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# Recruitment hotspots around a coral reef: the roles of hydrodynamics and habitats

Thesis submitted by

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# Abstract

The patterns and causes of variation in recruitment are widely acknowledged as major determinants of the spatial structure of coral reef communities, both for corals and reef-associated fishes. Atolls and isolated platform reefs often form discrete adult populations and management units for reef organisms. Recruitment to such reefs as a whole and spatial variation at the scale of whole reefs is, however, poorly understood. In addition, concomitant patterns in the recruitment of both corals and fishes have never been investigated. This study examined patterns of variation in coral and fish recruitment around a platform reef on the southern Great Barrier Reef (One Tree Reef) over three years. Using both descriptive and experimental approaches, it examined the roles of hydrodynamic processes and the composition of benthic assemblages as potential causes of recruitment variation across the reef. The aims were to detect persistent "recruitment hotspots" that may be vital to the replenishment and management of reef isolates, and to develop an understanding of why recruitment hotspots occur where they do.

Variation in hydrodynamic regimes in the boundary layer and in the free-stream flow around One Tree Reef was investigated to determine potential differences in larval supply to different areas around the reef. Plaster dissolution was used to assess net water movement on a hierarchy of scales: among locations one to three kilometres apart, among sites within one kilometre of each other and within metres at each site. In the boundary layer, the greatest amount of variation in water movement (69 %) was found within metres at sites, thus precluding comparisons among sites or among locations. In the free-stream, the greatest amount of variation (73 %) was attributable to differences

among sites. Relative ranks of sites according to water movement were consistent when measured at different times, although variability in wind direction affected locations. In the free-stream, mean water movement was 1.5 to 1.8 times greater at some sites compared with others. For flow in the free-stream, variability in water movement among sites could significantly affect cumulative larval supply and subsequent recruitment to assemblages in different areas. When larvae enter the boundary layer they are, however, also likely to be influenced by patterns of flow that are probably determined by small-scale (centimetres to metres) topography.

Patterns of variation in the composition of benthic coral reef assemblages around a reef were investigated to determine whether they persisted over time, and whether they were related to variation in net water movement. Benthic assemblage structure is known to influence recruitment patterns for coral and fish larvae, therefore, significant and predictable variation in the benthic composition among sites, and relationships between assemblages and water movement, could influence spatial patterns of recruitment at this scale. Two different types of sampling units were used to assess the benthic composition of coral reef assemblages: transects sampled the substratum under points spaced along 50 metres of the reef margin, while quadrats sampled the substratum under points located within a 1 $m^2$ area. The relative compositions of benthic assemblages were variable among sites, but patterns of relative variation persisted over two to three years using both types of sampling unit. The nature of linear relationships between benthic composition and net water flow, however, differed between sampling units. In quadrats the multivariate composition of coral assemblages was significantly linearly correlated with water flow, however, in transects only the percent cover of some particular benthic categories were linearly correlated with water flow. Nevertheless, overall patterns in the benthic composition of assemblages around One Tree Reef were relatively consistent over the length of the study period, related to patterns of water flow, and together defined stable characteristics of sites likely to be important to the recruitment of reef corals and fishes.

Variation in recruitment of scleractinian corals and potential associations with net water flow, adult abundance and settlement substrata were examined around One Tree Reef. Although overall recruitment rates were very low compared to other studies of recruitment on the Great Barrier Reef, particular sites, both on the reef slope and in the lagoon, had consistently higher recruitment. These ‘recruitment hotspots’ (two or greater recruits per tile on average for two or more deployment periods) were, however, at different sites for different coral families. Variation in recruitment of pocilloporids and poritids, but not acroporids, was related to the percentage cover of adult colonies at each site. Recruitment hotspots were more common at sites with medium levels of water flow in the lagoon (4.6 $cms^{-1}$), but there were no clear relationships on the slope. In contrast, in experimental aquaria, *Acropora nasuta* settlement was six to ten times greater under low water flow speeds (2.1 $cms^{-1}$), compared to medium water flow speeds. This indicated that recruitment hotspots in the field might be more related to larval supply than to larval selection for medium flow sites. Differences in patterns of recruitment among taxa may have also been due to brooding and spawning life history strategies.

Identifying congruent recruitment hotspots for reef corals and fishes and their causes, represents a potentially powerful tool for understanding reef-wide persistence and resilience, and prioritizing management areas within reefs. Spatial variation in recruitment around a reef was monitored for three species of planktivorous coral-dwelling fishes, *Pomcentrus moluccensis*, *Chromis viridis* and *Dascyllus aruanus* and relationships with net water flow and benthic composition were examined. As for coral taxa, for all species there were 'recruitment hotspots', where recruitment was two to three orders of magnitude (10's to 100's of fish per 100 $m^2$) greater than at other sites (less than 1 fish per 100 $m^2$). One site was a recruitment hotspot for all three species, but other sites were recruitment hotspots for just one or two species. Deterministic factors contributing to consistent patterns at this scale included positive relationships with the abundance of recruit microhabitats for *P. moluccensis* and *C. viridis*, and relationships with net water flow, though the nature of relationships with water flow differed between species, and also between the lagoon and slope environments. There was no clear relationship between recruitment and net water flow for *D. aruanus*, and recruitment was greatest at sites in the lagoon where the coral microhabitats to which this species recruited were intermediate in abundance. Relationships between recruiting fish and microhabitats may have been confounded by interactions between net water flow and microhabitats. Flow variation not only affected the abundances of coral taxa but also their morphology. Lower flows produced coral colonies with a wider branching morphology that were preferred by recruits. Nevertheless, recruitment hotspots for coral reef fishes were clear and could be predicted using a combination of hydrodynamic and benthic influences and their synergistic relationships.

In summary, patterns of spatial variability in hydrodynamics and benthic composition around a reef persisted over time and were two factors that influenced recruitment patterns in reef corals and fishes. 'Recruitment hotspots' were identifiable for all three coral families, and all three fish species, although these sites were not the same for all taxa, reflecting differences in their relationships with hydrodynamics and benthic composition. Interestingly, relationships between patterns of recruitment, hydrodynamics and benthic composition varied not only among taxa, but also between lagoon and slope environments for individual taxa. Sites in the lagoon and on the slope that were recruitment hotspots for more than one taxon were, however, clustered in one area on the leeward side of the reef, and may have related to patterns of larval accumulation at a larger scale. Although there is a general consensus among coral reef ecologists that recruitment is variable, this study adds to the growing body of literature suggesting that predictable and persistent recruitment hotspots occur around coral reefs. This variation should be taken into account in the selection of sites for ecological research and for reef management.

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# STATEMENT ON SOURCES

## ***Declaration***

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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# Chapter 1 - General Introduction

Identifying the processes that determine the structure and dynamics of populations and communities has been a major avenue of ecological research (Begon et al. 1996, Krebs 2001). As ecological theory developed, the early focus was on processes that operate within local assemblages, such as predation, competition and biological disturbance (Dayton 1971, Schoener 1974, Connell 1978, Sih et al. 1985). Later work highlighted that the structure of local assemblages could also be constrained by their regional context, and that large-scale factors such as climatic regimes and the regional species pool could be more important than local interactions (Ricklefs 1987, Caley & Schluter 1997). Given that processes operating at both local and regional scales may contribute to patterns observed at a range of spatial scales, a multi-scale approach is now advocated (Ricklefs & Schluter 1993, Cornell & Karlson 1996, Moerke & Lamberti 2006).

The shift in emphasis from local to large-scale processes was perhaps greatest in the field of benthic marine ecology (Roughgarden et al. 1988, Underwood & Fairweather 1989, Underwood & Keough 2001). Early work focused on local-scale patterns and interactions among adult individuals, and little attention was paid to where these individuals came from. While it was recognized that most benthic marine organisms are characterised by a life history that involves a pelagic larval stage, little attention was given to the processes operating during this early stage. Larval supply and recruitment were only later recognised as important factors contributing to the structure and dynamics of these types of assemblages –and so called “supply-side” ecology emerged (Connell 1985, Underwood & Fairweather 1989).

The relative importance of processes associated with supply and demand acting on local benthic marine assemblages has been the subject of much debate (Butman 1987, Olafsson et al. 1994, Caley et al. 1996, Brunton & Booth 2003). Current opinion is that for assemblages where recruitment is low and resources unlimited, supply-side processes are more important. In contrast, for assemblages where there is a surplus of recruits and resources are limited, local interactions such as predation, competition and biological disturbance are thought to be more important (Gaines & Roughgarden 1985, Connolly & Roughgarden 1998, Svensson et al. 2004). Larval supply and recruitment are, however, highly variable at almost every spatial or temporal scale that they have been measured (Caffey 1985, Doherty 1991, Caley et al. 1996). This means that the relative contribution of processes associated with either a limited supply or a surplus of recruits will also vary in space and time.

The debate over whether supply-side processes, or interactions resulting from a surplus of recruits, are more important has been prominent in the literature on tropical coral reefs. This is true not only for populations of key benthic organisms, such as reef-building scleractinian corals (Tanner et al. 1994, Connell et al. 1997), but also for the highly visible and diverse coral-associated fishes (Sale 1977, 1980, Robertson 1988, Hixon 1991, Jones 1991, Doherty 2002). The emphases of these previous studies have been on whether or not assemblages reach ‘equilibrium’ or ‘climax’ states governed by post-recruitment interactions, or whether variation in supply-side processes results in assemblages that are in a constant state of succession and are inherently variable. After almost thirty years of research, the general consensus is that both post-recruitment processes and larval supply are important contributors to assemblage structure (Caley et al. 1996, Doherty 2002), arguing for a multi-factorial approach.

The relative importance of processes associated with supply and surplus to the structure and dynamics of coral reef assemblages will, however, vary according to scale. At larger scales, the structure of coral reef assemblages shows distinctive patterns in response to historical factors and physical gradients. For example, both corals and fishes exhibit concordant changes in species composition with latitude (Caley 1995a, Hughes et al. 1999, Hughes et al. 2002) and distance from shore (Done 1982, Williams 1982, Sammarco 1983, Williams & Hatcher 1983, Ninio & Meekan 2002). Where the mechanisms driving these large-scale patterns have been explored, it appears that they are driven by patterns of recruitment, rather than being the consequence of post-recruitment processes (Hughes et al. 2000, Doherty 2002). In contrast, although larval supply is an important factor at small scales, species composition and abundance change over time according to the recent history of space occupancy, disturbance, competition and predation (Sale 1975, 1978, Hughes 1994, Tanner et al. 1994, Connell et al. 1997). The ultimate effects of processes operating at small and large scales are not independent, however, as large-scale processes will affect what happens at local scales (Karlson & Cornell 1998), and small-scale interactions can scale up to explain large scale patterns (Steele & Forrester 2005).

Coral reef habitats often exist as discrete platform reefs or atolls that may be hundreds of metres or many kilometres in diameter, and which may be separated from other coral reefs by many kilometres of open water (Veron 1986). Recurring patterns in the distribution of corals and fishes around discrete reef structures such as atolls or platform reefs are perhaps best viewed as intermediate in scale. They will be influenced by both small-scale biological interactions such as competition and predation (Bouchon-Navaro 1986, Eagle et al. 2001, Jompa & McCook 2002, Almany 2003, Munday 2004) and the regional scale supply of larvae of different species (Caley 1995b, Hughes et al. 2000). There will also be processes that inherently operate at the whole-reef scale, such as exposure gradients (Fabricius 1997, Friedlander et al. 2003, Fulton & Bellwood 2004, Nanami et al. 2005), variation between broad-scale habitats such as lagoons and reef slopes (Munday et al. 1997, Newman et al. 1997, Sale et al. 2005), and spatial patterns in hydrodynamics, larval supply and recruitment (Andrews et al. 1988, Cowen & Castro 1994, Milicich 1994). In general, however, processes operating at intermediate scales are poorly understood.

At intermediate scales around individual reefs, tracts of superficially similar reef habitat may extend for hundreds of metres to kilometers. However, even within such habitats, patterns in the distribution and abundance of reef organisms and in the recruitment of their pelagic larvae may be highly variable due to the interrelated influences of topography and hydrodynamics (Chiappone & Sullivan 1996, Edmunds & Bruno 1996, Archambault & Bourget 1999, Danilowicz et al. 2001, Eagle et al. 2001). Such patterns are usually the hidden "site" effects in sampling designs that take account of local variation, only in order to estimate larger scale patterns (e.g. Hughes et al. 1999, Murdoch & Aronson 1999, Sale et al. 2005). Site variation is rarely the focus of ecological studies. Where detected it is usually considered to be 'random' and there is little exploration of contributing mechanisms or temporal persistence of patterns (but see Booth et al. 2000, Hamilton et al. 2006). To date it remains unclear whether patterns of spatial variation in coral reef assemblages and recruitment at this scale are more predictable (as it appears to be at larger scales) or whether variation is more unpredictable (as it often is at smaller scales). The magnitudes of recruitment variation among areas at this scale, persistence of these patterns over time or potential causes have rarely been studied.

Ecological patterns at a reef-wide scale may be particularly important, given that this is often the scale at which coral reefs are divided up into management units (Beger et al. 2003, Sobel & Dahlgren 2004). In the selection of sites to maximize biodiversity in protected areas, knowledge of the degree of congruency among different taxa is very important (Gaston 1996, Beger et al. 2003) and diversity hotspots that coincide for a range of organisms represent conservation priorities. If recruitment is persistently higher in some reef areas, this could also be important to the selection of reef areas using ecological criteria for marine protected areas (Roberts et al. 2003). These ‘recruitment hotspots’ (sensu Booth et al. 2000) could be important if they support a higher diversity, recover more quickly after disturbances, and/or enhance fisheries productivity through larval export and spillover of highly productive populations. Furthermore, if areas of high recruitment are the same for many taxa, then careful allocation of these areas for use or conservation could affect desired reserve functions. Knowledge of the temporal consistency in recruitment patterns across reefs would not only contribute to our understanding of the processes structuring coral reef assemblages, but could also be applied to ensure the economic sustainability of our coral reef ecosystems.

### *Recruitment and hydrodynamics*

Hydrodynamic regimes around reefs and along reef tracts at intermediate scales are likely to influence the distribution patterns and subsequent recruitment of pelagic larvae. Interactions among prevailing large-scale currents, wind patterns, tides, local bathymetry, and coral reef shape, size and spacing cause hydrodynamic features such as convergences, eddies, and wakes behind islands and promontories (Hamner & Wolanski 1988, Wolanski 1988, Furukawa & Wolanski 1998, Wolanski et al. 2003). Under particular sets of tide and/or wind conditions hydrodynamic features are likely to consistently reoccur in certain reef areas (Alldredge & Hamner 1980), subsequently reef areas separated by tens of metres to a few kilometres might experience considerable variation in the extent of mass water movement, current speeds and directions.

Theoretically, reef areas that have consistently higher flow rates and therefore water exchange should receive greater supplies of larvae from outside assemblages than areas with low flow rates. Hydrodynamic features around reefs, however, not only modify current speeds and direction, but may accumulate passive larvae in or near these features, and more motile taxa may actively aggregate around existing accumulations for food or shelter (Hamner & Hauri 1981, Black 1988, Hamner et al. 1988, Wolanski & Hamner 1988, Kingsford 1990, Kingsford et al. 1991, Kingsford 1993, Rissik & Suthers 2000, Carleton et al. 2001a, Carleton et al. 2001b). To date, however, there are few detailed descriptions of patterns of water flow at scales relevant to potential rates of larval supply to assemblages at different sites within and around isolated coral reefs.

Hydrodynamic regimes could potentially generate similar spatial patterns of recruitment for different taxa, however, there have been no integrated studies of recruitment across key reef organisms. A natural choice for such a study is a comparison of recruitment in scleractinian corals and their associated coral-dwelling fishes. Many reef fish are highly dependent on corals for shelter (Hixon & Beets 1993, Jones & McCormick 2002, Almany 2004a, b) and the health of coral habitat is often dependent on key herbivorous and predatory fishes (Sammarco & Carleton 1981, Liberman et al. 1995, Gleason 1996, Bellwood et al. 2003). Therefore the recruitment dynamics of corals may have important implications for fishes and vice versa. The recruitment patterns of fishes may be constrained by recruitment patterns of corals even though the larvae of these two taxa differ in pelagic larval duration, sensory and swimming capabilities and responses to hydrodynamic and benthic settlement cues.

Patterns of distribution and abundance of pelagic larvae in response to hydrodynamic patterns have been studied for reef corals and fishes independently at two reefs on the Great Barrier Reef: Helix and Bowden Reefs (Black 1988, Sammarco & Andrews 1988, Willis & Oliver 1988, Carleton et al. 2001a). While not all of the same sites were sampled for both taxa, where sampling did overlap, sites of high recruit abundance for fish were in approximately the same areas as sites of high recruit abundance for corals. These areas were characterised by long water residence times demonstrating how ‘recruitment hotspots’ could be generated by hydrodynamic patterns for taxonomically distinct taxa, as has been found for closely related taxa (Booth et al. 2000).

The combined results of the Helix and Bowden studies are inconclusive, however, for two reasons. Firstly, the areas of larval accumulation were for the sum of all fish species and for the sum of all coral families. Individual distribution patterns within each of the coral and fish groups differed when broken into more detailed taxonomic categories as has been found in other studies of coral and fish recruitment patterns at this scale (Babcock 1988, Sponaugle & Cowen 1997, Tolimieri et al. 1998). At Helix and Bowden Reefs these patterns were thought to relate to brooding or spawning reproductive strategies in corals and swimming abilities for fishes. Secondly, these studies demonstrated that there were differences in patterns of distribution of larvae in the water column, but they did not demonstrate that these patterns translated into settlement and recruitment onto the reef itself. Variation among taxa in settlement cues and preferences could potentially disrupt initially similar patterns of pelagic distribution and abundance translating to patterns of settlement and recruitment to benthic habitats.

Even if larvae are aggregated in particular areas around reefs due to hydrodynamic processes, not all taxa may settle due to their settlement preferences for specific water flow regimes. For example, the larvae of two coral species from two different families exhibited different settlement responses to currents in aquaria. The percentage of larvae that settled remained constant with increasing current speed for *Pocillopora damicornis,* but decreased with increasing current speed for *Heliopora coerulea* (Harii & Kayanne 2002). Similarly, recruitment of three congeneric fishes in the field had contrasting relationships with current speed (Schmitt & Holbrook 2002b). Settlement increased linearly with current speed for *Dascyllus flavicaudus*, reached a maximum at low to medium current speeds after which it declined for *Dascyllus trimaculatus*, and formed an asymptote at low to medium current speeds for *Dascyllus aruanus*. While water movement has the potential to influence larval supply, specific hydrodynamic preferences of individual taxa ultimately influence whether or not they settle.

A detailed description of specific water flow regimes at intermediate scales and their temporal persistence is a precursor to the examination of the patterns and causes of recruitment variation in reef corals and fishes. There are two components to variation in water movement among sites around a reef. Water movement in the boundary layer constitutes the small-scale flow environment directly above the benthos. The boundary layer ends and free-stream flow begins where water movement ceases to be affected by bottom friction (Vogel 1994). Water movement in the boundary layer is determined by the interaction of free-stream currents with the structure or topographical complexity of the benthic environment (Shashar et al. 1996). To date there are few studies that compare the extent of variation in these two flow regimes around reefs, and there is a paucity of empirical data defining water movement at this scale.

### *Recruitment and habitats*

As well as their individual responses to hydrodynamics, coral and fish larvae have variable settlement responses according to the availability of suitable benthic habitats. Coral recruitment is increased in the presence of particular types of encrusting coralline algae (Heyward & Negri 1999, Negri et al. 2001, Baird & Morse 2004), in damselfish territories (Sammarco & Carleton 1981, Gleason 1996) and conspecific adults (Lewis 1974, Tioho et al. 2001, Soong et al. 2003), and decreased in the presence of soft corals (Maida et al. 1995a), macroalgae (Kuffner & Paul 2004) and tabulate corals (Wallace 1985, Fisk & Harriott 1992, Baird & Hughes 2000). For fishes, some species are habitat specialists and recruit to just one or a few coral or other invertebrate species (Danilowicz 1996, Munday et al. 1997, Elliott & Mariscal 2001), while other species have a less defined, but still highly dependent relationship on a more generalized recruitment habitat type, which incorporates features such as reef topography (Bell & Kramer 2000, Holbrook et al. 2002, Nanami & Nishihira 2004).

Particular areas around reefs may be recruitment hotspots due to their hydrodynamic patterns, but only if benthic characteristics are suitable for settlement. Benthic composition has the potential to vary over time, however, even if hydrodynamic conditions remain relatively constant. Variation in the benthic composition of coral reefs is predictable at large scale but becomes increasingly unpredictable at small scales (Green et al. 1987, Pandolfi 2002). At large scales the composition of benthic assemblages relates to physical gradients and regional species pools'. These assemblages persist over time, and even in the presence of a natural disturbance regime they may move back toward an 'equilibrium' state through succession (Done 1992, Ninio et al. 2000, Halford et al. 2004), though this may not be the case where disturbances are anthropogenic (Hughes 1989, 1994, Hughes & Connell 1999).

In contrast to variation at larger scales, at small scales (metres) assemblage structure may be less predictable at any one point in time (Tanner et al. 1994, 1996) While the species found within a particular plot will be a subset of all those found in the larger scale environmental niche, the composition will change over time according to the recent history of space occupancy, disturbance, competition, predation and larval availability (Hughes 1994; Tanner et al. 1994; Connell et al. 1997). The scale at which there is a transition from predictability to unpredictability has not yet been established. It is unknown whether variation in areas around reefs and along reef tracts in the same broad-scale habitats are unpredictable, as at small scales, or more predictable and related to physical parameters, such as hydrodynamics, at larger scales. Any study attempting to examine recruitment variation and the existence of recruitment hotspots that persist over time due to potential relationships with benthic composition must first determine whether benthic composition at this scale is variable over space and predictable over time.

### ***Recruitment, hydrodynamics and habitat in reef corals and fishes***

Successful recruitment of juveniles is an important aspect of the population biology and community structure of reef corals (Hughes 1985, Babcock 1991). Recruitment plays a critical role in the distribution and abundance of species (Connell et al. 1997), is postulated as a major determinant of scleractinian community structure (Connell 1973, Birkeland et al. 1981, Done 1982) and coral populations are dependent on sexual recruits for recovery after catastrophic disturbances (Sammarco 1985). Spatial variation in recruitment has been examined on a hierarchy of spatial scales (Hughes et al. 1999), however, temporal persistence in patterns of variation around reefs and causes of variation at this scale have not been examined. Coral settlement responds to both hydrodynamic processes (e.g. Andrews et al. 1988, Harii & Kayanne 2002) and benthic composition (e.g. Maida et al. 1995b, Baird & Hughes 2000) so it would be predicted that around reef variation in these two parameters would affect variation in recruitment around reefs. To date there have been no studies that simultaneously examine patterns in recruitment, hydrodynamics and benthic composition around reefs, their interrelationships and relative importance.

Temporal and spatial variation in recruitment of coral reef fishes and its consequences has been the subject of extensive study and review (Sale et al. 1984a, Doherty & Williams 1988, Doherty 1991, 2002). Variation in recruitment of coral reef fishes is thought to relate mostly to hydrodynamic phenomena and the regional supply of larvae at large scales (tens to hundreds of kilometres) (Caselle & Warner 1996, Cowen 2002, Nishimoto & Washburn 2002, Paris & Cowen 2004), and to the availability of suitable microhabitats at the smallest scales (tens to hundreds of metres) (Williams & Sale 1981, Booth 1992, Tolimieri 1995, Holbrook et al. 2000). At intermediate scales there is likely to be a transition in the relative importance of hydrodynamic versus habitat processes affecting recruitment, but where this occurs is unknown, mainly because the relative influence of hydrodynamics and habitat on patterns of variation in recruitment around reefs has rarely been explored simultaneously (but see Booth et al. 2000).

Hydrodynamics and habitats are, however, not independent factors. Variation in the abundance and morphology of coral habitats around reefs according to hydrodynamic regimes may further complicate patterns of recruitment in fishes reliant on coral shelters for recruitment habitat, but to date this has not been examined using a holistic approach.

## Objectives and outline

The aim of this research was to provide the first integrated study of patterns of coral and fish recruitment, and their association with hydrodynamic regimes and benthic composition at the scale of a discrete platform reef on the Great Barrier Reef. To do this, the substantially different lagoon and reef slope environments were partitioned. The hydrodynamic variation around the reef and the persistence of spatial variation over time was examined to determine the potential for variation in larval supply among sites. Spatial variation in benthic composition among sites was examined to describe differences in potential habitats for settlement among sites and to investigate how this related to hydrodynamic processes. Temporal persistence of spatial patterns in coral recruitment and fish recruitment among sites was examined in relation to variation in hydrodynamic conditions and benthic composition.

Chapter 2 details an experimental test of the hypothesis that significant variation in hydrodynamics among sites occurs around a coral reef and is consistent over time, which could lead to consistent differences in larval supply. Plaster dissolution was used to obtain a time-averaged index of relative water movement for each site, which was compared with coral reef assemblages and patterns of recruitment in subsequent chapters. Net water movement was examined both in the water column and at the substratum level, and the usefulness of these two techniques for measuring water movement in topographically heterogeneous habitats such as coral reefs was evaluated.

Chapter 3 investigated whether variation in the benthic composition among sites on a coral reef was predictable over short time scales, like at larger scales, or unpredictable, like at smaller scales. Two scales of benthic composition were examined, within 1 $m^2$ quadrats and along 50 m long transects, which are two techniques commonly used in studies on coral reefs. Furthermore, the relationship between the two scales of benthic composition was investigated, as were their relationships with site-specific net water movement.

Chapter 4 investigated the hypothesis that there was significant spatial variation in recruitment of three coral families (Pocilloporidae, Acroporidae and Poritidae) among sites around a reef, but that these patterns were persistent over time and likely to relate to variation among sites in net water movement and benthic composition. Two scales of benthic composition likely to be important to a settling larva were compared: within a metre of settlement tiles and over 150 metres along the reef tract defining a ‘site’. Furthermore, the relative importance of water flow and the site at which tiles were conditioned were examined in experimental aquaria for *Acropora nasuta* larvae.

Chapter 5 investigated the hypothesis that there was spatial variation in recruitment of three coral-dwelling species of pomacentrid fishes (*Pomacentrus moluccensis*, *Chromis viridis*, *Dascyllus aruanus*) among sites around a reef, which were persistent over time, and related to variation among sites in net water movement and benthic composition. Furthermore, the impact of the interaction between hydrodynamics and habitat on the recruitment of two of these species through effects on coral colony morphology was assessed using a settlement choice experiment.

Finally, chapter 6 provides an overview of the major findings of each chapter, compares recruitment hotspots for corals and fishes, and considers the significance and implications of this research, both in terms of contributing to our understanding of the structure and dynamics of coral reef assemblages at multiple scales and in different habitats, and to the management of coral reefs.

# Chapter 2 - Experimental evaluation of spatio-temporal variation in water flow near the substratum of a coral reef

## Abstract

Measurements of hydrodynamic regimes in coral reef environments often do not account for modified water flow around and across complex reef structures. We used plaster dissolution to assess spatial and temporal variation in boundary layer and free-stream flows in the lagoon at One Tree Reef (southern Great Barrier Reef). A hierarchical sampling design distinguished variation in water movement among locations one to three kilometres apart, among sites within one kilometre of each other, and within metres at each site. In the boundary layer (attached to the substratum), the greatest proportion of variation in water movement (69 %) was found within metres. In the 'free-stream' (1 metre from the reef), the greatest proportions of variation (73 %) were attributable to differences among sites. In the free-stream, site ranks according to water movement persisted over time and mean water movement was 1.5 to 1.7 times greater at some sites compared with others. These results show that flow in the boundary layer is relevant only for small-scale comparisons, and that flow in the 'free-stream' drives patterns at larger scales. For flow in the free-stream, variability in water movement among sites could significantly affect food and larval supplies to different areas.

## Introduction

Water movement is a key mechanism by which important physical (oxygen, nutrients) and biological (food, larvae) inputs are delivered to sedentary aquatic assemblages. The hydrodynamic regime also affects the removal of metabolic and food wastes, transports gametes and larvae away from natal assemblages, and influences physical parameters, such as water temperature and salinity, which affect biological processes (Riedl 1971). Two types of water movement are important to benthic aquatic assemblages (Vogel 1994): (1) water movement in the boundary layer constitutes the small-scale flow environment in which sedentary organisms live; (2) water movement in the free-stream flow relates to the overall supply of nutrients, food and larvae. The boundary layer ends and the free-stream flow begins where water movement ceases to be affected by bottom friction (Vogel 1994). Water movement in the boundary layer is determined by the interaction of free-stream currents with the structure or topographical complexity of the benthic environment (Shashar et al. 1996). Often studies that examine water movement, however, do not distinguish between boundary layer and free-stream flows.

Water movement patterns in both the boundary layer and free-stream are likely to be important to benthic organisms. Water movement in the boundary layer is important to the sessile organisms that live there (Wheeler 1980, Frechette & Bourget 1985, Frechette et al. 1989, Butman et al. 1994), but also influences the behaviour of motile species (Winterbottom et al. 1997, Gerstner 1998, Fulton et al. 2001). Water movement in the free-stream will have strong influences on aspects such as feeding in planktivorous fishes (Kingsford & MacDiarmid 1988, Kiflawi & Genin 1997) but affects both sessile and motile assemblages due to its role as a transport medium for food and larvae (e.g. Emerson 1990, Larned & Atkinson 1997). Studies that examine the effects of water movement on benthic organisms generally, however, only investigate either boundary layer or free-stream flows, depending on the mobility of the study organisms. For example, boundary layer flow is investigated for sessile organisms such as sponges (Vogel 1994) seagrasses (Schanz et al. 2002, Schanz & Asmus 2003) and bivalves (Vincent et al. 1988, Grizzle & Morin 1989), while free-stream flow is investigated for motile organisms, such as plankton and fish larvae (Hamner et al. 1988, Carleton et al. 2001a). To date there are no studies that examine both boundary layer and free-stream water movement simultaneously, the combination of which is likely to be an important physical and biological influence in benthic habitats.

