chrysiptera talboti	971	12	0.71	2	+	NS	-	-	-	-	NS	-	0	-	NS	-	+
Dascyllus melanurus	362	2	0.06	2B	0	0	0	0	0	0	0	+	+	0	0	0	0
Neoglyphidodon nigroris	415	13	0.93	2	+	+	-	-	-	NS	NS	NS	NS	-	+	NS	NS
Neopomacentrus azysron	1086	10	0.74	2(Fr)	0	-	+	0	0	+	+	+	-	+	NS	-	-
Plectroglyphidodon lacrymatus	203	11	0.62	0	+	+	-	NS	-	0	NS	-	-	-	NS	0	NS
Pomacentrus adelus	647	13	0.51	0	+	-	-	-	0	0	0	-	-	-	0	0	NS
Pomacentrus aurifrons	1732	11	0.58	2B	-	-	+	0	-	-	NS	+	+	-	+	0	NS
Pomacentrus bankanensis	401	7	0.44	0	+	+	-	-	-	0	0	0	0	-	-	0	0
Pomacentrus burroughi	600	8	0.41	6	+	NS	-	-	0	0	0	-	0	-	-	0	-
Pomacentrus lepidogenys	481	12	0.73	2	-	-	-	-	-	0	+	+	NS	NS	NS	-	NS

Table 3.1 (cont.)

Family/Species	N	NM	SI	depth	NL	TF	TB	MA	CA	Sp	SC	Acro	Poc	PMF	PMB	OCF	OCB
Pomacentridae																	
Pomacentrus moluccensis	2779	9	0.26	2	0	-	-	0	0	0	-	+	+	-	NS	-	NS
Pomacentrus nigromanus	1356	11	0.95	10	-	NS	-	NS	0	+	+	+	0	+	-	NS	NS
Pomacentrus simsiang	1067	11	0.72	2(Fr)	+	+	+	-	0	-	0	-	-	-	-	-	-
Labridae																	
Diproctacanthus xanthurus	118	9	0.68	10	0	-	-	-	0	NS	0	+	NS	-	+	0	+
Halichoeres argus	111	8	0.52	0	+	NS	-	0	0	0	NS	0	NS	-	NS	0	NS
Halichoeres chloropterus	846	10	0.24	2(B)	+	NS	-	-	0	-	0	-	0	-	NS	-	-
Halichoeres melanurus	4103	13	0.97	2(B)	-	NS	-	NS	-	NS	+	+	+	+	+	NS	NS
Halichoeres purpurescens	1623	13	0.95	10	-	+	-	-	-	-	NS	+	NS	+	NS	NS	+
Labrichthys unilineatus	541	12	0.94	2	0	0	0	0	0	0	-	+	+	-	-	0	-
Labroides dimidiatus	138	6	0.31	2	NS	NS	-	0	NS	NS	NS	+	NS	NS	+	NS	NS
Oxycheilinus celebicus	180	12	0.91	10	-	NS	-	NS	0	NS	NS	+	NS	NS	NS	NS	+
Paracheilinus filamentosus	712	7	0.50	10	+	+	-	NS	0	0	0	-	0	-	0	0	-
Thalassoma hardwicke	2445	12	0.64	0	-	-	-	-	-	0	+	+	+	-	NS	-	NS
Thalassoma lunare	2327	12	0.66	2	-	-	-	-	0	0	+	+	+	NS	-	-	-
Chaetodontidae																	
Chaetodon baronessa	128	3	0.06	2	0	0	0	0	0	0	0	+	NS	-	0	0	0
Chaetodon octofasciatus	312	2	0.04	2(Fr)	0	0	-	0	0	0	0	+	NS	-	-	0	-
Acanthuridae																	
Ctenochaetus binotatus	69	7	0.60	6	+	NS	-	0	0	0	NS	NS	0	NS	NS	0	0
Ctenochaetus strigosus	158	10	0.78	2	+	NS	NS	0	NS	0	NS	NS	0	-	NS	0	NS
Ctenochaetus tominiensis	614	11	0.78	6	+	+	-	-	-	NS	-	NS	0	-	+	0	NS
Serranidae																	
Pseudanthias tuka	500	6	0.68	10	0	0	0	0	+	+	+	+	0	-	0	0	+

3.4.2 Spatial patterns in recruitment among reef zones

When the positions and reef zones of peak recruitment were examined for 70 species, the number of species increased with increasing distance from shore, from just 9 species with peak recruitment on the fringing reefs to 37 species with peak recruitment on the 'far' platform reefs (Fig. 3.3). There was a hump shaped relationship for the depth/zone of peak recruitment, with the highest number of species (24) with peak recruitment at a depth of 2 m on the windward slope, and just 9 species with peak recruitment at depths of 10 m (windward slope) and 2 m on the leeward slope (Fig. 3.3). There were no obvious family-level differences in the large-scale spatial pattern in peak recruitment.

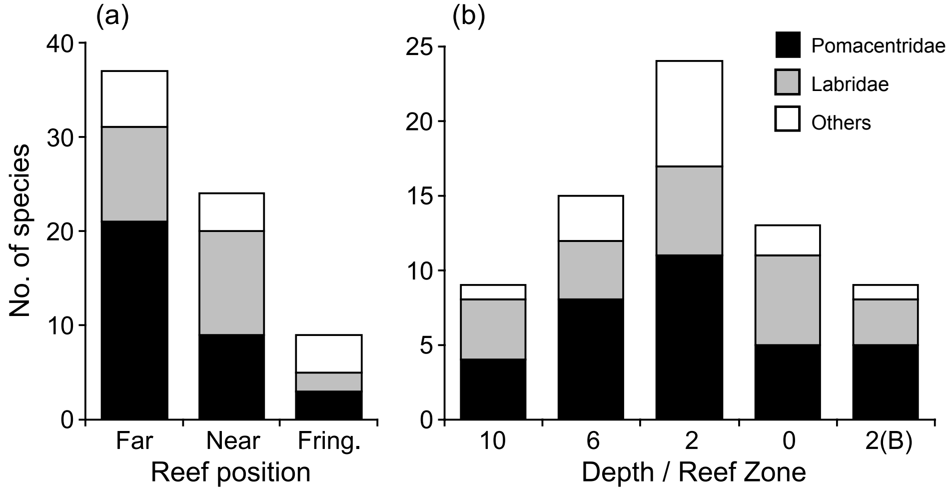


Figure 3.3: Summary of spatial recruitment data for 70 species, showing number of species with the highest densities of recruits at: (a) each reef position or distance from shore, and (b) each depth/reef zone.

Species that were abundant at both platform and fringing reefs were found at shallower depths on the fringing reefs compared to the platform reefs. For example, densities of *Chrysiptera parasema* and *Pomacentrus nigromanus* were greatest at 6m on the fringing reefs, compared with a depth of 10m on the platform reefs (Fig. 3.4), and *Halichoeres purpurescens* was most abundant at 10m on the 'near' platform reefs and at 6m on the fringing reefs (Fig. 3.5). There were also several species, for example, *Dascyllus melanurus* and *Halichoeres*

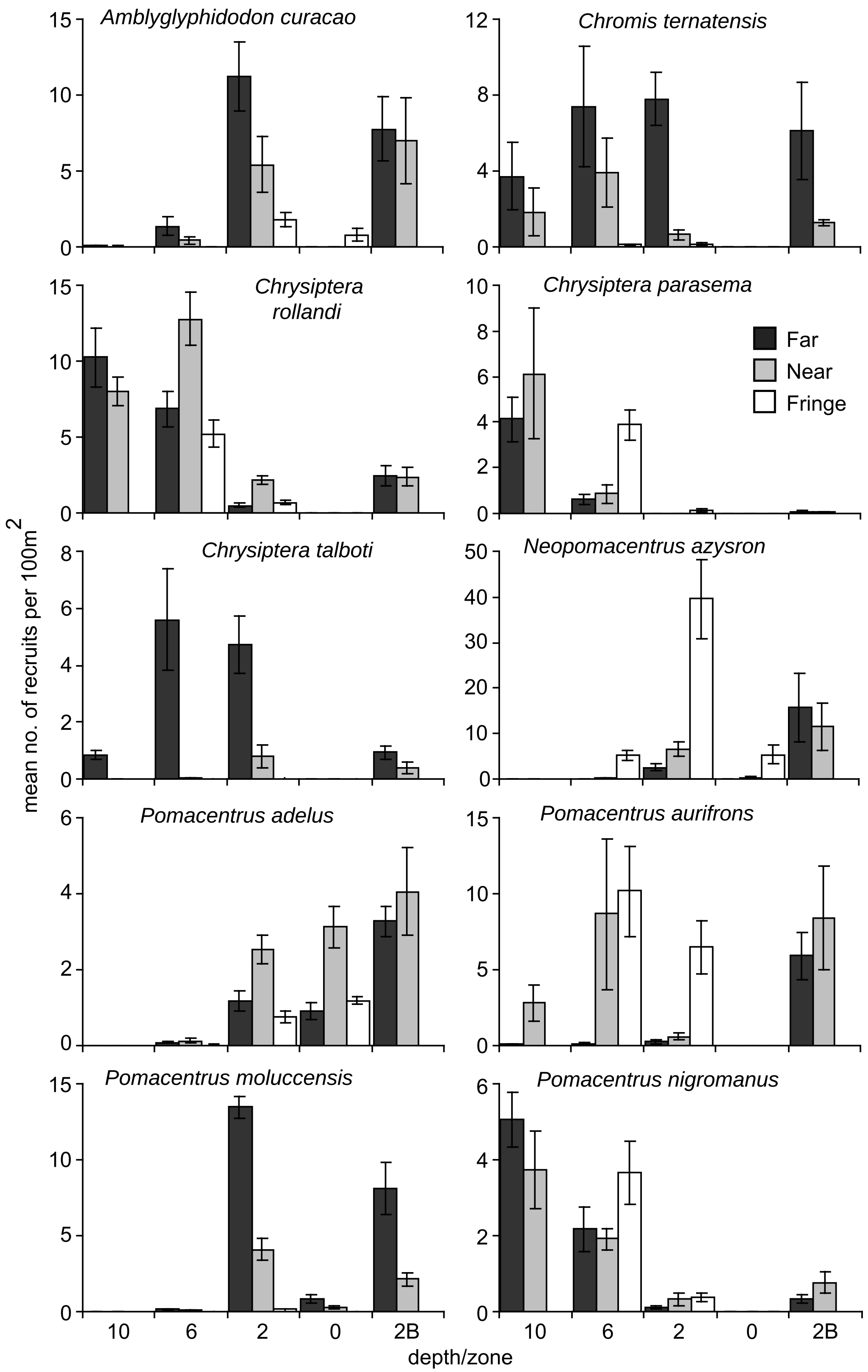


Figure 3.4: Mean recruit densities of the 10 most abundant damselfish species at each position and depth/reef zone. 2B = 2m on leeward side. Error bars = 1SE.

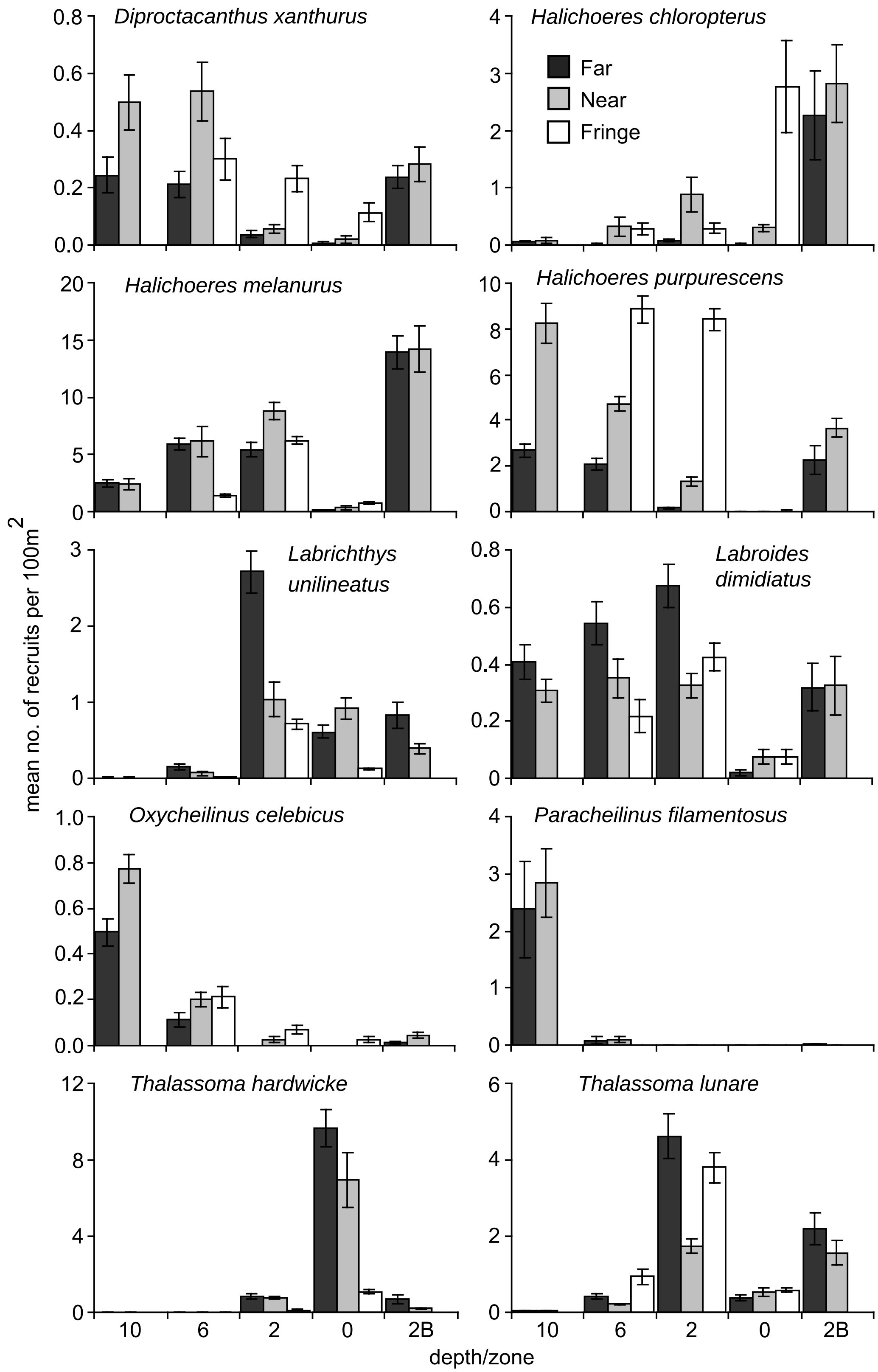


Figure 3.5: Mean recruit densities of the 10 most abundant damselfish species at each position and depth/reef zone. 2B = 2m on leeward side. Error bars = 1SE

chloropterus (Figs. 3.4 and 3.5) that only settled on the leeward sides of the platform reefs and on the fringing reefs

Family level

The summed abundances of the 10 most abundant damselfish and wrasse species made up 80% and 96% of the total abundance of each family respectively (among the 70 species with total recruit abundance ≥ 24), therefore these species were considered to represent a significant proportion of each family. Multivariate regression tree analyses for the damselfishes and wrasses resulted in modal tree sizes of 15 and 14 leaves, explaining 84% and 94% of the variation in the data, respectively (Figs. 3.6 and 3.7). In each of the two families, the largest percentage of the variance was explained by depth/reef zone (damselfishes: 44%, wrasses: 63%), followed by position (damselfishes: 10%, wrasses: 15%), and only a small percentage was explained by microhabitat (damselfishes: 7%, wrasses: 4%, Figs. 3.6 and 3.7). In both trees, the first two splits were determined by depth/reef zone, and these two splits together explained 41% and 54.5% of the variance in the damselfish and wrasse data, respectively (Figs. 3.6 and 3.7; Table 3.2). In both cases, the first two splits describe differences in the spatial data among: 10 and 6 m depths, 2 m (both windward and leeward), and reef flats (Figs. 3.6 and 3.7).

In the damselfish tree, the 10 and 6m depths were separated from the shallower depths in the first split. This split was influenced most strongly by *Chrysiptera rollandi* (most abundant at depths of 10 and 6m), *Neopomacentrus azysron* and *Pomacentrus adelus* (both most abundant at the shallower depths, Table 3.2a, Fig. 3.4). The second split separated the 2 m depths (both windward and leeward sides) from the reef flat, with *Pomacentrus adelus* (the most abundant damselfish on the reef flat) contributing the most to this split (Table 3.2a, Fig. 3.4). In the wrasse tree, the reef flat was first separated from the other depths, a split that was influenced mostly by *Thalassoma hardwicke* (most abundant on the reef flat), and by *Halichoeres melanurus* and *Halichoeres purpurescens* (both rarely seen on the reef flat, Table 3.2b, Fig. 3.5). The 10 and 6 m depths were then separated from

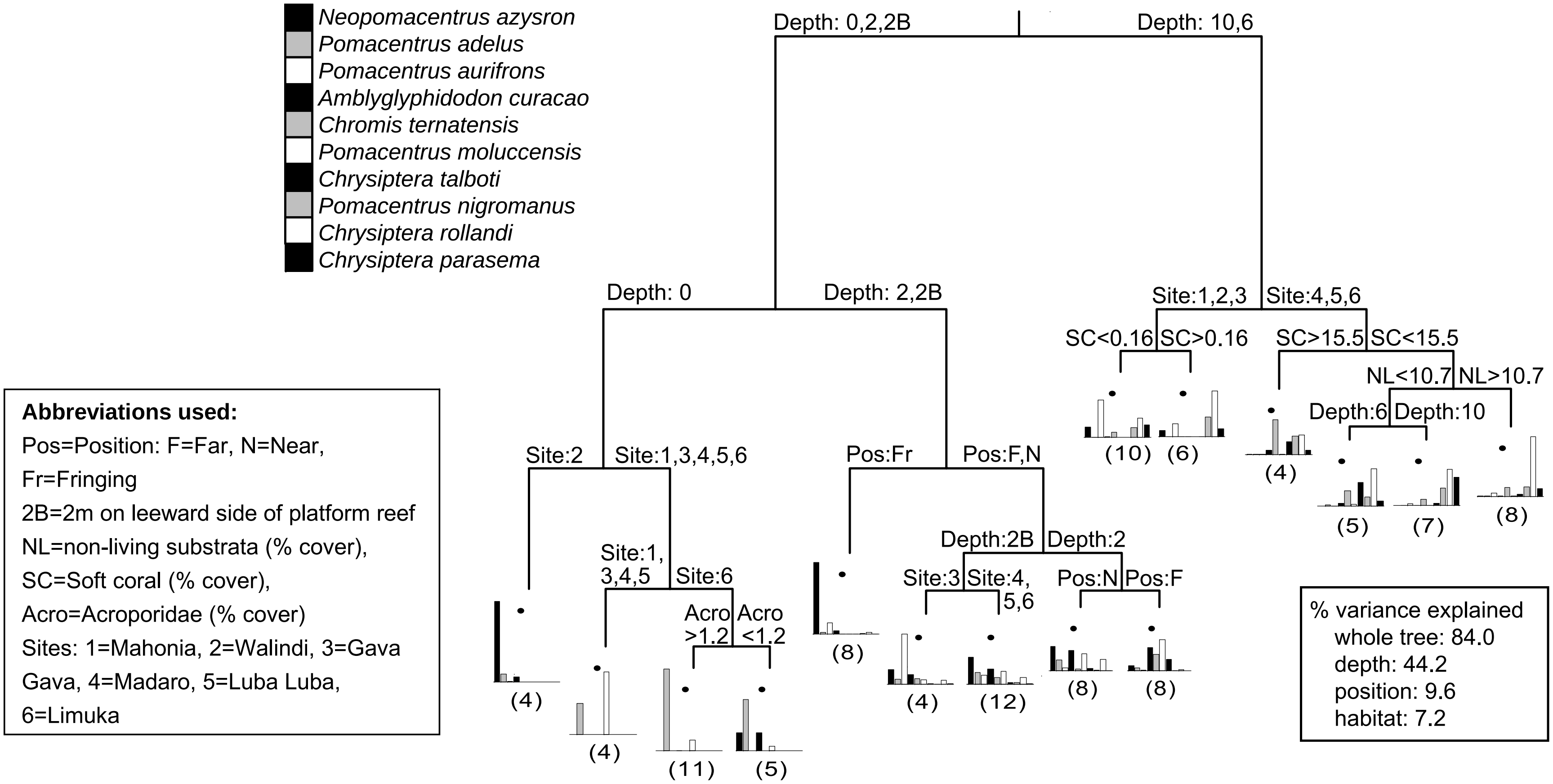


Figure 3.6: Multivariate regression tree for the spatial recruitment data of the 10 most abundant damselfish species. The bar plots show the relative abundance of the 10 species at each node, indicated using cyclical shading (black, grey and white) running from left to right, and the numbers in brackets are the numbers of replicates in each group.