Coral reefs have very complex water movement patterns, driven by factors such as prevailing large scale currents, depth, topography and the dominance of tide versus wind generated current patterns (Hamner & Wolanski 1988). Defining the complex hydrodynamic environments found around coral reefs has been the goal of many current modeling studies (e.g. Atkinson et al. 1981, Frith 1981, Wolanski & Pickard 1983, Wolanski & King 1990, Kench 1998, Kraines et al. 1998). However, few studies account for the modification of water flow between the boundary layer and free-stream at the highly complex water-reef interface. Here flow can potentially affect a range of important ecological processes. For reef-building corals, the mass transfer of nutrients, dissolved gases and toxins that affect rates of photosynthesis, respiration, growth and survivorship are reliant on water movement in the boundary layer (Dennison & Barnes 1988, Patterson et al. 1991, Stambler et al. 1991, Atkinson & Bilger 1992, Lesser et al. 1994, Thomas & Atkinson 1997, Nakamura & van Woesik 2001). Water movement in the boundary layer also affects particle capture by corals and other suspension feeders (Patterson 1984, Patterson 1991, Sebens et al. 1998) as well as the morphology, competitive outcomes and distribution patterns of sessile (e.g. corals, algae) and motile (e.g. urchins) organisms (Hubbard 1974, Russo 1977, Santelices 1977, Genin et al. 1986, Genin et al. 1994, Lesser et al. 1994). Water movement in the nearby free-stream, however, affects the distribution of zooplankton (Hamner & Hauri 1981, Hernandez-Leon 1991), invertebrate larvae (Black 1988, Willis & Oliver 1990, Carleton et al. 2001b) and pre-settlement fishes around reefs (Kingsford et al. 1991, Doherty & Carleton 1996, Carleton et al. 2001a), settlement patterns in invertebrates (Pawlik & Butman 1993, Harii & Kayanne 2002) and fish (Schmitt & Holbrook 2002b), and fish feeding rates (Kiflawi & Genin 1997). Hence, an accurate assessment of spatial patterns of variation in both boundary layer and free stream flow is required to understand processes that may cause patterns of variation in assemblages across and around coral reefs.

Differences in the hydrodynamics of the boundary layer and free-stream flow may vary across different spatial and temporal scales. Spatial variation may occur according to exposure to prevailing wind patterns (McGehee 1994, Fulton & Bellwood 2005) and along depth gradients (Jokiel 1978, Oliver et al. 1983, Dennison & Barnes 1988, Jokiel & Morrissey 1993, Fulton & Bellwood 2005). Smaller scale variation may occur due to unique flow features behind reef promontories (Alldredge & Hamner 1980, Murdoch 1989, Wolanski et al. 2003) near channels (Atkinson et al. 1981, Wolanski et al. 1988) and according to the proximity of large coral bommies or other substratum features (Jokiel 1978, Guichard & Bourget 1998, Guichard et al. 2001). Spatial patterns in water movement may also vary over time, depending on large-scale and tidal currents, and wind and swell conditions (Hamner & Wolanski 1988). Clearly descriptions of patterns in water movement need to be carried out at many spatial scales and repeated to determine if they are persistent over time. Few studies that examine patterns of water movement sample at more than one spatial scale or time.

Plaster dissolution is an inexpensive and widely used means of measuring cumulative water movement in aquatic habitats (e.g. Muus 1968, Doty 1971, Komatsu & Kawai 1992, Shashar et al. 1996). In reef habitats, plaster standards or 'clod cards' have been used as a water movement index with which to correlate patterns of distribution, growth and other ecological characteristics in algae (Santelices 1977, Glenn & Doty 1990, Ohta & Ninomiya 1990, Glenn & Doty 1992), corals (Jokiel 1978, Wellington 1982, Oliver et al. 1983, Dennison & Barnes 1988, Jokiel & Tyler 1992), fishes (McGehee 1994, Yamahira 1997, Fulton & Bellwood 2005), urchins (Russo 1977) and bivalves (Foyle et al. 1997, Hart et al. 1998). In general, studies that examine benthic organisms mount clod cards on the substratum, effectively measuring flow within the boundary layer, while studies that examine demersal fishes or caged bivalves mount clod cards on stakes or cages to measure free-stream flow. To date there have been no detailed attempts to compare the patterns and magnitude of variation in boundary layer versus free-stream flow as measured by plaster dissolution on coral reefs.

The aim of this study was to assess variation in cumulative spatial and temporal variation in water flow in the boundary layer and free-stream flow across and around One Tree Reef (southern Great Barrier Reef). Plaster dissolution was used to compare relative levels of water movement in the boundary layer and in the free-stream on a hierarchy of scales: among locations one to three kilometres apart, among sites within one kilometre of each other, and within metres at each site. Sampling was repeated over time to determine whether spatial variation among sites and locations were consistent.

The following specific questions were addressed: Are patterns of variability in water movement the same in the boundary layer as in the free-stream? How much does water movement vary around a reef? Are there some scales that show more variation than others? Are spatial patterns of water movement consistent over time?

## Methods

### *Study site*

One Tree (23°30'S, 153°67'E) is a platform reef located approximately 20 km from the continental shelf edge in the Capricorn-Bunker group of the southern Great Barrier Reef (GBR). Spring tides range from 2 - 3 m and neap tides range from 0.5 - 1 m. The southeasterly trade winds dominate the wind pattern in this area, although north and northwesterly winds may be common during summer. The East Australian Current (EAC) is deflected eastwards by the continental margin near the Swains group, north of the One Tree Reef, so local hydrodynamics are driven primarily by tidal fluctuations and wind generated surface circulation (Frith 1981, 1983).

One Tree Reef has a fully enclosed lagoon that 'ponds' during low tides. Due to the absence of a channel into the lagoon, areas where the reef rim is less built-up create important entry and exit points for water during tidal changeover. These water exchange points are found on all sides of the lagoon and reefs areas that are nearby to these points are predicted to have greater water movement than sites further away from them. However, while the circulation patterns within the lagoon are well known (Ludington 1979, Frith 1981, 1983, Frith & Mason 1986), the magnitude of the cumulative differences in water movement around the lagoon over time has not been measured. This study examines relative differences in cumulative water movement for twelve sites in four locations (South, East, North, West) approximately 2 to 5 km apart around the One Tree lagoon (Figure 1). The South, East and North locations are in the main lagoon, while sites within the West location are located in a smaller and deeper lagoon that is fully enclosed by reef. Within each location three sites were located along the continuous reef margin at approximately 500 m intervals.

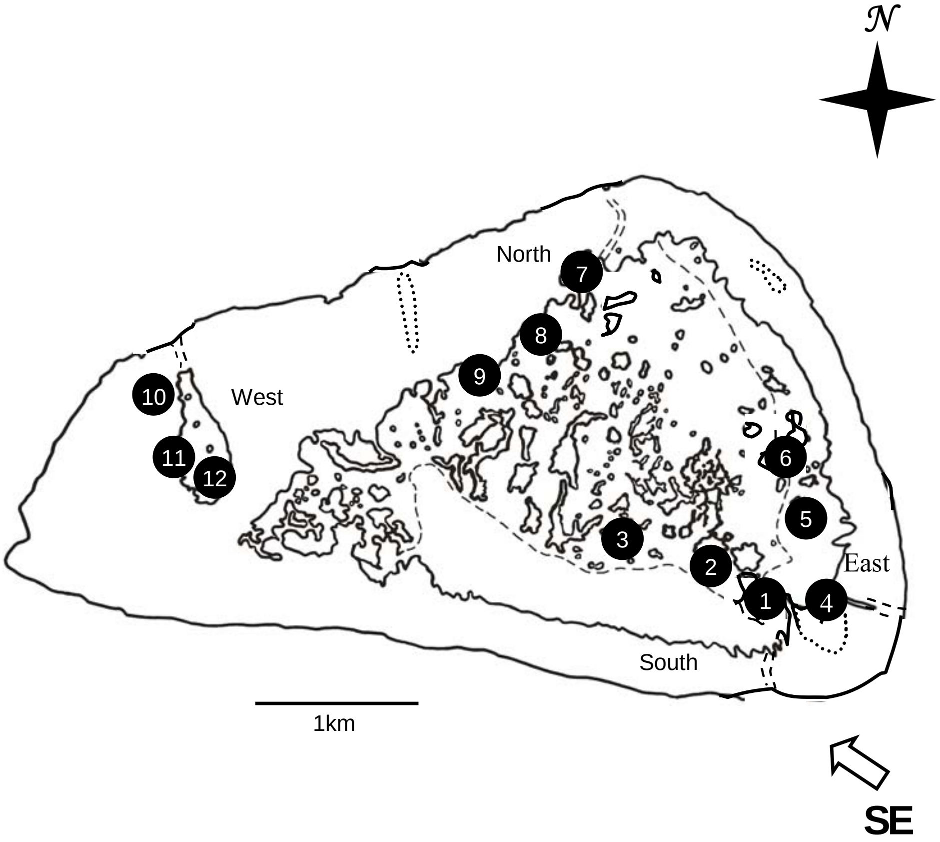


**Figure 1:** Map of study sites and locations around One Tree Reef lagoon (sites 1 to 12).

### *Estimation of water motion using Clod cards*

This study examined two types of water movement that are likely to be important to coral reef assemblages – boundary layer and free stream. Gypsum (calcium sulphate hemihydrate) was used to make both the 'boundary layer' clods (hemispherical clods that were glued to a base plate and attached directly to the reef substratum), and 'free-stream' clods (spherical clods that were suspended in the water column from star-pickets located approximately 1 metre away from the reef edge). The sheltered environment of One Tree lagoon are likely to be subject to primarily steady-type flows, rather than oscillatory or mixed-type flows, and are therefore amenable to use of gypsum dissolution to measure water movement (Porter et al. 2000).

Boundary layer clods were made by mixing 27 g of Yellowstone Dental Cement with 17ml cold water, which made one hemisphere of diameter 46 mm and average weight of 33 g in a plastic egg carton mould. Plaster hemispheres were removed from moulds after 24 hours, oven-dried for eight hours at 80°C and glued with silicon to stainless steel base plates (100 x 50 mm) (Figure 2a). After transferring to the field station, attached clods were dried in an air-conditioned lab for five days and then weighed before deployment. Base plates with clods were attached to the reef with plastic masonry push-mount plugs approximately 1.0 m below the reef crest (Figure 3a). The exact positions of clod cards on the reef were chosen at random where there was a suitable point of attachment at least 50 cm away from topographic projections greater than approximately 30 cm in diameter.

Free-stream clods were made from CSR casting plaster (following Fulton and Bellwood (2005)), which obtained an extremely hard consistency without oven drying and was more easily attainable. Free-stream clods were mixed at a ratio of 70 ml of water to 130 g plaster, which made one sphere with a diameter of 55 mm and average weight 110 g in a tennis ball mould. Thirty cm of 1.25 mm galvanized fencing wire was embedded in the plaster as an attachment point (Figure 2b). Balls were left to set for 24 hours, removed from the moulds and dried for five days in an air-conditioned room.  Spheres were fixed approximately 10 cm below each end of a 0.4 m piece of wood-ply tied perpendicularly to a star picket 0.2 m below the top (Figure 3b). Star pickets measured 1.4 m and protruded 1.1 m from the sandy bottom of the lagoon, thereby suspending the spheres approximately 0.9 m above the substratum.

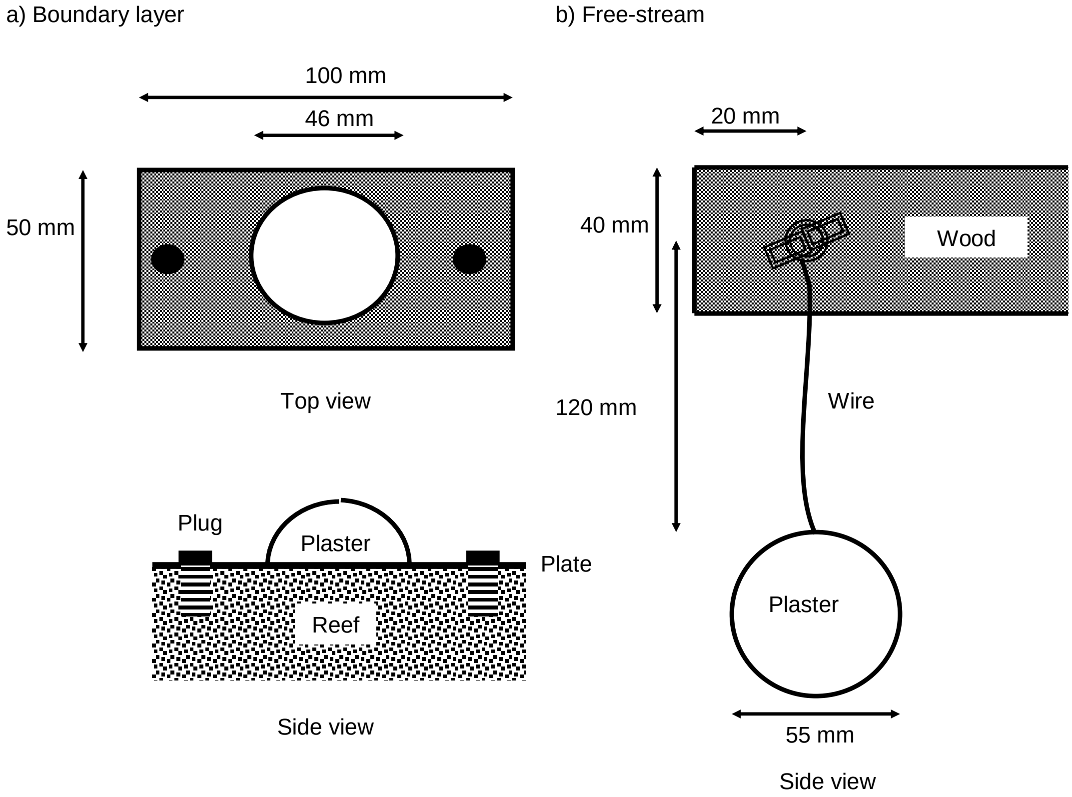


**Figure 2**: Dimensions and deployment of the two clod types: (a) boundary layer clods were glued to aluminium base plates and fixed to the reef with plastic masonry plugs (b) free-stream clods were hung in the water column with fencing wire from wooden cross-bars.

Since only relative flow rates among sites were of interest, rather than a comparison of absolute flows between boundary layer and free stream, it was decided best to select clod shapes according to those used in each flow regime in the literature. Spherical clods deployed on the substratum or hemispherical clods deployed in the free stream would change the flow dynamics around clods and cause interrupted rather than smooth flows. A pilot study using boundary layer clods made with CSR casting plaster that were deployed simultaneously with free-stream clods at one site showed similar levels of variance among clods located in close proximity to one another in the boundary layer as those made from dental cement confirming that variation in dissolution rates among clods within sites was due primarily to the clod type and location of deployment rather than the plaster type.

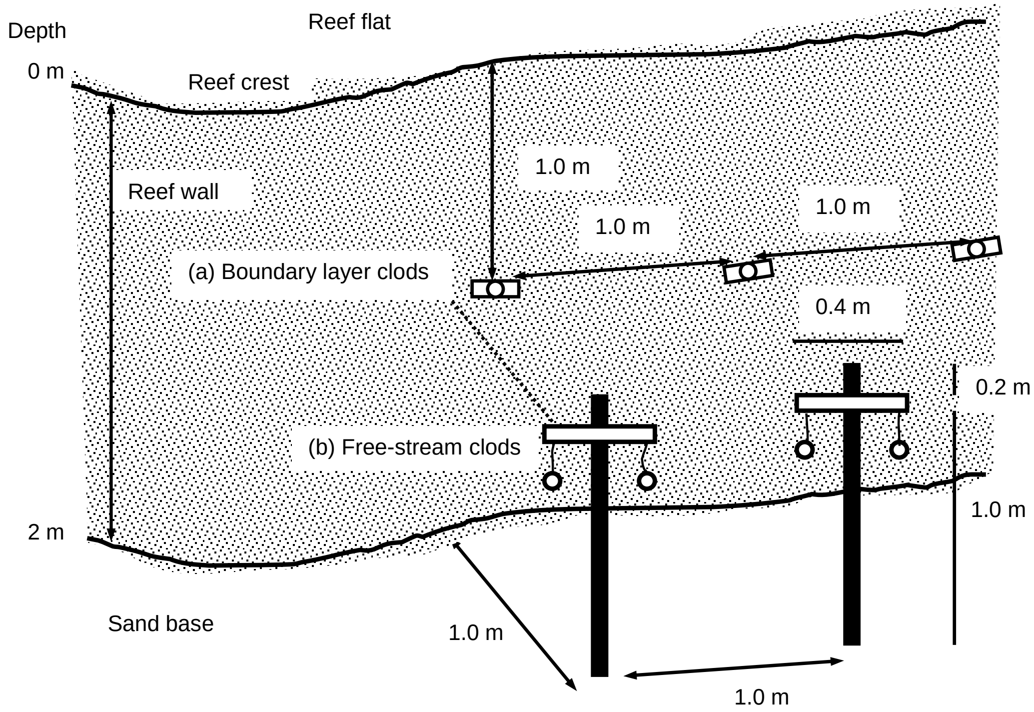


**Figure 3:** Placement of the two clod types on the reef. (a) boundary layer clods were fixed directly to the reef wall. (b) free-stream clods were hung from start pickets 1m away from the reef wall.

### *Sampling design*

Clods were deployed simultaneously at each of the 12 study sites in the lagoon on four separate occasions: twice for each of the two clod types (Figure 4). Boundary layer clods were deployed twice consecutively for 5 days in November 2002 (Times 1 and 2). Three base plates were deployed at each of the 12 sites, thereby giving a total of 36 clods for each deployment. A total of seven boundary layer clods were lost, four during

Time 1, and three during Time 2, but no more than one clod was lost from any site within a deployment time. Free-stream clods were deployed for 7 days in November 2003 and 6 days in January 2004. Two star pickets were placed 1 m apart at each site, giving a total of 48 spheres per deployment time in the lagoon. One of the four replicate free-stream clods for each site and each deployment time was chosen at random and excluded from analyses so that there were three replicates as for boundary layer clods. The position of the star pickets was chosen randomly at each site for each deployment time.

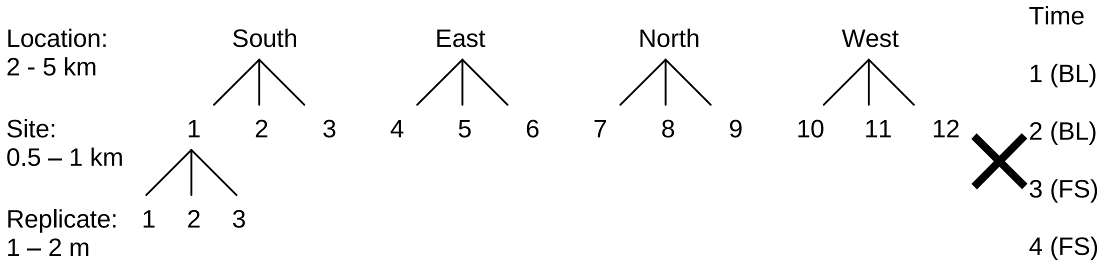


**Figure 4:** Figure 4: Clods were deployed four times at twelve sites in the lagoon, twice in the boundary layer (BL) (Times 1 and 2) and twice in the free-stream (FS) (Times 3 and 4).

### *Wind conditions*

Variability in wind speed may affect overall water movement between deployment times, and variability in wind direction may influence relative water movement among locations. Wind speed and direction, therefore, have the potential to influence the relative importance of different factors (i.e. spatial scales) in the analyses. The Australian Bureau of Meteorology provided hourly wind speeds and directions at One Tree Reef over each deployment time. T-test was used to compare average wind speeds during each deployment time separately for each clod type. An alpha level of 0.01 was used to determine significance for this analysis to account for non-homogeneous variances that could not be corrected with transformation.

### *Water Movement Index (WMI)*

Clods were deployed and collected at all sites during a single day. Clods were retrieved from all sites when clods at the fastest dissolving site for that deployment were approaching approximately one third of the original mass (assessed separately for lagoon and slope clods). This prevented non- linear dissolution at small sizes (Jokiel & Morrissey 1993). Clods were not necessarily deployed and collected from sites in the lagoon in the same order because not all sites could be accessed at all tides. Consequently, there were slight variations in the length of time clods were in the field and the amount of tidal movement experienced by clods in a 24 hour period was highly variable depending on the tidal state. To compensate for this variability, dissolution was calculated as a Water Movement Index (WMI): the percentage of the initial weight that was lost, divided by the number of days submerged and by the tidal amplitude experienced while in the water (calculation described below)

$$\text{Water Movement Index (WMI)} = [((W_f - W_i) \times W_i^{-1}) \text{ x } 100] \times T^{-1} \times t^{-1}$$

where $W_f$ = final weight (g), $W_i$ = initial weight (g), T = time in days (d) and t = tidal movement experienced in metres (m).

A value of 35 g for the boundary layer clods (the average weight of the base plate and glue), and 2.5 g for free-stream clods (the average weight of the wire) were subtracted from each $W_f$ and $W_i$ respectively. The duration that clods were in the field was recorded to the nearest minute. The metres of tidal movement experienced by each clod was calculated by summing the difference from the tidal height at the time of deployment of each clod to the next maxima or minima, and all subsequent differences until each clod was removed. All minima inside the lagoon were taken as 1.2 m, which is the lowest water level in the lagoon due to the ponding effect (Ludington 1979), however, actual tidal minima were used for the reef slope clods. This term simply standardized dissolution per day by removing the effect of different days having different amounts of tidal movement, which could affect variability, but had no effect on magnitudes of differences in the amount of plaster lost among sites.

### *Data analysis for WMI*

All data analyses were carried out separately for boundary layer and free-stream clods. An alpha value of 0.05 was used to determine significance unless otherwise stated. Untransformed WMI data met the assumptions of analyses in all cases. A mixed model, partially hierarchical analysis of variance (ANOVA) was used to test for significant differences in WMI for clods deployed in the lagoon among Sites, Locations and between Times. All factors were random and Site was nested in Location, which was orthogonal with Time. To calculate the partitioning of variation (variance components) among factors (Location, Site, Within Site – Residual) each deployment time was analysed separately as the method does not allow analysis of mixed models and partially hierarchical designs. Tukey's HSD post-hoc test (Quinn & Keough 2002) was carried out only for free-stream clods in the lagoon. Data from both times for the lagoon were combined because there was good correlation between Site means and ranks between Times 3 and 4. Only groupings with respect to Site were examined because this factor explained the greatest proportion of variation. This test was not carried out for boundary layer WMI's due to residual variation contributing the most to variance components. Pearson's correlation co-efficient and Linear Regression was used to examine the relationship in mean cumulative water movement at sites between deployment times and Spearman's Rank Correlation (Zar 1999) was used to determine whether relative ranks of water movement among sites were consistent between deployment times.

## Results

### *Are patterns of variability in water movement the same in the boundary layer as in the free-stream?*

Overall patterns of variability in water movement in the One Tree lagoon were not the same in the boundary layer and in the free-stream. The sites and locations with the highest values of WMI in the boundary layer (Sites 1, 3 and 5) did not closely match the sites and locations with highest values of WMI in the free-stream (Sites 4, 6 and 12) and relative differences among sites between times were not consistent (Figure 5). Furthermore the scale of greatest variation in WMI was different between the two clod types. There were, however, some similarities between water movement in boundary layer and free-stream flows. Water movement was 1.5 to 1.7 times greater at some sites compared with others and Site was a significant factor in both analyses (Table 1). Furthermore, sites with both low and high mean WMI's were found in all four locations of the One Tree Reef lagoon for both boundary layer and free-stream flows, and Location was not a significant factor in either analysis (Table 1). In the boundary layer average WMI was both lowest (Time 1, Site 2: 0.36 ± 0.18 % $d^{-1}m^{-1}$) and highest (Time 2, Site 3: 0.73 ± 0.05 % $d^{-1}m^{-1}$) at sites in the Southern area of the lagoon. In the free-stream, there were sites with both low and high WMI's in the South, East and West locations, although WMI at sites in the Northern location were all low (0.3 % $d^{-1}m^{-1}$ or less) to medium (0.3 to 0.4 % $d^{-1}m^{-1}$).

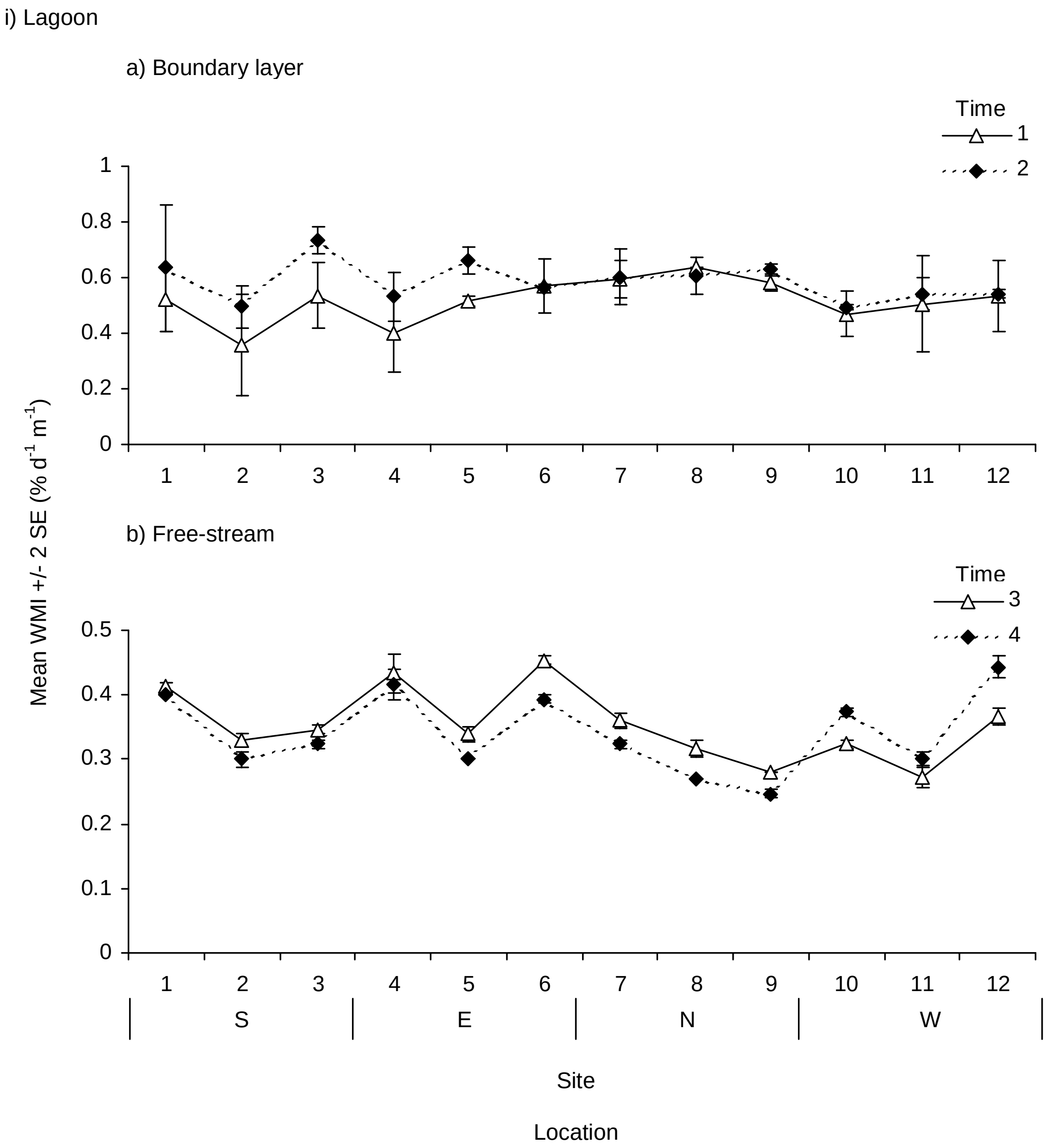


**Figure 5:** Average Water Movement Index (WMI) in % $d^{-1}$ $m^{-1}$ ± 2 standard errors at One Tree Reef for lagoon (a) boundary layer clods during Time 1and 2 and (b) free-stream clods during Time 3 and 4 at 12 sites within four locations

| | | a) Boundary layer | | b) Free-stream | |
|---|---|---|---|---|---|
| Source of Variation | df | MS | p | MS | p |
| Deployment | 1 | 0.072 | 0.120 | 0.003 | 0.589 |
| Location | 3 | 0.029 | 0.476 | 0.024 | 0.446 |
| Time * Location | 3 | 0.016 | 0.036 | 0.009 | 0.001 |
| Site (Location) | 8 | 0.019 | 0.013 | 0.017 | < 0.001 |
| Time * Site (Location) | 8 | 0.003 | 0.774 | < 0.001 | 0.001 |
| Residual | 41 | 0.006 | | < 0.001 | |

**Table 1:** Mixed-model ANOVA for plaster dissolution expressed as WMI. $\alpha = 0.05$

### *How much does water movement vary around a reef?*

Water movement ranged from 0.36 ± 0.18 % $d^{-1}m^{-1}$ (Site 2, Time 1) to 0.73 ± 0.05 % $d^{-1}m^{-1}$ (Site 3, Time 2) in the boundary layer and 0.25 ± 0.001 % $d^{-1}m^{-1}$ (Site 9, Time 2) to 0.45 ± 0.001 % $d^{-1}m^{-1}$ (Site 6, Time 1) in the free-stream (Figure 5). For the free-stream clods, a Tukey's post-hoc test on the combined data for both times grouped sites into five subsets (Table 2). The first four subsets contained the eight sites with lowest mean WMI's and these groups largely overlapped. The fifth subset contained the four sites with the highest values of mean WMI, and these were significantly different from all other sites.

|  | Group |  |  |  |  |
|---|---|---|---|---|---|
| Site Number | 1 | 2 | 3 | 4 | 5 |
| 9 | 0.263 |  |  |  |  |
| 11 | 0.285 | 0.285 |  |  |  |
| 8 | 0.293 | 0.293 | 0.293 |  |  |
| 2 |  | 0.314 | 0.314 | 0.314 |  |
| 5 |  | 0.320 | 0.320 | 0.320 |  |
| 3 |  |  | 0.335 | 0.335 |  |
| 7 |  |  |  | 0.344 |  |
| 10 |  |  |  | 0.348 |  |
| 12 |  |  |  |  | 0.405 |
| 1 |  |  |  |  | 0.407 |
| 6 |  |  |  |  | 0.422 |
| 4 |  |  |  |  | 0.424 |

**Table 2:** Tukey's groupings for sites based on WMI from the free stream. Means for sites in homogeneous groups are displayed and Sites and Groups are ranked in order of lowest to highest water movement where n = 6 because results were combined for Times 3 and 4 due to significant correlation of site means and concordance of site ranks

### *Are there some scales that show more variation than others?*

The amount that a particular scale contributed to variation in water movement differed between boundary layer and free-stream flows (Figure 6). For the WMI in the boundary layer, residual variation at the within site scale was the major component of variation, 78 % in Time 1 and 60 % in Time 2. In Time 1 Site contributed to only 7 % of the variation and was not a significant factor in the analysis (ANOVA, F = 1.343, d.f. = 8, p

= 0.279), but was significant in Time 2 (ANOVA, F = 3.229, d.f. = 8, p = 0.015) and contributed to 34 % of the variation. Variation in boundary layer WMI due to Location was low and non-significant for both times (Time 1: 15 %, ANOVA, F = 2.74, d.f. = 3, p = 0.112; Time 2: 6 %, ANOVA, F = 1.37, d.f. = 3, p = 0.320).