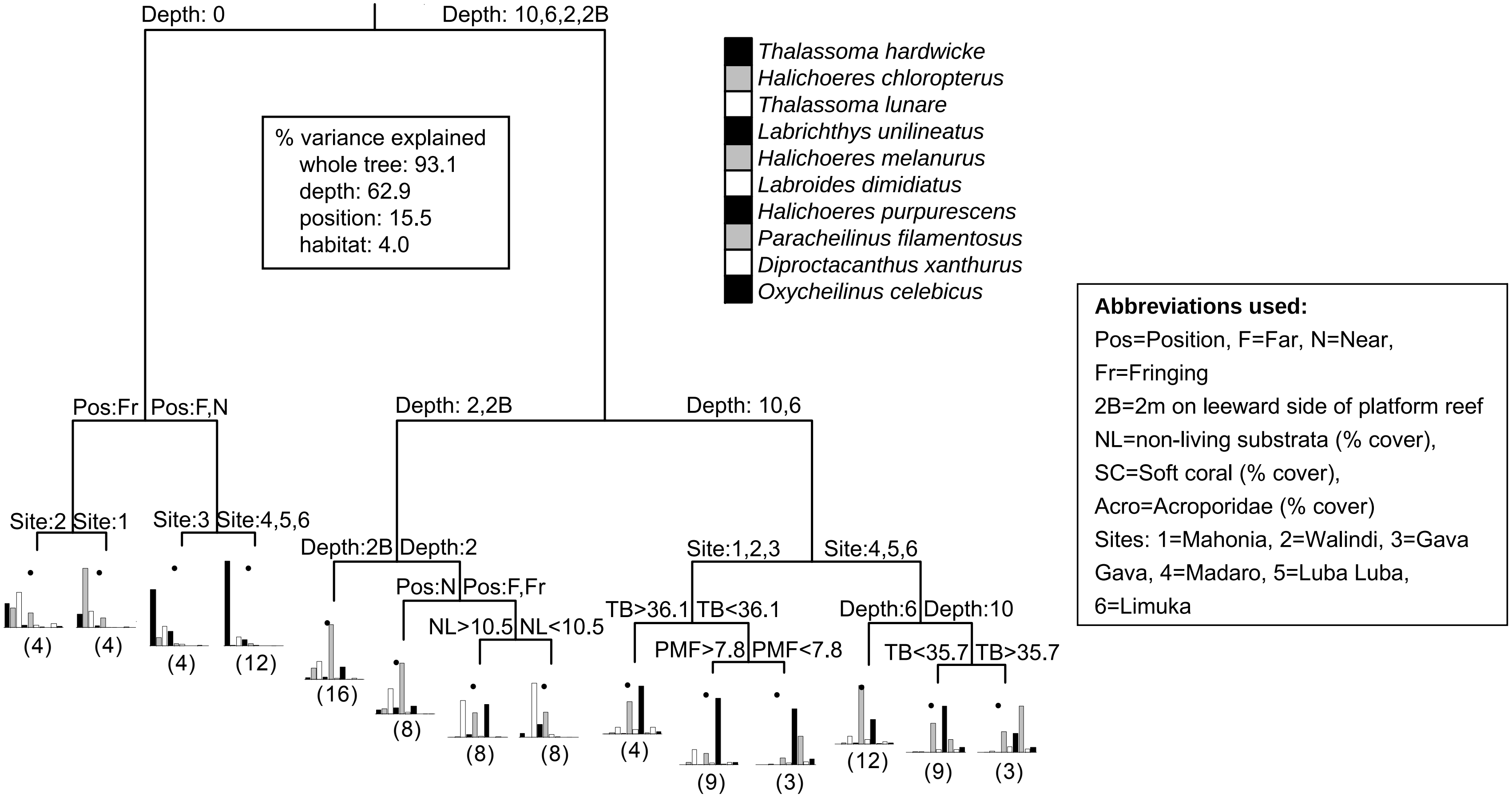


Figure 3.7: Multivariate regression tree for the spatial recruitment data of the 10 most abundant wrasse species. The bar plots show the relative abundance of the 10 species at each node, indicated using cyclical shading (black, grey and white) running from left to right), and the numbers in brackets are the numbers of replicates in each group.

Table 3.2: Summary of the splits in the multivariate regression tree for (a) the Pomacentridae and (b) the Labridae, showing the total percentage of the variation explained by each split, and the contribution of each species to each split. Abbreviations used in this table include the following: Pos = Position, F = Far, N = Near, Fr = Fringing, 2B = 2m on leeward side of platform reef, Acro = Acroporidae % cover, SC = soft coral % cover, NL = non-living substrata % cover. Sites: 1 = Mahonia Fringe, 2 = Walindi Fringe, 3 = Gava Gava, 4 = Madaro, 5 = Luba Luba, 6 = Limuka. The first four splits and the major contributions to each of these splits are highlighted.

(a) Pomacentridae

Split order	Nature of split	*A. cura*	*C. tern*	*C. para*	*C. roll*	*C. talb*	*N. azy*	*P. ad*	*P. au*	*P. mol*	*P. nig*	Split total
1	**Depth: 2,0,2B vs 10,6**	0.93	0.27	1.24	**9.88**	0.08	**4.24**	**5.55**	0.27	1.95	1.44	**26.85**
2	**Depth: 0 vs 2,2B**	0.59	0.23	0.00	0.16	0.06	0.90	**12.43**	0.64	0.04	0.00	**15.04**
4	**Pos: Fr vs F,N**	0.47	0.14	0.00	0.05	0.04	**6.54**	0.10	0.00	0.68	0.00	**8.02**
7	Depth: 2B vs 2	0.19	0.03	0.00	0.00	0.10	0.24	0.03	0.91	0.53	0.00	2.03
12	Pos: N vs F	0.01	0.31	0.00	0.15	0.12	0.53	0.10	0.01	0.31	0.00	1.54
7	Site: 3 vs 4,5,6	0.03	0.00	0.00	0.01	0.00	0.18	0.05	1.85	0.08	0.00	2.21
3	**Site: 2 vs 1,3,4,5,6**	0.00	0.00	0.00	0.00	0.00	**7.08**	**3.90**	0.00	0.48	0.00	**11.47**
5	Site: 1,3,4,5 vs 6	0.04	0.00	0.00	0.00	0.00	0.04	2.04	0.00	3.33	0.00	5.45
7	Acro>1.2 vs <1.2	0.41	0.00	0.00	0.00	0.00	0.41	1.12	0.00	0.05	0.00	1.99
6	Site: 1,2,3 vs 4,5,6	0.01	0.38	0.02	0.55	0.24	0.24	0.00	2.48	0.00	0.00	3.92
7	SC<0.16 vs >0.16	0.00	0.03	0.02	0.98	0.00	0.02	0.00	0.81	0.00	0.14	2.00
11	SC>15.5 vs <15.5	0.01	0.75	0.13	0.88	0.03	0.00	0.00	0.00	0.00	0.05	1.86
13	NL<10.7 vs >10.7	0.00	0.00	0.21	0.92	0.15	0.00	0.00	0.01	0.00	0.03	1.32
14	Depth: 6 vs 10	0.01	0.08	0.60	0.00	0.47	0.00	0.00	0.00	0.00	0.08	1.25
	Tree total	2.70	2.22	2.22	13.58	1.29	20.42	20.32	6.98	7.45	1.74	83.95

Table 3.2 (cont.)

(b) Labridae

Split order	Nature of split	*D. xan*	*H. chl*	*H. mel*	*H. purp*	*L. uni*	*L. dim*	*O. cel*	*P. fil*	*T. hard*	*T. lun*	Split total
1	**Depth: 2,0,2B vs 10,6**	0.01	1.00	**7.82**	**6.19**	0.08	0.02	0.02	0.16	**24.86**	0.04	**40.19**
3	**Pos: Fr vs F,N**	0.01	**3.05**	0.23	0.00	0.08	0.00	0.00	0.00	7.72	0.45	**11.54**
9	Site: 1 vs 2	0.01	1.37	0.02	0.00	0.00	0.00	0.00	0.00	0.09	0.30	1.78
11	Site: 3 vs 4,5,6	0.00	0.07	0.00	0.00	0.09	0.00	0.00	0.00	1.04	0.14	1.34
2	**Depth: 2,2B vs 10,6**	0.05	0.18	0.87	**7.60**	0.21	0.02	0.08	0.68	0.05	**4.77**	**14.50**
5	Depth: 2B vs 2	0.00	0.31	1.72	0.01	0.10	0.00	0.00	0.00	0.01	1.78	3.93
7	Pos: N vs F,Fr	0.00	0.04	1.49	0.19	0.01	0.00	0.00	0.00	0.01	0.92	2.66
8	NL>10.5 vs <10.5	0.00	0.00	0.00	1.75	0.19	0.00	0.00	0.00	0.03	0.51	2.48
4	**Site: 1,2,3 vs 4,5,6**	0.00	0.00	**2.97**	**3.10**	0.00	0.01	0.00	0.10	0.00	0.14	**6.34**
5	Depth: 6 vs 10	0.00	0.00	2.48	0.60	0.00	0.00	0.04	1.05	0.00	0.12	4.29
9	TB<35.7 vs >35.7	0.00	0.00	0.07	0.73	0.00	0.01	0.00	1.06	0.00	0.00	1.86
12	TB>36.1 vs <36.1	0.02	0.00	0.65	0.33	0.00	0.01	0.00	0.05	0.00	0.03	1.10
13	PMF>7.8 vs <7.8	0.00	0.00	0.02	0.12	0.00	0.00	0.01	0.73	0.00	0.19	1.07
	Tree total	0.10	6.02	18.34	20.62	0.76	0.07	0.15	3.83	33.81	9.39	93.08

the 2 m depths (both windward and leeward) in the second split, which was influenced mostly by *H. purpurescens* (most abundant at depths of 6 and 10 m) and *Thalassoma lunare* (most abundant at a depth of 2 m, Table 3.2b, Fig. 3.5).

In the damselfish tree, the third split separated the reef flats by site, between one of the fringing reef sites (Walindi) and the other 5 sites (Fig. 3.6). The fourth split separated the 2m depths by position, between the fringing reefs and the platform reefs (both 'far' and 'near', Fig. 3.6). Both of these splits were strongly influenced by *Neopomacentrus azysron* (Table 3.2a), which was most abundant at a depth of 2m on the fringing reef sites (Fig. 3.4), and the Walindi fringing reef was the only site where this species was abundant on the reef flat. The species that contributed the most to the whole-tree variance were *Pomacentrus adelus*, *N. azysron* and *Chrysiptera rollandi* (Table 3.2a).

In the wrasse tree, the third split separated the reef flats by position, between the fringing reef sites and the platform reefs (both 'far' and 'near', Fig. 3.7). This split was mostly influenced by *Thalassoma hardwicke* (most abundant on the platform reef flats) and *Halichoeres chloropterus* (abundant on the fringing reef flats, Table 3.2b, Fig. 3.5). The fourth split divided the 10m and 6m depths according to site, with the fringing reefs and the closest of the 'near' platform reefs (Gava Gava) in one group and the other 'near' platform reef (Madaro) and the two 'far' platform reefs in the other (Fig. 3.7). *Halichoeres melanurus* and *H. purpurescens* contributed the most to this split (Table 3.2b), with the latter species occurring in greater densities at the first group of sites, and the former species occurring in greater densities in the second group of sites. *Thalassoma hardwicke*, *H. purpurescens* and *H. melanurus* contributed the most to the whole-tree variance (Table 3.2b).

Species level

Regression trees explained significant variation in the spatial distributions of 36 of the 38 species. For 31 of the 36 species, the first split in the univariate regression tree was determined by depth (Table 3.3). These 31 species included 16 of the 20 damselfishes, 10 of the 11 wrasses, 1 of the 2 butterflyfishes and the 3

Table 3.3: Summary of univariate regression trees for 36 species, showing the size and percentage of the variation explained by the final tree, as well as the strength and nature of the first two splits of each tree. The nature of the first two splits is described by the factor causing the split (i.e. Position, Depth and Site) as well as the level(s) of that factor where the species is most abundant. The following abbreviations are used: (i) Position: F = Far, N = Near Fr = Fringing; (ii) Depth: number is depth in metres, B = leeward side (back) of platform reef; (iii) Sites: 1 = Mahonia Fringe, 2 = Walindi Fringe, 3 = Gava Gava, 4 = Madaro, 5 = Luba Luba, 6 = Limuka; (iv) Microhabitats: TF = algal turf (flat surface), TB = algal turf (branching), Acro = Acroporidae.

		tree		First split:		Second split:	
Family/Species	N	size	% var	determined by	% var	determined by	% var
Pomacentridae							
Amblyglyphidodon curacao	5735	3	71.2	Depth (2,2B)	60.6	Site (4,5,6)	10.6
Amblyglyphidodon leucogaster	976	3	86.3	Depth (10,6)	43.2	Site (6)	43.2
Chromis retrofasciata	901	3	73.9	Depth (10,6)	39.2	Position (F)	35.7
Chromis ternatensis	5284	3	36.0	Position (F)	18.9	Depth (10,6,2,2B)	17.1
Chrysiptera cyanea	1691	3	84.1	Depth (0)	45.7	Site (4,5)	38.4
Chrysiptera parasema	2541	4	76.1-	Depth (10,6)	53.8	Depth (10)/Site (1,2,4)	10.2/12.1
Chrysiptera rollandi	8208	3	80.2	Depth (10,6)	69.1	Depth (2,2B)	11.1
Chrysiptera talboti	2143	3	71.1	Position (F)	36.3	Depth (6,2)	34.8
Dascyllus melanurus	634	5	77.8	Depth (2B)	33.4	Site (3)/10,6,2,0 – Site (1)	17.3/16.5
Neoglyphidodon nigroris	646	3	63.2	Depth (2)	31.6	Position (F)	31.6
Neopomacentrus azysron	13983	9	85.7	Depth (2,2B)	45.3	10,6,0 – Position (Fr)	15.6
Plectroglyphidodon lacrymatus	346	3	85.1	Depth (0)	74.8	Site (1,3,4)	10.3
Pomacentrus adelus	2760	8	90.0	Depth (2,2B,0)	58.5	Site (4)	15.1
Pomacentrus aurifrons	6946	9	74.5	Depth (6,2B)	23.3	Site (1,3)	21.2
Pomacentrus bankanensis	439	3	94.1	Depth (0)	47.0	Site (4,5,6)	47.0
Pomacentrus burroughi	1896	7	87.7	Site (1,3)	32.5	Depth (10,6,2,2B)	28.8
Pomacentrus lepidogenys	512	3	56.5	Depth (2)	28.3	Position (F)	28.3
Pomacentrus moluccensis	4703	5	87.5	Depth (2,2B)	53.8	Site (4,5,6)	27.9
Pomacentrus nigromanus	2927	2	67.2	Depth (10,6)	67.8		

Table 3.3 (cont.)

				First split:		Second split:	
Family/Species	N	tree size	% var	determined by	% var	determined by	% var
Pomacentridae							
Pomacentrus simsiang	1817	8	95.7	Pos (Fr)	63.1	Depth (2)	10.7
Labridae							
Diproctacanthus xanthurus	444	2	37.2	Depth (10,6,2B)	37.2		
Halichoeres argus	298	2	42.1	Depth (0)	42.1		
Halichoeres chloropterus	1622	4	58.5	Depth (2B)	29.6	Site (1)/Depth (0)	12.3/15.6
Halichoeres melanurus	10843	5	86.9	Depth (6,2,2B)	56.8	Depth (2B)	11.6
Halichoeres purpurescens	6796	7	89.1	Depth (10,6,2,2B)	48.9	Position (N,Fr)	20.1
Labrichthys unilineatus	1210	5	81.6	Depth (2,0,2B)	40.1	Depth (2)/Position (F)	18.1/18.1
Labroides dimidiatus	650	5	60.0	TF (<16.8)	36.7	Acro (<8.1)	12.2
Oxycheilinus celebicus	315	3	82.4	Depth (10)	72.8	Depth (2)	9.6
Paracheilinus filamentosus	871	2	70.6	Depth (10)	70.6		
Thalassoma hardwicke	3231	9	96.3	Depth (0)	67.2	Site (4,5,6)	18.2
Thalassoma lunare	6816	8	90.3	Depth (2,2B)	67.5	Depth (6,0)	7.9
Chaetodontidae							
Chaetodon baronessa	334	2	33.4	Depth (2)	33.4		
Chaetodon octofasciatus	817	3	50.3	Position (Fr)	29.0	Depth (6,2)	21.4
Acanthuridae							
Ctenochaetus binotatus	293	3	38.2	Depth (6,2,2B)	24.0	Site (3)	14.2
Ctenochaetus strigosus	408	2	25.7	Depth (6,2,2B)	25.7		
Ctenochaetus tominiensis	1304	7	79.1	Depth (10,6)	27.2	TB (>34.2)	25.3

surgeonfishes (Table 3.3). Position determined the first tree split for 2 of the damselfish species (*Chromis ternatensis* and *Chrysiptera talboti*) both most abundant on the 'far' platform reefs (Fig. 3.5) and 1 butterflyfish, *Chaetodon octofasciatus*, which was most abundant on the fringing reefs. Site determined the first split for one damselfish species, *Pomacentrus burroughi* (Table 3.3), which was most abundant on one of the fringing reefs and one of the 'near' platform reefs. Microhabitat availability determined the first two splits for the cleaner wrasse, *Labroides dimidiatus* (Table 3.3), with the availability of turfing algae (flat surface) and Acroporid corals determining the first and second split respectively. When the total percentage variance explained by each factor was summed for each modal tree size and averaged across the 36 trees, depth explained the greatest amount of the variance (47%), position and site explained 26.5% and 21% of the variance respectively, and microhabitat availability (for all microhabitat types) explained the least amount of variance (14%). Regression tree analysis did not explain any of the variance in the spatial data for 2 of the 38 species, *Chromis viridis* and *Pseudanthias tuka*, probably due to their patchy spatial distributions.

3.4.3 Specialisation, the availability of preferred microhabitats and the distribution and abundance of recruits

The total abundance of recruits was not significantly correlated with the index of microhabitat specialisation, i.e. microhabitat specialists did not tend to be less abundant than generalists (Fig. 3.8a). In fact, several of the species which used just 3-4 microhabitats were among the most abundant species, e.g., *C. rollandi*, *P. moluccensis* and *C. parasema* were the 3rd, 10th and 14th most abundant species respectively. There was also no significant correlation between the indices of microhabitat and macrohabitat specialisation (Fig. 3.8b), that is, microhabitat specialists did not have more restricted spatial distributions than microhabitat generalists. The total abundance of recruits was not significantly correlated with the index of macrohabitat specialisation either (Fig. 3.8c). That is, species with restricted spatial distributions were not less abundant than those with broad spatial distributions. Again, there were no family-level distinctions in the relationships among recruit abundance, microhabitat and macrohabitat versatility.

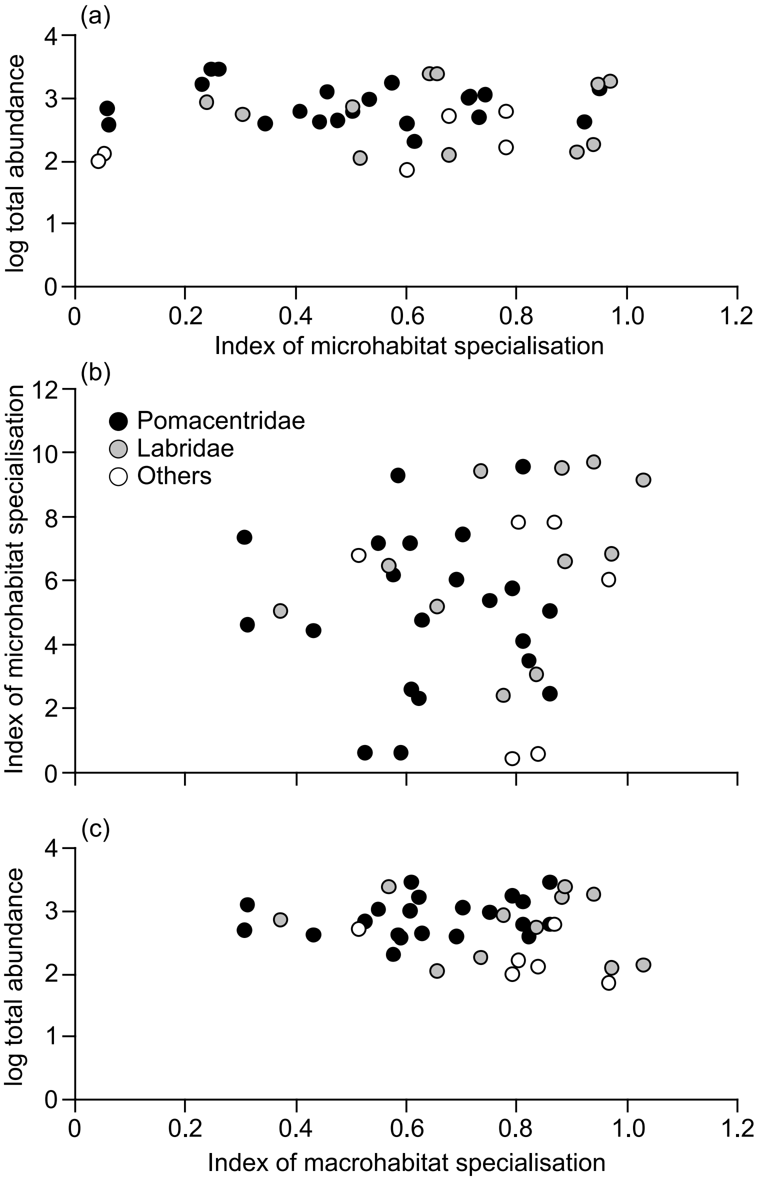


Figure 3.8: Scatterplots between: (a) total abundance (log transformed) and the index of microhabitat specialisation; (b) the index of microhabitat specialisation and the index of macrohabitat specialisation; and (c) total abundance (log transformed) and the index of macrohabitat specialisation. Each point represents a species.

There was a significant positive correlation between recruit density and the availability of preferred microhabitats within preferred depths/zones for just 10 of the 38 species. These included 2 damselfishes, *Chrysiptera talboti* (*r* = 0.356, *P* = 0.045) and *Pomacentrus burroughi* (*r* = 0.237, *P* = 0.010), 4 wrasses, *Diproctacanthus xanthurus* (*r* = 0.276, *P* = 0.016), *Labrichthys unilineatus* (*r* = 0.232, *P* = 0.034), *Paracheilinus filamentosus* (*r* = 0.513, *P* = 0.003) and *Thalassoma hardwicke* (*r* = 0.605, *P* < 0.001), 2 surgeonfishes, *Ctenochaetus binotatus* (*r* = 0.310, *P* = 0.004) and *C. tominiensis* (*r* = 0.395, *P* = 0.001), *Chaetodon baronessa* (*r* = 0.439, *P* = 0.005) and *Pseudanthias tuka* (*r* = 0.357, *P* = 0.002). There was a negative correlation between recruit density and microhabitat availability for one damselfish, *Neoglyphidodon nigroris* (*r* = -0.524, *P* < 0.001).

3.5 Discussion

This study revealed a high level of specialisation at the recruitment stage in the Kimbe Bay reef fish community, not only in the use of microhabitats, but also in the distribution of species across reef zones and down depth profiles. The majority of individuals in most of the species examined used a small proportion of the entire range of microhabitats occupied by the few more generalist species. There was also a high degree of partitioning among depths and reef zones, and, to a lesser extent, among reefs found at different distances from shore. However, the distinct large-scale spatial distributions were not explained by the availability of preferred microhabitats for most species. In addition, variation in the magnitude of recruitment among fish species could not be explained by the degree of specialisation on either micro- or macrohabitats (i.e. distances from shore, reef zones and depths). That is, specialists were not consistently less or more abundant than habitat generalists. Within preferred depths, spatial variation in the abundance of a significant fraction of species (~25%) could be explained by the availability of their preferred substrata. These results suggest that even in communities primarily composed of highly specialised species, the factors affecting the distribution and abundance of recruits are likely to be numerous and complex.

3.5.1 Microhabitat specialisation

This study adds to a growing number of studies indicating that many coral reef fishes recruit to a limited range of microhabitat types (Sale et al. 1984, 2005; Booth and Beretta 1994; Tolimieri 1995, 1998a, b; Holbrook et al. 2000; Shima 2001). It is likely that these specialised microhabitat associations are explained by settlement cues for particular substrata (Sale et al. 1984; Öhman et al. 1998). However, observed patterns are likely to be reinforced in species that also preferentially settle with conspecific juveniles (Sweatman 1985; Jones 1987b; Booth 1992; Forrester 1995; Öhman et al. 1998; Tolimieri 1998b; Lecchini, Planes et al. 2005; Lecchini, Shima et al. 2005). Observed patterns are also likely to be reinforced by early post settlement survival, for species in which juveniles grow and survive better on their preferred substrata (Jones 1997; Munday 2001; Caley and Munday 2003).

Clearly not all coral reef substrata represent good recruitment habitat. A large proportion of species in Kimbe Bay were predominantly associated with living corals as recruits, and among these, there were strong associations with *Acropora*, *Pocillipora* and other complex branching species. Massive and encrusting corals were generally avoided. Different fish species tended to specialise on different branching coral types. There was also a significant number of species disproportionately associated with dead coral, rubble and sand habitats. These different recruit microhabitat requirements will have important implications for how coral reef fish communities respond to habitat degradation, with some species likely to increase and others likely to decline in response to declining coral cover (Jones et al. 2004 – Appendix III; Bellwood et al. 2006). The potential impacts of coral loss on each species will depend upon which coral genera are lost and what the coral is replaced with (e.g. macroalgae, bare rock or rubble). At this stage, the ability of species to change recruitment habitat when preferred microhabitats disappear is unknown.

3.5.2 Macrohabitat specialisation: depth, reef zone and reef position

The regression tree analysis of larger scale recruitment patterns showed that depth and reef zone were critical in explaining the structure of recruit assemblages in Kimbe Bay, with most species primarily recruiting to a narrow range of depth strata. On average, depth/zone explained 47% of the spatial variation in the recruitment of common fish species. The composition of recruit assemblages also varied in relation to reef position or distance from shore. However, microhabitat availability explained very little of the larger scale variation in recruit abundance, suggesting that other factors are responsible for limiting spatial distributions on these coral reefs. These patterns confirm other studies showing that depth-related settlement patterns (Wellington 1992; Jones 1997; Srinivasan 2003) or other large-scale spatial patterns (Tolimieri 1995, 1998b; Caselle and Warner 1996; Jones 1997; Ault and Johnson 1998; Sale et al. 2005) are often independent of microhabitat requirements. For example, settlement of *Dascyllus melanurus* (Srinivasan 2003), *Stegastes leucostictus* and *S. variabilis* (Wellington 1992), was restricted to particular depths even when suitable microhabitats were available at other depths. For the same species, placing juveniles at depths outside, or at the extremes of the normal depth range at settlement resulted in reduced survival and growth, indicating that there are costs to recruiting outside preferred depth strata (Wellington 1992; Jones 1997; Srinivasan 2003).

In other studies, large-scale patterns in recruit abundance have been linked to microhabitat availability (e.g. Tolimieri 1998a, b; Schmitt and Holbrook 2000). It is likely that large-scale patterns in recruitment along typical coral reef gradients, whether driven by settlement or early post-settlement processes, are likely to be determined by many interacting factors that ultimately need to be identified using multifactorial experiments (Jones 1991; Shima 2001). In this study, the cleaner wrasse, *Labroides dimidiatus*, was the only species for which microhabitat explained a large proportion of the spatial variance in recruitment. Paradoxically, this species was one of the least specialised in terms of microhabitat use. It seems likely that the microhabitat types that influenced the first two splits in the regression tree for this species were surrogates for some other unmeasured habitat variable.

3.5.3 Microhabitat availability and spatial variation in abundance

Within preferred depth strata or reef zones, the abundance of recruits of only a quarter of the species was positively related to the availability of preferred microhabitats. The availability of preferred microhabitats is probably only one of several factors which may explain spatial variation in recruitment within macrohabitats. Indeed, during periods of high recruitment, new recruits appeared to occupy less preferred microhabitats in greater densities (Srinivasan, personal observation).

It is possible that the low number of statistically significant correlations between abundance and microhabitat availability may be the result of the large size of the sampling units used ($100m^2$ transects), which may incorporate a mix of microhabitat types. Microhabitat availability might have greater importance in determining recruit abundances at smaller spatial scales. For example, in studies where much smaller sampling units were used, the abundance of recruits over small spatial scales was related to microhabitat availability (Tolimieri 1995; 1998a; Caselle and Warner 1996). However, our results indicate that the spatial scale examined in this study was appropriate for roughly a quarter of the species examined (for which abundances were significantly correlated with microhabitat availability within their preferred depths and reef zones). The variation among species does highlight the importance of sampling at a variety of spatial scales.

Some of the unexplained patterns of distribution in this study might be related to horizontal habitat features, which were not measured. For example, some species tended to be more abundant on areas of high relief while others were more abundant in embayments, and some species were found mainly on areas of reef with vertical walls while others were only observed on more gently sloping areas of reef.

3.5.4 Habitat specialisation and the relative abundance of species

There were no clear differences between microhabitat specialists and generalists in terms of both their abundances and spatial distributions across broader habitat types (i.e. distances from shore, reef zones and depths). Species' abundances were also not related to the breadth of their spatial distributions. These results are contrary to predictions that specialists will either have lower abundances and/or narrower spatial distributions locally because they have access to a smaller proportion of recruitment sites (based on Brown 1984; McNally 1995; Morris 1996; Hughes 2000), or higher abundance and/or broader distributions because they are able to out-compete generalists by using resources more efficiently (Futuyma and Moreno 1988; Caley and Munday 2003).

3.5.5 Family-level differences in habitat specialisation – are wrasses and damselfishes different?

Unlike the notable differences between damselfish and wrasses in the temporal dynamics of recruitment (Chapter 2), the spatial variation in the patterns exhibited by these and other taxa were similar. That is, both families had representative species that were specialised on live branching coral, while others specialised on non-living substrata. Both families contained other species that had less specialised habitat requirements. In terms of larger-scale distributions, depth/zone was a critical factor in explaining the distribution and abundance of recruits of both damselfish and wrasses. Although wrasse species exhibit a greater range of maximum body sizes than damselfish (Choat and Bellwood 1991; Munday and Jones 1998), the larger wrasse species did not recruit in high numbers in this study. In the largest species, *Cheilinus undulatus*, recruitment appears to occur on non-reefal habitats (Dorenbosch et al. 2006). It appears likely that wrasses as a whole may exhibit a greater range and complexity in their habitat requirements at settlement. However for most small wrasse species and damselfish, the determinants of spatial patterns in recruitment are remarkably similar.

3.6.6. Geographic variation in habitat specialisation – are these results typical?

Depth may be a particularly important factor influencing recruitment on the steeply sloping platform reefs in very deep water that are typical of Kimbe Bay in Papua New Guinea. This was the first study to examine recruitment patterns of a large number of species across spatial gradients on these types of reefs. These reef formations do occur elsewhere in the Indo-Pacific, including the Great Barrier Reef. However, most of the studies on recruitment at higher latitudes have focused on variation across lagoonal systems (e.g. Lizard Island and One Tree Island, Williams and Sale 1981; Sale et al. 1984; Doherty 1991). Very few studies have examined recruitment across depth gradients at other Indo-Pacific locations. For four of the wrasse species examined in this study, Green (1996) demonstrated differences in recruitment among the reef flat, reef base and sand flat habitats at several sites at Lizard Island. The depth ranges of the reef base and sand flat varied at each site, precluding anything more than a rough qualitative comparison here. Three of the species I examined appear to have narrower distributions at Kimbe Bay than at Lizard Island. At Kimbe Bay, *Halichoeres melanurus* was most abundant at depths of 2m and 6m and *Thalassoma lunare* was most abundant at 2m, while both species were most abundant at depths of 5-20m at Lizard Island. *Thalassoma hardwicke* recruits were most abundant on the reef flat and reef crest at Lizard Island, but only occupied a narrow area of the reef flat at Kimbe Bay. The fourth species *Labroides dimidiatus* had a relatively broad distribution among reef zones and depths at both locations. However, for a comprehensive comparison of the degree of spatial segregation in recruitment among locations at different latitudes, descriptions of spatial patterns of recruitment at similar types of reefs at higher latitude locations in this region are required.

Studies on Australia's Great Barrier Reef have shown that there are major differences in larval supply and recruitment across gradients of exposure, e.g. among the windward side, leeward side and lagoon at Lizard Island (e.g. Milicich et al. 1992, Milicich and Doherty 1994) and between the inside and outside of One Tree Lagoon (e.g. Doherty et al 1996). In both of these locations, there are major differences in the physical environment across the exposure gradient. In contrast, such differences in environmental conditions do not occur among the inshore reefs I sampled in Kimbe Bay. Nevertheless, there were still significant differences in recruitment among reefs different distances from shore and between the windward and leeward sides of reefs. This suggests that the high species diversity here may have resulted in finer spatial partitioning or that the recruitment rate differences associated with exposure gradients shown in other studies may not be the direct result of these local conditions.

3.6.7 Conclusions

The high level of specialisation on and partitioning of micro- and macrohabitats has important implications for how reef fish communities are structured, and how this structure will change in response to habitat degradation. The independence of microhabitat specialisation, and broad scale patterns of distribution and abundance suggest that the spatial structure of reef fish communities will be explained by a complex interplay of factors. Depth stands out as a major factor structuring these communities, and the underlying basis of depth-related patterns is experimentally investigated in Chapter 4. The availability of preferred habitats alone does not explain the spatial variation in recruitment, although it is certainly a contributing factor for many species. However, while microhabitat availability may not explain broad spatial patterns, whether recruitment is modified over time through habitat loss is another issue. Patterns of recruitment are likely to be extremely susceptible to disturbances that cause a loss of particular microhabitats that are preferred by the majority of species, such as branching corals. Community-wide recruitment will also be susceptible to disturbances that impact in other ways on particularly important shallow depth strata (0 – 2m). The longer-term consequences of habitat change are examined in Chapter 5.

CHAPTER 4: DEPTH DISTRIBUTIONS OF CORAL REEF FISHES: THE INFLUENCE OF MICROHABITAT STRUCTURE, SETTLEMENT, AND POST-SETTLEMENT PROCESSES [2]

4.1 Abstract

Many coral reef fishes have restricted depth ranges that are established at settlement or soon after, but the factors limiting these distributions are largely unknown. This study examines whether the availability of microhabitats (reef substrata) explains depth limits, and evaluates whether juvenile growth and survival are lower beyond these limits. Depth-stratified surveys of reef fishes at Kimbe Bay (Papua New Guinea) showed that the abundance of new settlers and the cover of coral substrata differed significantly among depths. A field experiment investigated whether settling coral reef fishes preferred particular depths, and whether these depth preferences were dependent on microhabitat availability. Small patch reefs composed of identical coral substrata were set up at five depths (3, 6, 10, 15 and 20 m), and settlement patterns were compared to those on unmanipulated reef habitat at the same five depths. For all species, settlement on patch reefs differed significantly among depths despite uniform substratum composition. For four of the six species tested, depth-related settlement patterns on unmanipulated habitat and on patch reefs did not differ, while for the other two, depth ranges were greater on the patch reefs than on unmanipulated habitat. A second experiment examined whether depth preferences reflected variation in growth and survival when microhabitat was similar. Newly settled individuals of *Chrysiptera parasema* and *Dascyllus melanurus* were placed, separately, on patch reefs at five depths (as above) and their survival and growth monitored. *D. melanurus*, which is restricted to shallow depths, had highest survival and growth at the shallowest depth. Depth did not

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[2] Publication: **Srinivasan M** (2003) Depth distributions of coral reef fishes: the influence of microhabitat structure, settlement, and post-settlement processes. Oecologia 137:76-84 (Appendix II)

affect either survival or growth of *C. parasema*, which has a broader depth range than *D. melanurus* (between 6 and 15 m). This suggests that the fitness costs potentially incurred by settling outside a preferred depth range may depend on the strength of the depth preference.

4.2 Introduction

Among the most conspicuous patterns in nature are the changes in community structure and the limited distributions of species along environmental gradients such as altitude and depth. Both terrestrial and aquatic ecologists have investigated the factors that influence the distribution of species along these gradients and define the upper and lower limits of species' distributions (e.g. Connell 1961; Tranquillini 1979; Longhurst 1985; Hawkins 1999; Prenda and Gallardo-Mayenco 1999; Mark et al. 2001). These distributions can be influenced by a variety of physical and biological factors that covary along gradients, and it is often difficult to isolate the effects of any one factor. Hence few studies have attempted to do this (but see Connell 1961; Grosberg 1982; La Peyre et al. 2001).

Changes in community structure on steep environmental gradients are often attributed to changes in physical conditions. Along altitudinal gradients, high altitudes are generally associated with harsher environmental conditions and the upper limits of species distributions are frequently determined by their ability to tolerate these conditions (Whittaker and Niering 1965; Terborgh 1971; Hawkins 1999; Mark et al. 2001). Similarly, in intertidal habitats upper limits typically are controlled by species' tolerance to environmental factors such as desiccation and heat, while lower limits are influenced by biotic factors such as competition and predation (Connell 1961). One of the most important gradients for both freshwater and marine organisms is depth. In contrast to altitudinal and intertidal gradients, it is the lower limits of species' distributions along depth gradients that are likely to be controlled by physical factors such as pressure, low temperatures and low light intensity, while upper limits may be influenced by biotic interactions associated with greater diversity in shallow water.

On coral reefs, a large component in the spatial variation in fish community structure can be explained by depth (Choat and Bellwood 1985; Russ 1984; McGehee 1994; Meekan et al. 1995). Depth distributions may be established at settlement, either by physical processes and/or behaviour influencing the vertical distribution of larval fishes (Leis 1991b; Doherty and Carleton 1997; Leis and Carson-Ewart 2000), or by larvae selecting particular microhabitats and depths at settlement (Leis and Carson-Ewart 2002; Leis *et al* 2002). Habitat selection can occur at broad spatial scales (e.g., among reefs or among reef zones; Doherty et al 1996; Shima 1999; Wilson 2001) as well as at fine scales (e.g., among substratum types or microhabitats; Eckert 1985; Danilowicz 1996; Öhman et al. 1998; Shima 2001). Habitat choice can also be influenced, either positively or negatively, by the presence of resident conspecifics (Sweatman 1985; 1988; Jones 1987b; Booth 1992; Forrester 1995; Öhman et al. 1998) or heterospecifics (Shulman et al. 1983; Jones 1987b; Öhman et al. 1998). These fine-scale factors covary with depth, making it difficult to separate the influences of depth, microhabitat, and resident fishes.

Patterns of distribution at settlement can be either reinforced or disrupted by post-settlement survival rates (Jones 1997). For example, juveniles of a few species have been shown to have higher rates of survival at their preferred depths (Jones 1986; Wellington 1992), which would reinforce settlement distribution patterns. In addition, interspecific variation in depth ranges may be associated with variation in the effect of depth on post-settlement fitness traits (e.g., survival and growth). For example, species with narrow depth ranges may survive and grow better within their normal depth range than outside it, while the fitness traits of species with large depth ranges may be affected less by position along the gradient. The relationship between depth preferences and the fitness costs associated with settling outside preferred depth ranges has not yet been examined for coral reef fishes.

In this chapter, I examined, over a relatively broad depth range (3-20 m), the potential influence of depth preferences at settlement on patterns of distribution, and whether depth preferences were dependent on microhabitat structure. I investigated natural depth-related settlement patterns, microhabitat availability and microhabitat use. The effect of microhabitat structure was then removed experimentally to test the hypothesis that depth-related settlement patterns were dependent on the availability of preferred microhabitats. In a second experiment, I examined whether juvenile survival and growth also varied with depth on identical microhabitats. I tested the prediction that there are fitness costs, including reduced growth and life expectancy, associated with settling outside preferred depth ranges for two species.

4.3 Methods

4.3.1 Depth distribution of settlers on unmanipulated reefs

Patterns of distribution of newly settled fishes along a depth gradient were evaluated by conducting visual surveys on the leeward slopes of 2 inshore platform reefs in Kimbe Bay, Rakaru Diri and Madaro (Fig. 1.1), in June 1999. Both reefs are roughly oblong shaped, with their long axis running parallel to the coast, and are approximately 1km apart. Both reefs are similar distances (~500 m) from shore and are similar lengths (~300 m) but Diri Reef is approximately twice the width of Madaro Reef (~200 m compared to ~100 m). The reef flats of both reefs are usually exposed at low tide, and coral cover on the leeward slopes of these reefs generally extends down to 25-30 m. Surveys were conducted at 5 depths: 3, 6, 10, 15 and 20 m. I chose 20m as the maximum depth as I had observed little change in community structure beyond this depth and, in addition, there was often no solid substratum beyond 25-30 m on the leeward reef slopes surveyed. At each depth, I laid four 50 m x 2 m belt transects over areas of continuous reef and counted all non-cryptic, easily identifiable juveniles within each transect, estimated their size and recorded the microhabitats they occupied. I then used a cut-off size to separate settlers aged 0-2 weeks from older juveniles. Cut-off sizes varied among species and were based on observations of settlement sizes and growth of fishes that settled to natural patch reefs adjacent to the experimental patch reefs during 1999.

Separate one-way ANOVAs with post-hoc comparisons were used to test for differences in mean abundance of settlers among depths for each of the six most abundant species. These included four damselfishes (Pomacentridae: *Amblyglyphidodon curacao*, *Chrysiptera parasema*, *Dascyllus melanurus*, *Pomacentrus nigromanus*), one wrasse (Labridae: *Halichoeres melanurus*) and one butterflyfish (Chaetodontidae: *Chaetodon octofasciatus*). Data for *A. curacao*, *C. parasema*, *P. nigromanus* and *H. melanurus* were transformed to $\log_{10}(x+1)$ and data for *D. melanurus* were transformed to $\sqrt{(x+0.5)}$ to meet the assumption of equal variances in ANOVA.

4.3.2 Microhabitat availability and microhabitat use

To determine the availability of microhabitats (i.e. substrata) at each depth, benthic surveys were conducted using four 50 m transects at the same 5 depths on the same two reefs. I randomly marked 100 points on each 50 m transect tape, and recorded substrata directly under each of these points to obtain an estimate of percent cover per transect for each microhabitat. Substrata were grouped into seven broad categories: (1) non-living substrata (which included bare rock/dead coral, rubble and sand), (2) algae (including turf, crustose coralline algae and all macroalgae), (3) sponges, (4) soft corals (including gorgonians and anemones), (5) hard corals of the genus *Acropora*, (6) hard corals of the genus *Porites*, and (7) all other hard corals. Separate one-way ANOVAs were used to test for differences in mean percent cover of each microhabitat category among depths. Data for *Acropora* and *Porites* were transformed to $\log_{10}(x+1)$ to meet the assumptions of equal variances in ANOVA.

Data on microhabitat use by fishes from the surveys on unmanipulated habitat were used to compare microhabitat specificity among the 6 most abundant species of fish (see above). Additional data from several other surveys of newly settled fishes conducted during 1999 and 2000 (see Chapter 3) were added to increase the sample size for each species to 100 or more individuals. I calculated the percentages of fish of each species occupying each of the broad microhabitat categories above, with an additional category for fish that swim in schools and are not closely associated with any substrata.

4.3.3 Experiment 1: Is depth at settlement determined by microhabitat availability?

To separate effects of depth from microhabitat availability, five replicate patch reefs with similar microhabitats were constructed at each of five depths. The patch reefs were established on a sandy slope on the leeward side of Rakaru Diri, the larger of the two inshore platform reefs where surveys were conducted. This sandy area was approximately 70 m wide, extending from the reef flat down to the seafloor, and was bordered on each side by continuous reef. Patch reefs (~1m diameter) were placed 8-10 m apart and were constructed using a base of dead coral boulders and rubble, with live corals arranged on the boulders. The coral species used were *Acropora echinata*, *A. granulosa*, *Anacropora* sp., *Echinopora horrida*, *Pachyseris foliosa*, *Pavona cactus*, *Pocillopora verrucosa* and *Porites cylindrica*. These species were chosen in order to provide a combination of deep-water and shallow-water corals of a variety of growth forms. They were also species that I had observed to be settlement microhabitats of many species of fish.

Patch reefs were monitored every 3 to 4 days and all newly settled fishes were counted and removed each time. To minimise post-settlement mortality due to predation, all demersal predators were removed from patch reefs and from natural patch reefs at the edge of the sandy area, and there was sufficient coral to provide shelter to newly settled fishes. The experiment was run four times: (1) 6-weeks during April-May 1999 (period 1); (2) 10-weeks during September-November 1999 (period 2); (3) 6 weeks during March-April 2000 (period 3); and (4) 8 weeks during September-November 2000 (period 4). During periods 3 and 4, this experiment was run concurrently with a second experiment (see below), and resident juveniles of *C. parasema* and *D. melanurus* were present on the patch reefs. Coral species composition of patch reefs during periods 3 and 4 was different to that during periods 1 and 2 (see below).

I tested if the depth-related settlement patterns of each species were consistent among experimental periods using a 2-way ANOVA, with depth and period as factors (all 3-4 day surveys of patch reefs pooled within each experimental period). As the abundance of settlers differed substantially among the four periods, I used proportions rather than absolute abundances (i.e., number of settlers to each reef divided by the total number of settlers of that species observed in that period across all depths and replicates). Proportions were converted to a more appropriate scale for analysis using $\sqrt{x}$ transformation. A separate ANOVA was used for each of the 6 species mentioned above and an additional damselfish, *Pomacentrus amboinensis*, for which juveniles were not observed during the survey on un-manipulated habitat. If there was no interaction between depth and experimental period, a one-way ANOVA (using absolute abundances, with data from all 3-4 day surveys and all four experimental periods combined), with post-hoc comparisons, was used to test for differences in mean abundance of settlers among depths for each species. If necessary, data were transformed to either $\log_{10}(x+1)$ or $\sqrt{x}$ to meet the assumption of equal variances in ANOVA.