In contrast, for free-stream water movement, within site variation was negligible (< 5 %) in both deployment times, while Site contributed to the majority of variation, 65 % in Time 3 (ANOVA, F = 54.4, d.f. = 8, p = < 0.000) and 82 % in Time 4 (ANOVA, F = 121.2, d.f. = 8, p < 0.000) (Figure 6). For free-stream clods the effect of Location was also non-significant, though it contributed to approximately one third (30 %) of the variation in Time 3 (ANOVA, F = 2.37, d.f. = 3, p = 0.146) and 15 % of the variation in Time 4 (ANOVA, F = 1.55, d.f. = 3, p = 0.275).

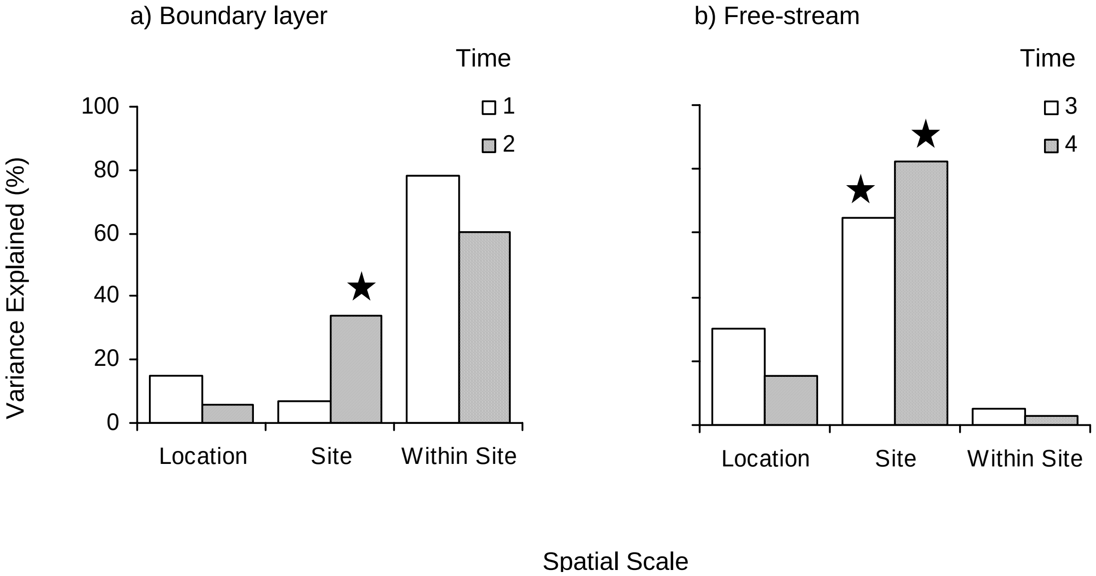


**Figure 6:** Variance components for WMI are partitioned among three spatial scales and expressed as a percentage of total for lagoon clods deployed in (a) boundary layer and (b) free-stream flow at four times. indicates spatial scales where variation is significant at $\alpha = 0.05$.

### *Are spatial patterns of water movement consistent over time?*

There was a significant linear relationship between the mean WMI at each site between times for the free-stream clods, but not for the boundary layer clods (Figure 7). For boundary layer clods the relationship between mean WMI per site in Time 1 and mean WMI per site in Time 2 had a coefficient of determination of only 28 % (Figure 7a). In contrast, for free-stream clods 58 % of the variation in WMI among sites was explained by this relationship (Figure 7b). The three Western sites, which are located in a separate part of the lagoon (Figure 1), are obvious outliers in this relationship. When they are examined independently to sites in the other three locations, the linear relationships for free-stream clods between WMI in Times 3 and 4 are an even closer fit, with 99 and 94 % of the variation explained by the two lines (Figure 7c).

A Spearman's Rank Correlation carried out for both data sets further supports this temporal consistency in relative patterns among sites of free-stream, but not boundary layer, mean WMI's. There was a significant correlation in site rankings by WMI between times 3 and 4 ($r_s = 0.816$, $p < 0.005$ where $r_{s\ crit} = 0.587$ for $\alpha = 0.05$ (2) and $n = 12$), the free-stream deployments, but not for times 1 and 2 ($r_s = 0.559$, $p > 0.05$ where $r_{s\ crit} = 0.587$ for $\alpha = 0.05$ (2) and $n = 12$), the boundary layer deployments.

For boundary layer and free-stream clods, the mean WMI varied between times for some sites, but not others, however, the relative proportion of sites that varied differed between clod types. For example, in the boundary layer, WMI for sites 3 and 5 were clearly higher in Time 2 than in Time 1, while all other sites showed little difference in mean WMI between times (Figure 5). In contrast, for the free-stream clods, all sites had different values for mean WMI between times, except for sites 1 and 4 (Figure 5).

Subsequently there was no significant interaction between Site and Time for boundary layer clods, but a significant interaction for free-stream clods (Table 1). This was, however, likely due to changes in rank between Time 3 and 4 in the western location (Figure 5).

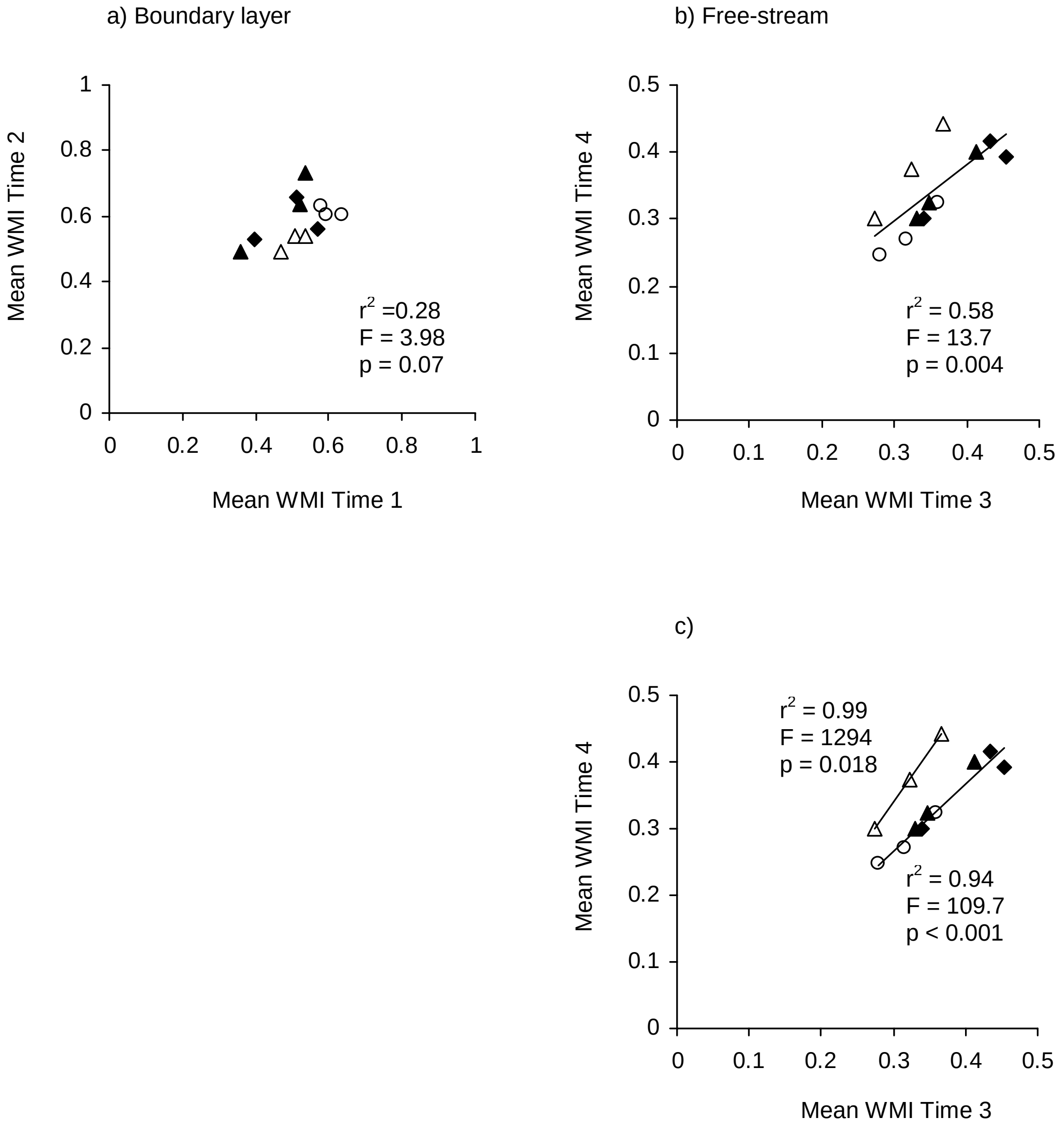
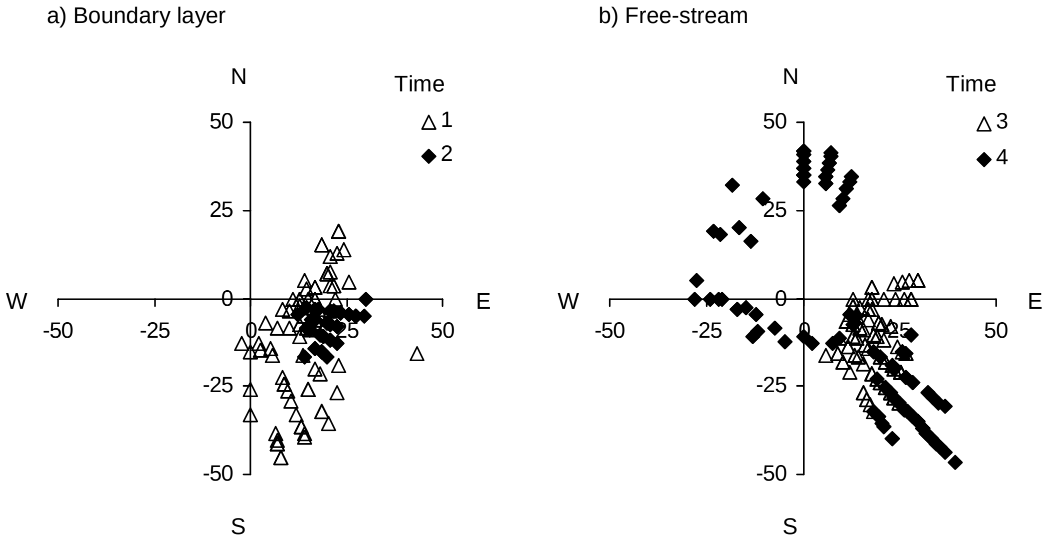


**Figure 7:** Relationship between average WMI for two deployment times at each of 12 lagoon sites for (a) boundary layer and (b) free-stream clods. ⬉ = South sites, ◆= East sites, o = North sites, Δ = West sites (c) shows best fit for free-stream clods separated into two groups based on location.

For boundary layer and free-stream clods, the mean WMI at a site varied significantly between times depending on its location, as confirmed by the significant Location x Time term in both ANOVA's (Table 1). For boundary layer clods, mean WMI's for five of the six sites in the Southern and Eastern locations (Sites 1 to 6) were 20 to 40 % greater in Time 2 than Time 1. There was, however, little difference in mean WMI between Times 1 and 2 for Site 6 and the sites in the Northern and Western locations (Sites 7 to 12) (Figure 5). For free-stream clods, WMI was between 11 and 66 % higher during Time 4 at the three sites in the western location, but 4 to 16 % lower during Time 4 at the other three locations.

Mean wind parameters were similar for the two boundary layer clod deployment times (Figure 8, Table 3). Wind direction was, however, almost four times as variable in Time 1 compared with Time 2. Wind direction in Time 1 ranged from Northeasterly to Southerly, but was consistently from the East-Southeast in Time 2. Although wind speeds during Time 1 were on average 10 % stronger than in Time 2, this difference was non-significant (t-test, t = 1.877, d.f. = 152, p = 0.062), probably because wind speeds were also almost three times as variable.

Wind directions and speeds for the first free-stream deployment (Time 3) were comparable to both of the boundary layer deployments (Times 1 and 2) (Figure 8, Table 3). In Time 3 wind direction was predominantly Easterly and Southeasterly. In Time 4, however, wind direction was highly variable, rotating over 300 ° from North Northeasterly to East Southeasterly. Despite this difference in the variability of wind direction, the mean angle for Times 3 and 4 was within 1 degree. The average wind speed was significantly stronger by almost 50 % in Time 4 than for Time 3 (t-test, t = 10.61, d.f. = 288, $p < 0.001$).



a) Boundary layer

b) Free-stream

**Figure 8:** Hourly wind speed and directions for (a) boundary layer and (b) free-stream clod deployment times. Points are on a compass bearing and represent the direction the wind was blowing from in degrees (°) and distance from the centre represents wind speed in km/hr.

| Time | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Mean Wind Speed (km/hr) (± SE) | 24.1 (1.1) | 21.8 (0.4) | 25.2 (0.6) | 37.1 (0.8) |
| Mean Wind Direction (°) (± A.D.) | 121.8 (40.8) | 111.5 (11.1) | 121.5 (23.3) | 122.5 (75.2) |

**Table 3:** Average wind speed (± standard error), and wind direction (± angular deviation) for four deployment times. Boundary layer clods were deployed in Times 1 and 2 and free-stream clods in Times 3 and 4.

## Discussion

This study confirmed that cumulative water movement differed between the boundary layer and the free-stream flow, with each showing distinct patterns of variation across One Tree Reef. The greatest variation in rates of plaster dissolution in the boundary layer was among replicates within metres of one another, emphasizing small-scale heterogeneity in hydrodynamic conditions. In contrast, the greatest variation in rates of plaster dissolution in the free-stream was among sites, where some sites had 50 to 70 % more water movement than others. Spatial patterns of variation among sites were consistent between times, although different wind conditions slightly affected relative water movement among locations.

### *Boundary layer versus free-stream flow*

Local-scale heterogeneity in cumulative water flow in the boundary layer is typical for benthic marine habitats comprised of complex habitat-forming organisms such as coral (McGehee 1994, West 1997), barnacles (Bertness et al. 1991) and kelp (Molloy & Bolton 1996). Topographic heterogeneity greatly affects small-scale variation in water movement in the boundary layer and using plaster dissolution techniques, significantly lower water movement has been found, for example, on the downstream sides of artificial bommies of a number of sizes (Guichard et al. 2001), in depressions such as scallop refuges (Arsenault et al. 1997) and behind coral heads in artificial aquaria (Jokiel 1978). This small scale variability results in high within treatment variation that can overshadow variation at larger scales. Studies that examine flow in the boundary layer in less complex habitats such as estuaries (Sanford et al. 1994), seagrass beds (Erftemeijer & Herman 1994) and *Sargassum* reefs (Ohta & Ninomiya 1990) have shown much less local-scale variation and, as a result, significant differences in water movement at larger scales. Hence, the complexity of the habitat is likely to be a useful predictor of the degree to which differences in movement at larger spatial scales can be detected.

Theoretically, flow in the boundary layer is not only a product of small-scale topographic heterogeneity, but also free-stream flow (Shashar et al. 1996). Previous studies in low complexity intertidal mudflat and estuary habitats have found good correlations between plaster dissolution in the boundary layer and velocity measured by current meters in the free-stream (Leonard et al. 1998, Congleton et al. 2003). In this study, however, sites with the highest levels of water movement in the boundary layer did not correspond to those with the highest levels of water movement in the free-stream, even though measurements were taken at adjacent sections of reef. This was also likely to have been related to the high topographical complexity of coral reef habitats. Our results imply that at One Tree Reef, boundary layer water movement is influenced more by topographic complexity than free-stream flow.

The free-stream flow measured in this study, which was only one metre away from the reef could, however, be viewed as part of the boundary layer depending on the magnitude of topographic projections out from the reef (*sensu* Shashar et al. 1996) and the scale at which flow is being assessed. Boundary layer clods were most variable at the smallest scale examined (within metres) and free-stream clods were the most variable at the intermediate scale examined (within one kilometre). If water movement was measured further away from the reef, for example four to five metres away, the scale contributing the most to variance components may become the Location (one to three kilometres) or greater scale, which would be an interesting point for further study.

### *Spatial patterns*

At One Tree Reef water movement in the free-stream was a more useful means of examining spatial variation at larger scales than water movement in the boundary layer. For free-stream clods, the site scale contributed the most to variance components. Water movement in the free-stream at high flow sites was 1.5 to 1.7 times greater than at the lowest flow sites, and highest flow sites differed significantly from the rest in post-hoc tests. These results are comparable to differences in free-stream water movement among seven beaches used as spawning sites by pufferfish, where one site was significantly different, having 1.5 times the water movement than the other six sites (Yamahira 1997).

Wind exposure has been found to greatly influence relative levels of water movement among sites in other studies, but this was not the case at One Tree Reef. Plaster dissolution was 1.5 to five times greater at exposed compared with sheltered sites on a kelp reef (Gerard & Mann 1979), and up to six times greater at exposed compared with sheltered sites on a coral reef, a difference which was amplified with increased wind speeds (Fulton & Bellwood 2005). Clod cards in both of those studies, however, were deployed on shallow reef crests where wave action is the primary determinant of water movement. In contrast, the lack of large differences in water movement at sites on the windward and leeward sides of the reef in this study was likely due to sites being located inside the lagoon.

### *Temporal patterns*

Despite some variability in wind conditions between deployment times, relative ranks of sites were consistent and there was a significant correlation in mean free-stream water movement between times at One Tree Reef. This was in contrast to boundary layer water movement, where site ranks changed between times, probably due to the high within site variation. Although wind was not a dominant force affecting relative water movement among locations, variability in wind direction between times did have some influence on plaster dissolution. The magnitude of water movement was roughly similar among locations in the One Tree lagoon, for both the boundary layer and free-stream, however, greater boundary layer water movement for sites on the southeastern side of the lagoon in Time 2, though not significant, appeared to correlate with lower variation in wind direction compared with Time 1. Furthermore, significantly greater free-stream water movement for sites on the western side of the lagoon in Time 4 appeared to correlate with the mere presence of westerly winds, despite greater wind speeds and mean wind direction being from the southeast. This is likely to be related to the reef profile, in which the reef walls on the windward side of the lagoon are more built up than the walls on the leeward side (Frith 1981), therefore offering greater protection from the prevailing wind pattern. Variability in wind direction appeared to be a more important influence on relative water movement among sites in the lagoon than mean wind direction, which was similar for all four deployment times, or mean wind speed, which was 1.5 times greater in Time 4 than in Times 1 to 3.

### *Implications for spatio-temporal patterns of water movement*

Relatively consistent and significant patterns in relative water movement among sites in the free-stream at One Tree Reef, despite variable wind conditions, means that over time some sites will be subject to greater water flux, and therefore potentially greater delivery of food and larvae, compared with others. Two of the sites with the highest values of WMI (Sites 1 and 6) are, in fact, known recruitment hotspots for fishes in the One Tree lagoon (Booth et al. 2000). It is a possibility that greater recruitment at these sites is a result of greater water fluxes delivering greater numbers of larvae. Reef fishes are, however, known to be highly discriminating in their choice of settlement sites and so it is also possible that they actively choose to settle in these higher flow areas, either because of the potential for delivery of planktivorous food, or because of habitat associations with flow-associated sessile organisms. Alternative, the timing of larval settlement according to tidal states may influence recruitment patterns. Once in the more variable boundary layer, however, larval swimming abilities and choice may drive patterns of supply.

### ***Plaster dissolution as a technique for measuring water movement***

Few studies measure water movement as a variable of interest *per se*. By the far the majority of studies use water movement indices calculated from clod cards as a variable to correlate with one or more biological variables (e.g. Doty 1971, Dawes et al. 1974, Russo 1977, Santelices 1977, Dennison & Barnes 1988, Glenn & Doty 1990, 1992, Jokiel & Tyler 1992, McGehee 1994, Foyle et al. 1997, Hart et al. 1998, McClanahan et al. 2005) even though the usefulness of the technique is somewhat contentious (Jokiel & Morrissey 1993, Thompson & Glenn 1994, Porter et al. 2000). The relationships between mean water movement and other variables in these studies may have described a considerable portion of the variation in the data, and/or have been significant in regression analyses. Most do not report, however, whether the differences in water movement among sites were significant, persisted over time, or described a substantial portion of variation in the data. Most do not even provide any estimate of variation around means. Our results suggest that greater care should be taken in correlating mean values of water movement in many cases. In our study, for example, site means of water movement in the boundary layer taken from Time 1, which were not significantly different, would be meaningless if used in a correlation with biological variables.

Only two studies have examined water movement indices in detail. One study found a correlation between water flow and barnacle settlement, despite the fact there were significant differences in water movement among multiple deployments at the same sites, as well as high within site variation and broadly overlapping variation around site means (Bushek 1988). The other found a correlation between flow velocity and the proportional representation of swimming modes for fish species in assemblages at Lizard Island (Fulton & Bellwood 2005). In Fulton and Bellwood (2005) the factors ‘sites’ and ‘locations’ examined were at approximately the same scales as for this study, however, water movement among sites were not significantly different compared with location and wind conditions. Differences in the importance of factors between this study and ours may have been because sites were not nested in locations in the analysis, or because of differences in the topographical complexity of the reefs at Lizard Island, which are fringing reefs surrounding a continental island, rather than an isolated platform reef such as One tree Reef.

It is possible that the high within site variability for boundary layer compared with free-stream clods may have been due to the experimental methods used in this study. For logistical reasons boundary layer clods were deployed at different times to free-stream clods. Differences in small-scale variability could have resulted from differences in the wind and tide conditions during deployment times, or because boundary layer and free-stream clods differed in the lengths of time they were immersed, and in the size, shape and type of plaster with which they were constructed. The method of calculating WMI was, however, designed to compensate for these inconsistencies in clod types and deployment times. The clod types were chosen to conform to the shapes of clods used in the literature. The only other study that has compared dissolution rates in two types of plaster standards, one glued to a base plate, the other spherical, found good agreement in flow values where both types were deployed in the ‘free-stream’ although mounted on cages (Hart et al. 2002). We believe that the differences in variability between boundary layer and free-stream clod cards in this study were primarily due to the different flow regimes in which they were deployed.

## Conclusion

This study demonstrates that water movement patterns in topographically heterogeneous habitats such as coral reefs are complex and spatially variable. Water movement in the boundary layer is variable at very small scales. In contrast, water movement in the free-stream flow is variable at larger scales, and relatively consistent under varying wind conditions. The free-stream plaster dissolution technique used in this study was most appropriate for comparing water flow among sites spaced at intervals of approximately 500m to one kilometre, and could probably also be used for distinctive flow regimes such as lagoons versus slopes, or windward versus leeward slopes. Patterns of variation in the water flow at different heights above the substratum may be used to generate hypotheses about the effects of water flow on important ecological patterns within the complex reef environment.

## Chapter 3 - Hydrodynamics as a potential determinant of the structure of coral assemblages across an isolated platform reef

### Abstract

Coral reef assemblages exhibit distinct patterns around atolls, platforms and patch reefs according to gradients in large scale environmental factors such as wave exposure and depth, however, smaller scale patterns in composition appear more random. Interactions between currents and reef contours result in recurrent near-reef hydrodynamic patterns, and these may play an important role in determining spatial patterns in assemblages at smaller scales. This study tests the hypothesis that spatial and temporal variation in the composition of coral assemblages among sites in the lagoon and on the slope of a platform reef (One Tree Reef, southern Great Barrier Reef) are associated with the magnitude of near-reef water flow. The composition of coral assemblages was sampled at two spatial scales: larger-scale transects (50 m) and point quadrats (1 $m^2$). Both scales showed that assemblages varied significantly among sites but that these patterns persisted over a two to three year period. While there was a close relationship between the two sampling units in percentage cover for ten out of twelve benthic categories in the lagoon (with $r^2$ explaining 40 to 80 % of the variation), the two sampling units generally detected different quantitative patterns on the slope. The two sampling units also had different relationships with cumulative water flow. In quadrats, the multivariate composition of coral assemblages was significantly correlated with water movement, however, in transects only the percent cover of a few individual benthic categories were significantly related. These results show that local hydrodynamic regimes are related to the structure of coral assemblages at small scales, however, the scale at which

communities are sampled must be closely matched to the scale at which variation in water movement is measured. Furthermore, relationships between water movement and coral assemblages may differ between larger scale reef habitat types such as lagoons and slopes.

## Introduction

The composition of coral reef assemblages varies across many spatial and temporal scales. On a geographic scale, reefs range from those at high latitudes containing only a few species of corals interspersed with macroalgae, to the highly diverse assemblages of the tropical Indo-Pacific (Bellwood & Hughes 2001, Karlson et al. 2004). On the scale of individual reefs, the composition of assemblages can change across broad reef habitat types, with flats dominated by coral species with a massive morphology (Endean et al. 1997), slopes by acroporid species (Done 1982), and walls by diverse benthic communities (Loya 1972, Sheppard 1981). Coral reef assemblages may also vary dramatically over time due to episodic disturbances followed by variable periods of recovery. Disturbances that directly affect corals include cyclones, bleaching and predation by crown-of-thorns *Acanthaster planci* (Done 1992, Connell et al. 1997, Hughes & Connell 1999), while the removal of herbivores by overfishing, which can result in algal overgrowth (Hughes 1994), can affect corals indirectly. In the current climate of coral reef degradation, baseline knowledge of patterns of spatial and temporal variation in the composition of coral assemblages and their causes is an increasingly important avenue of coral reef research.

While spatial variability in the composition of coral assemblages is usually predictable at larger scales, it may become increasingly unpredictable at smaller scales (Green et al.

1987, Pandolfi 2002). For example, at large spatial scales (tens to hundreds of kilometres) spatial variation in the composition of assemblages may be determined by the regional species pool and environmental gradients such as distance from shore (Done 1982, Fabricius 1997, Ninio & Meekan 2002), water temperature (Burns 1985, Chiappone & Sullivan 1994, Harriott & Banks 2002), wave exposure (Done 1982, Fabricius 1997) and depth/light (Sheppard 1981, Done 1982, Anthony & Hoegh-Guldberg 2003). Natural disturbances such as cyclones can temporarily alter the species composition of reefs, however, they appear to return to predictable assemblages (Done 1992, Ninio et al. 2000, Halford et al. 2004), unless combined with chronic and sustained anthropogenic effects (Hughes 1994, Hughes & Connell 1999). In contrast, at small scales (metres), assemblages have a number of different states that are less predictable. Species within a particular plot will be a subset of those in the larger scale environmental niche; however, the composition will change over time according to the recent history of space occupancy, disturbance, competition, predation and larval availability (Hughes 1994, Tanner et al. 1994, Connell et al. 1997). The scale at which there is a transition from predictable to unpredictable community structure is not evident from the literature.

While local scale variation among sites across whole reefs has been frequently quantified (e.g. Burns 1985, Edmunds & Bruno 1996, Murdoch & Aronson 1999, Chiappone et al. 2001, Ninio & Meekan 2002, Perez & Ballesteros 2004, Ruiz-Zarate & Arias-Gonzalez 2004) the causes or correlates of this variation are often not assessed. A better understanding of patterns in the distribution and abundance of corals at a "whole-reef" scale is important, as human impacts vary at this scale and different parts of individual reefs may be zoned for different activities.

Local scale variation in coral assemblages could be determined by predictable patterns in hydrodynamic regimes around reefs. Regional current patterns will be modified by reef shape and topography to cause spatially variable but temporally recurrent near-reef hydrodynamics across platform reefs and atolls (Wolanski & Pickard 1983, Hamner & Wolanski 1988, Black et al. 1990). Consistent hydrodynamic patterns are known to affect the distribution patterns (Black 1988, Sammarco & Andrews 1989) and settlement behaviour of coral larvae (Harii & Kayanne 2002). Furthermore, water movement has a role as a transport medium, delivering nutrients and planktonic food, removing metabolic wastes (Dennison & Barnes 1988, Patterson 1991, Patterson et al. 1991, Atkinson & Bilger 1992, Lesser et al. 1994, Jokiel et al. 1997, Thomas & Atkinson 1997, Sebens et al. 1998) and mediating temperature (Nakamura & van Woesik 2001) in established colonies and can influence the outcome of competitive interactions (Genin et al. 1994). These processes affect life history parameters including recruitment, survivorship, growth and reproduction (Jokiel 1978, Ferrier-Pages et al. 2003, Sebens et al. 2003), which ultimately result in distribution and abundance patterns related to water flow (Hubbard 1974, Baynes & Szmant 1989, Sebens & Johnson 1991). Despite the obvious potential for hydrodynamic regimes to affect the composition of benthic assemblages at local scales, there have been few studies that directly quantify this relationship.