To determine whether depth ranges at settlement were influenced by microhabitat availability, depth distributions on unmanipulated habitat and on the experimental patch reefs were compared using a separate 2-way ANOVA for each species, with unmanipulated/manipulated and depth as the factors. A significant interaction between the two factors would indicate that depth-related settlement patterns on the patch reefs were not consistent with depth-related settlement patterns on unmanipulated habitat. As data from the surveys and experiment were not scaled to one another, numbers of fish were standardised by dividing the number of fish in each transect or on each patch reef by the total number of fish observed (across all depths and replicates), and multiplying by the number of replicates at each depth (i.e., 8 for the survey data, 5 for the experimental data). These data were converted to a more appropriate scale for analysis using $\sqrt{x}$ transformation.

4.3.4 Experiment 2: Fitness costs of settling beyond preferred depth ranges

To determine if there are fitness costs of settling beyond preferred depth ranges, two fish species with contrasting depth preferences were placed on patch reefs at different depths and their survival and growth rates monitored. The two species chosen for this experiment were *D. melanurus*, which settled mostly to patch reefs at 3 m, and *C. parasema*, for which settlement rates were highest on patch reefs at 15 m. I predicted that survival and growth would be highest at the preferred depth for each species (i.e., 3 m for *D. melanurus*; 15 m for *C. parasema*; see Experiment 1 results below). In addition, I predicted that the broader preferred depth range of *C. parasema* might be explained by its ability to grow and survive over a greater range of depths than *D. melanurus*.

The same 25 patch reefs mentioned above were reconstructed using 4 coral species that *C. parasema* and *D. melanurus* usually settle into: *Acropora echinata*, *A. subglabra*, *A. granulosa*, *Pocillopora verrucosa*, with *Porites cylindrica* as a base. The experiment was run during two separate 6-week periods in 2000, during February-April for *C. parasema* and during September-November for *D. melanurus*. At the beginning of the experiment, newly settled fishes were collected and placed on patch reefs at a density of ten individuals per reef. This density was considerably lower than observed natural densities (e.g., up to 30 fish per patch reef) therefore I assumed that the effect of density on individual survival and growth would be minimal. Patch reefs were restocked each day for 4-5 days until numbers stabilised before the experiment was started. Patch reefs were cleared of all other fish prior to stocking them with *C. parasema* or *D. melanurus*. All fish were measured at the start of the experiment and again at the end of the 6-week period. The sizes of fish used ranged from 6.6 to 13 mm SL (mean=9.3 mm) for *C. parasema*, and from 7.0 to 14.2 mm SL (mean=10.0 mm) for *D. melanurus*. The mean size of individuals of each species per patch reef did not differ among depths at the start of the experiment. The number of fish on each patch reef was monitored every 3-4 days, and all new arrivals were recorded and removed. I was able to visually distinguish residents from newly settled conspecifics, as new settlers were smaller and differed slightly in colour.

For each patch reef, survival was calculated as the number of fish remaining at the end of the experiment (N_t) divided by the number of fish at the start of the experiment (N_o). Since many of the fish used were initially too small to be successfully tagged, it was not possible to determine individual growth rates.

Therefore, for each patch reef, a value for growth was obtained by calculating the difference between mean size per patch reef at the beginning and at the end of the experiment. Since the patch reefs were separated from each other and the adjacent reef by 8-10 m of sand, I assumed that they were sufficiently isolated to preclude movement of fish among them, particularly since *C. parasema* and *D. melanurus* both occupy live coral exclusively.

To help determine if any differences in growth rates could be attributed to temperature differences among depths, temperature was recorded at two depths (5 and 15 m) on the experimental site. A data logger set to record temperature every hour was placed at each depth between 16 November 2000 and 14 April 2001.

Separate one-way ANOVAs with planned comparisons were used to test for differences in mean survival and growth of each species among the 5 depths. Survival was converted to a more appropriate scale for analysis using $\sqrt{x}$ transformation. Planned comparisons were used to compare survival and growth of each species between its preferred depth and the other 4 depths (i.e. 3 m vs. other 4 depths for *D. melanurus*, 15 m vs. other 4 depths for *C. parasema*).

4.4 Results

4.4.1 Depth distribution of settlers on unmanipulated reefs

The mean abundance of settlers on unmanipulated habitat differed significantly among the 5 depths for all 6 species tested (Table 4.1a). *A. curacao* and *D. melanurus* had shallow distributions, with over 95% of settlers at 3 and 6 m, less than 5% at 10 m and none at 15 and 20 m (Fig. 4.1). Almost 90% of *C. parasema* settlers were at depths of 6 and 10m, and there were none at 3 m and 20 m (Fig. 4.1). *P. nigromanus* had a deeper distribution with 85% of settlers at 15 and 20 m and almost none at the two shallowest depths (Fig. 4.1). The two other species, *H. melanurus* and *C. octofasciatus*, had relatively broad depth ranges, with settlers present at all depths (except 20 m for *H. melanurus*), though *H. melanurus* was

Table 4.1: Summary of one-way ANOVAs and post-hoc comparisons of means for (a) the abundance of settlers on unmanipulated habitat at each depth surveyed and (b) the abundance of settlers on experimental patch reefs at each depth. Within a species, means at depths followed by the same letter did not differ significantly ($P<0.05$). To meet the assumption of equal variances in ANOVA, survey data for *Amblyglyphidodon curacao* and *Halichoeres melanurus,* and both survey and experimental data for *Chrysiptera parasema* and *Pomacentrus nigromanus* were transformed to $\log_{10}(x+1)$, and survey data for *Dascyllus melanurus* were transformed to $\sqrt{(x+0.5)}$.

	df effect	MS effect	*df* error	MS error	*F*	*P*	Summary of post-hoc comparisons				
(a) abundance of settlers on unmanipulated habitat (from surveys)											
Amblyglyphidodon curacao	4	0.42	35	0.13	3.16	0.026	3	6 a	10 a	15 a	20 a
Chrysiptera parasema	4	0.58	35	0.15	3.95	0.010	6 a	10 a	15 a,b	3 b	20 b
Dascyllus melanurus	4	6.14	35	1.32	4.66	0.004	3 a	6 a,b	10 b,c	15 c	20 c
Pomacentrus nigromanus	4	0.60	35	0.07	8.45	<0.001	20 a	15 a,b	10 b,c	6 c	3 c
Halichoeres melanurus	4	0.99	35	0.07	13.46	<0.001	3 a	6 a,b	10 b	15 b,c	20 c
Chaetodon octofasciatus	4	4.71	35	1.28	3.69	0.013	6 a	10 a,b	3 b,c	15 b,c	20 c
(b) abundance of settlers on experimental patch reefs											
Amblyglyphidodon curacao	4	3.66	20	0.46	7.91	0.001	3	6 a	10 a	15 a	20 a
Chrysiptera parasema	4	1.73	20	0.02	72.73	<0.001	3	6 a	20 a	10 b	15 b
Dascyllus melanurus	4	31.53	20	0.54	58.29	<0.001	3	6	10	15 a	20 a
Pomacentrus amboinensis	4	8.26	20	2.06	4.01	0.015	6 a	10 a,b	3 b	15 b	20 b
Pomacentrus nigromanus	4	0.45	20	0.04	11.77	<0.001	3 a	6 a	10 b	15 b	20 b
Halichoeres melanurus	4	169.30	20	22.64	7.48	0.001	6 a	10 a	3 a,b	15 b,c	20 c
Chaetodon octofasciatus	4	24.64	20	6.48	3.80	0.019	3 a	20 a,b	6 b	10 b	15

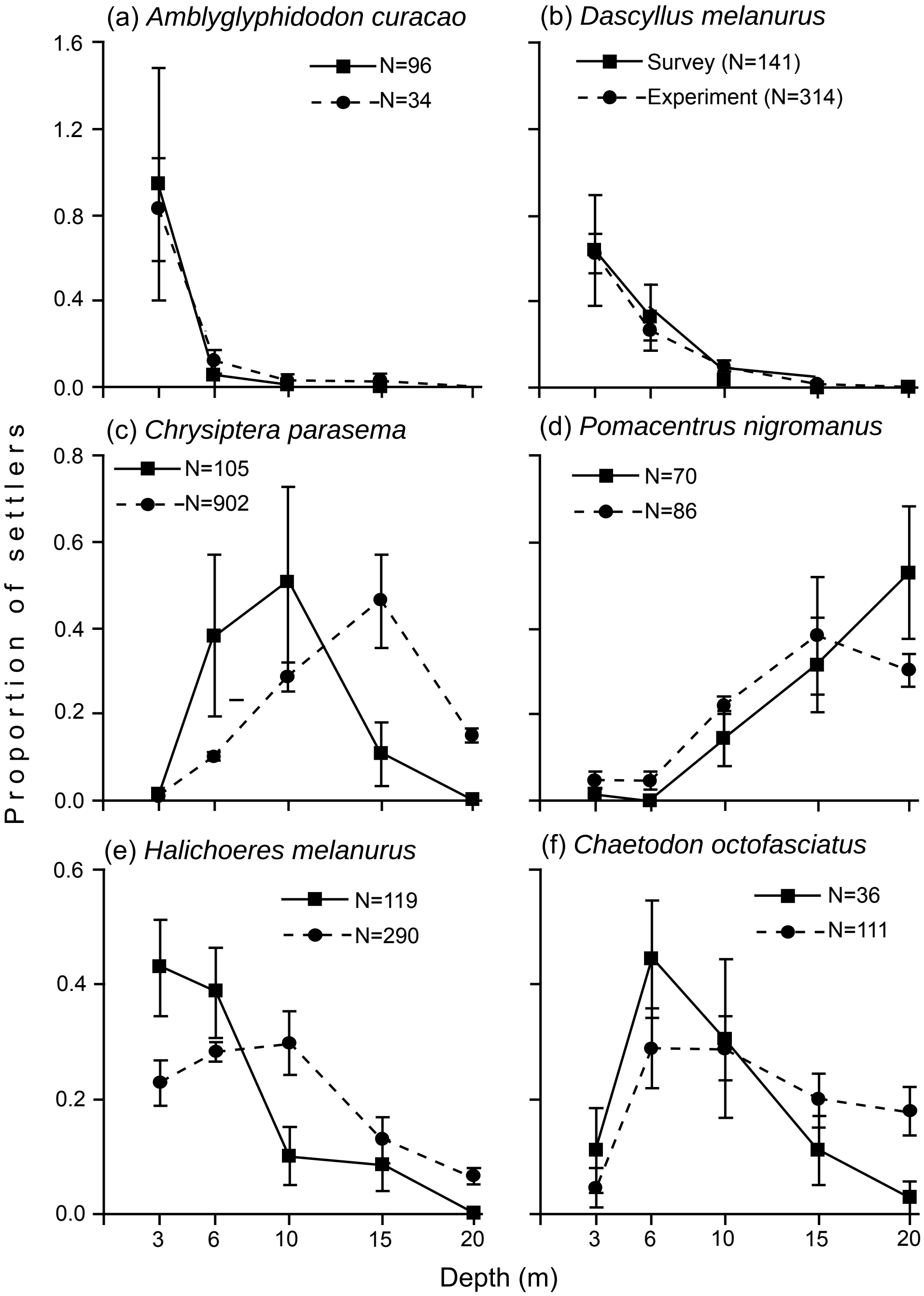

Figure 4.1: Settlement patterns of 6 species (a-f) among depths on unmanipulated habitat (—■—), estimated from visual surveys, and on experimental patch reefs (- -●- -) shown as the mean proportion of settlers per patch reef at each depth. N's give the total numbers of fish surveyed or that settled on patch reefs. Error bars are one standard error.

most abundant at 3 and 6 m (~80%), and *C. octofasciatus* was most abundant at 6 and 10 m (~75%, Fig. 4.1).

4.4.2 Microhabitat availability and microhabitat use

Percent cover of hard corals of the genera *Acropora* and *Porites* declined significantly with increasing depth (Fig. 4.2, Table 4.2), from roughly 3% cover of *Acropora* at 3 and 6 m to less than 1% at 20 m, and from 15% cover of *Porites* at 3 and 6 m to less than 3% at 20 m. For other hard corals, cover was highest at 10 m (26%), declining to 13-14% at 3 and 6 m, and to 17% at 20 m. There were no significant differences among depths for the other microhabitat categories (Fig. 4.2, Table 4.2).

Three of the 6 fish species, *C. parasema*, *D. melanurus* and *C. octofasciatus*, are live coral specialists, with 100% of settlers surveyed occupying live hard coral, usually of the genus *Acropora* (Table 4.3). Over 70% of *C. parasema* and *D. melanurus* settlers, and roughly 65% of *C. octofasciatus* settlers occupied species of *Acropora* of just two growth forms (corymbose and bottlebrush). Fifty percent of *A. curacao*, 55% of *P. nigromanus* and 64% of *H. melanurus* settlers occupied live coral, though these species appeared to be less selective of the species of coral occupied. These three species also occupied live substrata other than hard corals (e.g. sponges and soft coral). In addition, 10% of *A. curacao* settlers were in schools of juveniles, both conspecific and heterospecific, and not closely associated with any substrata, 20% of *P. nigromanus* settlers were found on turf-covered dead coral or rock, and 15% of *H. melanurus* settlers occupied areas of rubble and sand.

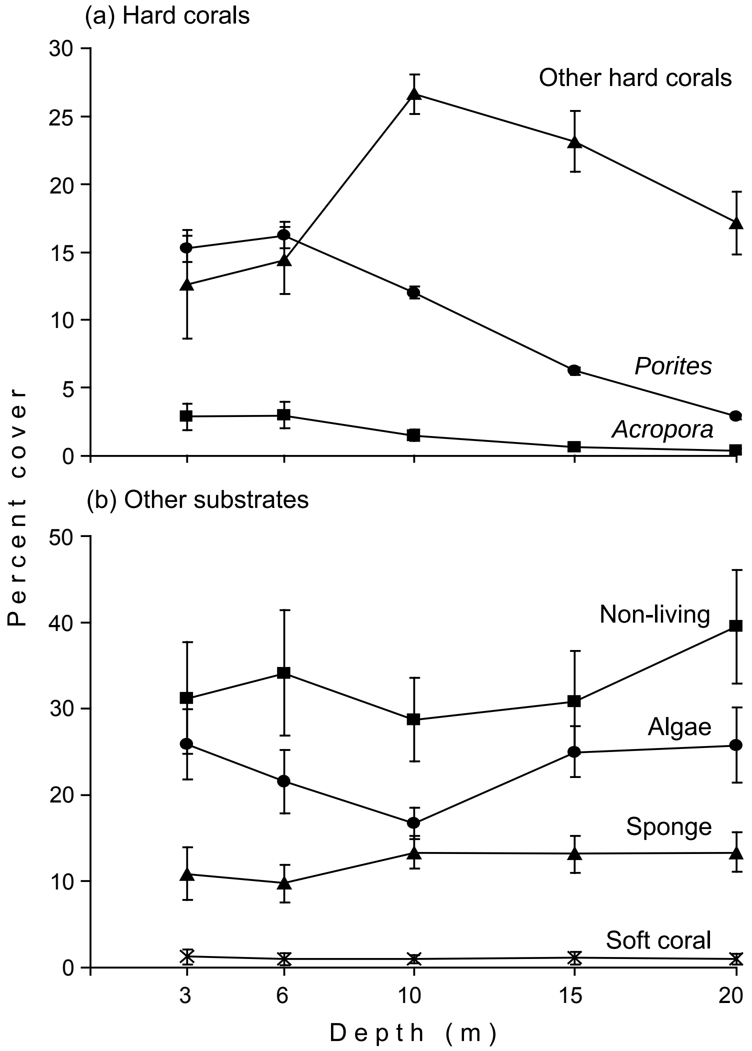

Figure 4.2: Percent cover of (a) hard corals of the genera Acropora and Porites, and all other genera combined, and (b) non-living substrata (bare rock/dead coral, rubble and sand), soft coral (including gorgonians and anemones), algae (crustose coralline algae, turf and macroalgae), and sponges at each depth. Error bars are 1SE.

Table 4.2: Summary of one-way ANOVAs and post-hoc comparisons of mean cover of microhabitats among depths. Within a microhabitat, means at depths followed by the same letter did not differ significantly (*P*<0.05).

	df effect	MS effect	*df* error	MS error	*F*	*P*	Summary of post-hoc comparisons				
Non-living	4	139.25	35	314.67	0.44	0.777	3 a	6 a	10 a	15 a	20 a
Algae	4	122.28	35	97.54	1.25	0.307	3 a	6 a	10 a	15 a	20 a
Sponge	4	22.65	35	44.49	0.51	0.729	3 a	6 a	10 a	15 a	20 a
Soft coral	4	0.10	35	3.67	0.03	0.999	3 a	6 a	10 a	15 a	20 a
Acropora	4	0.26	35	0.06	4.42	0.005	3 a	6 a	10 a,b	15 b	20 b
Porites	4	0.49	35	0.06	8.12	<0.001	3 a	6 a	10 a	15	20
Other hard coral	4	280.90	35	55.18	5.09	0.002	10 a	15 a,b	20 b,c	3 c	6 c

Table 4.3: Summary of microhabitat use by new recruits of each fish species, shown as the percentage of fish found in each of eight microhabitats.

	N	Not in any substrata	Non-living	Algae	Sponge	Soft coral	*Acropora*	*Porites*	Other hard coral
Amblyglyphidodon curacao	498	9.6	0.0	1.4	7.6	30.3	42.0	5.4	3.6
Chrysiptera parasema	391	0.0	0.0	0.0	0.0	0.0	99.5	0.0	0.5
Dascyllus melanurus	161	0.0	0.0	0.0	0.0	0.0	90.7	0.0	9.3
Pomacentrus nigromanus	136	0.0	1.5	19.9	11.8	11.8	19.1	11.8	24.3
Halichoeres melanurus	634	0.0	16.7	2.5	3.0	3.8	26.2	32.2	15.6
Chaetodon octofasciatus	146	0.0	0.0	0.0	0.0	0.0	89.7	2.7	7.5

4.4.3 Experiment 1: Is depth at settlement determined by microhabitat availability?

Settlement rates to identical patch reefs differed significantly among the 5 depths for all species tested (Table 4.1b). Therefore, there are microhabitat independent effects on the depth distributions of all species. The shapes of the depth distributions on experimental patch reefs were very similar to depth distributions on unmanipulated habitat (Fig. 4.1). Patterns of distribution among depths differed significantly between the experimental patch reefs and unmanipulated habitat for only two species, *C. parasema* and *H. melanurus* (2-way ANOVA interaction: $F_{4,55}$=2.647, *P*=0.043 for *C. parasema*, $F_{4,55}$=3.926, *P*=0.007 for *H. melanurus*). The depth distributions of both species extended deeper on the experimental patch reefs. The depth of greatest settlement for *C. parasema* was 15 m on the experimental patch reefs (46% of settlers), compared to 10 m on unmanipulated habitat (50%), and more fish settled at 20 m on the experimental patch reefs (15%) than on unmanipulated habitat (0%, Fig. 4.1). On unmanipulated habitat, *H. melanurus* settled mainly at 3 m and 6 m (80% of settlers), but on the experimental patch reefs settlement was roughly equal at 3, 6 and 10 m patch reefs (23, 28 and 30% respectively), and a higher proportion of fish settled deeper (7% at 20 m compared to 0% on unmanipulated habitat, Fig. 4.1).

The depth-related settlement patterns of the other four species did not differ between unmanipulated habitat and experimental patch reefs. The two shallow species settled mostly at 3 m and 6 m on the experimental patch reefs (94% of *A. curacao* and 88% of *D. melanurus*), *C. octofasciatus* settled mostly at 6 and 10 m (60% of settlers) and *P. nigromanus* settled mostly at 10 m and deeper (91%, Fig. 4.1).

There was no interaction between depth and experimental period for all 7 species tested, indicating that depth-related settlement patterns were consistent among experimental periods. That is, there was no temporal variation in depth-related settlement patterns, and the presence of juvenile *C. parasema* and *D. melanurus* residents during periods 3 and 4 respectively did not influence settlement patterns of either conspecifics or heterospecifics.

4.4.4 Experiment 2: Fitness costs of settling beyond preferred depth ranges

Survival of *D. melanurus* was significantly higher at 3 m than at the other 4 depths (Table 4.4, Fig. 4.3) with an average of 9 out of 10 fish per patch reef surviving to the end of the experiment, compared to averages of 6 to 7 at the other 4 depths. Growth of *D. melanurus* was also significantly higher at 3 m than at the other 4 depths (Table 4.4, Figure 4.3), with an average size difference of 10 mm at 3m compared to averages of 7 to 8 mm at the other 4 depths. Fish at 3 m ranged in size from 15.8 to 25.6 mm SL (average=20.3 mm), while fish at 20 m ranged in size from 9.9 to 21.5 mm (average=16.8 mm) at the end of the 6-week period. Neither survival nor growth of *C. parasema* was higher at 15 m than at the other 4 depths (Table 4.4, Fig. 4.3).

Table 4.4: Summary of one-way ANOVAs and planned comparisons of means for survival and growth at each depth for *Dascyllus melanurus* and *Chrysiptera parasema.*

	effect		error					
	df	MS	*df*	MS	*F*	*P*	Planned comparison	*P*
Survival								
C. parasema	4	0.26	20	0.19	1.38	0.278	15m vs. other 4 depths	0.133
D. melanurus	4	0.17	20	0.10	1.73	0.182	3 m vs. other 4 depths	0.021
Growth								
C. parasema	4	0.68	20	0.79	0.86	0.507	15m vs. other 4 depths	0.441
D. melanurus	4	7.50	20	1.28	5.88	0.003	3 m vs. other 4 depths	<0.001

Mean temperatures at 3 and 15m were very similar (31.4°C and 31.6°C respectively) and it is, therefore, unlikely that any differences in growth rates of *D. melanurus* were influenced by temperature.