The description of local scale patterns in the structure of reef assemblages may be dependent upon the scale of sampling. Hence, correlations between hydrodynamics and assemblage structure may also be scale dependent. A number of sampling techniques are used to quantify corals and benthic reef composition. These include counting colonies (Adjeroud 1997, Chiappone et al. 2001) or censusing points within quadrats or photoquadrats as small as $1m^2$ (Chiappone & Sullivan 1994, Edmunds & Bruno 1996, Connell et al. 1997, Adjeroud et al. 2005). On a larger scale (usually greater than 5m), line intercept transects (Burns 1985, Green et al. 1987, Adjeroud 1997, McGehee 1997, van Woesik et al. 1999, Hughes et al. 2000), belt transects (Adjeroud 1997, Perez & Ballesteros 2004), and more recently, point censuses of frames taken from video transects (Murdoch & Aronson 1999, Ninio & Meekan 2002, Friedlander et al. 2003) are often used. Given that the scale at which communities may respond to local-scale variation in hydrodynamic regimes is unknown, employing a number of different sampling units increases the chances of detecting these relationships.

The main objective of this study was to examine spatial and temporal variation in the structure of benthic assemblages across and around an isolated platform reef (One Tree Reef) and to test the hypothesis that these patterns are related to near-reef, time-averaged flow patterns. Quantitative descriptions of coral reef community structure sampled at two different spatial scales are used to address the following questions: (1) Are spatial patterns in benthic composition around a reef persistent among years? (2) How do spatial and temporal patterns in benthic composition and their relationships with water flow around a reef compare using small-scale quadrat and larger-scale transects as sampling units? (3) Are there relationships between benthic composition and around-reef variation in water movement?

## Methods

### *Study site and habitats*

Patterns of variation in coral composition were examined at One Tree Reef (23°30'S, 153°67'E) a platform reef located approximately 20 km from the continental shelf edge in the Capricorn-Bunker group of the southern Great Barrier Reef (GBR). One Tree Reef is a highly exposed outer shelf lagoonal reef. The local hydrodynamic regime in this area is driven primarily by tidal fluctuations and wind-generated surface circulation (Frith 1981), which interact with local topography. One Tree Reef forms an enclosed lagoon that ponds at low tide due to the absence of any significant reef channels. Over the period of this study, tabulate, branching and digitate growth forms of *Acropora* dominated the slope, as has been found for this location in other studies (e.g. Ninio & Meekan 2002). In the past high levels of storm damage and recovery have, however, been recorded in this area (Halford et al. 2004). In the lagoon, massive and digitate growth forms of *Porites* were the main habitat forming organisms.

### *Sampling design and surveys of benthic composition*

Temporal patterns of variation in coral assemblages were monitored over a period of three years at twelve lagoon sites, and over two years at eight slope sites. Sites were separated by distances of 100 m to 5 km apart (Figure 1). In the lagoon there were three sites nested in each of four locations, and on the slope there were two sites nested in each of four locations. Slope locations were chosen on the basis of accessibility from the research station during predominant wind and tide conditions. Due to non-significant differences between locations and significant differences between sites within locations in hydrodynamic patterns, only variation among sites was examined in subsequent analyses.

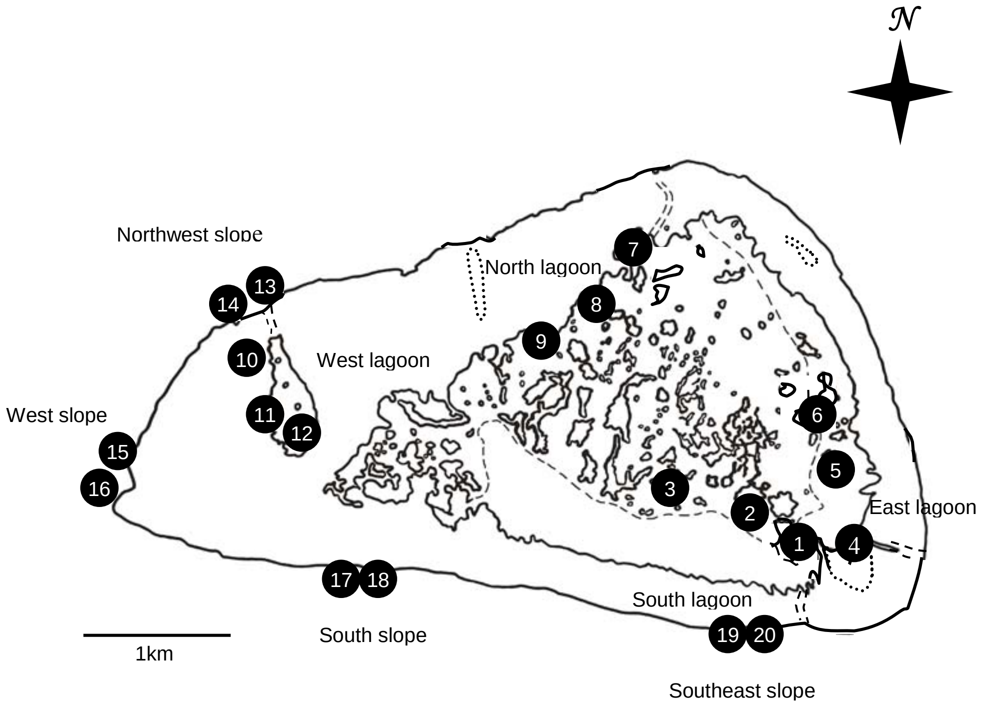


**Figure 1:** Location of study sites around One Tree Reef in the lagoon and on the reef slope. Lagoon sites are labelled 1 to 12 and slope sites are labelled 13 to 20.

The percentage composition of coral reef assemblages was assessed using two types of surveys. Larger scale transects sampled 150 points over a section of reef 160 to 200 m long at each site. Three 50 m tapes were laid parallel to the reef crest with a few metres between transects. The habitat under 50 points per transect, sampled at 1 m intervals was recorded. In the lagoon, transects were 1 to 2 m below the crest and on the slope they were 5 to 6 m below the crest. Transect surveys were repeated annually for three years in the lagoon (2002, 2003, 2004) and two years on the slope (2002, 2003).

Smaller scale quadrats surveyed 1 $m^2$ patches and sampled up to 490 points within a section of reef 25 to 50 m long. Habitats were recorded at the points where seven wires crossed in a 1 $m^2$ grid, which gave a total of 49 points per quadrat. Quadrats were placed haphazardly on the reef along the same contours as transect surveys. Seven to ten quadrats were sampled at each site and this was repeated annually for three years in the lagoon (2002, 2003 and 2004) and two years on the slope (2003 and 2004). The total numbers of replicates in each year were: 120, 119 and 117 quadrats out of a potential 120 per year in the lagoon and 72 and 70 quadrats out of a potential 80 per year on the slope.

The substratum under points in quadrats and transects were classified into one of 52 categories in the field that included: 40 scleractinian coral genera/growth forms, four non-living substrata, two types of algae and six types of invertebrates other than scleractinians (Table 1). To reduce the number of zero values in the data set these benthic categories were compressed into 11 categories based on taxonomy, morphology and abundance for multivariate analysis, and a twelfth category, benthic diversity, was added, which was the number of categories present in the replicate. High benthic diversity indicated that benthic composition was not dominated by one or two categories.

### *Spatio-temporal patterns in benthic composition*

Canonical discriminant analysis (CDA) was used to obtain multivariate descriptors of benthic composition for quadrats and transects in the lagoon and on the slope for each site and time combination. Where observations can be *a priori* divided into groups (in this case Sites and Times), CDA provides a means to classify and describe variation in multiple response variables for a data set. Data for the slope and lagoon environments were tested separately in all analyses due to differences in the frequency of sampling.

| Field | Analysis | Contents |
|---|---|---|
| Scleractinian Corals (40) | Acroporidae | Corals from the genus *Acropora* (including subgenus Isopora) in the family Acroporidae, which have branching/complex growth forms, but not including the genus *Astreopora,* which forms massive colonies, or the genus *Montipora,* which forms encrusting/foliose/submassive colonies. |
| | Pocilloporidae | Corals from the family Pocilloporidae including species from the genera *Stylophora*, *Seriatopora* and *Pocillopora*. |
| | Poritidae | Corals from the family Poritidae including species from the genera *Porites* and *Gonipora* and also all *Montipora* (Acroporidae) species because many were too difficult to distinguish from some *Porites* species in the field. |
| | Massive Corals | Corals of massive growth form primarily from the families Faviidae and Mussidae, but also including corals from the genera *Astreopora* (Acroporidae), *Fungia* (Fungiidae), *Euphyllia* (Caryophyllidae), and *Galaxea* (Oculinidae). |
| | Foliose and Encrusting Corals | Corals from a variety of families that had complex growth forms including encrusting, foliose, branching and digitate forms but did not fit into the three main families above. Examples include: *Echinopora* (Faviidae), *Merulina* (Merulinidae), *Psammacora* (Siderastreidae), *Pavona* (Agariciidae), *Galaxea* (Oculinidae) |
| Non-living substratum (4) | Dead Corals | Dead reef-building corals retaining their structural integrity including old massive colonies and relatively new branching colonies |
| | Coral Rock | Flat sections of coral pavement |
| | Rubble | Loose rocks and rubble that ranged in size from 1 to 10 cm or greater in diameter |
| | Sand | Sand or silt containing few rocks or rubble pieces greater than 1cm in diameter |
| Algae (2) | Algae | Macroalgae, microalgae (epilithic algal turfs), crustose coralline algae, coralline paint and other calcareous algal forms. |
| Invertebrates (6) | Other Invertebrates | Includes soft corals, anemones, sponges, clams, anthozoans and the hydrocoral *Millepora*. |
| | Benthic Diversity | The number of categories contained per replicate out of the 11 categories above |

**Table 1:** Habitat categories used to define coral reef composition including 52 field-assessed categories and 12 analysis categories. Values in parentheses () represent number of categories used in the field from which categories for the analysis were pooled.

These new variables were analysed for variation among sites and times using univariate tests on the first and second multivariate canonical discriminant function scores (Can 1 and Can 2), which, summed together, described approximately half to two thirds of the variation in the data for all four data sets (lagoon quadrats 63 %, lagoon transects 59 %, slope quadrats 55 % and slope transects 64 %). Random factor ANOVA's were used to test for significant differences in benthic composition for Can 1 and Can 2 among years (Time) and sites (Site) and the interaction between these two factors for each of the four data sets. Kendall's Coefficient of Concordance (W) tested for consistency in site ranks by Can 1 and Can 2 for twelve sites in the lagoon over three years and Spearman's Rank Correlation Coefficient ($r_s$) tested for consistency in site ranks for eight sites on the slope over two years. Significance of ranked correlations was taken at $\alpha < 0.05$ (2-tailed) where in the lagoon $n = 11$, $\chi_r^2\text{crit} = 19.675$ and on the slope $n = 8$, $r_s\text{ crit} = 0.738$ (Zar 1999). Despite some complexities, benthic composition was variable among sites but appeared to be persistent over time. Therefore, the percentage cover of each benthic category averaged over time was examined to obtain a summary of benthic composition in quadrats and transects at each site for further analyses.

### *Comparison of quadrats and transects*

In order to assess whether the methods of benthic assessment at the quadrat and transect scales were comparable, Least Squares Linear Regression on the quadrat means versus the transect means for each of the 12 variables was carried out for lagoon and slope environments. For this analysis the benthic composition in quadrats was the dependent variable and benthic composition in transects was the independent variable, according to the assumption that the benthic composition in quadrats at a site would be a subset of what was available over the extent of transects.

### *Relationship between benthic compositions and hydrodynamics*

Plaster standards or 'clod cards' were used to evaluate time-averaged flow at each site in the One Tree lagoon. Four spherical plaster balls measured water flow by dissolution within the area that habitat quadrats were sampled, which was within the area that habitat transects were sampled, at each of the twelve sites for approximately one week in November 2003 and one week in January 2004. As relative magnitudes of water movement were consistent among sites between times the November data was used for further analysis because during this time winds were from the prevailing southeasterly direction. This method gave values of water flux for each site in terms of a Water Movement Index (WMI) in the units of % $d^{-1}$ $m^{-1}$. A hydrodynamic model for the One Tree Reef slope, which was based on the tidal regime experienced at One Tree Reef during a 10-day period starting 11th January 2001 and under conditions of no wind. (Black 1983, Burgess et al. 2007), was used to derive average current speeds in m $s^{-1}$ for the eight slope sites. Average current speeds were extracted at 30-minute intervals from the model output for each site. Relationships were examined between mean water flow at each site, in terms of WMI for the lagoon and average current speed for the slope, and (1) the mean percent cover of each benthic category, (2) the mean benthic diversity for quadrats and transects and (3) the mean multivariate composition of coral assemblages (Can 1 and Can 2). Water flow was the independent variable and benthic characteristics were the dependent variables.

## Results

### *Spatio-temporal patterns of benthic composition*

#### *Lagoon quadrats*

Relative patterns of benthic composition in quadrats among sites persisted over three years in the One Tree lagoon (Figure 2). The majority of sites maintained their relative benthic compositions (positive or negative) for all three years for both Can 1 and Can 2, though there were some exceptions (e.g., sites 11 and 12 for Can 1 and Can 2, and sites 1 and 9 for Can 2). Can 1 explained 49 % of the variation in the data and segregated sites on the basis of whether they were in the south and east locations (sites 1-6), which had negative values for Can 1 and high proportions of dead corals, sand, and algae, and higher benthic diversity, or in the north and west locations (sites 7-12), which had positive values of Can 1 and greater percentage cover of acroporids, pocilloporids and poritids (FC1). Can 2 explained 14 % of the variation in benthic composition among sites and times and primarily distinguished site 4 in the eastern location, which had had high proportions of coral rock, poritids and other massive corals relative to all other sites (FC2). The site by time interaction was significant for both Can 1 and Can 2 in the two-way ANOVA for lagoon quadrat composition (Table 2 a), indicating that the composition of coral assemblages changed significantly at each site among times. There was, however, a significant degree of concordance among site ranks from year to year for both Can 1 ($W = 0.894$, $\chi_r^2 = 29.5$, $p < 0.005$) and Can 2 ($W = 0.686$, $\chi_r^2 = 22.6$, $p < 0.025$). This meant that sites generally maintained their relative ranks over the three years, and that changes over time were more related to variation in the magnitude of changes among years.

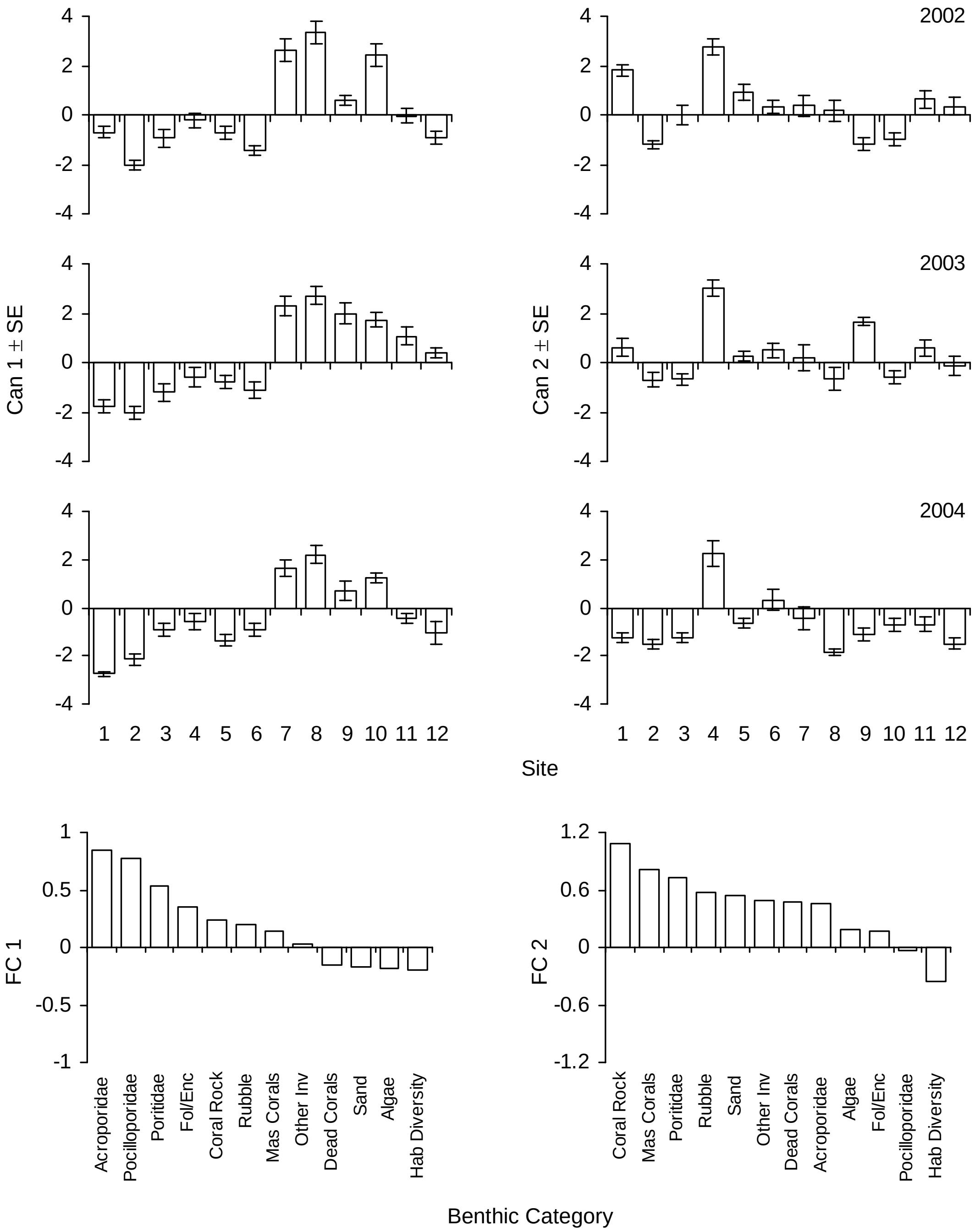


**Figure 2:** Variation in the multivariate benthic composition among sites and years around One Tree lagoon for quadrats (n = 7-10). Values are the mean value ± SE of canonical discriminant function 1 = Can 1 and canonical discriminant function 2 = Can 2. Functional coefficients of response variables in ranked order are shown for FC 1 and FC 2 below. Sites/years with positive values for Can 1 or 2 have high proportions of benthic categories with positive values in FC1 and FC2 respectively.

| (a) | | Can 1 | | Can 2 | |
|---|---|---|---|---|---|
| Factors | df | MS | p | MS | p |
| Time | 2 | 12.3 | 0.019 | 41.5 | 0.001 |
| Site | 11 | 74.1 | < 0.001 | 28.7 | < 0.001 |
| Time x Site | 22 | 2.59 | < 0.001 | 4.33 | < 0.001 |
| Residual | 320 | 1.00 | | 1.00 | |

| (b) | | Can 1 | | Can 2 | |
|---|---|---|---|---|---|
| Factors | df | MS | p | MS | p |
| Time | 2 | 5.64 | 0.061 | 0.520 | 0.691 |
| Site | 11 | 30.4 | < 0.001 | 17.2 | < 0.001 |
| Time x Site | 22 | 1.77 | 0.001 | 1.38 | 0.087 |
| Residual | 72 | 0.637 | | 0.896 | |

| (c) | | Can 1 | | Can 2 | |
|---|---|---|---|---|---|
| Factors | df | MS | p | MS | p |
| Time | 1 | 4.21 | 0.121 | 2.88 | 0.187 |
| Site | 7 | 47.0 | < 0.001 | 27.1 | < 0.001 |
| Time x Site | 7 | 1.36 | 0.230 | 1.36 | 0.230 |
| Residual | 126 | 1.00 | | 1.00 | |

| (d) | | Can 1 | | Can 2 | |
|---|---|---|---|---|---|
| Factors | df | MS | p | MS | p |
| Time | 1 | 2.82 | 0.455 | 0.596 | 0.57 |
| Site | 7 | 46.4 | 0.003 | 37.4 | < 0.001 |
| Time x Site | 7 | 4.51 | 0.001 | 1.68 | 0.15 |
| Residual | 32 | 1.00 | | 1.00 | |

**Table 2:** Two-way ANOVA's for multivariate canonical discriminant function scores, Can 1 and Can 2, for (a) quadrats in the lagoon (b) transects in the lagoon (c) quadrats on the slope (d) transects on the slope.

*Slope quadrats*

Similarly to the lagoon, patterns of benthic composition in quadrats for the One Tree slope sites were generally persistent between years and the distinction among sites was maintained over time (Figure 4). Can 1 described 33 % of the variation in benthic composition and distinguished sites 13, 14 and 16 on the leeward side of the reef, due to their higher percentage cover of sand, other invertebrates, and acroporids (FC1). Can 2 described 22 % of the variation in benthic composition and separated site 16 on the western tip of the reef and site 19 on the eastern windward side, which had higher proportions of non-living substrata, from sites 17 and 18, also on the windward side, which had high proportions of poritids, foliose/encrusting corals, and pocilloporids (FC2). The other four sites were intermediate in their benthic composition between these two extremes. For both Can 1 and Can 2 the site by time interaction was not significant in the two-way ANOVA for benthic composition of slope quadrats and there was no significant difference in benthic composition between times. Only differences among sites were significant (Table 2 c). Subsequently, there were significant correlations between site rankings between years for both of these variables according to Spearman's rank correlation (Can 1: $r_S = 0.94$, $p < 0.005$, Can 2: $r_S = 0.98$, $p < 0.005$).

*Slope transects*

Like patterns of benthic composition in the lagoon and for quadrats on the slope, relative patterns of benthic composition in transects for the slope sites were persistent between years (Figure 5). Can 1, which explained 36 % of the variation in the data for slope transects differentiated sites into two groups. Sites from the north western and south eastern locations had positive values for Can 1 due to their greater coverage of coral rock, poritids and other invertebrates, while sites from the western and southern locations had negative values of Can 1 and greater benthic diversity (FC1). Can 2, which described a further 28 % of the variation in benthic composition, distinguished site 13 in the north western location, and sites 15 and 16 in the western location, which had higher proportions of acroporids, dead corals and coral rock in transects than the other five sites (FC2). The relative benthic composition of some sites on the slope changed over time (significant time by site interaction) according to Can 1 (Table 2 d), although relative site ranks were correlated between years ($r_{est} = 0.88$, $p < 0.02$). This was not the case with Can 2, however, where there was no site by time interaction and benthic composition was persistent over time, but there were significant differences among sites (Table 2 d). Despite a non-significant interaction, and the relative pattern among sites appearing consistent, site ranks between years was not consistent according to the Spearman's rank correlation for Can 2 ($r_S = 0.55$, $p > 0.05$). This insignificant result was probably due to changes in the ranked order of multivariate benthic composition for sites (that were unlikely to be significantly different from each other) on the positive axis only, as sites on the negative axis remained the same.

### *Lagoon transects*

Patterns of benthic composition in transects in the One Tree lagoon were similar to patterns in quadrats. Benthic composition in transects varied among sites but persisted over three years (Figure 3). As for habitat quadrats, Can 1, which described 44 % of the variation in the data, separated sites on the basis of their locations (South and East versus North and West) while Can 2, which described another 15 % of the variation in the data, separated out site 4 from all other sites. Sites with positive values of Can 1 had high proportions of poritids, algae and all categories of non-living substrata (FC1). Site

4 had high abundances of sand, acroporids, other invertebrates relative to other sites (FC2). There was a significant site by time interaction for Can 1, but not Can 2, where instead differences among sites were significant, but there were no significant differences among times (Table 2 b). As for lagoon quadrats, relative site rankings did not change over the three years for either Can 1 ($W = 0.891$, $\chi_r^2 = 29.4$, $p < 0.005$) or Can 2 ($W = 0.829$, $\chi_r^2 = 27.4$, $p < 0.005$), suggesting that relative benthic composition among sites was temporally persistent over the study period and that only the magnitude of difference in Can 1 among sites changed over time.

### ***Time-averaged patterns of benthic composition***

Despite some complexities, the benthic composition in quadrats and transects generally persisted over time in the lagoon and on the slope at One Tree Reef. Consequently, the percent cover of habitats could be averaged over time to compare benthic composition among sites. Three benthic categories: dead corals, coral rock and acroporids, were abundant in both lagoon and slope environments for quadrats and transects. Dead corals and acroporids covered up to two thirds of the substratum and coral rock up to half of the substratum in either of the sampling units at particular sites (Table 3). The lagoon and slope differed in their relative compositions of these categories, however, and also in that poritids were an additional dominant benthic category in the lagoon, comprising up to half of the substratum in transects, while other invertebrates (primarily soft corals) were the next most important category on the slope comprising up to one quarter of the substratum.

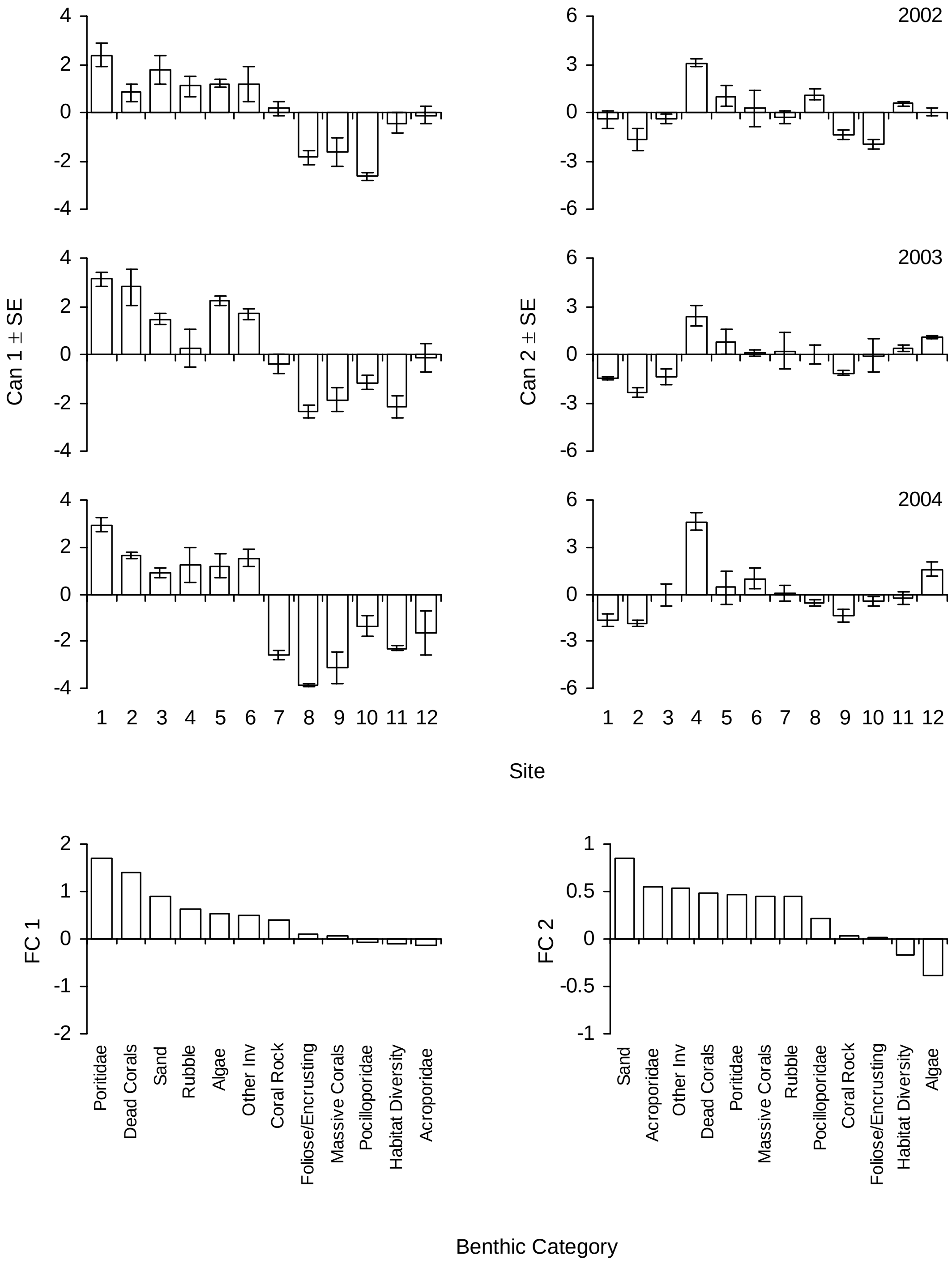


**Figure 3:** Variation in the multivariate benthic composition among sites and years around One Tree lagoon for transects (n = 3). Values are the mean value ± SE of canonical discriminant function 1 = Can 1 and canonical discriminant function 2 = Can 2. Functional coefficients of response variables in ranked order are shown for FC 1 and FC 2 below. Sites/years with positive values for Can 1 or 2 have high proportions of benthic categories with positive values in FC1 and FC2 respectively.

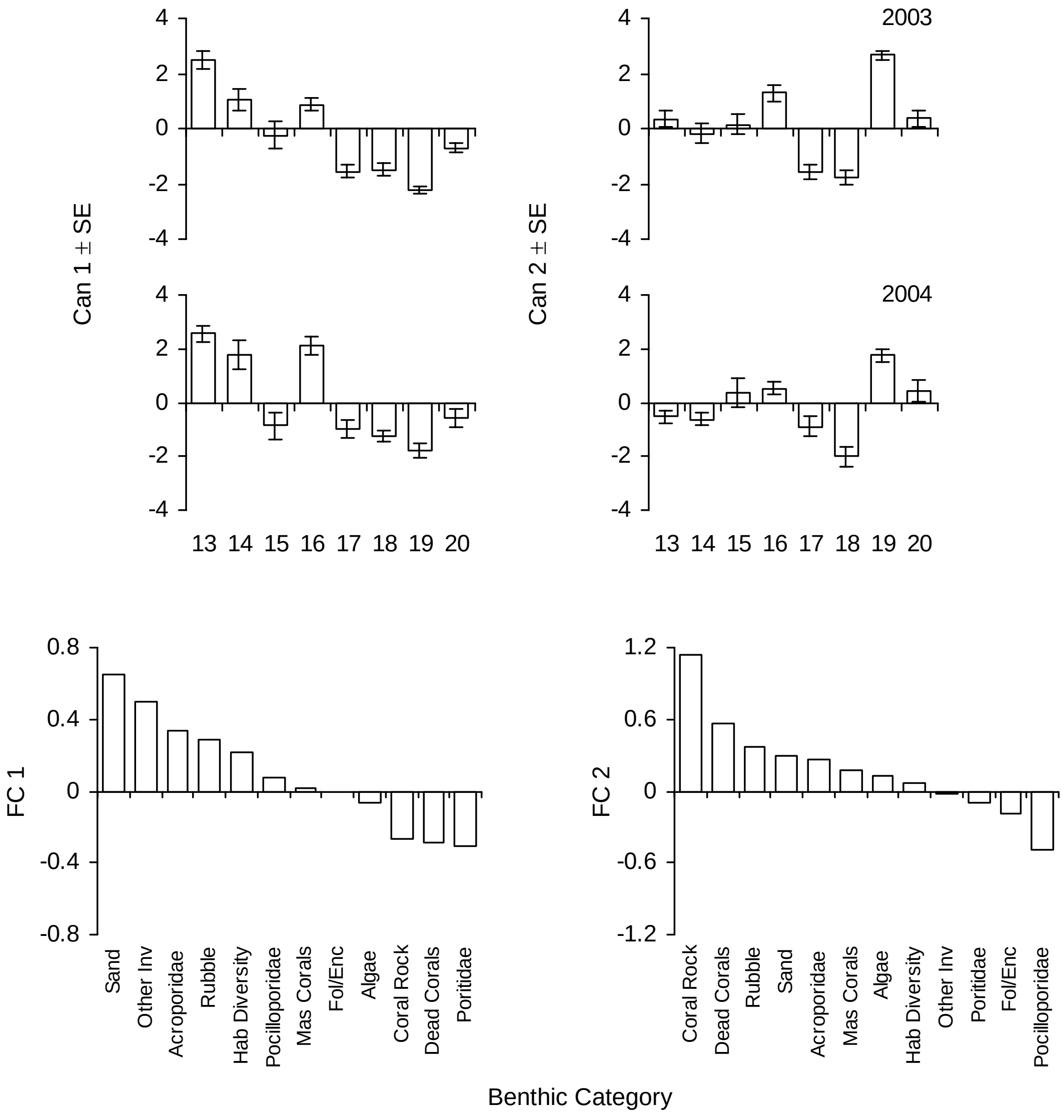


**Figure 4:** Variation in the multivariate benthic composition among sites and years around the One Tree reef slope for quadrats (n = 7 - 10). Values are the mean value ± SE of canonical discriminant function 1 = Can 1 and canonical discriminant function 2 = Can 2. Functional coefficients of response variables in ranked order are shown for FC 1 and FC 2 below. Sites/years with positive values for Can 1 or 2 have high proportions of benthic categories with positive values in FC1 and FC2 respectively.

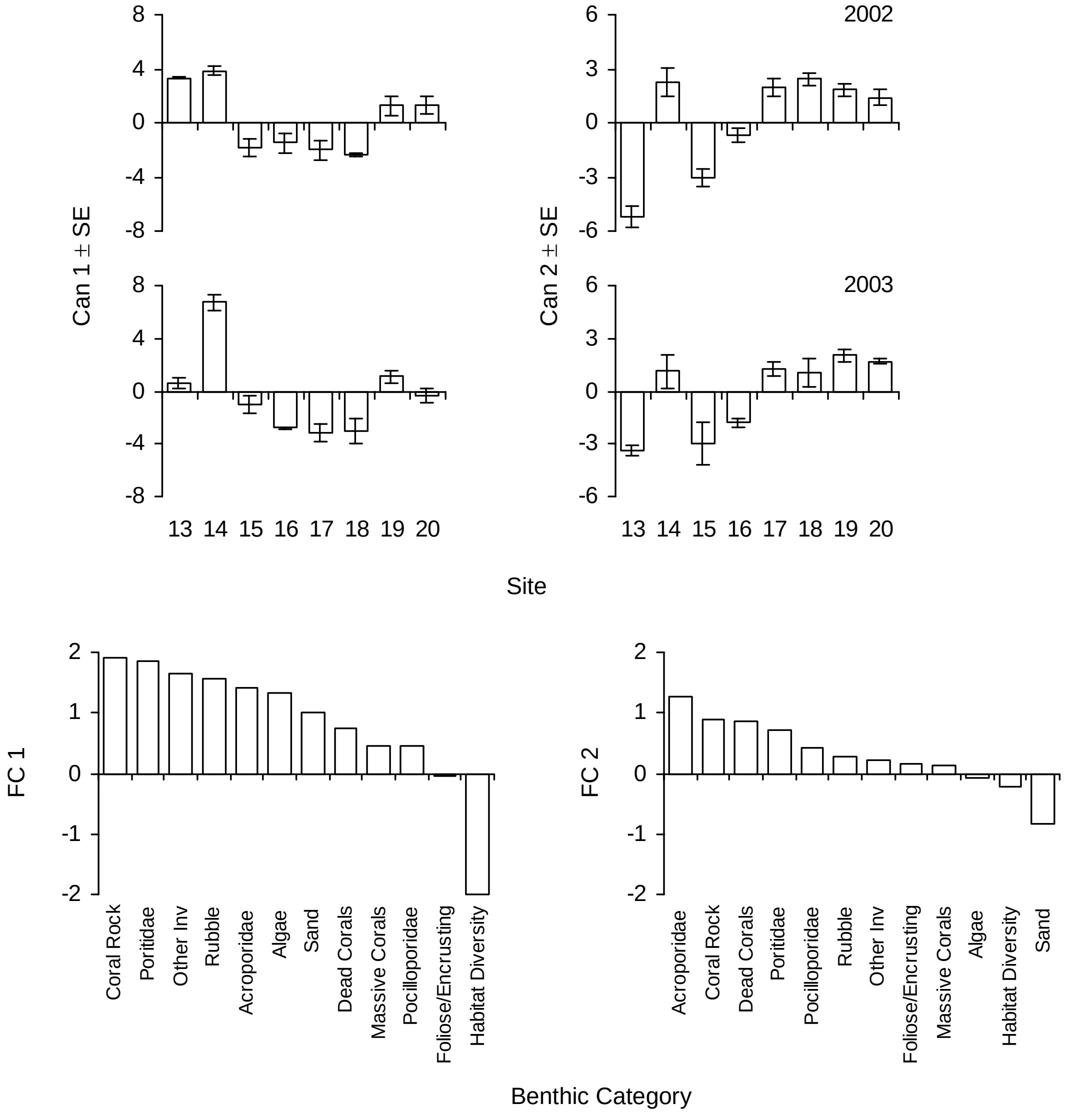


**Figure 5:** Variation in the multivariate benthic composition among sites and years around the One Tree reef slope for transects (n = 3). Values are the mean value ± SE of canonical discriminant function 1 = Can 1 and canonical discriminant function 2 = Can 2. Functional coefficients of response variables in ranked order are shown for FC 1 and FC 2 below. Sites/years with positive values for Can 1 or 2 have high proportions of benthic categories with positive values in FC1 and FC2 respectively.

| Site | Acroporidae | Pocilloporidae | Poritidae | Massive Corals | Foliose & Encrusting Corals | Dead Corals | Coral Rock | Rubble | Sand | Algae | Other Invertebrates | Habitat Diversity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.0 (0.4) | 0.1 (0.1) | 19.4 (1.5) | 0.9 (0.3) | 0.1 (0.1) | 39.1 (5.3) | 16.1 (3.7) | 0.1 (0.1) | 12.0 (2.7) | 11.0 (1.8) | 0.2 (0.2) | 4.4 (0.2) |
| 2 | 0.4 (0.3) | 0.8 (0.3) | 9.2 (1.3) | 0.3 (0.2) | 0.7 (0.3) | 66.8 (3.8) | 1.3 (1.3) | 8.0 (2.0) | 9.4 (2.0) | 3.2 (0.8) | 0 | 4.2 (0.2) |
| 3 | 3.1 (1.0) | 2.6 (0.6) | 10.3 (1.3) | 0.5 (0.3) | 0.8 (0.5) | 44.8 (4.4) | 5.7 (2.3) | 14.4 (3.9) | 11.2 (2.4) | 6.7 (2.2) | 0.1 (0.1) | 5.3 (0.2) |
| 4 | 1.2 (0.6) | 0.9 (0.4) | 17.1 (1.6) | 12.0 (1.4) | 2.9 (0.9) | 33.6 (3.3) | 12.2 (2.5) | 6.6 (1.9) | 8.6 (2.0) | 1.4 (0.8) | 3.5 (0.7) | 6.2 (0.2) |
| 5 | 2.0 (0.6) | 0.7 (0.3) | 19.9 (2.4) | 0.9 (0.4) | 0 | 44.8 (4.6) | 7.5 (2.7) | 13.3 (3.5) | 9.0 (2.0) | 0.6 (0.3) | 1.3 (0.5) | 4.8 (0.2) |
| 6 | 0.5 (0.3) | 1.4 (0.5) | 16.2 (1.9) | 2.3 (0.6) | 0.5 (0.3) | 41.8 (3.9) | 12.4 (4.8) | 7.0 (1.4) | 15.4 (2.8) | 2.3 (1.2) | 0.1 (0.1) | 5.0 (0.2) |
| 7 | 12.4 (3.1) | 8.0 (1.2) | 27.2 (4.9) | 1.7 (0.6) | 1.1 (0.4) | 23.4 (3.9) | 9.0 (2.8) | 12.8 (4.4) | 0.7 (0.4) | 0.6 (0.3) | 3.0 (3.0) | 4.9 (0.3) |
| 8 | 24.8 (4.3) | 11.2 (1.4) | 10.5 (1.8) | 0.7(0.3) | 1.8 (0.8) | 33.8 (4.5) | 13.5 (4.2) | 1.2 (0.5) | 1.4 (0.6) | 1.2 (0.5) | 0 | 4.8 (0.3) |
| 9 | 4.6 (1.3) | 6.9 (1.0) | 16.3 (1.3) | 1.1 (0.4) | 2.5 (0.7) | 43.9 (5.3) | 20.3 (5.0) | 0.8 (0.6) | 2.8 (0.8) | 0.7 (0.4) | 0 | 4.9 (0.2) |
| 10 | 11.6 (1.1) | 8.6 (2.0) | 24.9 (1.4) | 1.0 (0.5) | 0 | 45.0 (2.9) | 0 | 2.2 (0.8) | 6.4 (1.9) | 0.3 (0.2) | 0 | 4.9 (0.2) |
| 11 | 7.1 (2.1) | 3.6 (1.1) | 17.0 (2.2) | 3.9 (0.7) | 0.1 (0.1) | 56.3 (3.3) | 5.9 (2.0) | 3.0 (1.3) | 2.6 (1.2) | 0.4 (0.3) | 0 | 4.8 (0.3) |
| 12 | 5.4 (1.9) | 5.4 (0.9) | 6.9 (2.0) | 2.7 (0.6) | 0.1 (0.1) | 44.1 (3.6) | 3.5 (1.3) | 10.9 (2.0) | 16.0 (3.5) | 3.5 (1.1) | 1.5 (1.3) | 5.7 (0.2) |
| All | 6.1 (0.6) | 4.1 (0.3) | 16.2 (0.7) | 2.4 (0.2) | 0.9 (0.1) | 43.2 (1.3) | 9.0 (0.9) | 6.6 (0.7) | 8.0 (0.6) | 2.7 (0.3) | 0.8 (0.3) | 5.0 (0.1) |

**Table 3 (a):** Mean (± SE) percentage cover in quadrats of 11 habitat categories and habitat diversity for twelve lagoon sites at One Tree Reef

| Site | Acroporidae | Pocilloporidae | Poritidae | Massive Corals | Foliose & Encrusting Corals | Dead Corals | Coral Rock | Rubble | Sand | Algae | Other Invertebrates | Habitat Diversity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.4 (0.3) | 0.7 (0.3) | 44.7 (5.2) | 0.7 (0.3) | 0.9 (0.6) | 33.1 (4.6) | 8.2 (2.9) | 1.3 (0.6) | 4.9 (1.9) | 4.7 (1.5) | 0.4 (0.3) | 5.9 (0.6) |
| 2 | 2.2 (0.6) | 2.9 (0.8) | 36.2 (9.5) | 0 | 0 | 35.8 (6.7) | 10.4 (5.2) | 2.4 (1.7) | 4.9 (2.6) | 5.1 (3.1) | 0 | 5.1 (0.4) |
| 3 | 3.8 (1.2) | 2.9 (0.9) | 14.7 (4.0) | 0.4 (0.3) | 0.2 (0.2) | 50.0 (4.2) | 10.2 (2.9) | 7.8 (1.5) | 7.3 (1.7) | 2.2 (2.0) | 0.4 (0.3) | 6.7 (0.3) |
| 4 | 4.4 (2.0) | 1.6 (0.6) | 19.1 (3.1) | 5.3 (0.7) | 4.9 (1.5) | 23.6 (2.3) | 7.3 (1.7) | 12.2 (1.4) | 16.9 (4.9) | 0 | 4.7 (2.0) | 8.2 (0.4) |
| 5 | 2.2 (0.8) | 1.1 (0.6) | 28.4 (2.0) | 1.3 (0.5) | 1.8 (0.7) | 33.3 (3.3) | 10.7 (2.5) | 8.4 (1.9) | 10.4 (3.0) | 0.2 (0.2) | 2.0 (1.8) | 7.3 (0.3) |
| 6 | 4.7 (1.3) | 0.7 (0.5) | 17.1 (2.3) | 2.4 (0.6) | 1.1 (0.8) | 43.6 (4.9) | 16.2 (3.9) | 5.6 (1.7) | 8.0 (1.5) | 0.2 (0.2) | 0.4 (0.3) | 7.2 (0.3) |
| 7 | 14.0 (4.9) | 5.8 (1.4) | 40.0 (6.0) | 0.9 (0.6) | 2.0 (0.7) | 19.8 (2.1) | 1.8 (0.9) | 12.9 (3.4) | 1.6 (0.6) | 0.7 (0.5) | 0.7 (0.3) | 7.1 (0.4) |
| 8 | 34.0 (3.9) | 7.3 (0.8) | 11.8 (2.3) | 1.3 (0.7) | 4.9 (1.4) | 24.7 (3.1) | 8.7 (2.6) | 5.8 (1.5) | 1.6 (0.7) | 0 | 0 | 7.6 (0.4) |
| 9 | 29.8 (4.8) | 6.9 (1.6) | 10.4 (3.0) | 0.4 (0.3) | 3.6 (0.7) | 20.4 (2.9) | 26.4 (31) | 1.6 (0.7) | 0.4 (0.4) | 0 | 0 | 6.6 (0.3) |
| 10 | 32.0 (4.9) | 3.0 (0.9) | 37.3 (2.8) | 0.7 (0.5) | 0.7 (0.5) | 16.0 (3.5) | 2.9 (1.5) | 5.3 (2.3) | 1.8 (1.1) | 0.4 (0.4) | 0 | 5.6 (0.3) |
| 11 | 30.9 (5.4) | 2.9 (1.0) | 6.7 (1.7) | 0.7 (0.3) | 0.7 (0.5) | 29.2 (3.7) | 3.6 (1.7) | 6.7 (1.3) | 18.7 (6.5) | 0 | 0 | 6.8 (0.5) |
| 12 | 15.3 (2.0) | 4.9 (1.3) | 7.1 (1.9) | 1.6 (0.7) | 0.2 (0.2) | 36.0 (3.5) | 3.3 (1.5) | 12.0 (2.4) | 18.4 (3.6) | 0.7 (0.5) | 0.4 (0.4) | 7.1 (0.4) |
| All | 14.5 (1.5) | 3.4 (0.3) | 22.8 (1.7) | 1.3 (0.2) | 1.7 (0.3) | 30.5 (1.4) | 9.1 (1.0) | 6.8 (0.6) | 7.9 (1.0) | 1.2 (0.4) | 0.8 (0.2) | 6.8 (0.1) |

**Table 3(b):** Mean (± SE) percentage cover in transects of 11 habitat categories and habitat diversity for twelve lagoon sites at One Tree Reef

| Site | Acroporidae | Pocilloporidae | Poritidae | Massive Corals | Foliose & Encrusting Corals | Dead Corals | Coral Rock | Rubble | Sand | Algae | Other Invertebrates | Habitat Diversity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 13 | 31.0 (2.9) | 3.1 (1.0) | 1.2 (0.6) | 4.8 (1.1) | 1.1 (0.7) | 9.4 (2.6) | 8.5 (2.8) | 1.6 (0.9) | 15.5 (2.3) | 0 | 23.8 (2.7) | 5.4 (0.3) |
| 14 | 22.8 (3.1) | 5.5 (1.5) | 5.0 (1.1) | 4.4 (1.5) | 1.6 (0.9) | 7.1 (2.4) | 14.6 (3.6) | 3.2 (1.6) | 9.3 (2.9) | 1.1 (0.6) | 25.3 (4.3) | 5.7 (0.4) |
| 15 | 35.6 (4.6) | 4.6 (1.1) | 7.2 (1.6) | 3.5 (1.8) | 0 | 18.5 (4.4) | 19.7 (5.0) | 2.9 (1.6) | 4.7 (1.5) | 1.7 (0.8) | 1.6 (0.8) | 4.4 (0.3) |
| 16 | 43.0 (3.1) | 1.6 (0.8) | 2.2 (1.0) | 5.7 (2.2) | 0 | 13.4 (2.8) | 5.4 (1.8) | 11.1 (2.4) | 11.3 (2.6) | 3.3 (1.2) | 3.1 (1.3) | 5.1 (0.2) |
| 17 | 23.3 (2.7) | 5.2 (0.8) | 8.8 (2.0) | 1.8 (0.8) | 4.9 (1.7) | 45.9 (3.7) | 2.4 (1.8) | 0 | 0 | 1.5 (1.0) | 6.3 (1.9) | 5.4 (0.4) |
| 18 | 27.2 (3.0) | 9.6 (1.6) | 10.4 (1.7) | 1.9 (0.9) | 6.2 (1.9) | 36.2 (4.2) | 1.4 (1.4) | 0 | 0 | 3.5 (1.7) | 3.5 (1.4) | 5.1 (0.1) |
| 19 | 14.8 (2.8) | 0.3 (0.3) | 4.8 (1.9) | 8.0 (1.5) | 1.7 (0.8) | 15.2 (3.1) | 52.0 (5.3) | 0 | 0 | 0.5 (0.5) | 2.7 (0.9) | 4.8 (0.3) |
| 20 | 23.9 (2.6) | 4.3 (0.9) | 4.6 (1.6) | 11.8 (2.4) | 3.4 (0.7) | 15.5 (3.4) | 25.8 (4.5) | 0 | 0 | 1.6 (0.9) | 9.2 (2.8) | 6.4 (0.3) |
| All | 28.1 (1.3) | 4.3 (0.4) | 5.5 (0.6) | 5.2 (0.6) | 2.3 (0.4) | 19.7 (1.6) | 15.9 (1.8) | 2.4 (0.2) | 5.3 (0.8) | 1.7 (0.3) | 9.6 (1.1) | 5.3 (0.1) |

**Table 3(c):** Mean (± SE) percentage cover in quadrats of 11 habitat categories and habitat diversity for eight reef slope sites at One Tree Reef.

| Site | Acroporidae | Pocilloporidae | Poritidae | Massive Corals | Foliose & Encrusting Corals | Dead Corals | Coral Rock | Rubble | Sand | Algae | Other Invertebrates | Habitat Diversity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 13 | 35.6 (4.2) | 2.7 (1.3) | 1.0 (0.5) | 1.8 (0.5) | 0.2 (0.2) | 13.4 (2.2) | 6.0 (1.0) | 6.0 (1.4) | 9.4 (2.9) | 1.6 (1.0) | 22.3 (5.1) | 8.8 (0.5) |
| 14 | 36.2 (3.3) | 6.4 (1.4) | 18.9 (3.1) | 1.3 (0.7) | 0 | 8.1 (2.1) | 15.0 (2.1) | 2.2 (1.2) | 0.9 (0.6) | 1.3 (1.3) | 9.7 (2.8) | 7.3 (0.3) |
| 15 | 55.0 (5.2) | 0.3 (0.3) | 1.7 (0.8) | 1.7 (1.7) | 0.3 (0.3) | 20.1 (4.7) | 2.5 (1.6) | 11.2 (6.3) | 5.1 (1.3) | 0.7 (0.7) | 1.3 (1.0) | 5.3 (0.4) |
| 16 | 70.9 (3.9) | 0.3 (0.3) | 0.3 (0.3) | 0 | 0 | 13.2 (2.3) | 2.5 (1.3) | 9.5 (3.6) | 2.3 (0.8) | 0 | 1.1 (0.5) | 4.8 (0.7) |
| 17 | 64.4 (5.2) | 0.3 (0.3) | 2.5 (0.7) | 3.1 (1.5) | 0.4 (0.4) | 21.3 (2.6) | 5.9 (2.1) | 1.7 (1.3) | 0 | 0 | 0.4 (0.4) | 5.2 (0.3) |
| 18 | 61.0 (6.6) | 2.8 (1.2) | 8.8 (3.0) | 5.4 (2.1) | 2.1 (0.6) | 13.7 (2.6) | 4.1 (2.5) | 0.3 (0.3) | 0 | 0.4 (0.4) | 1.5 (0.1) | 6.5 (0.8) |
| 19 | 53.4 (8.9) | 0 | 5.0 (1.2) | 4.3 (1.7) | 0.7 (0.5) | 14.4 (4.5) | 17.3 (1.9) | 2.0 (1.6) | 0 | 0.4 (0.4) | 2.5 (1.0) | 6.0 (0.7) |
| 20 | 50.8 (6.0) | 1.1 (0.7) | 1.0 (0.7) | 3.4 (1.3) | 0.3 (0.3) | 11.7 (4.5) | 27.3 (4.0) | 0.7 (0.4) | 0 | 0 | 3.7 (1.4) | 5.3 (0.8) |
| All | 53.4 (2.5) | 1.7 (0.4) | 4.9 (1.0) | 2.6 (0.5) | 0.5 (0.1) | 14.5 (1.2) | 10.1 (1.4) | 4.2 (1.1) | 2.2 (0.6) | 0.5 (0.2) | 5.3 (1.2) | 6.2 (0.3) |

**Table 3(d):** Mean (± SE) percentage cover in transects of 11 habitat categories and habitat diversity for eight reef slope sites at One Tree Reef.

Other live categories of substratum were mostly rare but did distinguish some sites. In the lagoon these included pocilloporid corals for site 8, massive corals and other invertebrates for site 4, foliose and encrusting corals for sites 4, 8 and 9 and algae for sites 1, 2 and 3. On the slope sites 14 and 18 were characterised by relatively high cover of pocilloporids, site 18 also by higher cover of foliose and encrusting corals and sites 17 and 18 by higher cover of poritids.

### *Comparisons of patterns detected by quadrat and transect sampling units*

The relationships between percentage cover estimates for quadrats and transects were stronger for the lagoon compared to the reef slope (Table 4). The percentage composition of ten out of the twelve benthic variables were significantly positively linearly correlated between quadrats and transects for the lagoon and linear relationships accounted for 40 to 80 % of the variation. This indicated that the description of local benthic structure was not sensitive to these two scales of sampling. The only categories for which the percentage cover in transects could not predict the percentage cover in quadrats were Sand ($r^2 = 0.150$) and Dead Corals ($r^2 = 0.116$). In contrast, for the reef slope, results for the two sampling scales were only correlated for three of the twelve variables examined. On the reef slope the percent cover in transects could significantly predict the percent cover in quadrats only for Foliose and Encrusting Corals ($r^2 = 0.530$), Sand ($r^2 = 0.591$) and Other Invertebrates ($r^2 = 0.723$).

| | Lagoon | | | Slope | | |
|---|---|---|---|---|---|---|
| | $r^2$ | F | p | $r^2$ | F | p |
| Acroporidae | **0.539** | **11.7** | **0.007** | 0.118 | 0.806 | 0.404 |
| Pocilloporidae | **0.725** | **26.4** | **< 0.001** | 0.202 | 1.51 | 0.264 |
| Poritidae | **0.342** | **5.20** | **0.046** | 0.062 | 0.397 | 0.552 |
| Massive Corals | **0.809** | **42.4** | **< 0.0** | < 0.000 | 0.003 | 0.959 |
| Foliose and Encrusting Corals | **0.707** | **24.1** | **< 0.001** | **0.530** | **6.78** | **0.040** |
| Dead Corals | 0.116 | 1.32 | 0.278 | 0.433 | 4.58 | 0.076 |
| Coral Rock | **0.407** | **6.87** | **0.026** | 0.384 | 3.74 | 0.101 |
| Rubble | **0.424** | **7.35** | **0.022** | 0.457 | 5.05 | 0.066 |
| Sand | 0.150 | 1.76 | 0.214 | **0.591** | **8.67** | **0.026** |
| Algae | **0.547** | **12.1** | **0.006** | 0.332 | 2.98 | 0.135 |
| Other Invertebrates | **0.584** | **14.1** | **0.004** | **0.723** | **15.6** | **0.007** |
| Benthic Diversity | **0.486** | **9.45** | **0.012** | 0.029 | 0.172 | 0.692 |

**Table 4:** Linear relationships between the mean percent cover of 11 benthic categories in quadrats and their mean percent cover in transects, and between the mean benthic diversity in quadrats and the mean benthic diversity in transects, for the lagoon and slope. Significant relationships are in bold type.

### *Relationships between water flow and habitats*

Linear relationships between estimates of site-specific water movement and benthic composition were detected for both lagoon and slope environments, and for both quadrat and transect sampling units. The benthic categories that were related to water movement, however, differed between sampling units and environments. In the lagoon the multivariate composition of habitat quadrats (Can 2) and the percentage over of Sand in quadrats were significantly positively linearly related to time-averaged water movement (Table 5 a and Figure 6 a). For lagoon transects, greater water movement was inversely proportional to the percentage cover of acroporids, while conversely, the percentage cover of massive corals increased significantly with greater water movement (Table 5 b and Figure 6 b). For slope quadrats there were significant positive linear relationships between current speeds and the multivariate composition of assemblages (Can 1) and also with the percentage cover of Other Invertebrates (Table 5 c and Figure 6 c). For slope transects, 75% of the variation in benthic diversity among sites was explained by an increase in average current speeds (Table 5 d and Figure 6 d), and there were also significant positive linear relationships between increasing water movement and the percentage cover of Other Invertebrates and Algae. In contrast, however, Acroporid cover declined significantly with increasing water movement.

## Discussion

Spatial patterns in the composition of coral assemblages among sites around One Tree reef persisted over time and were correlated with the magnitude of time-averaged flow. This has not been previously quantified at scales among sites within reefs, but was not unexpected, as many benthic species found on coral reefs occur primarily in either low or high flow habitats (Veron 1986). This study supports those showing a strong association between reef assemblages and water flow at both larger (Done 1982, Fabricius 1997, Ninio & Meekan 2002) and smaller scales (Hubbard 1974, Baynes & Szmant 1989, Sebens & Johnson 1991) and demonstrates that variation in coral assemblages among sites is not random or unpredictable.

| | (a) | | | (b) | | | (c) | | | (d) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $r^2$ | F | p | $r^2$ | F | p | $r^2$ | F | p | $r^2$ | F | p |
| Acroporidae | 0.176 | 2.135 | 0.175 | **0.460** | **8.531** | **0.015** | 0.021 | 0.127 | 0.734 | **0.520** | **6.499** | **0.044** |
| Pocilloporidae | 0.232 | 3.020 | 0.113 | 0.323 | 4.764 | 0.054 | 0.003 | 0.015 | 0.905 | 0.177 | 1.293 | 0.299 |
| Poritidae | 0.004 | 0.043 | 0.839 | 0.053 | 0.555 | 0.474 | 0.145 | 1.016 | 0.352 | < 0.001 | 0.003 | 0.958 |
| Massive Corals | 0.176 | 2.141 | 0.174 | **0.426** | **7.432** | **0.021** | 0.002 | 0.012 | 0.917 | 0.001 | 0.004 | 0.950 |
| Foliose and Encrusting Corals | 0.006 | 0.057 | 0.815 | 0.003 | 0.033 | 0.859 | 0.004 | 0.025 | 0.879 | 0.018 | 0.109 | 0.753 |
| Dead Corals | 0.177 | 2.157 | 0.173 | 0.108 | 1.210 | 0.297 | 0.039 | 0.246 | 0.637 | 0.052 | 0.331 | 0.586 |
| Coral Rock | 0.046 | 0.487 | 0.501 | 0.001 | 0.010 | 0.923 | 0.051 | 0.320 | 0.592 | 0.003 | 0.017 | 0.901 |
| Rubble | 0.037 | 0.387 | 0.548 | 0.069 | 0.746 | 0.408 | 0.110 | 0.740 | 0.423 | 0.038 | 0.235 | 0.645 |
| Sand | **0.426** | **7.415** | **0.021** | 0.031 | 0.317 | 0.586 | 0.258 | 2.088 | 0.199 | 0.375 | 3.601 | 0.107 |
| Algae | 0.161 | 1.925 | 0.195 | 0.014 | 0.142 | 0.715 | 0.375 | 3.595 | 0.107 | **0.527** | **6.676** | **0.042** |
| Other Invertebrates | 0.176 | 2.139 | 0.174 | 0.271 | 3.723 | 0.083 | **0.628** | **10.134** | **0.019** | **0.858** | **36.20** | **0.001** |
| Benthic Diversity | 0.158 | 1.876 | 0.201 | 0.109 | 1.229 | 0.294 | 0.171 | 1.234 | 0.309 | **0.748** | **17.84** | **0.006** |
| Can 1 | 0.057 | 0.602 | 0.456 | 0.253 | 3.389 | 0.095 | **0.643** | **10.801** | **0.017** | 0.001 | 0.007 | 0.935 |
| Can 2 | **0.386** | **6.285** | **0.031** | 0.002 | 0.015 | 0.905 | 0.299 | 2.564 | 0.160 | 0.119 | 0.808 | 0.403 |

**Table 5:** Linear relationships between mean water movement index (WMI in g $d^{-1}$ $m^{-1}$) and the percent cover of 11 benthic categories and benthic diversity in quadrats for (a) quadrats in the lagoon (b) transects in the lagoon (c) quadrats on the slope (d) transects on the slope. Significant relationships are in bold type.