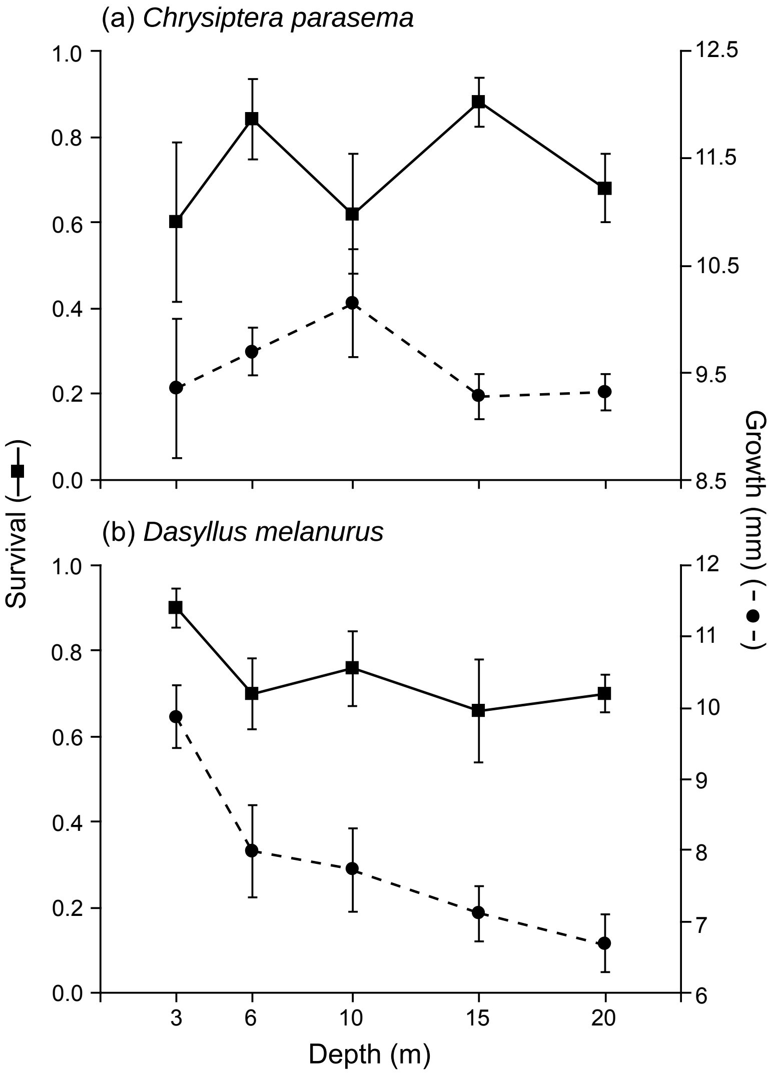

Figure 4.3: Mean survival (the proportion of fish that survived to the end of the experiment per patch reef) and growth (the increase in size per patch reef) for (a) *Chrysiptera parasema* and (b) *Dascyllus melanurus* at each of the 5 depths. Error bars indicate 1 SE.

4.5 Discussion

Despite the strong association between species distributions and environmental gradients, few studies have isolated specific factors that limit distributions or explain preferred positions along such gradients. Both experimental manipulations of physical and biological conditions, and transplants of focal species to different positions along gradients have proven the most successful ways to distinguish among potentially important factors (Connell 1961; Grosberg 1982; Wellington 1992; Jones 1997; Van der Wal et al. 2000; La Peyre et al. 2001).

Many coral reef fishes settle preferentially into certain microhabitats (Eckert 1985; Danilowicz 1996; Öhman et al. 1998). Because microhabitat structure often changes with depth (Done 1982), depth distributions of fishes could be explained by the availability of preferred microhabitats. However, by providing identical patch reefs at different depths (Experiment 1), I showed that distributions among depths are established at settlement and are to a great degree independent of microhabitat structure. All 6 species examined settled at particular depths despite uniform microhabitat structure.

Patterns of distribution among depths on experimental patch reefs and on unmanipulated habitat were almost identical for 4 of the 6 species (*A. curacao*, *D. melanurus*, *P. nigromanus* and *C. octofasciatus*). This indicates that for these species, distributions among depths are established at settlement and are not limited by the availability of microhabitats. This result is not surprising for *A. curacao* and *P. nigromanus* as both species settle into a wide range of microhabitats. However, *D. melanurus* and *C. octofasciatus* are both microhabitat specialists, settling only into live corals, usually of the genus *Acropora*. Although the decrease in percent cover of *Acropora* with increasing depth could explain the depth distribution of *D. melanurus*, when equal amounts of *Acropora* was present at all depths, *D. melanurus* still always settled in shallow water. Surveys on unmanipulated habitat included recruits that had been on the reef for up to 2 weeks, therefore the similarity between depth distributions on experimental patch reefs and on unmanipulated habitat also suggests that the depth distributions of *A. curacao*, *D. melanurus*, *P. nigromanus* and *C. octofasciatus* are not modified by post-settlement mortality or movement, at least during the first week or two following settlement.

These results support other studies on marine taxa, including barnacles (Grosberg 1982), ascidians (Hurlbut 1991) and fishes (Wellington 1992; Jones 1997; Gutierrez 1998, Leis et al. 2002), which have shown that settlers have preferences for particular depths and that differences between depths in settler abundances persist when identical substrata are provided. Two species, *C. parasema* and *H. melanurus*, did extend their depth distributions into deeper water when suitable microhabitats were provided. However, as in the case of the other 4 species, these 2 species were not similar in other ecological characteristics. *C. parasema* is a microhabitat specialist, almost always settling into live *Acropora*. The presence of equal amounts of live coral, particularly *Acropora*, on patch reefs may have made it possible to settle deeper than normal. This may also be the case for *H. melanurus*, which is more of a microhabitat generalist. For both these species, however, settlement on patch reefs was not uniform among depths and the general shapes of the two depth distributions (on patch reefs and on unmanipulated habitat) were similar. Therefore, depth preferences of both species appear to some degree to be independent of microhabitat structure. It is also possible that settlement patterns on unmanipulated habitat were identical to those on the patch reefs but the original settlement patterns had been modified by post-settlement mortality. Since the fish surveyed on unmanipulated habitat included individuals that had been on the reef for up to 2 weeks, post-settlement mortality acting during the first week or two could have shaped the observed depth settlement patterns.

Because patch reefs were monitored every 3-4 days in Experiment 1, it is possible that post-settlement mortality could have influenced the observed depth-related patterns to some degree. High levels of post-settlement mortality in the first few days have been observed in other studies in which new settlers were monitored daily (Doherty and Sale 1985; Steele and Forrester 2002; Webster 2002). However, in this study the potential for predation was minimised by regular removal of demersal predators from experimental patch reefs. Even though it is likely that some post-settlement mortality did occur, it would have to be substantial to account for the observed differences in settler densities among depths. The actual post-settlement mortality measured in the second experiment (30-40% mortality over 6 weeks) was insufficient to account for the depth distributions observed in Experiment 1.

There are a number of factors that may be limiting depth distributions in the absence of microhabitat effects. Firstly, these patterns could arise because larval fish have species-specific vertical distributions prior to settlement (Leis 1991b; Leis and Carson-Ewart 2000; Hendricks 2001) and simply contact the reef at specific depths. Leis and Carson-Ewart (2002) suggest that larvae may swim at particular depths in order to use either the water surface or the seafloor to orient themselves horizontally (i.e. shallow enough that the water surface is visible, or deep enough that the seafloor is visible). Secondly, the physical factors that covary with depth (e.g., water pressure, temperature and light intensity) may be what are influencing the observed depth distributions. Species' may become adapted to the combinations of these physical factors associated with a particular depth, to the point that settling beyond their normal depth ranges results in reduced fitness. Finally, there may be intrinsic depth preferences exhibited by larvae at the time of settlement (Eckert 1985; Wellington 1992; Gutierrez 1998; Leis 2002). These preferences may relate to factors other than microhabitats, which may affect their growth and survival once they have settled. None of the above factors are mutually exclusive and all may play a role in explaining microhabitat-independent settlement patterns.

The second experiment supports the conclusion that there are factors other than microhabitat structure that affect growth and survival. Depth had a dramatic effect on the survival and growth of *D. melanurus* on identical microhabitats, suggesting that settlement patterns among depths can be modified by post-settlement mortality. However, because *D. melanurus* rarely settle beyond their normal depth range, and because reduced survival was only observed outside the normal range, it is unlikely that post-settlement mortality plays a major role in determining the depth range of this species. A more likely explanation is that the preference for shallow depths in this species has evolved as a result of reduced fitness (in the form of increased post settlement mortality and reduced growth rates) at depths beyond its normal range. For *C. parasema* there was no effect of depth on either mortality or growth. This indicates that the settlement depth range of this species is not modified by post-settlement mortality, and the preference for 10-15 m depths is unlikely to be a response to reduced fitness beyond the normal depth range.

One explanation for the difference in the effect of depth on fitness between the two species might be that their prey or predators have different depth distributions. Alternatively, species with relatively broad depth ranges (e.g., *C. parasema*) may have reduced costs associated with settling to depths beyond the normal range. That is, specialists (e.g., *D. melanurus*) may survive and grow better than generalists within their preferred depth strata, but generalists may do moderately well over a greater range of depths (Futuyma and Moreno 1988; McNally 1995).

In conclusion, I have shown that, for most of the coral reef fish considered here, depth-related patterns in settlement and early post-settlement processes are largely independent of the availability of microhabitats. Factors associated with depth may explain differences in settlement, growth and survival, and warrant further investigation. In addition, the results suggest that species with narrow depth preferences may have evolved such preferences because of the fitness costs associated with straying beyond these limits. The potential trade-off between depth specialisation and fitness needs to be rigorously tested using a wider range of coral reef fishes.

CHAPTER 5: HABITAT DEGRADATION, RECRUITMENT, AND THEIR CONSEQUENCES FOR THE DYNAMICS OF CORAL REEF FISH POPULATIONS

5.1 Abstract

Many marine species are undergoing long-term changes in abundance in response to habitat degradation. While recruitment is known to be a primary driver of the temporal and spatial dynamics of open marine populations, its role in determining responses to habitat change is poorly understood. Also, the degree to which species-specific patterns in recruit-adult relationships characterise whole reef fish families has not been examined. Here, I examine the influence of declining coral cover and fish recruitment on long-term trends, short-term fluctuations and spatial patterns in the abundance of the common coral reef fishes in Kimbe Bay (Papua New Guinea). Species-specific and family-level patterns were compared for the two most common reef-associated taxa: the damselfishes (Pomacentridae) and wrasses (Labridae). A comparison of recruit-adult relationships among species and between the two families established that a given average density of recruits resulted in greater average densities of adult damselfishes, compared with wrasses. Within each family, species with higher recruitment exhibited higher adult densities, but the magnitude of the increase in adult numbers declined as a function of increasing recruitment. Coral cover on the inshore reefs in Kimbe Bay gradually declined from 70% to less than 10% between 1997 and 2002. Associated with this, 75% of the common reef fish species declined in abundance, with 50% declining to less than half their original numbers. Wrasses exhibited the greatest range of responses, including species that increased, species that declined and others that remained stable, while the majority of damselfish species declined. The magnitude and direction of the long-term change in fish abundance was inversely correlated with the degree of association between recruits and live branching corals. Species that did not recruit into live coral tended to increase in abundance, while the greater the dependence of recruits on live coral, the greater the adult decline. For many species, long-term trends in adult numbers were interrupted by a spike of increased abundance in 2001, which was associated with high recruitment the previous year. Spatial patterns in the

abundance of adults across reefs and depths were positively correlated with recruitment levels for 80% of the species examined. For some species, adult distributions tended to be more even than recruit distributions, indicating post-settlement expansion in distributions. I suggest that short-term fluctuations in adult abundance arise through fluctuations in larval supply, while longer-term trends reflect a combination of changes in habitat availability, habitat-limited recruitment and adult survival. In contrast, adult spatial distributions are primarily explained by strong habitat-specific settlement preferences. The family-level differences between damselfish and wrasses may reflect fundamental differences in their life history traits, reliance on living corals and the carrying capacities of the habitat.

5.2 Introduction

Many shallow water marine species are contending with degrading pelagic environments and benthic habitats (Hoegh-Guldberg 1999; Duarte 2002; Kennish 2002; Thompson et al. 2002; Verity et al. 2002; Steneck et al. 2002; Lotze et al. 2006). There is increasing evidence that many are declining in response to habitat loss (Short and Wyllie-Echeverria 1996; Jones et al. 2004 – Appendix III; Wilson et al. 2006) and some may be at risk of extinction (Roberts and Hawkins 1999; Powles et al. 2000; Kappel 2005). However, the demographic mechanisms responsible for declining numbers and the consequences for the structure of whole assemblages are unclear. Local populations of the majority of marine species appear to function as open (or at least partially open) units, with considerable import and export of pelagic larvae (Palmer et al. 1996; Jones et al. 1999; Cowen et al. 2000; Hixon et al. 2002; Grantham et al. 2003). The dynamics of such populations appears to be limited (or at least partially limited) by larval supply and recruitment (Connell 1985; Gaines and Roughgarden 1985; Roughgarden et al. 1988; Caley et al. 1996; Armsworth 2002). Hence, any effects of habitat degradation on recruitment are likely to have important implications for long-term trends in population size (Butler et al. 2005). While there is increasing evidence that the magnitude of recruitment can be governed by the availability of suitable juvenile habitat (e.g., Carr 1994; Schmitt and Holbrook 2000; Reed et al. 2004), few studies have addressed the effects of habitat change on recruitment, and the consequent effects on distribution and abundance.

In recent years there has been much concern over a global decline in the health of coral reefs due to a variety of disturbances, including global warming (and associated bleaching), over-fishing and coastal pollution (Hughes 1994; Sebens 1994; McClanahan 2002; Gardner et al. 2003; Hughes et al 2003; Wilson et al. 2006). Coral reefs support a high diversity of fishes and it is clear that there are strong links between fish assemblages and the structure of the underlying habitat. There is increasing evidence of a decline in abundance and diversity of coral reef fishes in response to reef degradation (Booth and Beretta 2002; Jones et al. 2004; Graham et al. 2006; Bellwood et al. 2006; Wilson et al. 2006). In the few cases where coral cover has recovered, fish communities have also recovered (Halford et al. 2004; Berumen and Pratchett 2006). Coral specialists (including coralivores and coral-dwelling species) are particularly susceptible to loss of their preferred coral substrata (Munday et al. 1997; Kokita and Nakazono 2001; Cheal et al. 2002; Spalding and Jarvis 2002; Syms and Jones 2002; Sano 2004; Pratchett et al. 2006), and local extinctions have been recorded (Munday 2004; Graham et al. 2006). Fish species associated with dead coral or algal covered substrata may increase in response to declining coral cover (Jones et al. 2004; Graham et al. 2006), while substrate generalists may exhibit a high degree of variability that is independent of habitat structure (Sale and Douglas 1984; Williams 1986; Doherty and Fowler 1994; Doherty 2002; Cheal et al. 2002; Spalding and Jarvis 2002). Comprehensive strategies for protecting coral reef fish biodiversity require an understanding of mechanisms responsible for this diversity in demographic responses to habitat change.

It is widely acknowledged that variation in recruitment plays a major role in determining the structure and dynamics of coral reef fish populations (Sale 1980; Doherty and Fowler 1994; Caley et al. 1996; Doherty 2002; Jones and McCormick 2002). While the magnitude of recruitment can be substantially modified by post-recruitment interactions or regulatory mechanisms (Jones 1990, 1991; Caley et al. 1996; Osenberg et al. 2002), adult population size often increases as a declining function of the magnitude of recruitment (Jones 1990, 1991; Schmitt et al. 1999; Shima 1999). Hence, the factors determining variation in recruitment can be critical to explaining year-to-year fluctuations and long-term trends in population size. Temporal patterns in recruitment may be determined not only by larval supply (Doherty and Williams 1988;

Doherty 2002), but also by the availability of suitable recruitment habitat (Booth and Beretta 2002; Schmitt and Holbrook 2000; Syms and Jones 2002; Jones et al. 2004). If recruitment is generally habitat-limited, than major changes to habitat structure can be predicted to have profound effects on temporal trends in adult population size and community structure.

Recruitment also appears to be extremely important in determining the spatial distributions of adult fishes on coral reefs (Williams 1991; Jones 1997; Booth and Wellington 1998). Spatial variation in recruitment may explain distinct adult distributions across broad reef zones, or along gradients of exposure and depth (Green 1996; Jones 1997; Srinivasan 2003 – Appendix II). Many species exhibit strong substrate preferences at settlement (Danilowicz 1996; Öhman et al. 1998; Chapter 3) and variation in substrate availability can have a major influence on spatial patterns in recruitment, and consequently, adult distributions (e.g., Danilowicz et al. 2001; Booth 1992; Wellington 1992). Habitat choice at settlement can also be influenced, either positively or negatively, by the presence of resident conspecifics (Sweatman 1985, 1988; Jones 1987b; Booth 1992; Forrester 1995; Öhman et al. 1998) or heterospecifics (Shulman et al. 1983; Jones 1987b). Patterns in the spatial distribution of recruits may subsequently be either reinforced or disrupted by factors affecting post-settlement mortality or ontogenetic shifts to other habitat (Jones 1990, 1991, 1997; McCormick and Makey 1997). However, the degree to which species-specific adult distributions within fish communities are already evident at the time of recruitment is unknown.

Much of our knowledge of recruitment as a determinant of spatial and temporal patterns in adult abundance has come from the gradual accumulation of case studies on individual species (e.g. reviews by Doherty 2002; Hixon and Webster 2002; Osenberg et al. 2002). If the generalisations that have emerged apply to coral reef fishes as a whole, then patterns in recruit-adult relationships should be evident at the level of the community. However, few studies have taken a multi-species approach to assess whether recruitment is a primary driver of adult distribution and abundance, and whether the relative abundance of different species can be explained by differences in their levels of recruitment. Also, family-level differences in the role of recruitment should be expected, given obvious contrasts among the different reef fish families in life history strategies, including growth, reproduction and longevity (Choat and Robertson

2002; Doherty 2002). Many small reef fish families are intimately associated with reef substrata throughout their lives (Munday et al. 1997; Gardiner and Jones 2005), while other taxa may recruit elsewhere and migrate onto coral reefs at a later ontogenetic stage (Mumby et al. 2004; Dorenbosch et al. 2006). In general, recruit-adult relationships and the response of coral reef fishes to habitat degradation at the family level are poorly understood.

The aim of this chapter was to assess the role of recruitment in explaining temporal and spatial patterns in the abundance of coral reef fish species on the inshore fringing reefs of Kimbe Bay, Papua New Guinea. The study began during a period of long-term decline in coral reef health, with cover of branching corals decreasing from approximately 70% in 1996 to less than 10% in 2002, with a corresponding increase in the cover of turfing algae (Jones et al. 2004). The coral decline appeared to have been caused by a combination of coral bleaching (observed in 1997, 1998, 2000 and 2001 - Srinivasan 2000), as well as a gradual increase in sedimentation from terrestrial run-off and outbreaks of Crown-of-Thorns starfish (Srinivasan, personal observation). While the decline in coral cover resulted in a decline in reef fish biodiversity and a change in the structure of adult communities, the role of recruitment in explaining community-wide and family-wide changes in adult numbers requires further attention. Here I use the recruitment data reported in Chapters 2 and 3 to assess the effect of recruitment on short-term population dynamics, and examine whether the degree of substrate specificity explains long-term trends in adult numbers. In addition, I examine whether spatial patterns in recruitment explain the distribution and abundance of adults across different reef habitats. As shown in Chapter 2, the total recruitment of fishes to the inshore reefs was dominated by wrasses (Labridae) and damselfishes (Pomacentridae). Here, these two families are compared, to assess whether there are taxonomic differences in recruit-adult relationships that explain differences in the relative abundance of species, and family-level differences in the long-term response to habitat degradation.

5.3 Methods

5.3.1 Visual surveys of adults and recruits

Visual surveys of adult fishes were carried out annually from 1997 to 2003 at 8 inshore platform reefs near the township of Kimbe (Fig. 1.1). During each survey, depths of 10, 6 and 2 m on the windward slope, and the reef flat (0 m), of each site were surveyed using four 50 m belt transects at each depth. In each transect, all non-cryptic reef fishes were counted simultaneously by two divers. Damselfish species (Pomacentridae) were surveyed using 50 x 1m transects. Species in other families, including the wrasses (Labridae), surgeonfishes (Acanthuridae), parrotfishes (Scaridae), butterflyfishes (Chaetodontidae) and fairy basslets (Serranidae) were surveyed using 50 x 4 m transects. Four transects were surveyed at each depth. Data were standardised to the number of fish per 100 m^2 for all species.

Visual surveys of new recruits from the same families were carried out every 1-2 months from December 1998 to April 2001, at four of the reefs at which adult fishes were surveyed (Gava Gava, Limuka, Luba Luba and Madaro, Fig. 1.1), and at the same depths. Four 50 x 2 m transects were surveyed at each depth. New recruits and adults were surveyed simultaneously during two months (November 1999 and 2000). All non-cryptic juveniles below a certain cut-off size were counted, and the substratum type occupied by each fish was recorded (see Chapters 2 and 3). In addition to the recruit surveys, microhabitat use for species not included in these surveys (e.g. cryptic or rare species, and species which recruit at depths and habitats other than those sampled) was estimated by conducting random searches, recording substratum types occupied, until at least 20 individuals of each species had been found.

5.3.2 Family level relationships between recruit and adult densities

The relationships between average recruitment levels and adult densities were examined for all species for which there were data on both adult and recruit abundances. Non-linear regression analysis was used to examine the relationships between log mean adult density (averaged across years, from 1999 to 2001) and log recruit density (averaged across all surveys). Separate regression analyses were carried out for each of the two families with sufficient numbers of species: the damselfishes (32 species) and wrasses (21 species).

5.3.3 Temporal patterns in adult density and the influence of recruitment

To examine long-term trends in the structure of the whole community, the magnitude of change in adult densities between 1997 and 2003 was calculated for all species with average abundance (averaged across the first two years - 1997 and 1998) ≥ 2 fish per ha (a total of 77 species). Percentage change was calculated from the difference in density averaged across the first two years (1996-1997) and the final two years (2002-2003) of monitoring. The 77 species included 32 damselfish species, 27 wrasse species, 10 butterflyfish species and 8 surgeonfish species.

To examine whether the dependence of recruits on live branching coral explained long-term changes in adult abundance, the relationship between the percentage change in adult density and the percentage of new recruits observed occupying live branching coral was examined using 3 separate linear regressions for: (1) all 77 species; (2) the damselfishes (32 species); and (3) the wrasses (28 species). An ANCOVA was used to test if the slopes of this relationship differed between the damselfishes and wrasses.

Long-term trends and short-term fluctuations in adult numbers were examined for the ten most commonly recruiting damselfish and wrasses. In addition, to examine whether yearly variation in recruitment may explain short-term fluctuations in adult numbers, recruitment differences between 1999 and 2000 (see Chapter 2) were compared with adult population changes between 2000 and 2001 for all species. For each species, the magnitude and direction of change in total recruit abundance (summed across all sites, depths and survey periods) between 1999 and 2000, was related to the magnitude and direction of change in total adult abundance (summed across all sites and depths) between 2000 and 2001. These data were log transformed, and the relationship was compared using linear regression, including species for which a change in recruit abundance and adult abundance occurred in the same direction (i.e. either an increase in both or a decline in both).