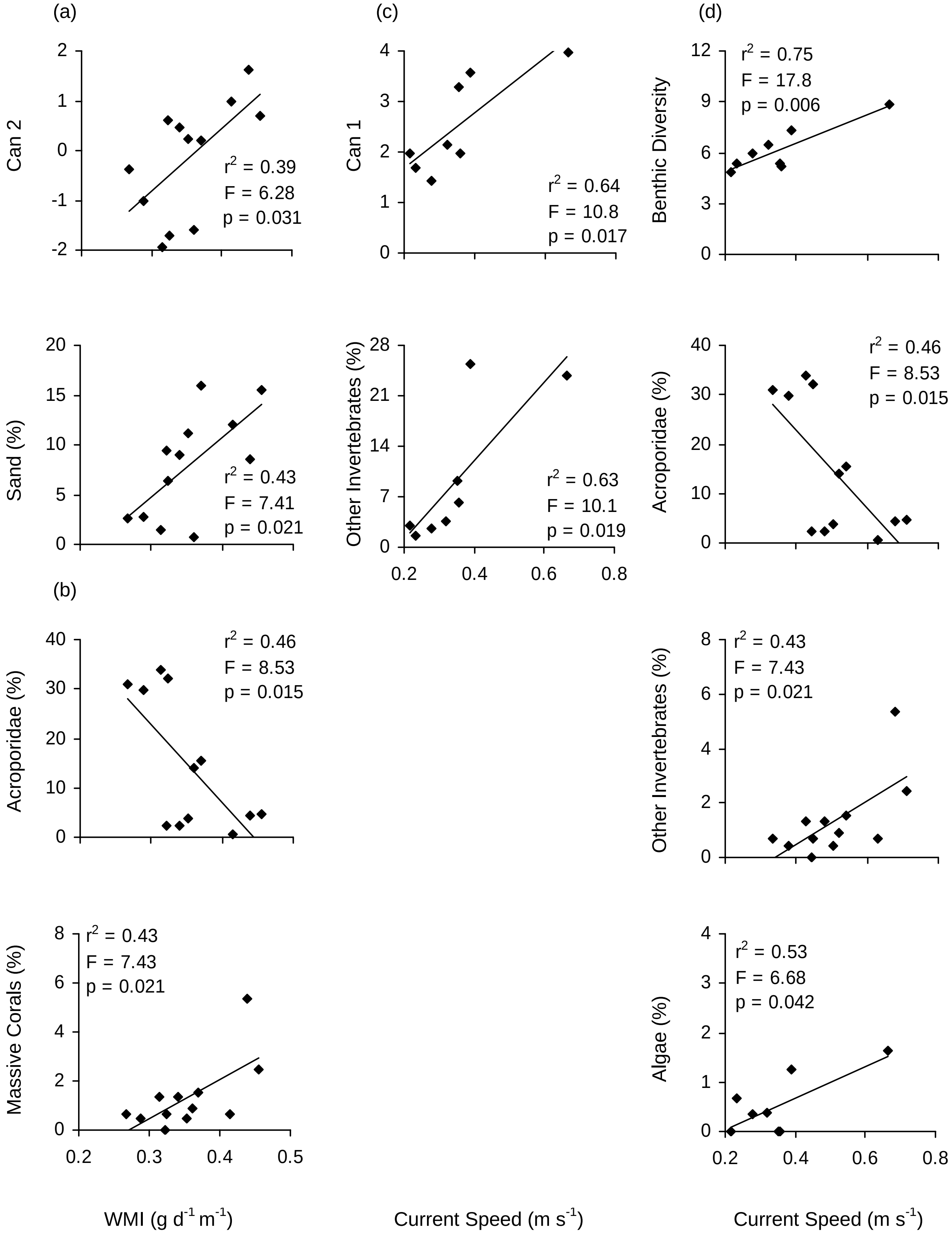


**Figure 6:** Linear relationships between water flow (lagoon: WMI in % d$^{-1}$ m$^{-1}$, slope: average current speed in m s$^{-1}$) and the percentage cover of benthic categories for (a) quadrats in the lagoon (b) transects in the lagoon (c) quadrats on the slope (d) transects on the slope.

While the conclusion that there is a strong association between benthic coral assemblages and water flow is robust, the quantitative patterns described were sensitive to the scale of sampling. For example, while the multivariate description of the composition of assemblages was correlated with water flow for small quadrats (1m$^2$), only the percent cover of a few individual taxa were correlated with water flow using larger transects (50m). This suggests that the scale of measuring hydrodynamics should very closely match the scale of sampling the coral community and an interesting area for future research would be to determine whether sampling water movement at a greater scale at One Tree reef would detect relationships between multivariate benthic composition and hydrodynamics.

For the lagoon benthic composition in quadrats was strongly dependent on the benthic composition in transects. The scale of sampling did, however, affect quantitative descriptions of benthic composition for the slope. This may have been because bays and projections along the reef wall in the lagoon are much smaller compared to the slope (metres compared to tens of metres) and so the composition of reef in the lagoon may be more homogenous. A modern technique for surveying coral reef habitats involves censusing multiple points within photo or video frames spaced along transects (Murdoch & Aronson 1999, Ninio & Meekan 2002, Friedlander et al. 2003), which is roughly equivalent to censusing multiple quadrats along transects (Chiappone & Sullivan 1994, Edmunds & Bruno 1996, Sluka et al. 2001). This technique represents a good compromise of sampling at two spatial scales simultaneously to avoid sensitivity of conclusions to sampling scale.

### *Spatial and temporal patterns in benthic composition*

The composition of coral assemblages varied significantly among sites around the One Tree lagoon and slope. This variation was, however, more subtle than differences reported among depths (Burns 1985, Chiappone et al. 2001, Friedlander et al. 2003, Karlson et al. 2004) or due to wave exposure (Done 1982, Fabricius 1997, Ninio & Meekan 2002) where the identity of the dominant taxa vary. At One Tree Reef, the same four benthic categories were dominant in both quadrats and transects at all sites within the lagoon and three of these were also dominant in quadrats and transects on the reef. Within the lagoon and slope environments sites could, however, be clearly distinguished on the basis of their relative proportions of these dominant categories, as well as the presence of less abundant taxa.

Variation in the composition of reef assemblages at kilometre-wide scales has been found previously in other studies (e.g. Burns 1985, Edmunds & Bruno 1996, Chiappone et al. 2001, Perez & Ballesteros 2004, Ruiz-Zarate & Arias-Gonzalez 2004), although this is not always the case (e.g. Murdoch & Aronson 1999). Even where significant variation among sites is found, for example in the density of acroporid colonies, the proportion of variation explained at within reef spatial scales may be small (Hughes et al. 1999). Whether or not studies find significant and predictable variation at this scale may depend on the heterogeneity of the reef tract at which the study is conducted. For example, the study that found no significant variation in species richness and coral cover among sites examined three sites on the seaward facing edge on each of three elongated reefs running parallel to the edge of the shelf in the Florida Straits (Murdoch & Aronson 1999). In contrast, there were significant differences in coral reef characteristics among sites around St John Island in the Caribbean where the coastline topography appears to be extremely convoluted (Edmunds & Bruno 1996).

On the Great Barrier Reef, reefs range from roughly circular mid-shelf platform reefs, to inshore fringing reefs around topographically convoluted islands and elongated ribbon reefs on the northern outer shelf (Hopley 2006). One study that compared average annual changes in hard coral cover (in terms of > 5 % increase, >5 % decrease or < 5 % change) at sites on many reefs all along the GBR, found that for the majority of reefs adjacent sites showed the same pattern (Ninio et al. 2000). There were some areas, however, where within reef patterns among sites were more variable, and these areas included the Capricorn Bunker group where One Tree is located, as well as reefs in the nearby Swains group, and inshore reefs. All of these reef groups show greater heterogeneity in reef topography than northern and offshore reefs (Hopley 2006). It is likely that whether or not there is important variation in the composition of coral reef assemblages at within reef scales is dependent on the particular reef being examined.

In general, spatial variation in benthic composition among sites at One Tree reef was maintained over the duration of the study for both lagoon and slope environments and using both types of replicate units. This was expected given that One Tree reef was not subjected to destructive biotic influences such as crown-of-thorns starfish or bleaching during the course of this study, and physical disturbances such as cyclones occur only randomly and over much larger temporal scales. Clearly the temporal range of this study, three years in the lagoon and two years on the slope, is very short, well below the life span of many corals, and not comparable to longer term studies of coral composition at both small (Tanner et al. 1994, Connell et al. 1997) and large (Ninio &

Meekan 2002, Halford et al. 2004) scales on the Great Barrier Reef. One Tree Reef was, however, one of the reefs surveyed by Ninio and Meekan (2002) where for all benthic categories there was less than a 10 % change in coral cover at sites over seven years. The results of our study and Ninio and Meekan (2002) suggest that in the absence of major disturbances, relative patterns of coral composition among sites at One Tree Reef will remain stable over time, and therefore be subject to hydrodynamic influences, although effects such as bleaching may at times affect some individual patches (Booth & Beretta 2002).

### ***Relationships between benthic composition and water movement***

There were relationships between mass water flux and the abundance of some individual benthic categories in both quadrats and transects in the lagoon and on the slope. Only one category showed the same pattern in both environments, and this was the percentage cover of acroporids in transects that decreased with increasing flow among sites in the One Tree lagoon and on the slope. This is interesting because time-averaged water flow at even the lowest flow site on the slope was still three to four times the flow at the highest flow site in the lagoon, but overall acroporids were much more abundant on the slope (15 to 71 %) than in the lagoon (half a percent to 34 %). A possible explanation for this pattern is that at One Tree Reef, different suites of acroporids species inhabit the lagoon and slope environments, as is the case among other broad scale habitats (Done 1982).

Only one benthic category showed the same relationship with water movement for both quadrat and transect sampling units. The percent cover of Invertebrates (mostly soft corals) on the slope increased in proportion to increasing water movement. This result may have been because the percent cover in quadrats was positively correlated with the percentage cover in transects, however, similar trends with water flow did not occur for taxa that were similarly correlated between quadrats and transects in the lagoon. At One Tree Reef, soft corals were found only on the slope and they reached their greatest percentage cover (5-10 %) at one site on the leeward side of the reef (Site 13) that was characterised by the highest flows. This result is in agreement with Fabricius (1997) who found that highest cover and abundances of soft corals (12 to 17 %) occurred on outer-shelf reefs exposed to relatively strong currents but low wave energy, and the relationship may not be scale-dependent.

Time-averaged flow was significantly related to overall benthic composition for both the lagoon and slope at One Tree Reef, but only at the quadrat sampling scale. These relationships may result from the fact that current flow affects the size, morphology, structure and outcome of competitive interactions for reef corals and other benthic reef organisms (Sebens 1984, Genin et al. 1994, Sebens et al. 1997, Sebens et al. 2003). All of these aspects of coral life history would interact at small scales because nearby points on the substratum are subject to influences from the surrounding colonies. Sizes of individual colonies, for example, are known to affect percent coverage data (Hughes 1985). The lack of relationships between water flow and the benthic composition in transects is most likely due to differences in the dependence of census points within transects compared to within quadrats. For benthic transects on the slope the number of benthic categories (benthic diversity index) was, however, positively correlated with water flow, perhaps because water flow is also related to species diversity (Jokiel & Tyler 1992, Barnes & Bell 2002).

## Conclusion

In conclusion, the composition of coral assemblages varied significantly among sites around a reef, but relative patterns of variation were persistent over time and related to near-reef hydrodynamics. This conclusion is robust to the scale of sampling but details of the benthic composition-water movement relationship are scale-dependent and in some cases, also particular to individual reef environments such as reef lagoons and slopes. While this study is unique in that it is the first to quantify ultimate relationships between water movement and the benthic composition of coral habitats at scales across and within reefs, further studies are required to clarify proximate causes.

# Chapter 4 - Recruitment hotspots for scleractinian corals: the roles of water flow, adults and substratum selection

## Abstract

Sites on coral reefs that receive consistently higher recruitment than the norm (“recruitment hotspots”) may be crucial to the persistence of populations and should be considered in reef management. However, the locations of such sites and what causes them is poorly understood. The aim of this study was to detect sites of high coral recruitment at One Tree Reef (southern Great Barrier Reef) and examine associations between hotspots, hydrodynamics, adult abundance and settlement substrata. Recruitment hotspots (two or greater recruits per tile on average for two or more times) were detected on the reef slope and in the lagoon. Almost all hotspots were located on the western side of the reef, however, there was limited congruence among hotspots for different coral families. A clear recruitment hotspot for two families in the lagoon had medium levels of water flow (~ 4 cm $s^{-1}$), but there was no relationship with water flow on the slope. In experimental aquaria, *Acropora nasuta* settlement was six to ten times greater under low (2.1 cm $s^{-1}$) compared to medium water flow (4.6 cm $s^{-1}$). Variation in recruitment of pocilloporids and poritids, but not acroporids, was related to the percentage cover of adult colonies at each site. These differences among families may have been related to their brooding versus spawning life history strategies. Since recruitment hotspots for at least some taxa of corals may be both sources and sinks, detecting and conserving them should be a high priority in the design of marine reserve networks.

## Introduction

Successful recruitment of juveniles plays a critical role in the distribution and abundance of species, is an important aspect of population biology, and is a major determinant of assemblage structure for reef corals (Done 1982, Rogers et al. 1984, Hughes 1985, Babcock 1991, Connell et al. 1997). Coral populations are also dependent on sexual recruits for recovery after catastrophic disturbances (Sammarco 1985). Since determining the mechanisms underlying recruitment variation is critical to understanding population and community dynamics, there has been an increasing number of studies on coral recruitment, and the causes and outcomes of recruitment variation at various scales (see reviews by Hughes et al. 2002, Glassom et al. 2004). In open marine populations, sites that support consistently higher recruitment than the norm, known as “recruitment hotspots” (*sensu* Booth et al. 2000), may play a major role in the determining the size and persistence of sub-populations through subsequent growth and asexual reproduction. However, the location and causes of recruitment hotspots in scleractinian corals have not been previously investigated.

Many studies have examined spatial variation in coral recruitment at the scale of individual reefs (hundreds of metres to kilometres). The emphasis of these studies has, however, been on either very small (millimetres to metres) (Sammarco & Carleton 1981, Fisk & Harriott 1992, Gleason 1996, Maida et al. 2001, Kuffner & Paul 2004) or very large (thousands of kilometres) scales (Smith 1992, Hughes et al. 1999, 2000). Variation at the scale of individual reefs, such as platform reefs or atolls is, however, often significant (Fitzhardinge 1985, Babcock 1988, Dunstan & Johnson 1998, Soong et al. 2003) and contributes to a substantial portion of overall variation (Hughes & Connell 1999, Glassom et al. 2004). Knowledge of patterns occurring at the whole-reef scale are particularly important, because this is often the scale at which coral reefs are managed and marine reserve boundaries are designated (e.g. Sobel & Dahlgren 2004). Knowledge of spatial predictability and congruence in recruitment hotspots could be vital to the optimal placement of such protected areas. Recruitment hotspots are a logical choice for protection due their potential for rapid recovery from disturbances; however, they may also be good sites for reef usage due to their natural resilience.

The composition of the microhabitat and substratum features that affect coral recruitment, vary around reefs (Sheppard 1981, Done 1982, Fabricius 1997, Ninio & Meekan 2002). The location of adult conspecifics may be particularly important, and many studies report greater recruitment associated with the presence of adults of the same species (Babcock 1988, Vermeij 2005). Larvae may choose to settle in areas where adults are already abundant, indicating that conditions are suitable for growth and development i.e. aggregative settlement, as appears to be the case for variation in recruitment among depths (Mundy & Babcock 2000, Carlon 2002, Baird et al. 2003). A positive relationship between the settlement of recruits and adults would also be apparent, however, for planulae larvae produced by brooding species, which are released ready to swim and often settle in close proximity to parent colonies (Lewis 1974, Harriott 1992, Tioho et al. 2001, Harii & Kayanne 2003, Soong et al. 2003). Spatial variation in the composition of adult assemblages is a factor that warrants examination in studies investigating causes of variation in recruitment around reefs.

Recruitment variation around reefs and the location of hotspots may also be influenced by hydrodynamic regimes, which largely determine the delivery of planktonic larvae to particular areas of reefs (Hamner & Hauri 1981, Black 1988, Black & Moran 1991, Carleton et al. 2001b). Since these patterns are likely to recur (Oliver et al. 1992, Sammarco 1994) due to currents interacting with local topography (Alldredge & Hamner 1980, Wolanski & Hamner 1988), differences in recruitment among areas around a reef may have a cumulative effect on assemblages over many years. Instantaneous current speeds also affect settlement in many species of invertebrate larvae (Butman et al. 1988, Pawlik & Butman 1993, Watson & Barnes 2004) including corals (Harii & Kayanne 2002), so any study seeking to examine the causes of recruitment variation around individual reefs needs to examine hydrodynamic patterns at this scale.

Most studies of coral recruitment monitor field patterns of variation. Only a handful of studies have performed experimental manipulations to test recruitment hypotheses, such as responses to settlement substrata or current strength (Babcock & Mundy 1996, Mundy & Babcock 2000, Harii & Kayanne 2002, Baird et al. 2003). This is mainly due to the logistical constraints of obtaining coral larvae, which in many species are produced infrequently. Field manipulations are clearly the most desirable technique to investigate larval settlement choices, however, a diversity of environmental factors, which include light, availability of suitable substrata, chemical cues and water flow, all of which affect the decision of larvae to settle and metamorphose(Morse & Morse 1996, Baird & Morse 2004, Harrington et al. 2004) make identifying causal mechanisms difficult. Consequently, assessing the relative importance of only one or two cues in controlled conditions is necessary. This study tested whether coral larvae preferred tiles conditioned at different sites, and whether these preferences varied with current strength. This will allow an evaluation of the relative importance of water flow and settlement substrata to coral larvae, and assist interpretation of whether flow-related patterns in field recruitment might be related to larval supply or settlement choices.

The primary objective of this study was to identify recruitment hotspots for three coral families at One Tree Reef and whether these hotspots were associated with hydrodynamic patterns, adult abundance and/or habitat. The specific questions were: (1) Do some sites consistently receive greater numbers of recruits than others and are these patterns consistent across different coral taxa? (2) If so, do these recruitment hotspots have greater cover of adult conspecifics? (3) Are recruitment hotspots associated with higher or lower levels of water flow? And (4) how is larval settlement choice influenced by water flow and site-specific settlement substrata?

## Methods

### *Spatial and temporal patterns in coral recruitment*

One Tree (23°30'S, 153°67'E) is a platform reef located approximately 20 km from the continental shelf edge in the Capricorn-Bunker group of the southern Great Barrier Reef (GBR). Coral recruitment was monitored at twenty sites chosen to represent the range of hydrographic conditions and habitat structure occurring in the lagoon and on the reef slope (Figure 1). Twelve sites were located in the lagoon and 8 around the perimeter of the reef slope. Sites were separated by a few hundred metres to five kilometres.

To monitor coral recruitment, 10 replicate 11 x 11x 1 cm unglazed terracotta tiles were attached individually to the reef (Mundy 2000) at each of the 20 sites on five occasions over the three-year study period. Tiles were spaced randomly along the reef wall where suitable attachment sites could be found, and were between one and three metres apart.

In the first deployment (January 2002 to March 2002) only 8 sites in the lagoon were used, giving a total of 16 sites. Two of the five tile deployments (November 2002 to January 2003 and November 2003 to January 2004) coincided with the mass spawning period of corals on the GBR (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986). The other three deployments were from January to March in the years 2002, 2003 and 2004 and were to monitor recruitment from corals that may spawn later in the year, or brooding species that release larvae over a longer period (Wallace 1985, Tanner 1996). Recruitment monitored over the five month period from November to March would be expected to capture the majority of annual recruitment (Wallace 1985).

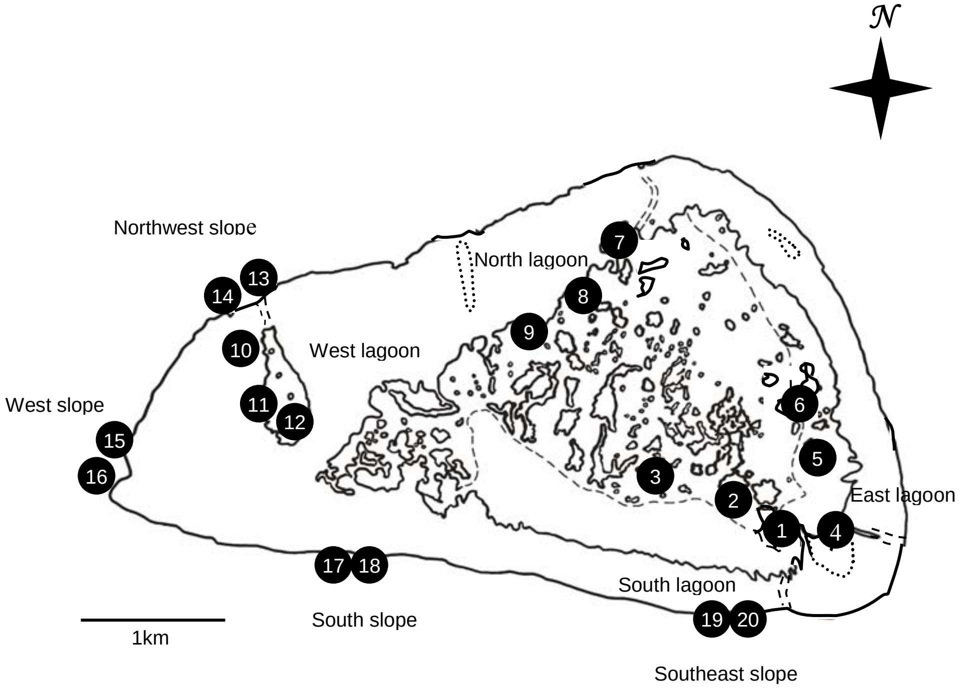


**Figure 1:** Locations of study sites around One Tree Reef in the lagoon and on the reef slope. Lagoon sites are labelled 1 to 12 and slope sites are labelled 13 to 20. Distances between sites are between 100 m and 5 km.

Tiles were attached to the reef at depths of 1-2 m below the crest in the lagoon and 5-7 m below the reef crest on the slope, approximately 2 weeks before the full moon preceding mass-spawning events in November. This allowed them to obtain appropriate coverage of encrusting organisms e.g. biofilms and crustose coralline algae required to induce settlement (Morse & Morse 1996, Raimondi & Morse 2000). Tiles were collected eight weeks later and the next set of tiles was deployed. An 8-week interval was chosen as this is commonly accepted as a reasonable time period to minimise losses due to post-settlement mortality, but to allow sufficient development to facilitate taxonomic resolution. Once removed, tiles were bleached in a dilute chlorine solution to remove all organic material and coral recruit skeletons were counted using a stereo-dissector microscope and identified to family level (Babcock et al. 2003).

All analyses were carried out separately for the slope and lagoon habitats and for each coral family. Two-way ANOVA was used to test for differences in coral recruitment among the five deployment periods (Time) and among sites (Site). Both Time and Site were random factors. Data were square root transformed to reduce heterogeneity of variances. Concordance analysis (Kendall's Coefficient of Concordance with Correction for Tied Values) where $\chi_r^2{}_{crit} = 19.7$ and $\nu = 11$ was used to determine whether relative ranks of sites according to mean recruitment were consistent among the five deployment periods (Zar 1999). Significance was taken at $\alpha < 0.05$ unless otherwise stated.

***Surveys of habitat composition***

Two types of surveys of habitat composition were carried out to assess the percentage composition of each coral family: (1) Larger scale transects sampled 150 points over

160 to 200 m and represented the broad-scale habitat defining each site that an incoming larvae would encounter. Three 50 m tapes were laid parallel to the reef crest with a few metres between them. In the lagoon, transects were 1 to 2 m and on the reef slope they were 5 to 6 m below the reef crest. The habitat type under 50 points per transect, sampled at 1 m intervals, was recorded. (2) Smaller scale quadrats surveyed 1 $m^2$ patches directly around each tile, sampled up to 490 points per site over 25 to 50 m and represented microhabitat that could influence ultimate settlement. Quadrats were placed on the reef at the location of each recruitment tile, therefore the number of quadrats sampled at each site varied according to the number of tiles remaining (between 7 and 10). Habitats were recorded at the points where 7 bars crossed in a 1 $m^2$ grid, which gave a total of 49 points per quadrat. Habitats were classified into 52 field categories and compressed into 10 major analysis categories: acroporids, pocilloporids, poritids, other massive corals, other foliose and encrusting corals, dead corals, coral rock, rubble, sand, algae and other invertebrates. Both types of surveys were repeated annually for 3 years in the lagoon (2002, 2003, 2004) and 2 years on the slope (transects 2002, 2003 and quadrats 2003 and 2004) and because patterns of percentage cover remained relatively consistent, averages for each coral family over the three years were used in analyses.

Relationships between the mean number of recruits and mean percent cover of adults at each site were examined for each family for both transects and quadrats. Pearson's Correlation Coefficient was used to determine the amount of variation described by each relationship and Least Squares Regression and Curve Estimation were used to determine significance. Use of regression assumes that recruitment is dependent on adult habitats rather than adults being dependent on recruitment.

### *Measurements of hydrodynamic regime*

Plaster standards or 'clod cards' were used to compare mass water flux among sites in the One Tree lagoon. This method was used as the integrated effect of circulation over a critical period is thought to be more important to recruitment than currents at any one time (Sammarco & Andrews 1989). Four spherical plaster balls measured water flow by dissolution at each site. Balls were deployed at 12 sites in the lagoon for approximately one week immediately following the full moon in November 2003 and coincided with mass-spawning. For the reef slope, clod cards were deployed at the four leeward sites in January 2004. To obtain water flow estimates in terms of plaster dissolution (Water Movement Index (WMI)) for all eight reef slope sites, the relationship between dissolution data at four sites was extrapolated from a relationship with mean current speed at each site calculated from a hydrodynamic model of the One Tree Reef region (Black 1983, Burgess et al. 2007) modelled on the tidal regime experienced at One Tree Reef during a 10-day period starting January 11th 2001 under zero wind conditions. Average current speeds were extracted from the model output at 30-minute intervals for each site.

The relationship between the mean number of recruits and the mean WMI in units of percentage weight lost per day per metre of tidal movement (% $d^{-1}$ $m^{-1}$) at each site was examined separately for each family. To enable comparisons to flow speeds used in experimental aquaria, the average weight lost from balls in a 24-hour period was converted to a value in $cms^{-1}$ using equations from Fulton and Bellwood (2005) where $WL$ = weight lost in grams in 24 hours and $v$ = flow velocity in cm $s^{-1}$. $WL_{24°C} = 0.915v + 5.395$ was used for the November deployment and $WL_{28°C} = 0.921v + 10.812$ was used for the January deployment in accordance with average water temperatures measured on the reef using Onset TidBits © (23.4 ± 0.11 °C (mean ± SE) in November 2003 and 26.6 ± 0.18 °C in January 2004).

### *Settlement choice experiment*

A larval settlement choice experiment using *Acropora nasuta* larvae was carried out to compare the relative influences of hydrodynamics and settlement substrata, 2 factors which may co-vary in the field. This experiment tested whether larvae preferred tiles conditioned at 4 different sites and low (2.1 cm $s^{-1}$) or medium (4.6 cm $s^{-1}$) flow speeds. Part (a) of the experiment tested settlement choice among tiles conditioned in the lagoon, and part (b) among tiles conditioned on the reef slope. These flow speeds were equivalent to average current speeds integrated over a tidal cycle at low and medium flow lagoonal sites measured in the field (2.1 to 7.1 cm $s^{-1}$), but much lower than maximum current speeds, which can reach up to 130 cm $s^{-1}$ (Kingsford & Finn 1997). Medium flow speeds were used rather than high flow speeds due to field patterns showing greater recruitment at sites with medium flow.

Six gravid colonies of *Acropora nasuta* were collected from the leeward reef slope (near sites 15 and 16) a few days before the predicted mass spawning and held in large coral aquaria with flow-through lagoon water. Five of the six colonies spawned and after 68 hours approximately 2,500 swimming larvae were added to each of 10 larval aquaria. Larval aquaria consisted of circular plastic 35 l tubs of diameter 38 cm filled by a tap and drained from the centre of the tub through a 210-micron mesh sock that slid over a perforated 100 mm diameter PVC pipe, which created a doughnut shaped tank with water circulating in one direction. Flow speeds were verified by the speed of circulating drops of red dye, while all other parameters e.g. temperature, light, water quality were kept constant between treatments. Each aquarium contained 4 settlement tiles that had been conditioned at different sites on the reef for the previous nine months. This time period was chosen as it was the maximum time available and ensured good coverage of encrusting organisms that would be specific to individual sites. Tiles were placed on the bottom of tubs and because of the slight curve in the base and sides of tubs a small gap between tiles and the tub bottom provided the type of "gap" habitat often preferred by coral larvae (Harriott & Fisk 1988, Mundy 2000).

In part (a), each of six tubs, three set to each flow speed, contained one tile conditioned at each of 4 lagoon sites, 1, 4, 7 and 10 representing sites with a range of field recruitment levels. In part (b) each of four tubs, two set to each flow speed, contained one tile conditioned at each of the 4 leeward reef slope sites, 13, 14, 15 and 16, which also represented a range of recruitment levels. More replicate tubs could not be used in part (b) due to limits on the number of conditioned tiles available from each site. Four days after larvae were introduced into the tubs, tiles were removed and the number of coral larvae attached to all surfaces on each tile was counted live under a dissecting microscope. Presumably the difference in the number larvae added to each tub and those that settled remained in the water column or perished during the experiment. Data were analysed using a fully fixed orthogonal two-factor ANOVA on log $(x + 1)$ transformed data, which improved homogeneity.

## Results

### *Pocilloporidae*

Relative spatial patterns of pocilloporid recruits among sites were highly consistent over time (Figure 2). Recruit densities ranged from zero to a maximum of 6.2 ± 1.7 (mean ± SE) spat per tile at site 14 on the leeward side of the reef slope (north-west) in November 2003 to January 2004. At all times there were sites where no recruits were recorded, though no site had zero recruitment at all five times. In all times on the reef slope mean recruitment was highest at site 14, and second highest at site 13, the two sites in the north-west location. Site 14 had 1.5 to 2.7 times the mean recruitment of site 13, and 1.8 to 8.5 times the mean recruitment of the next highest site. There was significant concordance in site ranks among times ($W_c = 0.68$; $(\chi_r^2)_c = 23.8$; $p < 0.005$), and despite changes in the rank order of low recruitment sites, there was no significant interaction between Site and Time in the ANOVA (Table 1), indicating that the magnitude of relative differences among sites were persistent.

Pocilloporid recruitment was lower in the lagoon than on the reef slope but patterns among sites were similarly consistent in rank over repeated times. Site 7 in the northern location of the lagoon was ranked first for the mean number of recruits in five out of five times, and site 8, also in the northern location, was ranked second in four out of five times. Site 7 had between 1.2 and 2.6 times the recruitment rate of site 8, and 2.5 to 7.2 times higher than recruitment at the next highest site. There was a significant concordance in site ranks among times ($W_c = 0.59$; $(\chi_r^2)_c = 32.5$; $p < 0.001$), however, the significant interaction between Site and Time was indicative of variation in the magnitude of differences among sites during different times (Table 1).

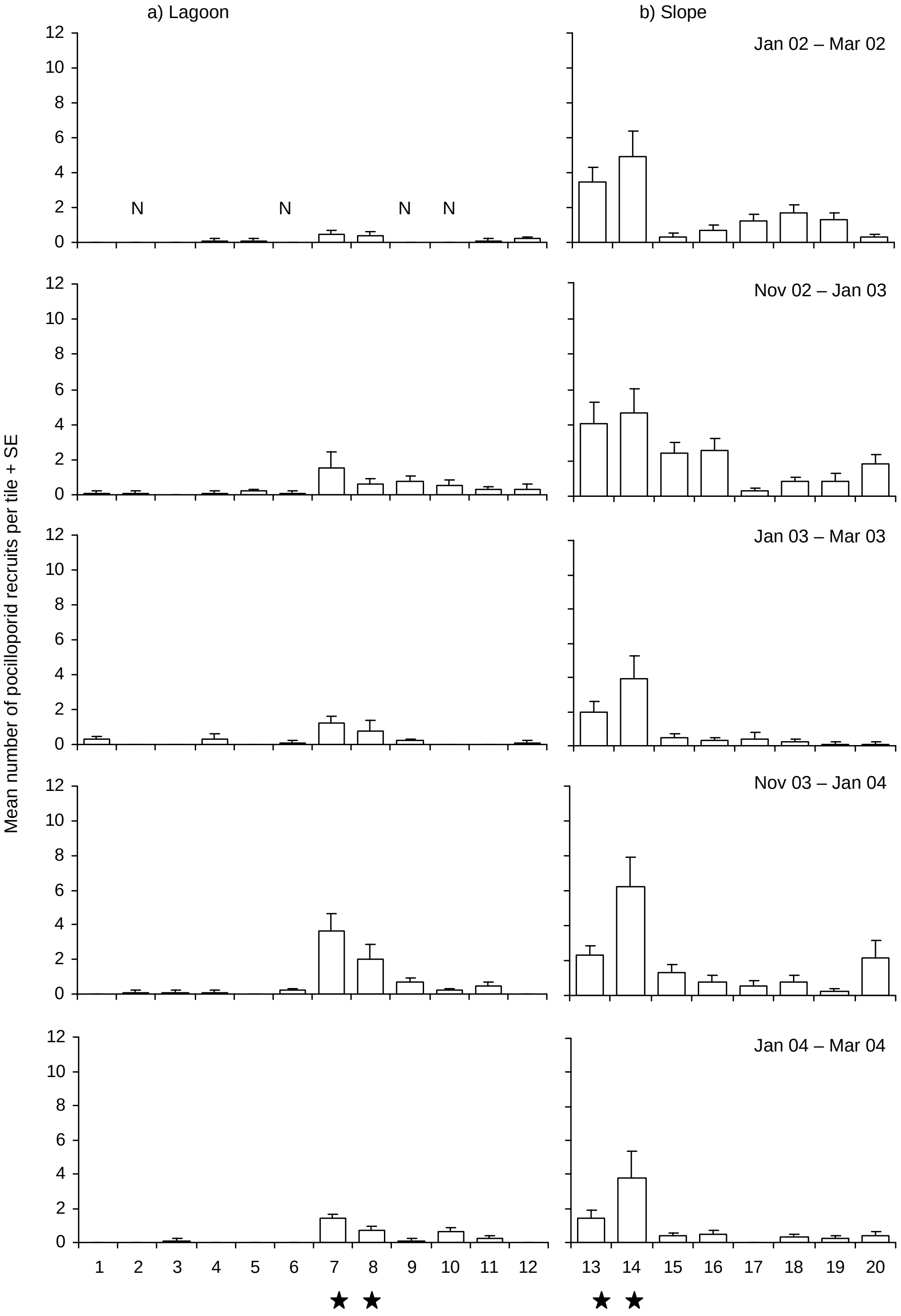


**Figure 2** Mean pocilloporid recruitment per tile + SE at 8 reef slope and 12 lagoon sites at One Tree Reef for five 8-week deployment periods over three summer recruitment seasons (n ~ 10). N denotes sites not included in the first deployment. ∃ = a recruitment hotspot i.e. the site was ranked first or second in order of greatest average recruitment per tile in three or greater times out of the five times sampled.

|  |  |  | Pocilloporidae |  | Acroporidae |  | Poritidae |  |
|---|---|---|---|---|---|---|---|---|
| Habitat | Factors | df | MS | p | MS | p | MS | p |
| Lagoon | Time | 4 | 0.920 | .054 | 0.127 | 0.594 | 1.502 | 0.008 |
|  | Site | 11 | 3.727 | < 0.001 | 0.384 | 0.040 | 0.752 | 0.052 |
|  | Time x Site | 40 | 0.361 | 0.001 | 0.180 | 0.409 | 0.374 | < 0.001 |
|  | Residual | 495 | 0.194 |  | 0.173 |  | 0.178 |  |
| Slope | Time | 4 | 5.961 | < 0.001 | 28.0 | < 0.001 | 2.277 | < 0.001 |
|  | Site | 7 | 11.717 | < 0.001 | 1.369 | 0.022 | 0.635 | .091 |
|  | Time x Site | 28 | 0.718 | 0.170 | 0.477 | 0.173 | 0.319 | < 0.001 |
|  | Residual | 325 | 0.566 |  | 0.378 |  | 0.119 |  |

**Table 1:** Two-way ANOVA's for field recruitment patterns. Data are square root transformed number of larvae per tile and $p < 0.05$ denotes a significant effect.

### *Acroporidae*

Mean recruitment of acroporids was relatively low at all sites and ranged from zero to a maximum of 5.6 ± 1.1 (mean ± SE) spat per tile at site 17, which was located on the windward side of the reef slope (south), during November 2002 to January 2003. As for pocilloporid recruitment, no site had zero recruits for all five times (Figure 3). On the slope, recruitment rates were less than 2 recruits per tile at all sites during all times except November 2002 to January 2003 when mean recruitment ranged from 1.5 ± 0.60 per tile at site 15 on the western edge of the leeward side of the reef, to the maximum described above. Site 19 on the exposed south eastern corner, and site 14 on the leeward northern side (where pocilloporid recruitment was highest), were the only sites where acroporids recruited every time, site 19 was ranked first or second in five of five times sampled, and site 14 in four of five times.

In the lagoon, mean recruitment rates were less than one recruit per tile at all sites and at all times, with the single exception of site 11 during November 2002 to January 2003, which had a mean recruitment of 2.5 ± 2.5. Only site 5 had acroporid recruits at all times, and along with site 6, was ranked either first or second in three of the five times. Both these sites were located in the east of the lagoon. For both the slope and lagoon, relative site ranks were consistent among times (slope: $W_c = 0.49$; $(\chi_r^2)_c = 17.2$; $p < 0.025$, lagoon: $W_c = 0.39$; $(\chi_r^2)_c = 21.4$; $p < 0.05$) and there was no significant interaction between Site and Time indicating that recruitment patterns among sites were persistent. Exceptionally low recruitment rates overall, however, meant that these results may reflect similarly low recruitment at all sites at all times, rather than similar patterns of high and low recruitment among sites during each time.

### *Poritidae*

For all times there were low levels of recruitment of poritids in the lagoon and on the slope relative to other taxa (Figure 4). Mean recruitment ranged from zero to a maximum of 2.7 ± 1.4 (mean ± SE) spat per tile in November 2003 to January 2004 at site 7, which is located in the northern section of the lagoon. There was virtually no recruitment of poritids in January 2002 to March 2002 in either the slope or lagoon, and one site in the western location of the lagoon (site 12) did not receive any poritid recruits over the entire five times. Less than one recruit per tile was recorded at almost all sites and times. The exceptions were a northern lagoon site (site 7) and two windward reef slope sites (sites 17 and 18) in November 2002 to January 2003, and two northern lagoon sites (7 and 8) in November 2003 to January 2004. Site 7 in the lagoon was ranked highest in mean recruitment and sites 17 and 18 on the reef slope were ranked either first or second in three out of five times and site ranks were concordant across times on the slope ($W_c = 0.65$; $(\chi_r^2)_c = 18.3$; $p < 0.025$) and in the lagoon ($W_c = 0.66$; $(\chi_r^2)_c = 29.2$; $p < 0.005$). Significant Site by Time interactions, however, for both habitats (Table 1) indicated that relative patterns of poritid recruitment varied in the magnitude of differences among sites over time.

### ***Coral recruitment v adult coral cover.***

Mean recruitment of pocilloporids and poritids was positively related to the percentage cover of conspecifics but not for all habitats (lagoon and slope) or scales (quadrats and transects). There was no correlation between recruitment and cover of acroporids in either habitat or at either scale. In the lagoon (Figure 5a), there were significant positive exponential relationships between recruitment and the abundance of adults at both transect and quadrat scales and adult abundance described 55 and 72 % of the variation respectively. There were no relationships between recruits and adults for poritids at either scale in the lagoon. On the reef slope (Figure 5b) the mean percent of poritids comprising the coral habitat in quadrats explained 68 % of the variation in mean poritid recruitment, but there was no relationship between recruitment and the abundance of poritid adults in transects. The mean percent cover of adults in transects explained 82 % of the variation in mean pocilloporid recruitment, but there was no relationship between adults in quadrats and recruitment.

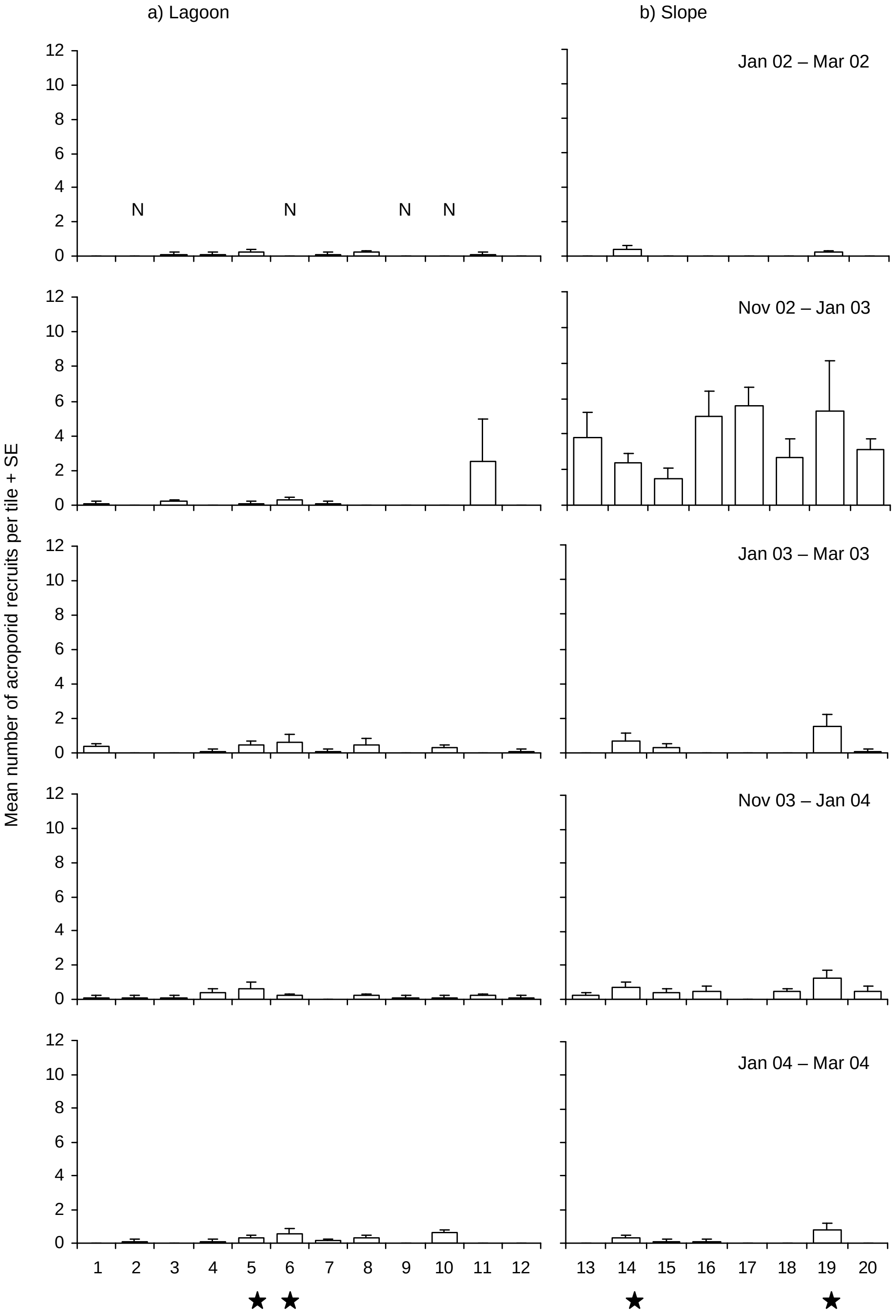


**Figure 3:** Mean acroporid recruitment per tile + SE at 8 reef slope sites and 12 lagoon sites at One Tree Reef for five 8-week deployment periods over three summer recruitment seasons (n ~ 10). N denotes sites not included in the first deployment. ∃ = a recruitment hotspot i.e. the site was ranked first or second in order of greatest average recruitment per tile in three or greater times out of the five times sampled.

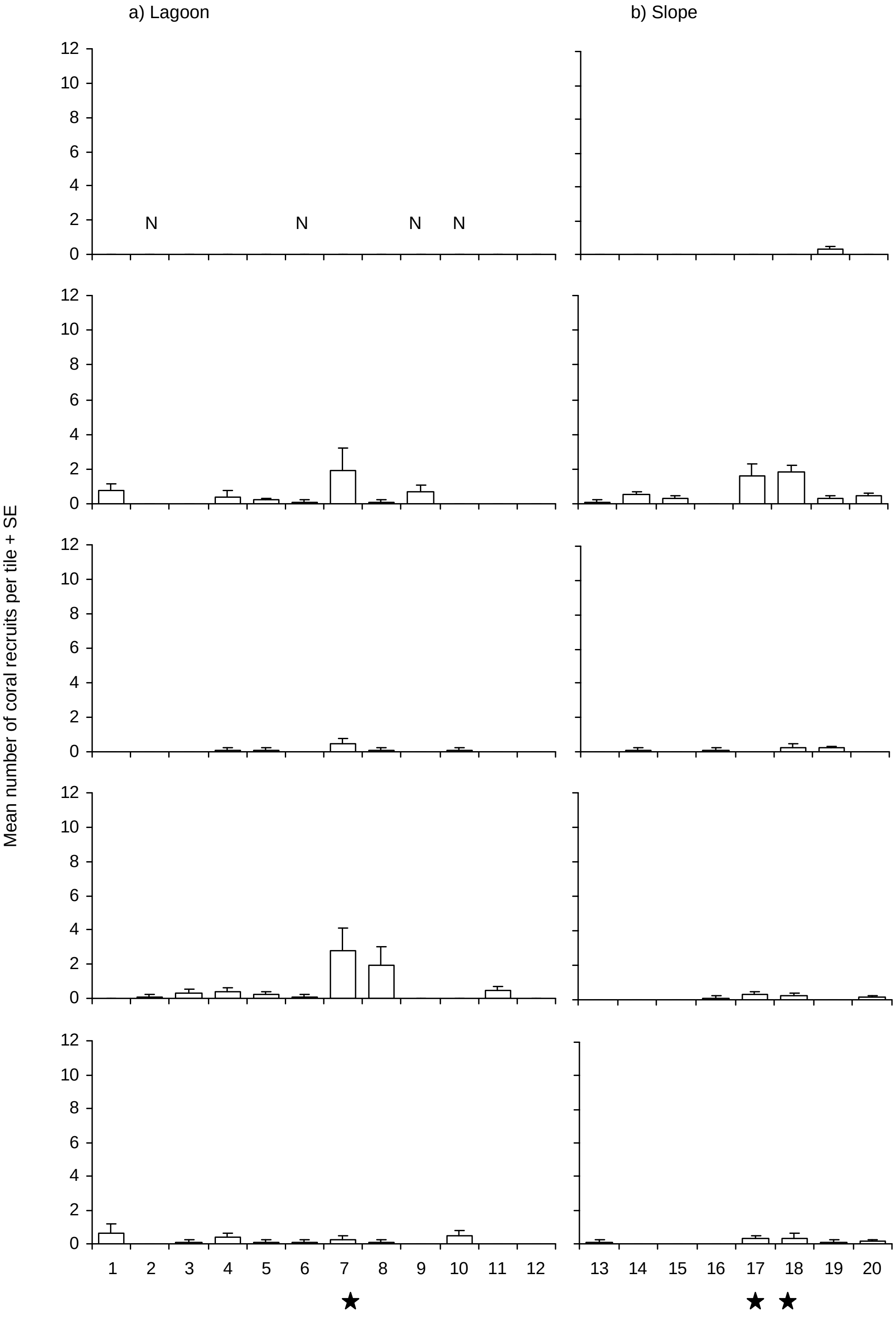


**Figure 4:** Mean poritid recruitment per tile + SE at 8 reef slope sites and 12 lagoon sites at One Tree Reef for five 8-week deployment periods over three summer recruitment seasons (n ~ 10). N denotes sites not included in the first deployment. ∃ = a recruitment hotspot i.e. the site was ranked first or second in order of greatest average recruitment per tile in three or greater times out of the five times sampled.

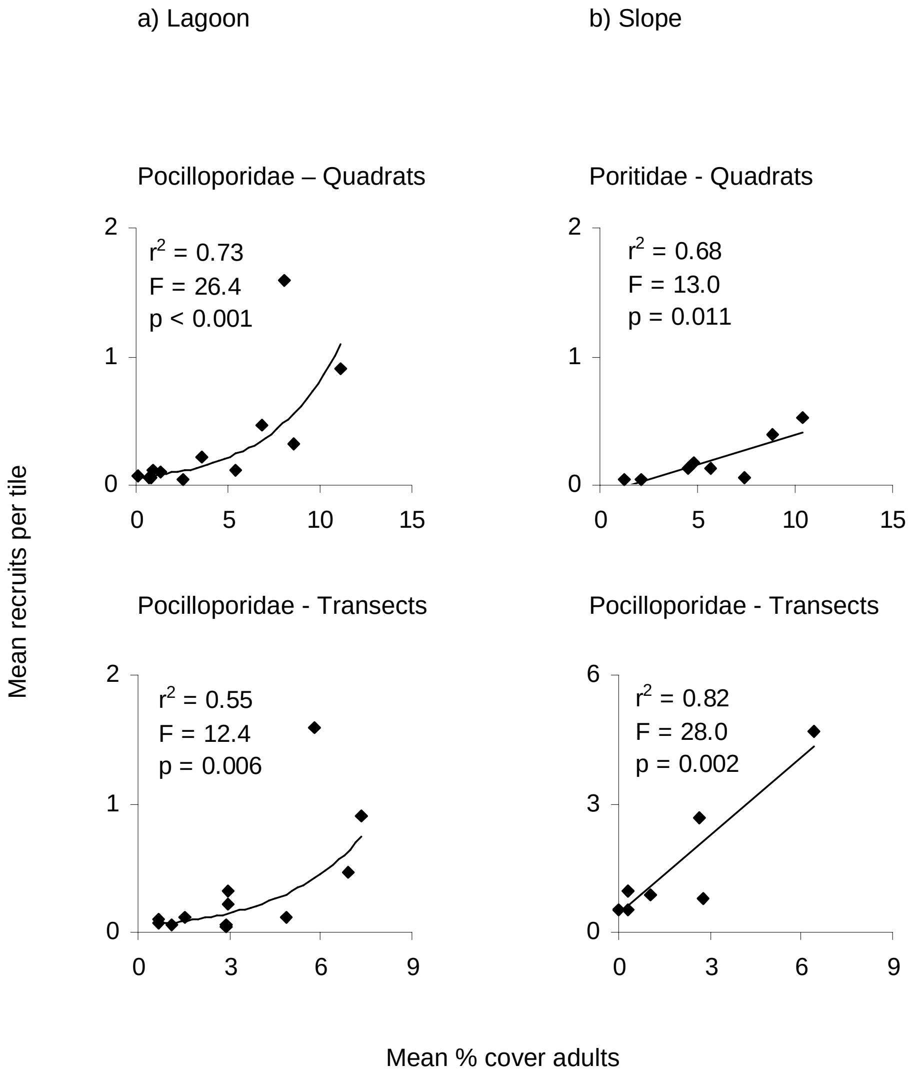


**Figure 5:** Significant relationships between the mean number of recruits per tile at each site and the mean percent cover of adult corals for (a) lagoon and (b) slope.

### *Coral recruitment v hydrodynamics*

Mean recruitment and water flow were not linearly related for any of the three coral families in either the slope or lagoon. In the lagoon, (Figure 6a) average recruitment over the five study periods among sites appeared similar between pocilloporids and poritids. Recruitment in these two families was highest at a medium flow (~ 0.35 % $d^{-1}$ $m^{-1}$ or 4.5 cm $s^{-1}$) site, but was low at sites with low (~ 0.27 % $d^{-1}m^{-1}$ or 2.1 $cms^{-1}$), medium or high (~ 0.43 % $d^{-1}$ $m^{-1}$ or 7.1 cm $s^{-1}$) average flows. In contrast, on the reef slope (Figure 6b), there were no clear relationships between mean recruitment for these two families and water flow. There were no relationship between recruit abundance and adult percent cover for acroporids on either the slope or lagoon.

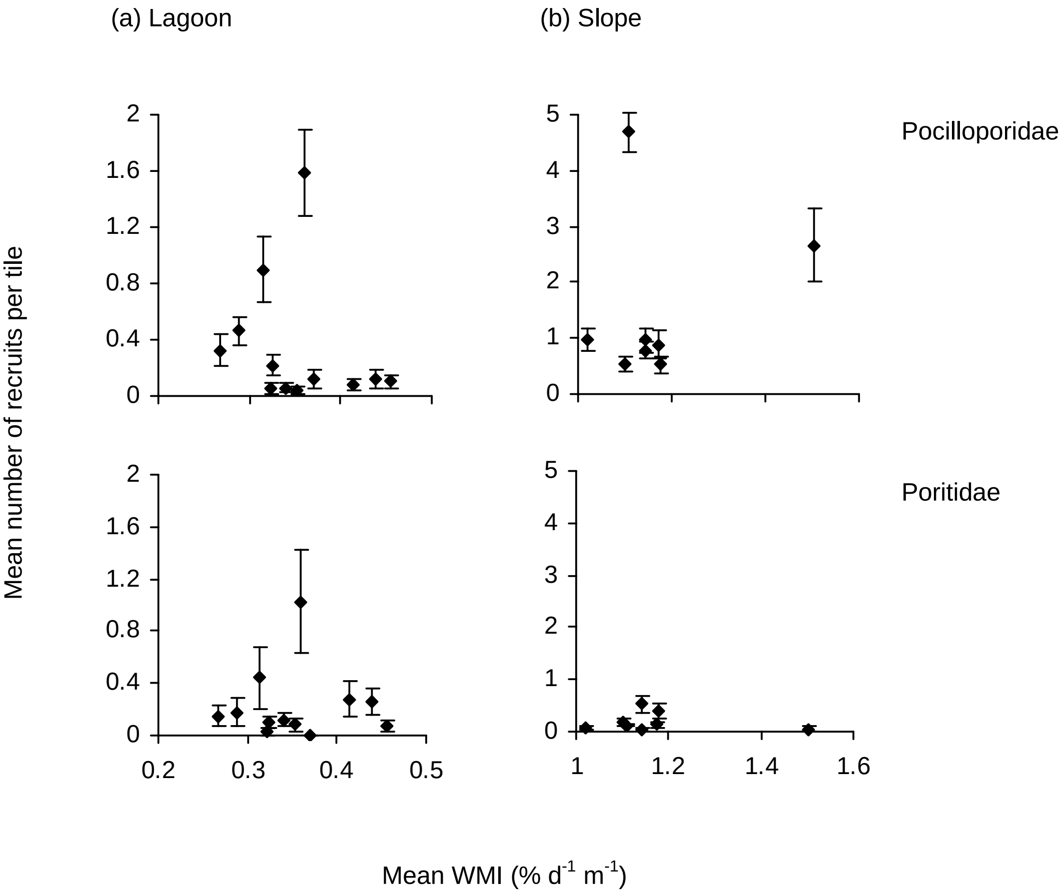


**Figure 6:** Relationship between mean Water Movement Index (WMI) and mean recruitment per tile per site for coral families for (a) lagoon and (b) slope. Current flow in cms$^{-1}$ estimated using equations from Fulton and Bellwood (2005) are 2.7 to 7.4 cm s$^{-1}$ in the lagoon, and 11.6 to 22.4 cm s$^{-1}$ on the slope.

### *Experimental test of water flow and substratum effects on coral settlement*

In experimental aquaria, *Acropora nasuta* larvae were six to ten times more abundant on tiles held under low (2.1 cm s$^{-1}$) compared to medium (4.6 cm s$^{-1}$) flow speeds (Figure 7). Recruitment varied by two orders of magnitude, ranging from 2.0 ± 1.0 to 111.0 ± 83.6 (mean ± SE) recruits per tile.

For tiles conditioned in the lagoon, settlement of *Acropora nasuta* was ten times greater onto tiles in low 61.0 ± 23.0 (mean ± SE) compared with medium 6.0 ± 2.0 flow treatments (ANOVA: df = 1, 16, F = 11.9, p = 0.003) and there was no significant interaction or effect of site (Figure 7a). For tiles conditioned on the reef slope *A. nasuta* larvae also showed significant settlement preferences according to flow speed but not substrata (Figure 7b). Settlement of larvae was six times greater in the low (40.0 ± 14.0) compared to the medium (6.0 ± 3.0) flow treatment (ANOVA: df = 1, 8, F = 30.3, p = 0.001) and there were no significant effects of sites or an interaction.

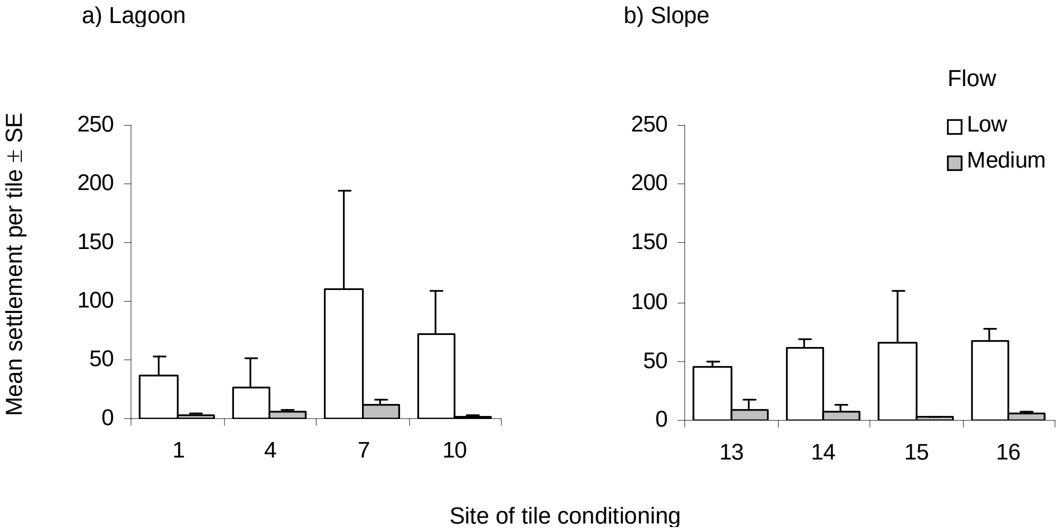


**Figure 7:** Settlement choice experiment for *Acropora nasuta* larvae. Bars represent the mean number of larvae per tile per flow regime with ± SE indicating variation among aquaria. Larvae in a tub were subject to either low or medium flow conditions and the x-axis shows the choice of four settlement tiles available. Tiles were conditions at sites labelled as in Figure 1. (a) shows larval settlement choice for tiles conditioned at four lagoon sites (n = 3) and (b) for tiles conditioned at four reef slope sites (n = 2).

## Discussion

Recruitment hotspots were identified for all coral families in both lagoon and slope environments according to concordance in site ranks among recruitment times. Densities of coral recruits at these hotspots at One Tree Reef were, however, relatively low compared to reports of recruitment onto similar substrata elsewhere on the Great Barrier Reef (up to one hundred recruits per tile) (Hughes et al. 1999). In previous studies, temporal variation has often been too high to detect any persistent spatial patterns in recruitment at around reef scales (Fitzhardinge 1985, Dunstan & Johnson 1998, Hughes et al. 2000, Soong et al. 2003). This study shows, however, that spatial variation in mean recruitment among sites around a reef may be predictable in terms of the rank order of recruitment, even though the magnitude of differences among sites may vary from year to year. It is concluded that both deterministic and stochastic processes affect recruitment variation at across reef scales.