5.3.4 Spatial distributions of adults and the influence of recruitment

The spatial distributions of recruits and adults in 1999 and 2000 were compared for the 40 highest recruiting species at the depths and sites surveyed. This included 21 damselfish species, 12 wrasse species, 3 surgeonfish species, 2 butterflyfish species, *Pseudanthias tuka* (Serranidae) and *Scarus niger* (Scaridae). Separate regression analyses for the years 1999 and 2000 were used to examine the relationship between the mean density of adults in November, and the mean density of recruits averaged across all survey periods in the 12 months before, at each of the 16 depth-site combinations. Adult densities in November 1999 were compared with recruit densities averaged across 9 survey periods (December 1998 to November 1999 inclusive), and adult densities in November 2000 were compared with recruit densities averaged across 8 survey periods (February 2000 to November 2000 inclusive). Data for both recruits and adults were transformed to $\log(x+1)$.

For each species, a Kolmogorov-Smirnof (KS) two-sample test was used to examine if the shapes of the spatial distributions of recruits and adults differed significantly in each of the two years. As above, adult distributions in each year were compared with recruit distributions from the previous 12 months. The total number of individuals at each depth-site combination was obtained by summing across transects for adults, and across transects and survey periods for recruits. The KS test examines the cumulative frequency of ordered data and is based on the largest difference between the ordered cumulative frequencies of each group (Sokal and Rohlf 1981), in this case recruits and adults. Simpson's Index of Evenness was then used to compare the breadth of recruit and adult distributions among sites and depths. This index is calculated using the formula, $ED=1/\Sigma P_i * 1/S$, where P_i is the proportion of individuals at site-depth combination i, and S is the number of site-depth combinations (16 in this case) (Krebs 1999). Evenness indices were compared between recruits and adults at the family level for the damselfishes and wrasses in each of the two years using paired t-tests. Depth distributions of recruits and adults of the 10 most common damselfishes and wrasses were compared qualitatively by plotting the mean proportion of adults and recruits at each depth (averaged among the 4 sites).

5.4 Results

5.4.1 Family-specific patterns in recruit-adult relationships

The relative densities of adult fishes among the common reef fish species could be explained largely by their average levels of recruitment (Fig. 5.1). That is, species with higher recruitment exhibited higher adult densities, although the relationships between recruit and adult densities were non-linear and differed for damselfishes and wrasses, the two most common reef fish families (Fig. 5.1). There were significant curvilinear relationships between log-transformed average densities of adults and recruits for both the damselfishes ($r^2 = 0.692$, $P < 0.001$) and the wrasses ($r^2 = 0.682$, $P < 0.001$, Fig. 5.1). Adult numbers tended toward an asymptote at high recruitment levels for species in both families. That is, adult densities increased more steeply as a function of increasing recruitment at low to moderate levels of recruitment. Species with very high recruitment did not produce proportionally higher numbers of adults. A given level of

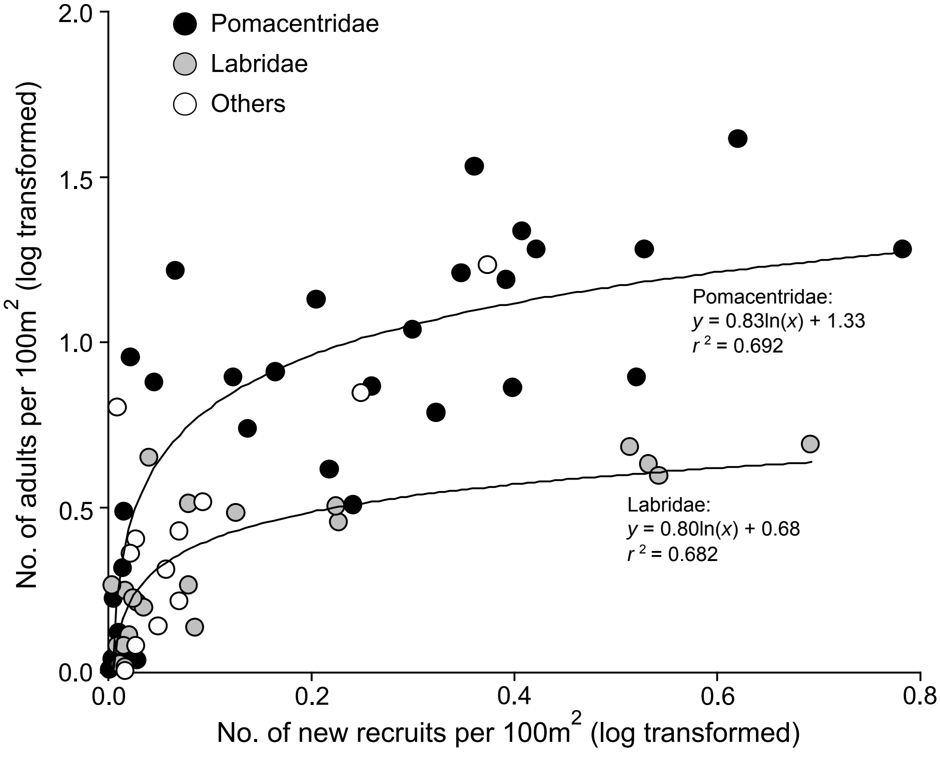

Figure 5.1: Relationships between the densities of adults and recruits for the damselfishes and the wrasses. Each point represents a species. Points representing species in other families were added for comparison.

recruitment resulted in higher densities of adult damselfish, compared with wrasses (Fig. 5.1). The difference between the two families was greatest for high recruiting species, with adult damselfish densities typically twice as high as wrasses. There were too few species in other families to examine the shape of recruit-adult relationships.

5.4.2 Long-term trends in reef fish abundance and the role of recruitment substrata

About 75% of the fish species surveyed declined in abundance from the beginning to the end of the survey period, with roughly half of the species declining by over 50% (Fig. 5.2). The remaining 25% of species increased in abundance, with numbers of some dead coral or rubble associated species rising dramatically. The majority of the damselfish species declined in abundance, and along with butterflyfish, accounted for the most dramatic declines in numbers over the study period (Fig. 5.2). The labrids exhibited a great range of changes over this period including many species that increased dramatically and some undergoing moderate declines in abundance. The species from other taxa also exhibited the full spectrum of population changes.

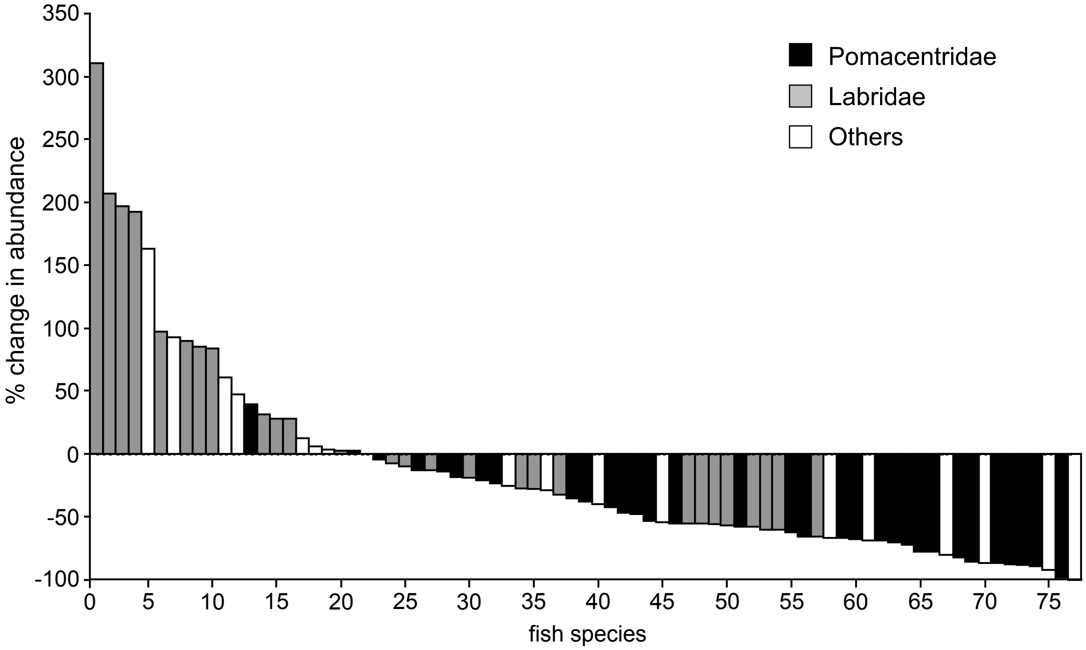

Figure 5.2: Percentage change in adult fish abundance between 1997 and 2003. The numbers on the x-axis represent individual species (1-77), ranked from largest increase to largest decline.

When all 77 species were examined, there was a negative relationship between the magnitude of change in fish abundance and the proportion of juveniles found settling on live coral (linear regression, $r^2 = 0.351$, $P < 0.001$) (Fig. 5.3). Species varied on a continuum of those that only ever settled onto live coral substrata to those that never settled onto coral (Fig. 5.3). About 65% of fish species settled onto live coral in proportions significantly greater than expected given the average cover of live coral during 2000 and 2001 (~35%). Species with the highest degree of coral dependence as juveniles exhibited the greatest magnitudes of decline in adult numbers. In general, the few species that increased in abundance exhibited low levels of recruitment into live coral. There was a significant negative relationship between these two variables at the family level for both the damselfishes ($r^2 = 0.327$, $P < 0.001$) and the wrasses ($r^2 = 0.377$, $P < 0.001$). The slope of this relationship was significantly steeper among the wrasses than among the damselfishes (ANCOVA homogeneity of slopes: $F = 7.13$, $P = 0.01$). That is, for a given level of coral-dependence, damselfishes exhibited a greater magnitude of decline over the study period (Fig. 5.3).

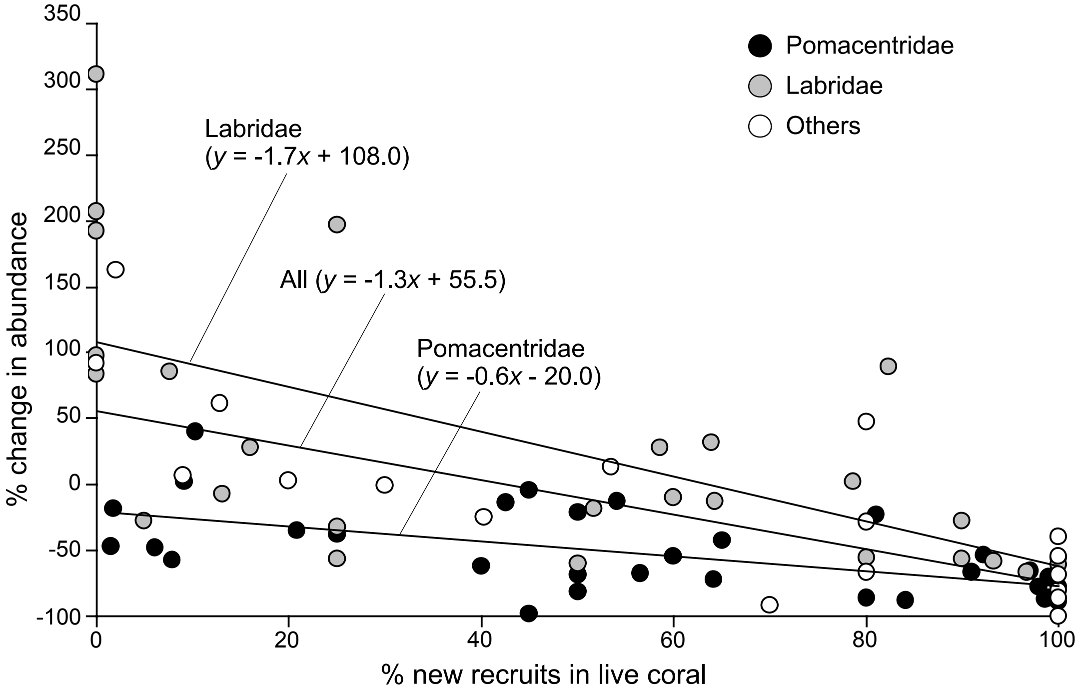

Figure 5.3: Relationships between the direction and magnitude of change in fish abundance between 1997 and 2003, and the proportion of all juveniles observed to be associated with live branching coral at settlement, for the damselfishes, wrasses, and all 77 species.

5.4.3 Species-specific patterns: long-term trends and short-term fluctuations

Among the 10 highest recruiting damselfish and wrasse species, a range of long-term trends and short-term fluctuations were evident. There was a long-term decline in adult densities of five of the ten damselfish species (*Ambyglyphidodon curacao*, *Chromis ternatensis*, *Chrysiptera parasema*, *Pomacentrus aurifrons* and *Pomacentrus moluccensis*) between 1997 and 2003 (Fig. 5.4). The magnitude of the decline varied, with two coral-associated species (*Chrysiptera parasema* and *Pomacentrus aurifrons*) reduced to less than 10% of their initial numbers. The other five species exhibited similar short-term temporal fluctuations in adult numbers, all recording highest densities in 2001. This peak appears to correspond with a short-term increase in recruitment from 1999 to 2000 (Fig. 5.4). Even for most species exhibiting a long-term decline, this trend was interrupted by a spike of increased abundance in 2001.

Compared to the damselfishes, the wrasses appeared to exhibit a greater variation among species in the temporal change in adult abundance (Fig. 5.5). Two of the coral-associated wrasses (*Diproctacanthus xanthurus* and *Labrichthys unilineatus*) exhibited a long-term decline in adult density that mirrored the declining coral cover, while three other species (*Halichoeres chloropterus*, *Paracheilinus filamentosus* and *Thalassoma lunare*) exhibited long-term increases in adult numbers (Fig. 5.5). The remaining five species did not appear to exhibit any long-term trends in adult densities, with one maintaining virtually constant densities (*Thalassoma hardwicke*) and others exhibiting short-term fluctuations. As with the damselfish, a large number of wrasses exhibited a spike of increased adult abundance in 2001, which for most reflected high recruitment in 2000 compared with the previous year.

Recruitment differences between the two years appeared to explain short-term changes in adult abundance. There was a significant linear relationship between the magnitude of change in total adult abundance between 2000 and 2001, and the magnitude of change in total recruit abundance between 1999 and 2000 ($r^2 = 0.764$, $P < 0.001$, Fig. 5.6), for 42 species for which the change adult and recruit abundance occurred in the same direction. That is, the bigger the increase in recruit abundance over one year, the

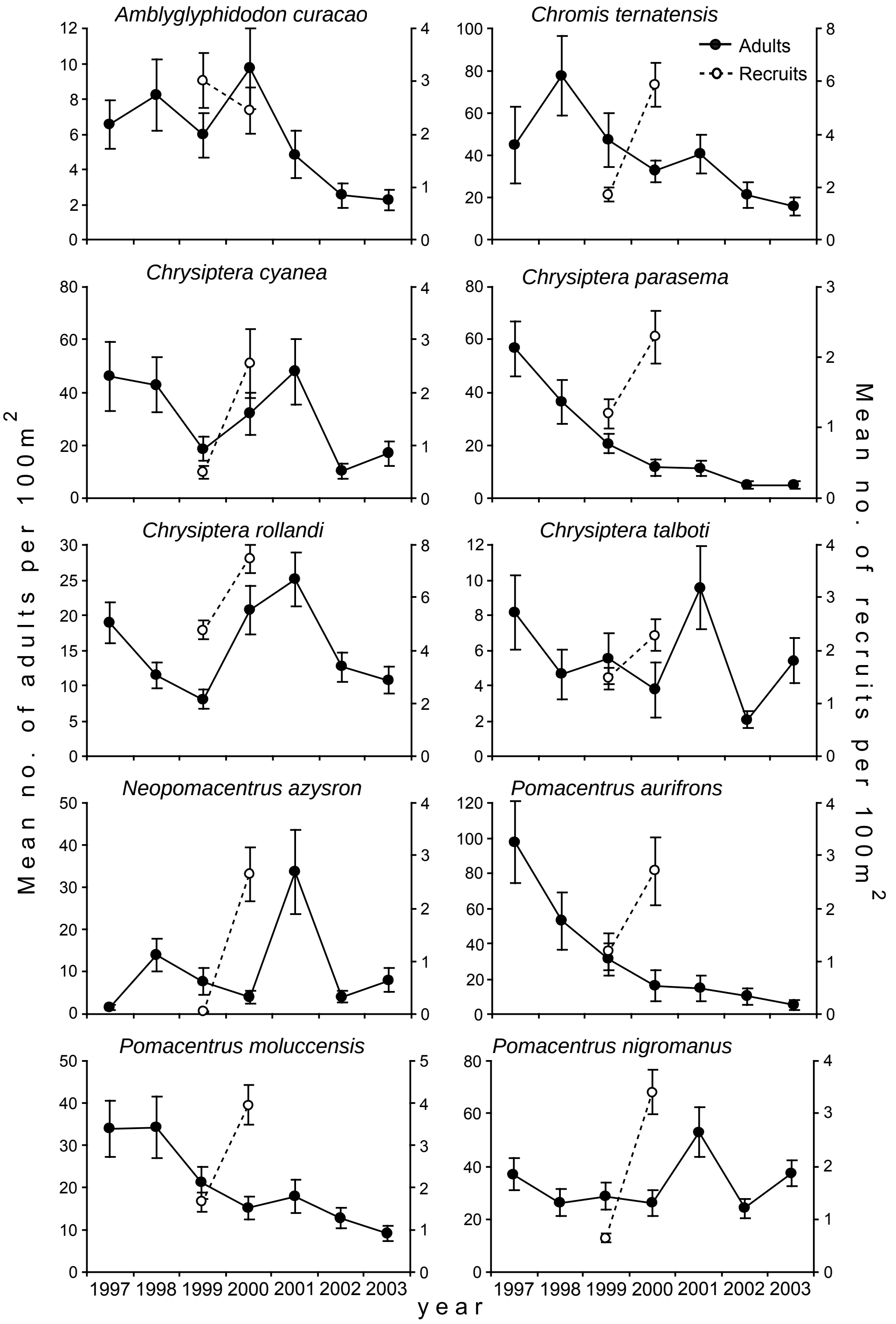

Figure 5.4: Temporal patterns of adult and recruit density for the 10 highest recruiting damselfish species. Recruit density was sampled for just two full years (1999 and 2000).

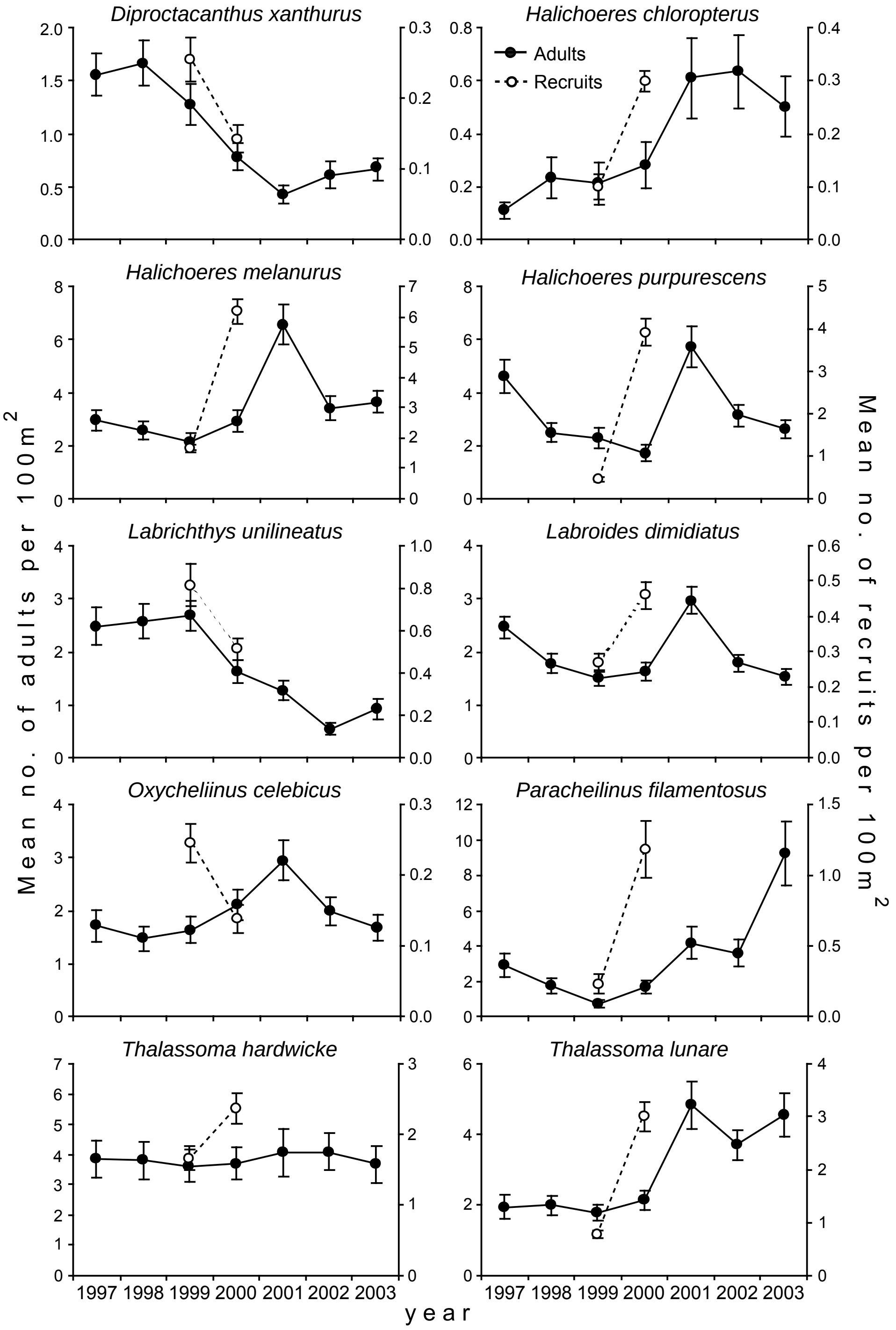

Figure 5.5: Temporal patterns of adult and recruit density for the 10 highest recruiting wrasse species. Recruit density was sampled for just two full years (1999 and 2000).

bigger the increase in adult numbers the following year. Similarly, a larger decline in recruitment resulted in a larger decline in adult numbers.

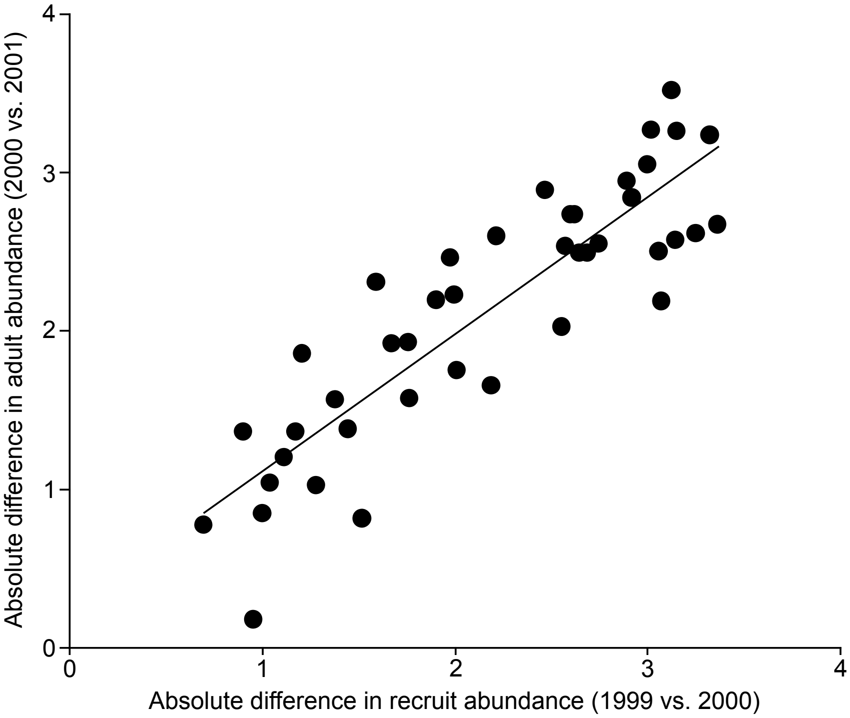

Figure 5.6: Relationship between the absolute differences in adult and recruit abundance over two years (1999 to 2000 for recruits, and 2000 to 2001 for adults) for 42 species.

5.3.4 Spatial distributions of recruits and adults

In general, spatial variation in the abundance of adults was largely explained by patterns in recruit densities. For most of the species (32 out of 40) there were significant positive relationships between adult and recruit densities in both 1999 and 2000 (Table 5.1). For these species, recruitment explained 60%, on average, of the variation in adult numbers. All but one species exhibited a significant positive linear relationship between recruitment and adult densities in 2000. The exception was *Ctenochaetus strigosus* for which the relationship had borderline significance in both years (Table 5.1). There were no obvious differences among families in the strength of these relationships, although most of the examples of non-significant relationships were for damselfishes in 1999 only.

Table 5.1: Summary of the comparisons between spatial distributions of adults and new recruits of each of the 40 highest recruiting species, including the results of linear regressions (adult density vs. recruit density at the 16 site-depth combinations), KS tests (NS = $P > 0.05$, * = $0.01 < P < 0.05$, ** = $P < 0.01$), and Simpson's Index of Evenness for adults and recruits (with differences greater than 0.08 highlighted) in the years 1999 and 2000.

	1999							**2000**						
Family and Species	Total abundance		Regression		KS	Evenness		Total abundance		Regression		KS	Evenness	
	Recruit	Adult	r^2	*P*	test	Recruit	Adult	Recruit	Adult	r^2	*P*	test	Recruit	Adult
Pomacentridae														
Acanthochromis polyacanthus	105	274	0.439	0.003	**	**0.063**	**0.155**	939	466	0.485	0.002	**	0.152	0.175
Amblyglyphidodon curacao	1544	622	0.737	<0.001	**	0.243	0.269	1250	308	0.442	0.003	**	0.249	0.285
Amblyglyphidodon leucogaster	362	142	0.339	0.011	**	**0.322**	**0.507**	546	122	0.533	0.001	**	0.210	0.265
Chromis amboinensis	5	418	0.061	0.357	*	**0.223**	**0.372**	132	220	0.268	0.023	**	0.186	0.175
Chromis retrofasciata	244	782	0.799	<0.001	NS	0.344	0.323	507	666	0.784	<0.001	**	0.317	0.270
Chromis ternatensis	886	2078	0.636	<0.001	**	**0.469**	**0.595**	2997	2608	0.833	<0.001	**	0.426	0.460
Chromis viridis	104	32	0.010	0.716	**	**0.242**	**0.110**	499	346	0.986	<0.001	*	0.142	0.118
Chrysiptera cyanea	254	2036	0.806	<0.001	**	0.190	0.248	1300	3058	0.622	<0.001	**	**0.115**	**0.209**
Chrysiptera parasema	658	738	0.813	<0.001	**	0.241	0.286	1170	718	0.904	<0.001	**	0.221	0.258
Chrysiptera rollandi	2513	1324	0.530	<0.001	**	**0.508**	**0.424**	3828	1602	0.856	<0.001	**	**0.532**	**0.449**
Chrysiptera talboti	754	240	0.359	0.008	**	**0.273**	**0.112**	1168	612	0.704	<0.001	**	0.282	0.289
Neoglyphidodon nigroris	107	348	0.024	0.569	**	**0.201**	**0.443**	482	570	0.382	0.006	**	**0.327**	**0.482**
Neopomacentrus azysron	22	252	0.417	0.004	**	0.233	0.185	1352	2148	0.771	<0.001	**	0.205	0.171
Plectroglyphidodon lacrymatus	80	768	0.176	0.060	**	**0.205**	**0.460**	94	1048	0.443	0.003	**	**0.250**	**0.373**
Pomacentrus adelus	352	630	0.799	<0.001	**	0.364	0.409	791	688	0.453	0.003	**	**0.450**	**0.272**
Pomacentrus aurifrons	603	1022	0.828	<0.001	**	0.132	0.110	1386	940	0.895	<0.001	**	0.135	0.090
Pomacentrus bankanensis	123	430	0.849	<0.001	*	0.215	0.219	286	528	0.893	<0.001	NS	0.217	0.211
Pomacentrus burroughi	209	324	0.577	<0.001	**	0.226	0.249	763	570	0.684	<0.001	**	0.280	0.275
Pomacentrus lepidogenys	191	278	0.647	<0.001	**	**0.148**	**0.241**	287	286	0.439	0.003	**	0.165	0.204
Pomacentrus moluccensis	852	968	0.361	0.002	**	**0.220**	**0.366**	2024	1142	0.503	0.001	**	**0.216**	**0.299**
Pomacentrus nigromanus	329	836	0.612	<0.001	**	0.362	0.410	1739	1698	0.943	<0.001	**	0.425	0.430

Table 5.1 (cont.)

Family and Species	1999							2000						
	Total abundance		Regression		KS	Evenness		Total abundance		Regression		KS	Evenness	
	Recruit	Adult	r^2	P	test	Recruit	Adult	Recruit	Adult	r^2	P	test	Recruit	Adult
Labridae														
Diproctacanthus xanthurus	135	50	0.361	0.008	**	**0.462**	**0.629**	73	27	0.679	<0.001	NS	0.454	0.465
Halichoeres argus	28	188	0.612	<0.001	NS	**0.170**	**0.252**	66	304	0.284	0.020	**	**0.130**	**0.280**
Halichoeres chloropterus	51	18	0.716	<0.001	**	0.235	0.224	153	39	0.503	0.001	NS	0.211	0.250
Halichoeres melanurus	1036	187	0.790	<0.001	NS	0.583	0.534	3162	420	0.837	<0.001	**	0.621	0.613
Halichoeres prosopeion	55	40	0.716	<0.001	NS	0.214	0.260	50	33	0.815	<0.001	NS		
Halichoeres purpurescens	279	110	0.727	<0.001	**	0.294	0.359	2006	367	0.916	<0.001	**	0.459	0.470
Labrichthys unilineatus	485	104	0.320	0.013	**	**0.352**	**0.618**	263	81	0.431	0.003	**	**0.378**	**0.539**
Labroides dimidiatus	144	104	0.556	0.001	NS	0.726	0.702	236	190	0.596	<0.001	**	**0.654**	**0.759**
Oxycheilinus celebicus	136	136	0.692	<0.001	**	**0.340**	**0.504**	71	189	0.447	0.003	**	**0.325**	**0.554**
Pseudocheilinus filamentosus	136	107	0.534	0.001	**	**0.204**	**0.381**	604	267	0.260	0.025	**	**0.214**	**0.396**
Thalassoma hardwicke	1100	238	0.617	<0.001	**	**0.282**	**0.453**	1209	260	0.371	0.007	**	0.261	0.311
Thalassoma lunare	517	137	0.263	0.024	**	**0.367**	**0.593**	1534	309	0.524	0.001	**	**0.282**	**0.466**
Serranidae														
Pseudanthias tuka	337	823	0.243	0.030	**	**0.179**	**0.302**	1326	1270	0.695	<0.001	**	0.291	0.268
Scaridae														
Scarus niger	86	22	0.107	0.117	NS	0.416	0.433	56	23	0.272	0.022	NS	0.356	0.321
Acanthuridae														
Ctenochaetus binotatus	112	67	0.088	0.140	**	**0.488**	**0.634**	65	74	0.385	0.006	NS	**0.686**	**0.537**
Ctenochaetus strigosus	197	122	0.198	0.048	**	**0.291**	**0.566**	95	183	0.171	0.062	**	**0.374**	**0.508**
Ctenochaetus tominiensis	432	313	0.482	0.002	**	**0.373**	**0.505**	494	514	0.765	<0.001	**	**0.399**	**0.506**
Chaetodontidae														
Chaetodon baronessa	92	109	0.391	0.006	**	**0.209**	**0.444**	111	85	0.448	0.003	**	0.325	0.363
Chaetodon octofasciatus	100	34	0.042	0.219	**	**0.235**	**0.513**	110	24	0.497	0.001	NS	0.457	0.416

Although there were strong relationships between recruit and adult densities, for almost three quarters of the species (29 out of 40), the actual shapes of spatial distributions differed for adults and juveniles in both 1999 and 2000 (KS tests, Table 5.1). Adult and recruit distributions differed significantly in one year (either 1999 or 2000) but not in the other for 9 species (Table 5.1). For the remaining two species, *Halichoeres prosopeion* (a wrasse) and *Scarus niger* (a parrotfish), the shapes of adult and recruit spatial distributions did not differ significantly in either year (Table 5.1). These differences were largely explained by the fact that adults were often more broadly distributed than recruits (Table 5.1, Evenness Indices). For the vast majority of species and in both years, adults were more evenly distributed among the depth-site combinations than recruits

The 10 highest recruiting damselfish species exhibited distinct depth distributions, with almost identical patterns for recruits and adults (Fig. 5.7). There were very slight differences in adult and recruit depth distributions of just 2 species, *Chrysiptera rollandi* and *Chrysiptera talboti*, where juveniles had slightly shallower distributions (Fig. 5.7). The 10 highest recruiting wrasse species also exhibited narrow species-specific depth distributions and a close match between recruits and adults (Fig. 5.8). There were just three species for which the depth distributions of recruits and adults were almost identical (*Halichoeres chloropterus*, *Halichoeres melanurus* and *Halichoeres purpurescens*, Fig. 5.8). In the other species, adult depth distributions tended to be broader than those of recruits, however the shapes of adult and recruit distributions were still quite similar. For example, *Paracheilinus filamentosus* recruits were found almost always at 10 m, however the adults were found in roughly equal proportions at 6 and 10 m (Fig. 5.8).

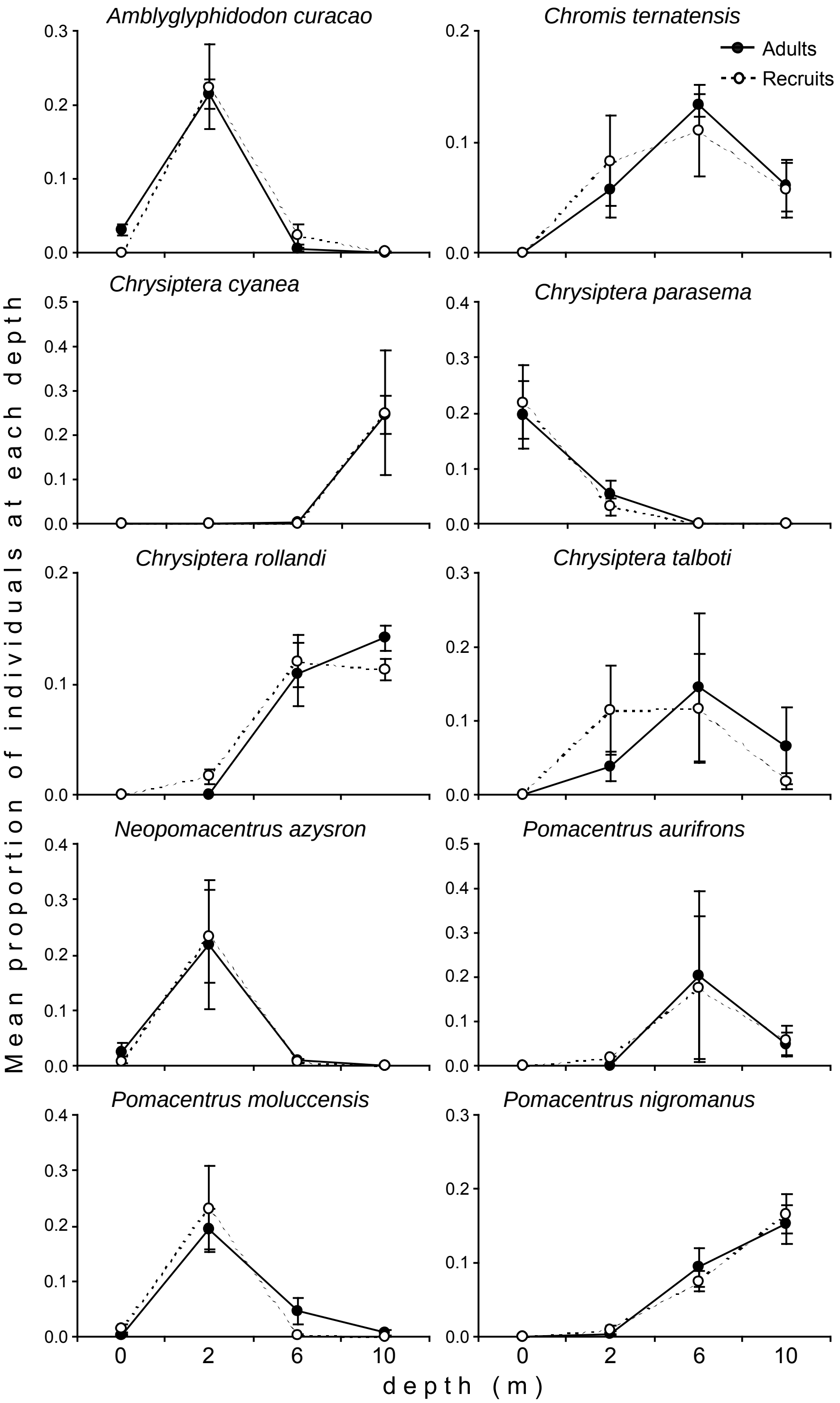

Figure 5.7: Depth distributions of adults and recruits of the 10 highest recruiting damselfish species, shown as the mean proportion of individuals (summed across sampling periods and averaged across four reefs) at each of 4 depths on the windward side of 4 reefs. Error bars are 1 SE.

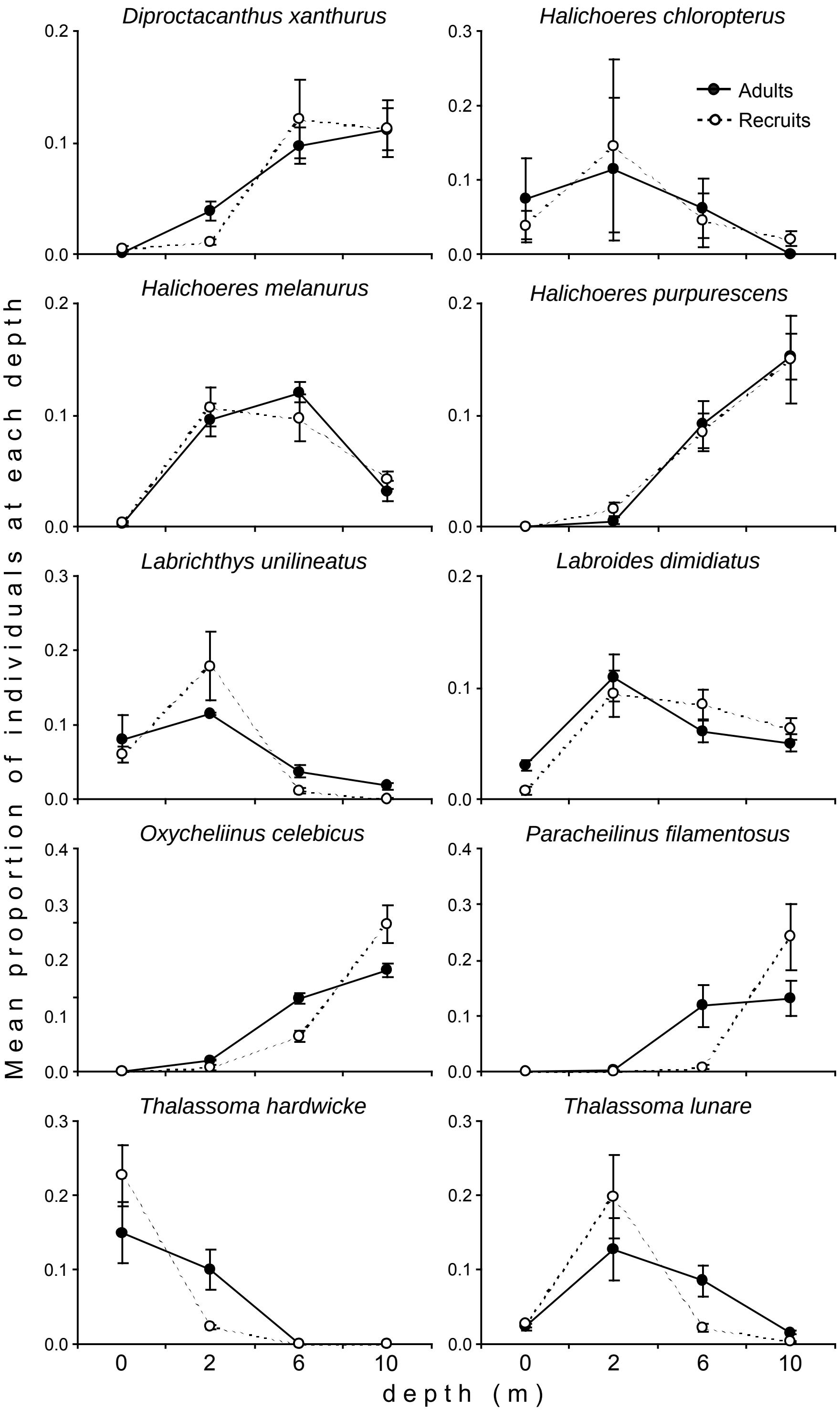

Figure 5.8: Depth distributions of adults and recruits of the 10 highest recruiting wrasse species, shown as the mean proportion of individuals (summed across sampling periods and averaged across four reefs) at each of 4 depths on the windward side of 4 reefs. Error bars are 1 SE.

5.5 Discussion

This work highlights the importance of recruitment as a determinant of temporal and spatial patterns in the abundance of adults for the majority of fish recruiting to coral reefs in Kimbe Bay, Papua New Guinea. The multi-species approach also exposed emergent phylogenetic patterns in recruit-adult relationships that have not previously been recorded. The strength and diversity of the relationships between recruitment and adult densities, and the responses to habitat change, clearly differed between damselfish and wrasses, the two reef fish families that accounted for most of the recruitment to Kimbe Bay reefs. The five-year period of habitat degradation provided useful insights into the role of habitat change in determining the abundance of the majority of species in this community. Patterns of change were clearly associated with the degree to which recruiting fishes depend on live branching coral. However, year-to-year, habitat-independent variation in recruitment clearly contributed to the shorter-term fluctuations in adult numbers in many species. Spatial patterns in adult numbers appear to reflect strong spatial gradients in recruitment, much of which may be conservative with respect to the long-term changes in habitat structure. Clearly, the mechanisms by which recruitment drives the observed patterns are likely to differ, depending on whether the focus is temporal or spatial patterns, and the different temporal or spatial scales over which these patterns are observed.

5.5.1 Long-term trends

The previously described decline between 1997 and 2002 in the cover of branching corals in Kimbe Bay has clearly had major consequences for the biodiversity of coral reef fishes (Jones et al. 2004). Here, the dramatic changes in the species-specific and family-wide structure of the fish communities are highlighted in more detail. The high level of dependence on live branching coral as a recruitment substratum suggests that these changes are largely driven by habitat-limited recruitment. The availability of suitable recruitment substrata has been implicated in other studies of reef fish populations (Holbrook et al. 2000) and communities (Holbrook et al. 2002; Syms and Jones 2002). In Kimbe Bay, approximately 75% of species declined in abundance, and the majority of these were observed to recruit into live branching coral in proportions greater than expected if species recruited at random. With a few exceptions, species that mainly settled into live branching coral declined, and those largely recruiting to non-coral substrata increased in abundance. By 2002, over half of the reef fish species had declined by more than 50% and a large number of species that settled almost exclusively into live branching coral were close to local extinction.

The extent of change in the fish community on these inshore reefs indicates that reef fish communities may be more dependent on their underlying habitat than has previously been considered. It supports an increasing number of studies and an alarming picture of the magnitude of the effect of habitat degradation on coral reef fish communities (Booth and Beretta 2002; Jones et al. 2004; Graham et al. 2006; Bellwood et al. 2006; Wilson et al. 2006). In Kimbe Bay, the changes in habitat structure and fish assemblages were contemporaneous, whereas at other locations, changes to fish communities have lagged some years behind that of habitat change (e.g. Graham et al. 2006). The rapid response in Kimbe Bay suggests that, in addition to declining recruitment, adult mortality through declining food and shelter may also be important. For example, for species in which adults are dependent on live coral either for food (e.g. the wrasses, *Diproctacanthus xanthurus* and *Labrichthys unilineatus*, and many of the butterflyfishes) or shelter (e.g. the damselfishes *Chromis viridis* and *Chrysiptera parasema*), declines in abundance were likely caused by a combination of adult mortality and habitat-limited recruitment. However, for many of the species, the declines in abundance would not have been predicted based on the adult habitat and/or food requirements of adults.

5.5.2 Short-term patterns

In addition, there were short-term fluctuations in adult abundance that were likely related to inter-annual variation in the magnitude of recruitment. For many of the species, recruitment in 2000 was much higher than in 1999, despite the decline in coral cover, and this increase in recruitment corresponded with an increase in adult abundance in 2001. Despite this, adult numbers continued to decline in many species. These results suggest that, for many of the species reliant on live coral for settlement, the amount of coral available for settlement in 2000 was sufficient (despite the increased recruitment rates), but that there was increased post-settlement mortality as a result of overcrowding. However, the numbers of recruits in each coral head were not recorded during recruit surveys, therefore I cannot determine if this was the case. An alternative explanation is that a greater proportion of individuals settled into less preferred habitats in 2000, resulting in increased post-settlement mortality.

5.5.3 Spatial patterns

Spatial distributions of adults were very similar to those of recruits, which suggests that adult distributions are established at settlement, and remain largely unmodified by post-settlement processes. In some species, the spatial distributions of adults were slightly broader than those of recruits, indicating that the level of post-settlement modification of these patterns varies among species.

The spatial segregation in settlement patterns apparent from the recruitment data (Chapter 3) appears to translate into a similar pattern among adults. For over three quarters of the species examined, adult densities at the four depths within each of the four sites were related to recruit densities, however, for many species, the adult distributions were slightly broader than recruit distributions. Studies on different species and at different geographic locations have demonstrated that spatial patterns at settlement can be either reinforced (Wellington 1992; Jones 1997) or modified (Robertson 1997; Lecchini and Galzin 2005) by post-settlement processes (e.g., movement, spatial variation in post-settlement mortality). Therefore, the effect of post-settlement processes on spatial patterns of recruitment must vary among species and locations. In this study, there were several species for which there was high overlap among adult and recruit distributions in one year and not the other. This may have simply been due to lower sample sizes in one year affecting the outcome, or it may be that the importance of post-settlement processes varies among time periods.

The presence of adults or larger juveniles can influence settlement either positively or negatively. For example, new settlers might be attracted by the presence of conspecific adults or juveniles (Sweatman 1985, 1988; Jones 1987b; Booth 1992; Öhman et al. 1998; Lecchini, Planes et al. 2005; Lecchini, Shima et al. 2005), or they may be repelled by agonistic interactions with resident conspecifics (Öhman et al. 1998) or heterospecifics (Forrester 1995). For some of the species for which adult and recruit distributions overlapped, it may be that the adult distributions determine the spatial pattern of recruitment, rather than the other way around.

5.5.4 Family-level patterns

A number of family-level differences in recruit adult relationships, and the population responses of different species to habitat change emerged from this study. Damselfishes and wrasses dominate the Kimbe Bay reef fish communities, both in terms of recruit and adult densities (Jones et al. 2004; Chapter 2). However, although damselfish and wrasse species could exhibit similar levels of recruitment, damselfishes were consistently more abundant than wrasses. The large majority of damselfish species declined in abundance over the 5-year period. In contrast, wrasses exhibited a wide diversity of responses, including species that increased dramatically and others that declined in abundance. For all species that declined in abundance (75% of the whole community), damselfishes exhibited greater declines than wrasses. Although the degree of coral-dependence by new settlers appears to be important in explaining the magnitude and direction of population changes for both taxa, for damselfish and wrasse species with a similar apparent dependence on live coral, damselfish usually suffered a greater proportional decline in abundance when coral declined.

The reasons for the differences between the damselfishes and wrasses, and perhaps also among other reef fish families, require further investigation. Clearly, the magnitude of recruitment and its effect on adult numbers can vary according to life history traits such as growth, reproduction and longevity (Warner and Hughes 1988; Doherty 2002). Many life history traits are phylogenetically conservative at the family level. For example, parrotfishes (Scaridae) tend to be shorter-lived and exhibit more indeterminate growth trajectories compared with surgeonfishes (Acanthuridae) (Choat and Robertson 2002). Tropical wrasses tend to exhibit a greater range of body sizes and longevities than damselfishes (Choat and Bellwood 1991; Munday and Jones 1998), which may explain the greater diversity in their responses to habitat change. However, ecological factors may be equally important in explaining the observed patterns. On average, damselfishes are smaller, and small size is often associated with greater abundance (Jones et al. 2002), and may also be associated with a greater dependence on branching corals as both recruitment sites and adult habitat (Munday and Jones 1998). Also, the majority of damselfish species are planktivorous, while wrasses are more often benthic invertebrate feeders. Healthy coral reef environments may potentially support higher densities of planktivores, but equally, planktivores may be more susceptible to loss of coral habitat because of their mode of feeding requires them to forage above the substratum. Whatever the reasons, the distinct family-level patterns support calls not to base generalisations about the dynamics of coral reef fishes on studies of a few model species.

5.5.5 Recruitment as a determinant of adult density

The nature of the relationship between recruit and adult densities has provided useful insights into the role of density-dependence and the mechanisms of population regulation in coral reef fishes (Jones 1990, 1991; Caley et al. 1996; Hixon and Webster 2002; Osenberg et al. 2002). The recurring pattern that such relationships tend toward an asymptote at high recruitment levels has provided evidence of the increasing intensity of density-dependent processes acting on high recruiting populations. However, the importance of density dependence in coral reef fish populations has been a contentious issue (e.g., Jones 1991; Doherty 1991, 2002; Hixon and Webster 2002). An unexpected observation from this study was that recruit-adult relationships across whole reef fish communities also flatten out at high levels of recruitment. This suggests that high recruiting species may be more subject to regulatory mechanisms, while low recruiting species may often be recruit-limited. The reasons why some species consistently have higher recruitment than others, and why high recruitment does not translate into higher adult densities require further investigation. Again, the results support calls for a pluralistic approach to understanding population regulation

5.5.6 Fish-habitat associations and the future

The magnitude of the decline in coral cover in Kimbe Bay is not atypical of other geographic locations where coral has also been largely replaced by turfing algae (Hughes 1994; Sebens 1994; McClanahan 2002; Hughes et al. 2003; Gardner et al. 2003). Reefs without corals will no longer support diverse fish faunas, but rather will be numerically dominated by a small subset of species preferring algal or rubble substrata. There may also be a shift towards reef fish families that are less reliant on corals and a shift in the relative diversity of species in the different families. Although there is considerable potential for recovery from local disturbance if the habitat recovers (Halford et al. 2004; Berumen and

Pratchett 2006), the spatial extent of habitat devastation appears to be expanding rather than contracting (Hughes et al. 2003; Gardner et al. 2003).

Clearly, we must continue long-term studies of fish communities into the uncertain future that coral reef environments face. Our understanding of the dynamics of reef fish populations has grown as the longer-term patterns and trends have emerged. The increasing knowledge of species-specific differences in habitat specialisation and responses to habitat change has given us a greater appreciation of the real threats to reef fish biodiversity. However, even more fundamentally, as the family-wide ecological characteristics of coral reef fish faunas are unearthed, the threat to the deeper phylogenetic diversity of coral reefs is becoming apparent.

CHAPTER 6: GENERAL DISCUSSION

This first investigation into the recruitment of fishes on coral reefs in Papua New Guinea significantly extends our knowledge and understanding of the replenishment of coral reef fish populations. The study has added to the known global diversity of patterns in reef fish recruitment and has provided new insights into processes that establish these patterns on low latitude coral reefs. Five key discoveries can be highlighted: (1) Chapter 2 demonstrated that recruitment of most reef fishes in Kimbe Bay occurs over extended periods, with recruitment of many species occurring throughout the year; (2) A high level of specialisation on living corals as recruitment substrata and a strong response to depth gradients were identified in Chapter 3; (3) Chapter 4 experimentally established that depth-related settlement patterns are largely independent of the availability of preferred recruitment substrata, and quantified the fitness costs associated with settling at the extremes of, or beyond, the normal depth range; (4) In contrast, chapter 5 showed that while inter-annual variation in the magnitude of recruitment clearly influences population dynamics in the short term, long-term trends in population size appear to be driven by habitat-limited recruitment and habitat change; (5) Throughout the thesis, the multi-species comparisons provided a new family-level perspective on the recruitment strategies of the common fishes that settle onto equatorial reefs in the Indo-Pacific.

In this chapter, I will discuss the links between these recruitment phenomena, and highlight their significance for understanding population responses to climate change and coral reef degradation.

6.1 Recruitment in time: short-term patterns

As predicted, given the negligible variation in water temperature throughout the year, recruitment of most species occurred throughout the year or for extended periods (i.e. over 8 months of the year), although there was significant variation in the magnitude of recruitment among months for all but one species (Chapter 2). The majority of species had broad periods of peak recruitment, usually between April and November each year, with low or negligible recruitment during the wet season (December – February). This contrasts with recruitment patterns from higher latitudes in the southwestern Pacific (for example, Lizard Island on the Great Barrier Reef), where December – February (the Austral summer) is the period of peak recruitment (Doherty and Williams 1988; Doherty 1991). These results suggest that there are fundamental geographic differences in recruitment strategies and support the hypothesis that the monsoon climate of low latitude coral reefs in the Indo-Pacific is a major driver of seasonal spawning and recruitment patterns.

Monsoonal climate patterns have also been implicated as a determinant of recruitment seasonality at the San Blas Archipelago, the only other low latitude location for which there are comparative long-term data on seasonal patterns of reproduction and recruitment (Robertson 1990, 1992; Clifton 1995; Robertson et al. 1993, 1999). The recruitment patterns described for San Blas and Kimbe Bay are similar in that year-round recruitment occurs, with broad seasonal peaks and inter-annual variation in recruitment rates. The main difference between these two locations is that the temporal recruitment patterns appear to be driven by different climatic factors. In San Blas, onshore winds during the dry season have a negative influence on spawning and recruitment (Robertson 1990; Clifton 1995; Robertson et al. 1999), while in Kimbe Bay, recruitment rates of many species are lowest during the wet season. There is evidence that the seasonal pattern of spawning at San Blas is reversed at inshore reefs, where freshwater inputs during the wet season have a negative impact on productivity (Clifton 1995), and this suggests that seasonal patterns at low latitudes are contingent upon the exposure of reefs to prevailing winds and the strength of these winds, as well as the proximity of reefs to rivers/streams and the volume of rainfall during the wet season. In Kimbe Bay, even offshore reefs have similar patterns of recruitment (personal observation), which suggests that it is rainfall itself rather than freshwater inputs from land that might affect recruitment. A freshwater lens several metres deep can often be seen at the surface following periods of intense rain, and this is likely to have a negative impact on the survival of larvae found close to the surface. The extent of the geographic differences highlights the need for temporal recruitment studies at a greater range of low latitude locations around the globe. The specific factors that influence recruitment patterns, such as fluctuations in sea surface salinity during the wet season, and the influence of these fluctuations on larval survival and growth, require further investigation.

The extended spawning and recruitment periods in fishes on low latitude reefs are likely to have a number of important demographic consequences. Preliminary observations suggest that continuous breeding and recruitment may be associated with shorter life spans and smaller maximum body size in this region (Srinivasan 1997; Bray 2001; Hubble 2003). The combination of these factors may promote the sensitivity of these communities to gradually changing climatic conditions and/or habitat degradation. The extent of the recruitment period itself may explain differences in abundance among species and families, the data suggesting that species with longer recruitment seasons reach greater local abundance (Chapter 2). While continuous recruitment may reduce the potential for year-class phenomena, intensive sampling over 2.5 years did show short-term fluctuations in adult abundance that were strongly associated with an inter-annual variation in recruitment magnitude (Chapter 5). Higher recruitment in 2000 compared to 1999 translated to a short-term increase in adult numbers in 2001. Clearly, the demographic and life history consequences of continuous breeding and recruitment require further investigation.

6.2 Recruitment in space: response to microhabitats

There was a high level of specialisation of new recruits in terms of the microhabitats occupied (Chapter 3). Branching corals of the genera *Acropora* and *Pocillopora* were particularly important settlement microhabitats for the majority of coral specialists. There was also a suite of species in which new recruits were associated with non-living substrata. These extremes of microhabitat specialisation were clearly implicated in explaining long-term shifts in community structure, with a decline in coral specialists and an increase in species associated with non-living substrata and some of the generalists (Chapter 5). New recruits of over 65% of fish species occupied live branching corals in proportions greater than the availability of these corals would suggest. This high level of dependence on living corals for a reef fish community has not been previously demonstrated and is likely to be of major significance in predicting long-term responses to habitat change (see next section).

The degree of specialisation on microhabitats did not explain variation among species in the magnitude of recruitment or their distribution among macrohabitats (Chapter 3). The lack of relationships among these factors does not support the predictions that specialists will generally be less abundant and/or more narrowly distributed than generalists, due to being restricted to a smaller range of recruitment sites (Brown 1984; McNally 1995; Morris 1996; Hughes 2000). There was also no evidence that microhabitat specialists were more abundant than generalists in their preferred microhabitats due to efficient use of resources and competitive dominance in their preferred recruitment sites (Futuyma and Moreno 1988; Caley and Munday 2003). While specialisation on branching corals clearly has implications for abundance when coral cover changes, the degree of specialisation may be less important than understanding the specific microhabitat requirements of each species. In future, descriptions of microhabitat specialisation at settlement need to be refined to take account of potential species-specific associations between fish recruits and corals.

6.3 Recruitment in time: long-term patterns

The long-term decline in coral cover on the inshore reefs in Kimbe Bay between 1997 and 2002 resulted in a decline in population size for the majority of the fish species examined, and a shift in community structure (Chapter 5). The magnitude of change in population size was related to the degree of dependence on live branching coral at settlement, which suggests that long-term population dynamics of many of the species are driven largely by habitat-limited recruitment. This result supports those from other studies, demonstrating the importance of the availability of suitable settlement microhabitats on the dynamics of populations (Holbrook et al. 2000) and communities (Holbrook et al. 2002; Syms and Jones 2002). Although short-term fluctuations in larval supply may also influence populations, periods of high recruitment may be associated with overcrowding in restricted microhabitats. Thus, density-dependent mortality may further exacerbate the effects of habitat loss and fragmentation.

The role of recruitment in explaining long-term responses to habitat change requires further investigation. There is increasing evidence that fish communities are changing, not just as a result of the immediate loss of living corals, but also due to longer-term changes in the topographic complexity of reefs (Graham et al. 2006; Wilson et al 2006). Unfortunately patterns of recruitment of many of the larger species are poorly understood, as they recruit in low numbers and/or into complex reef habitat. Hence, whether changes to these species are due to effects on recruitment or reduced survival associated with loss of shelter needs to be evaluated. The clear dependence of many reef fish species on shallow water macrohabitats (see next section), suggests that the long-term erosion of reefs will expose a new suite of species to the effects of reef degradation.

6.4 Recruitment in space: response to macrohabitats

A number of larger scale spatial patterns in recruitment were detected, primarily in response to depth gradients, but also differences among reef zones, and reefs at different distances from shore (Chapter 3). Both species-level and family-level regression tree analyses found that most of the variation in recruitment was explained by depth. In chapter 5, I show that these large-scale patterns in recruitment are a primary determinant of the spatial distributions of adult fishes. Unlike the long-term temporal response to declining coral cover, larger scale spatial distributions were not explained by the spatial distribution of suitable microhabitats. Even within preferred depth ranges and reef zones, microhabitat availability explained a limited amount of the variation in the abundance of new recruits of most species. An experiment in which the same microhabitats were provided at different depths clearly demonstrated that depth-related settlement patterns were largely independent of microhabitat availability (Chapter 4), suggesting that species are sensitive to other depth-related factors. However, further work is required to establish what these factors are.

These results are supported by those from other studies that highlight the minor role that microhabitat characteristics may have in determining large-scale spatial (Tolimieri 1995, 1998b; Caselle and Warner 1996; Jones 1997; Ault and Johnson 1998; Sale et al. 2005) or depth (Wellington 1992; Jones 1997) distributions of juvenile fishes. Nevertheless, other studies have shown that microhabitat availability can explain large-scale patterns in the abundance of recruits (e.g. Tolimieri 1998a, b; Schmitt and Holbrook 2000). The diversity of findings suggests that spatial patterns of recruitment can be limited by many factors other than microhabitat availability, and that the importance of microhabitat availability in determining spatial recruitment patters may vary among species, families, spatial scales and locations.

In another experiment, I demonstrated that there are fitness costs associated with settling outside or at the extremes of a species' normal depth range (Chapter 4). These costs are likely to reinforce the effects of recruit depth distributions on the spatial distribution of adults. The results also suggested that these costs are likely to vary depending on the level of depth specialisation of the species. For one of the species examined, *Dascyllus melanurus*, which is restricted to shallow water (< 6 m), placing juveniles at greater depths resulted in higher mortality and reduced growth. For another species, *Chrysiptera parasema*, which settles mostly in deeper water (10 – 15 m) but has a broader depth range than *D. melanurus*, growth and mortality rates of juveniles did not differ among depths. These results support the prediction that habitat specialists might have greater survival and growth rates than generalists within their preferred habitat, but generalists are able to do moderately well over a greater range of habitats (Futuyma and Moreno 1988; McNally 1995). Further support for this prediction comes from a recent study in Kimbe Bay, which has demonstrated that when juveniles of these two species are placed together, *D. melanurus* is competitively dominant over *C. parasema* (Bonin et al. unpublished ms).

Although recruitment was the primary factor in explaining the larger-scale spatial distributions of adults for the majority of species (Chapter 5), for some species, adult distributions were slightly broader than those of new recruits. Clearly, spatial patterns established at settlement have the potential to be either reinforced or modified by movement or spatial variations in mortality following settlement (Jones 1997; Robertson 1997; Lecchini and Galzin 2005). The results of this study indicate that spatial distributions established at settlement remained largely unchanged by post-settlement processes in some species, while in other species, some post-settlement expansion was occurring. There were also some species for which there was high overlap between adult and recruit distributions in one year but not the other. These results suggest that the effects of post-settlement processes on spatial distributions can vary among species and temporal periods, and possibly among locations.

6.5 Family-specific recruitment strategies and recruit-adult relationships

The two focal families in this thesis, the damselfishes and wrasses, together accounted for 90% of the total recruitment recorded. These two families exhibited several notable differences in their recruitment strategies. Temporal recruitment patterns of wrasses were typically less seasonal than those of damselfishes, with an average recruitment period of 11 months per year for the wrasses and 9 months per year for the damselfishes (Chapter 2).

There were a few species of damselfish for which recruitment periods of 6 months of the year or less were recorded, while over half the wrasses had recruitment occurring during all months of the year (Chapter 2). Recruitment of most of the damselfishes was low or negligible during (and just after) the wet season, however, for many of the wrasse species, recruitment was often high during (or just after) the wet season. This contrast might be explained by differences between the two families in the susceptibility of their larvae to fluctuations in salinity in shallow water during periods of intense rainfall, and/or in the vertical distributions of their larvae (Doherty and Carleton 1997; Leis 1991a, b; Fisher 2004).

In term of their spatial distributions the two families were quite similar. Their larger scale distributions were most strongly influenced by depth (Chapter 3). In addition, there were species in both families that were specialised either on live branching coral or on non-living substrata, as well as species that were less specialised.

There were notable similarities and differences among families in recruit-adult abundance relationships. Although both damselfishes and wrasses exhibited strong relationships between recruit and adult abundances, the same level of recruitment translated to a greater number of adults among damselfish species compared to the wrasses (Chapter 5). Despite this (and the similarities in the degree of dependence on live coral between the two families), the decline in coral cover appeared to have a greater impact on the damselfishes than the wrasses, with proportionally more species declining in abundance, and with greater magnitudes of decline, among the damselfishes. Life history characteristics such as longevity, reproduction and growth can determine the influence of recruitment on population size (Warner and Hughes 1988; Doherty 2002), and can be phylogenetically conservative at the family level. The greater range of responses to habitat change among the wrasses could be a result of the greater range of body sizes and longevities among wrasse species compared to the damselfishes (Choat and Bellwood 1991). An alternative explanation is that the smaller average size of damselfishes is associated with greater abundance (Jones et al. 2002) and/or greater dependence on branching corals as recruit/adult habitat (Munday and Jones 1998).

Although differences and similarities among damselfishes and wrasses were a recurring theme of this thesis, further work is required to determine whether family-level patterns in recruitment strategies and their consequences extend to other reef fish families. In addition, relationships between recruitment and other life history strategies such as growth and longevity require further investigation. Within families, the recruit-adult relationships suggest that low recruiting species may be recruitment-limited (sensu Doherty and Fowler 1994), while high recruiting species may be subject to stronger regulation by post recruitment processes. While most investigations into the relative importance of recruitment and density-dependent processes focus on variation within individual species (e.g. Jones 1991; Hixon 1991; Doherty 2002; Osenberg et al. 2002), the results presented in this thesis suggest that comparisons of low and high recruiting species may assist in explaining the relative importance of the processes limiting the sizes of reef fish populations.

6.6 The future: coral reefs in crisis and research priorities

My study on coral reef fish recruitment in Papua New Guinea began at the turn of the millennium. At the same time, the detrimental effects of human activities on coral reef fishes were first being documented for this region (Jones et al. 2004, Munday 2004). Given the dire predictions that have been made for coral reefs in the coming decades (Hoegh-Guldberg 1999; Hughes et al. 2003; Donner et al. 2005), we face a steep learning curve if we are to significantly improve the predicted fate of coral reefs. The low latitude coral reefs in the Indo-Pacific are likely to be among the first severe coral reef casualties and should remain a high research priority. They may be particularly sensitive to global warming as most of the corals here are already living close to their thermal limit. In addition, reefs in the region may lack resilience as many are already subject to severe impacts associated with human population growth, dependence on marine resources and coastal land use.

The new information provided here suggests that the recruitment strategies of coral reef fishes in the region place them at risk of severe depletion or extinction from climate change. Global warming may directly modify the monsoonal climatic conditions, which I predict will drastically impact on the reproduction, larval survivorship and recruitment of reef fishes. The effects of climate change on bleaching and loss of branching corals will further reduce recruitment and the survival of juveniles of the majority of species. The high level of specialisation at this location, combined with consistently high water temperatures, will mean that the fish communities are more susceptible to a range of human impacts, particularly those associated with global warming. Further research on fish recruitment in PNG and other low latitude locations is vitally important, as the clues for how best to protect reef fish species will come from understanding what is happening to them.

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