Recruitment hotspots at One Tree Reef were most obvious for pocilloporids, for which there were clear differences among sites that were consistent through time, but less obvious for acroporids and poritids. In fact, recruitment for acroporids appeared to more closely resemble the phenomenon of the ‘rogue wave’ recruitment hypothesis where recruitment peaks may occur occasionally at all sites due to a combination of favourable conditions all co-occurring, making variation among sites in most years background noise (Neill et al. 1994). One site in the lagoon was a hotspot for pocilloporids and poritids, and many sites of high recruitment for all families were on the western side of the island, however, there was little congruence in the specific sites of highest recruitment among the three families overall. Consistency in spatial patterns of pocilloporid, but not acroporid recruitment between years has also been found in the

Red Sea (Glassom et al. 2004) and greater differences among sites for pocilloporid recruitment compared with acroporid recruitment has been noted for other reefs on the GBR (Babcock 1988, Dunstan & Johnson 1998). Better resolution of patterns for pocilloporids compared with acroporids and poritids is probably related to greater abundances of pocilloporid recruits and potentially greater local retention in brooders.

Persistent temporal patterns maintaining recruitment hotspots may be due to the production of brooded planulae, which are ready to settle on release, by some coral species within each family. The dominant pocilloporids on the GBR produce brooded larvae (Richmond 1981, Stoddart & Black 1985, Harrison & Wallace 1990) and planulation in three pocilloporid species at Heron Reef co-occurs with the mass spawning period (Tanner 1996). For pocilloporids, recruits and adult abundances were correlated in both the lagoon and on the slope at One Tree reef, as has been previously found in other studies both on the GBR and elsewhere (Babcock 1988, Harriott 1992, Smith 1997, Tioho et al. 2001, Soong et al. 2003). Whether or not these recruits persist and ultimately maintain the adult population is unknown, particularly since brooded larvae are thought not to contribute substantially to populations of adult populations at One Tree reef on the basis of genotypic diversity (Sherman et al. 2006). Further study on the fate of larvae and juveniles in recruitment hotspots is required to determine this.

A relationship between recruits and adults was also found for poritids on the reef slope, which suggests that a proportion of poritid recruits on the reef slope at One Tree Reef may also be from brooded larvae. Interestingly, there were no relationships between recruits and adults for this family in the lagoon. The majority of poritids are broadcast spawners, however, some species brood larvae (Szmant 1986, Chornesky & Peters 1987, Harrison & Wallace 1990, Smith 1992, Shlesinger et al. 1998, Harii et al. 2001) including *Porites heronensis* (Harriott 1992, Harriott & Banks 1995), which occurs at the southern end of the GBR and *Porites murrayensis,* which planulates from November to April at nearby Heron Island (Kojis & Quinn 1981). The relative occurrence of these two species either in the lagoon or on the slope at One Tree reef has not been documented, however, differences in poritid recruit-adult relationships between the lagoon and slope may indicate differences in poritid species recruiting in each habitat.

There were no relationships between acroporid recruits and adults at either the quadrat or transect scale in either the lagoon or slope habitats. Most acroporid corals are broadcast spawners, however, isoporan acroporids brood planulae (Harrison & Wallace 1990, Richmond & Hunter 1990). At Heron Reef, planulae are released once a year by *Acropora palifera* between January and March and *Acropora cuneata* between November and January (Kojis 1986). Acroporids recruiting to settlement tiles at One Tree Reef could have been from both brooded and spawned larvae, but recruits would have to be examined at greater taxonomic resolution to investigate this. Sites 5 and 6 in the eastern lagoon and sites 14 (northwest) and 19 (southeast) on the reef slope were recruitment hotspots according to site ranks, however, abundances of neither acroporid corals, nor specifically isoporans were greater at these sites. If brooding is a precursor to the existence of recruitment hotspots, and given that the majority of acroporid corals are broadcast spawners, it is not surprising that the abundance of acroporid recruits did not relate to the abundance of adults at One Tree Reef. To properly elucidate the nature of the relationship between recruits and adults, that is, whether adults determine recruits or recruits determine and the ultimate mechanisms, further studies are required, and these should include an examination of distribution and abundance of juvenile corals.

In the lagoon, one site was a recruitment hotspot for two out of the three families, and this site was an area of medium water flow. Not all sites with medium levels of water flow were, however, recruitment hotspots. Greatest recruitment at a medium flow site may have been in part because sites with the lowest levels of water flow are supplied with very few larvae (Black & Moran 1991, Harriott & Simpson 1997), while at sites with the highest levels of water flow, larvae enter the lagoon at times when currents are fastest and they are subsequently unable to settle. In contrast, recruitment hotspots were not clearly related to hydrodynamic regimes on the reef slope for any family, perhaps because ambient flows are on average very fast, so recruitment may depend entirely on settlement windows afforded by infrequent low wind and current conditions, as may have occurred in November 2002.

Hydrodynamic structure may also be an important influence on recruitment patterns due to its affect on recruit patchiness. Hydrodynamic features such as fronts accumulate pelagic larvae (Wolanski & Hamner 1988, Kingsford 1990, McCulloch & Shanks 2003) and often form between lagoon and inter-reefal waters (Willis & Oliver 1990, Kingsford et al. 1991). During the course of this study, we observed fronts forming along the reef margin in the location of sites 7 and 8 in the lagoon and sites 13 and 14 on the reef slope, corresponding with recruitment hotspots for pocilloporids. Fronts are more likely to affect the recruitment patterns for coral species that release brooded planulae over a longer time period e.g. pocilloporids compared with species where recruitment is dominated by an annual broadcast spawning e.g. acroporids. Other hydrodynamic characteristics such as turbulence, boundary layers and complex micro-topography may also affect the ultimate settlement of coral larvae and warrant investigation in future studies.

Settlement of *Acropora nasuta* larvae in experimental aquaria was up to ten times greater in low (2.1 cm $s^{-1}$) compared to medium current flow (4.6 cm $s^{-1}$). This may be due either to poor abilities to swim or adhere to the substratum in higher flows, or due to settlement preferences for low flow. Coral larvae are weak swimmers and have been observed to swim in the laboratory at speeds of only 0.1 to 0.5 cm $s^{-1}$ (Harrison & Wallace 1990). However, swimming abilities and/or preferences may differ considerably among taxa. In experimental aquaria Harii and Kayanne (2002) found greatest settlement rates in *Pocillopora damicornis* larvae (70 %) occurred under high flows (9.8 cm $s^{-1}$) while greatest settlement in *Heliopora coerulea* larvae (50 %) occurred in still water. The combined experimental and field results from this study suggest that greatest acroporid recruitment may occur under very low flow conditions affecting all sites simultaneously.

## Conclusion

Recruitment 'hotspots' were identified for three coral families in the lagoon and on the slope at One Tree Reef. Recruitment hotspots were related to the percent cover of adults for pocilloporids and poritids but not acroporids, possibly reflecting principle reproductive modes of these taxa (brooding versus spawning). In the lagoon, recruitment hotspots were located in areas with medium levels of water flow. Flow speed in experimental aquaria was a more important determinant of settlement in *Acropora nasuta* larvae than the site that tiles were conditioned. Recruitment hotspots may be of particular importance when assessing the recovery capabilities of different reef areas and designating reef areas for use or conservation. Further work is required to determine whether recruitment hotspots occur at predictable sites on other platform reefs within the GBR and in other locations.

## Chapter 5 – Recruitment hotspots for coral reef fishes

### Abstract

Recruitment is a critical determinant of the abundance and population dynamics for coral reef fishes. Sites that continually receive high levels of recruitment, or "recruitment hotspots", may be especially important in sustaining certain populations. Identifying and protecting such sites is important, but little information exists on where recruitment hotspots are and what causes them. The aim of this study was to identify recruitment hotspots at One Tree Reef (southern Great Barrier Reef) and to assess the roles of hydrodynamic factors and habitat structure in governing localized recruitment patterns. We identified many recruitment hotspots, where recruitment by three coral-dwelling damselfishes (*Pomacentrus moluccensis*, *Chromis viridis* and *Dascyllus aruanus*) was consistently higher (~ 1 fish per $m^2$) compared to average levels of recruitment (~ 0.1 fish per $m^2$) recorded around One Tree Reef. Hydrodynamic factors (moderate current flows) and availability of suitable micro-habitats (the abundance of preferred corals) partly accounted for higher than expected recruitment at certain sites. However, relationships between recruit abundance versus hydrodynamic flow and habitat availability were complex, non-linear and inconsistent among the three study species. The lack of simple linear relationships between recruit abundance, hydrodynamics and habitats may have been due, at least in part, to interactions between hydrodynamics and habitat structure. Notably, there were marked differences in the morphology (branch-spacing) of preferred micro-habitats among sites with different hydrodynamics. Nevertheless, at One Tree Reef, specific hydrodynamic regimes and

habitat structure were fundamental in making some sites recruitment hotspots for coral reef fishes, contributing to increased determinism in spatial patterns of recruitment.

## Introduction

Recruitment of pelagic larvae into adult habitats is a fundamental process ensuring long-term persistence of marine populations (Connell 1975, Gaines & Roughgarden 1985, Underwood & Fairweather 1989, Caley et al. 1996, Doherty 2002). In general, recruitment is highly stochastic and unpredictable due to vagaries associated with the production, dispersal and complex behaviour of pelagic larvae (Doherty 1991, Caley et al. 1996, Watson & Barnes 2004, Sale et al. 2005). However, researchers are increasingly discovering that particular sites consistently receive disproportionately high numbers of new recruits (Connolly & Roughgarden 1998, Hughes et al. 1999, Booth et al. 2000, Hamilton et al. 2006). These sites, termed “recruitment hotspots” (Booth et al. 2000) make a major contribution to population replenishment of open populations and may be fundamental to the persistence of marine species. Importantly, recruitment hotspots may warrant increased protection from habitat degradation to ensure ongoing population replenishment, especially following major disturbance events. Currently, there is very limited information on where recruitment hotspots occur and what causes them. Most likely, recruitment hotspots result from hydrodynamic peculiarities (e.g., current and eddies) that collect and concentrate pelagic larvae (e.g. Cowen & Castro 1994, Carleton et al. 2001a) or specific habitat attributes that attract and maximize survival of settling larvae (Holbrook et al. 2000, Schmitt & Holbrook 2000, Jones et al. 2004).

Hydrodynamic regimes around reefs are complex because regional currents interact with reef topography to form irregular hydrodynamic features, such as island wakes and topographic fronts (Wolanski et al. 1984, Black 1988, Wolanski & Hamner 1988). However, many of these hydrodynamic features persist through time (Wolanski & Pickard 1983, Hamner & Wolanski 1988, Black et al. 1990), contributing to establishment of recruitment hotspots (Booth et al. 2000). Hydrodynamic features affect the distribution patterns of larval fishes through passive accumulation of larvae in wakes and slicks, as well as active aggregation by those species and developmental stages with better swimming capabilities (Kingsford & Choat 1986, Kingsford 1990, Kingsford et al. 1991, Doherty & Carleton 1996, Carleton et al. 2001a). Recruitment patterns may also result from physical delivery of larvae via currents to particular areas (Milicich et al. 1992, Sponaugle & Cowen 1996b, Hamilton et al. 2006) or from relationships between individual species and ambient current flow (Schmitt & Holbrook 2002b). For lagoons, recruitment hotspots might be predicted to occur in lagoon openings or areas of greatest water influx, due to either increased densities of passive larvae (Booth et al. 2000) or active swimming by larvae up lagoonal plumes (Gerlach et al. 2007). In contrast, areas that are more distant from lagoon entrances will have lower recruitment due to "shadow-effects", where larvae quickly settle out of the water column when they first encounter the reef substrates (Shapiro 1987, Booth 1995, Jones 1997). To date many of these patterns remain unexplored, and it is unknown whether greater recruitment occurs in areas of reef with greater water movement, and therefore, larval flux, or alternatively, in areas with lower water flux where larvae may be retained or choose to settle.

The abundances and composition of microhabitats vary around reefs, partly in response to physical factors such as wave exposure and hydrodynamic flow (Sheppard 1981, Done 1982, Fabricius 1997, Ninio & Meekan 2002). Settlement preferences by coral reef fish larvae for particular microhabitats are well established (Sale et al. 1984b, Eckert 1985, Eggleston 1995, Danilowicz 1996, Ohman et al. 1998). Coral reef fishes range from generalists that associate with subtle microhabitat features not always immediately obvious (Bell & Kramer 2000, Bergman et al. 2000, Eagle et al. 2001, Sale et al. 2005) to specialists that associate exclusively with particular species of habitat-forming invertebrates (Elliott et al. 1995, Munday et al. 1997, Munday 2002). It is no surprise that recruitment of reef fishes among locations within reefs often reflects the distribution and abundance of suitable microhabitat (Shulman 1985, Eggleston 1995, Tolimieri 1995, 1998b, a, Holbrook et al. 2000), however, this is not always the case (Levin 1994, Caselle & Warner 1996, Sale et al. 2005). There has been little exploration of this dichotomy amongst species with similar habitat preferences.

The relative importance of hydrodynamics versus microhabitat availability in determining recruitment patterns of coral reef fishes has rarely been explored (but see Booth et al. 2000), though it is known that the physical and biological structure of benthic reef habitats co-varies with hydrodynamics. For example, hydrodynamic processes affect coral habitats in a number of ways, influencing species composition and abundance (Sheppard 1981, Done 1982, Fabricius 1997, Ninio & Meekan 2002), rates of calcification, growth, reproduction and mortality (Jokiel 1978, Dennison & Barnes 1988, Sebens et al. 2003), susceptibility to bleaching (Nakamura & van Woesik 2001), competitive abilities (Maida et al. 1995a), and morphological characteristics such as branch-spacing (Chamberlain & Graus 1975, Veron & Pichon 1976). Whether or not hydrodynamics affect coral colonies to an extent that they more or less ‘suitable’ (*sensu* Holbrook et al. 2000) as recruit habitats, has not been tested. However, coral reef fishes are known to exhibit settlement choices among closely related coral species (Munday et al. 1997) and so it is possible that they may also exhibit settlement choices among morphologically different colonies within species. If so, use of coral habitats in the field may vary among sites with different hydrodynamics regimes.

The primary objectives of this study were to locate areas that consistently receive disproportionate recruitment for three fish species at One Tree Reef (southern Great Barrier Reef) and to examine the roles of hydrodynamic factors and habitat structure as determinants of these recruitment hotspots. We quantified temporal persistence of spatial patterns in recruitment across the lagoon and around the slope of this isolated platform reef. The specific questions addressed were: (1) Do some sites consistently receive disproportionately high levels of recruitment? (2) If so, is there congruence in recruitment hotspots among different fishes? Are recruitment hotspots associated with (3) high or low levels of water flow, or (4) greater cover of coral microhabitats? Finally, given that hydrodynamic factors may directly alter the quantity and quality of recruitment habitat, (5) does water flow influence the morphology of coral habitats and (6) do recruit fishes have preferences for corals with different flow-related morphologies?

## Methods

### *Field recruitment patterns*

One Tree (23°30’S, 153°67’E) is a platform reef located approximately 20 km from the continental shelf edge in the Capricorn-Bunker group of the southern Great Barrier Reef

(GBR). Recruitment was monitored at 20 sites, located 100 m to 5 km apart (Figure 1). Local hydrodynamics are driven primarily by tidal fluctuations and wind-generated surface circulation (Frith 1981), which interact with local topography. The prevailing wind pattern is from the south-east. One Tree lagoon is conspicuous for its lack of a clear lagoon entrance; there are no channels through the reef matrix enclosing the large shallow lagoon, which subsequently 'ponds' at low tide. However, slight variations in the height of the rim around the reef (<1m) create areas of low and high flow around the reef during tidal changeover. Habitat composition around the reef ranges from slopes with >70% cover of acroporid corals, to lagoonal areas dominated by sand, poritids and turf algae.

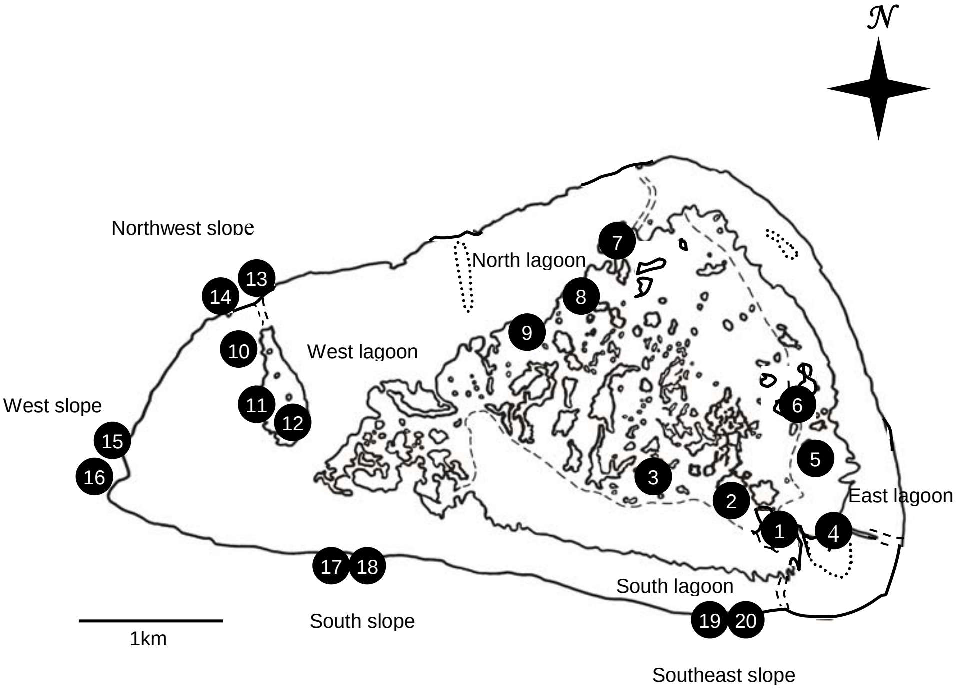


**Figure 1:** Location of study sites around One Tree Reef in the lagoon and on the reef slope. Lagoon sites are labelled 1 to 12 and slope sites are labelled 13 to 20. Distances between sites are between 100 m and 5 km.

Recruitment was monitored between January and March for three species of damselfish: *Pomacentrus moluccensis*, *Chromis viridis*, *Dascyllus aruanus*. All three species lay demersal eggs and once hatched, larvae have a pelagic larval duration of 19, 20-30 and 25 days, respectively (Brothers et al. 1983, Planes 2002, Bay et al. 2006). Competent larvae of all three species settle directly in live coral colonies, with which they remain strongly associated throughout their adult lives. Young-of-the-year (<3 cm TL) were counted within three replicate 50 × 2 m belt transects at each of the 20 study sites. All transects were laid parallel to the crest and run from haphazardly selected starting points within specified habitats. In the lagoon, transects were run 1-2 m below the crest, whereas on the outer slope, transects were run 5–6 m below the crest. Sampling was undertaken during January and March of 2002, 2003 and 2004 within the lagoon, and in March of 2002 and 2003 on the slope. Surveys were carried out twice during the summer recruitment season in the lagoon to account for the arrival of the recruits early in the season, but which would not be present at the end of the season due to post-settlement mortality, and results were averaged across the two surveys for each year to account for the fact that some individuals would have been counted twice. Only one survey per year was possible on the slope. Settlement patterns for most damselfishes are highly seasonal, concentrated in January-March on the Great Barrier Reef (Williams et al. 1994). Therefore, no additional sampling was conducted outside of this period.

All analyses were carried out separately for different habitats (lagoon versus slope) and for different fish species. Two-way ANOVAs tested for significant differences in recruitment rates among years (Time) and sites (Site), both random factors. Data were log10 (x + 1) transformed to improve normality and heterogeneity in raw counts. Concordance analysis (Kendall’s Coefficient of Concordance with Correction for Tied

Values) where $\chi_{r\ crit}^{2} = 19.7$ and $\nu = 11$ was used to determine whether relative site ranks in the lagoon were persistent among three years. Further, Spearman's Rank Correlation with Corrections for Tied Values, where $r_{s\ crit} = 0.738$ and $n = 8$, was used to determine whether relative site ranks on the slope were persistent between years (Zar 1999).

***Recruitment and hydrodynamics***

To quantify spatial variation in hydrodynamics, we deployed plaster standards or 'clod cards' at the 12 study sites within One Tree lagoon. Four spherical plaster balls (ca. 54 cm diameter) were deployed at each site one week following the full moon in January 2004. The average weight lost from balls in a 24-hour period was converted to a value in cm $s^{-1}$ using the equation $WL_{28°C} = 0.921v + 10.812$ from Fulton and Bellwood (2005) where $WL$ = weight lost in grams in 24 hours and $v$ = flow velocity in cm $s^{-1}$.This method was used as currents were thought to be less important in affecting recruitment than the integrated effect of the circulation over a critical period (Sammarco and Andrews 1989).

To estimate water flow on the slope, data was extrapolated from a hydrodynamic model (Black 1983) of the One Tree Reef region modelled over a 10 day period in January 2001 (Burgess et al. 2007). Current speeds for each of the eight slope sites were extracted at 30-minute intervals and averaged. To calibrate the model, plaster standards were deployed at only the four leeward sites (13, 14, 15 and 16). Four spherical plaster balls (ca. 54cm diameter) were deployed at each site in January 2004, recording the change in weight over a 3 day period. Relationships between recruitment rates of each fish species versus hydrodynamic regimes were tested using the mean Water Movement

Index (WMI) expressed in units of percentage weight lost per day per metre of tidal movement (% $d^{-1}$ $m^{-1}$), calculated separately for each site.

### *Recruitment and microhabitats*

Availability of suitable micro-habitats (specific coral colonies) is likely to exert a major influence on recruitment rates for coral-dwelling damselfishes (Holbrook et al. 2000). To assess availability of different micro-habitats, the proportional abundance of different coral species was quantified using 50-m point-intercept transects (PIT). Fifty uniformly spaced points (1-m apart) were sampled along each of the three transects used to survey fishes during the March surveys, recording the coral species or substrate-type underlying each point. Surveys were repeated annually for three years in the lagoon (2002, 2003, 2004) and two years on the slope (2002, 2003). The coral microhabitats into which each *Pomacentrus moluccensis*, *Chromis viridis* and *Dascyllus aruanus* recruited during the 2003 and 2004 recruitment surveys were also recorded. Habitats were grouped into five categories: pocilloporid corals, acroporid corals, poritid corals, corals from other families, and non-living substrata/turf algae. Recruitment for each year was examined with respect to the percent cover of each major coral family into which each species recruited, as well as the sum of all coral families into which they recruited and Least Squares Regression (LSR) was carried out to determine significant relationships.

### *Hydrodynamics and microhabitats*

Electivity indices were used to quantify patterns of micro-habitat use by two of the three damselfishes (*Pomacentrus moluccensis* and *Dascyllus aruanus*) at three sites in the northern part of the lagoon where water flow varied among sites within a location. Two sites (sites 8 and 9) had low levels of water movement (2.1 to 2.7 $\text{cms}^{-1}$), and one site (site 7) had medium levels of water movement (4.9 $\text{cms}^{-1}$), Electivity indices (Vanderploeg & Scavia 1979) established whether fish used different coral microhabitats in accordance with their proportional abundance on the reef (i.e. no selection), or whether they used coral microhabitats disproportionately to their abundance (i.e. strong selection). An electivity coefficient (E*) was calculated for recruits for each substratum category using the formula:

$E^* = [W_i - (n^{-1})] \,.\, [W_i + (n^{-1})]^{-1}$

where $n$ = the number of habitat types (categories)

$W_i = (r_i \,.\, p_i^{-1}) / \sum(r_i \,.\, p_i^{-1})$

$r$ = proportion of resources utilized

$p$ = proportion of resources available

Positive values indicated that these habitats were used in greater proportions than expected from their abundance. Negative values indicate that habitats are used less than expected.

Synergies between hydrodynamics and micro-habitats were apparent based on morphological differences in the most preferred coral habitat, *Pocillopora damicornis*, among sites with marked differences in water flux. To quantify these differences, four inter-branch spaces were measured directly for eight colonies at each of three sites (7, 8 and 9). Additional colonies of *P. damicornis* were collected from each of these sites for use in settlement choice experiments, conducted in flow-through aquaria at One Tree Island Research Station. Two nested one-way ANOVA's were used to examine differences in mean inter-branch spacing among colonies within sites and among sites for colonies measured in the field, and colonies collected for settlement experiments.

Untransformed data met the assumptions of ANOVA. In all analyses Tukey's post-hoc tests were used to determine the locations of significant differences. Settlement choice trials were carried out for *Pomacentrus moluccensis* and *Dascyllus aruanus* to examine whether recruits had habitat preferences according to contrasting flow-related morphologies of *P. damicornis*. *C. viridis* recruits were not used because they did not recruit to *Pocillopora* colonies at the three northern lagoon sites. Eighteen recruits from each species were collected from areas close to sites 4 and 12. Three *Pocillopora* colonies, one from each of the three sites, 7, 8 and 9, were placed approximately ~ 40 cm apart in a 200 L plastic aquarium. A similar sized piece of dead coral was placed in the center of the tub that was equidistant (~ 20 cm) from all three coral colonies. At the start of each trial an individual fish was released beneath the dead coral. After 2 hours, we then scored the coral colony to which the fish had moved and settled. The position of different colonies was randomized both within and between tanks. Finally, a chi-square goodness of fit test was carried out separately for each fish species to test preferences of recruits for small or wide-branching colonies based on a 2:1 ratio of different coral types in each tank where $\chi^2_{0.05,\,1}$ critical value = 3.841 (Zar 1999).

## Results

### *Recruitment patterns*

*Pomacentrus moluccensis* recruits were very cosmopolitan in their habitat use, consistently occurring at all 20 study sites (Figure 2a). However, mean densities of *P. moluccensis* recruits varied by two orders of magnitude among sites, ranging from 1.2 recruits (± 0.4 SE) per 100 $m^2$ at site 5 in 2004 to 98.5 recruits (± 20.5 SE) per 100 $m^2$ at site 10 in 2003. Despite marked inter-annual variation in the abundance of *P. moluccensis* recruits (Table 1) relative abundance among sites was very consistent.

Most notably, the ranking of sites according to abundance of *P. moluccensis* recruits was highly concordant among years ($W_c = 0.805$, $(\chi_r^2)_c = 26.5$, $p < 0.01$). Within the lagoon, highest densities of *P. moluccensis* recruits consistently occurred at sites 10 & 11 (Figure 2). At these sites mean densities of *P. moluccensis* recruits were 60 recruits per 100 $m^2$ across all three years, compared to 7 to 20 recruits per 100 $m^2$ for most other sites. On the slope, highest densities of *P. moluccensis* (76.7 ±18.7) were recorded at site 15 on the western corner of the reef. All three sites at this location (14, 15 and 16) consistently had highest densities of *P. moluccensis* recruits, averaging between 30 and 50 fish per 100 $m^2$, which was three to ten times greater than densities recorded at other slope sites (4 to 10 fish per 100 $m^2$). Although relative patterns of recruitment among sites were consistent, the magnitudes of the differences among sites changed between the two years that recruitment was monitored, as indicated by a significant Site by Time interaction in the ANOVA (Table 1). Site ranks were not statistically concordant between years ($(r_s)_c = 0.659$, $p > 0.05$).

Recruitment rates for *Chromis viridis* were much lower and more variable, compared to *P. moluccensis* (Figure 2). Inside the lagoon, highest densities of *Chromis viridis* recruits (94.3 ±51.4 fish per 100 $m^2$) occurred at site 11 and were close to the maximum densities recorded for *Pomacentrus moluccensis* (Figure 2b). However, recruitment rates were spatially variable and there were several sites to which *C. viridis* never recruited. The mean recruitment rate at site 11 (40 fish per 100 $m^2$) is four times greater than other lagoonal sites that had intermediate levels of recruitment (site 8 ~ 10 fish per 100 $m^2$ and site 9 ~ 12 fish per 100 $m^2$) and several orders of magnitude greater than at poor recruitment sites (0.2 to 0.5 fish per 100 $m^2$). Relative rates of recruitment among sites were very consistent among years ($W_c = 0.720$, $(\chi_r^2)_c = 23.7$, $p < 0.025$) but the magnitude of difference in recruitment among sites varied among years (Table 1). On the slope, *Chromis viridis* recruits were most abundant at site 15, where densities reached a maximum in 2002 of 271.7 ± 139.5 fish per 100 $m^2$. Sites 14 and 16 also had high recruitment in 2002 (site 16: 90.0 ± 58.6 and site 14: 40.0 ± 7.6) and were ranked highly in both years. On average, recruit densities at site 15 were three to four times the densities at sites 14 and 16, and two orders of magnitude greater than at sites with the lowest recruitment rates (1 to 10 fish per 100 $m^2$). However, no *C. viridis* recruited to site 13, located within 500m of site 14. Spatial patterns in recruitment for *C. viridis* did not vary significantly among years (Table 1). Spearmans Rank Correlation, however, revealed that rankings of sites did vary among years ($(r_s)_c = 0.659$, $p > 0.05$).

| | | | *Pomacentrus moluccensis* | | *Chromis viridis* | | *Dascyllus aruanus* | |
|---|---|---|---|---|---|---|---|---|
| Habitat | Factors | df | MS | p | MS | p | MS | p |
| Lagoon | Time | 2 | 2.594 | 0.006 | 0.576 | 0.182 | 0.459 | 0.043 |
| | Site | 11 | 2.217 | <0.001 | 1.515 | 0.001 | 2.195 | <0.001 |
| | Time x Site | 22 | 0.400 | <0.001 | 0.313 | 0.010 | 0.126 | 0.005 |
| | Residual | 180 | 0.072 | | 0.162 | | 0.060 | |
| Slope | Time | 1 | 0.009 | 0.862 | 0.444 | 0.481 | | |
| | Site | 7 | 0.948 | 0.071 | 2.663 | 0.068 | | |
| | Time x Site | 7 | 0.291 | 0.003 | 0.881 | 0.124 | | |
| | Residual | 32 | 0.074 | | 0.448 | | | |

**Table 1:** Two-way ANOVA's for field recruitment patterns. Data are log (x+1) transformed number of fish per transect.

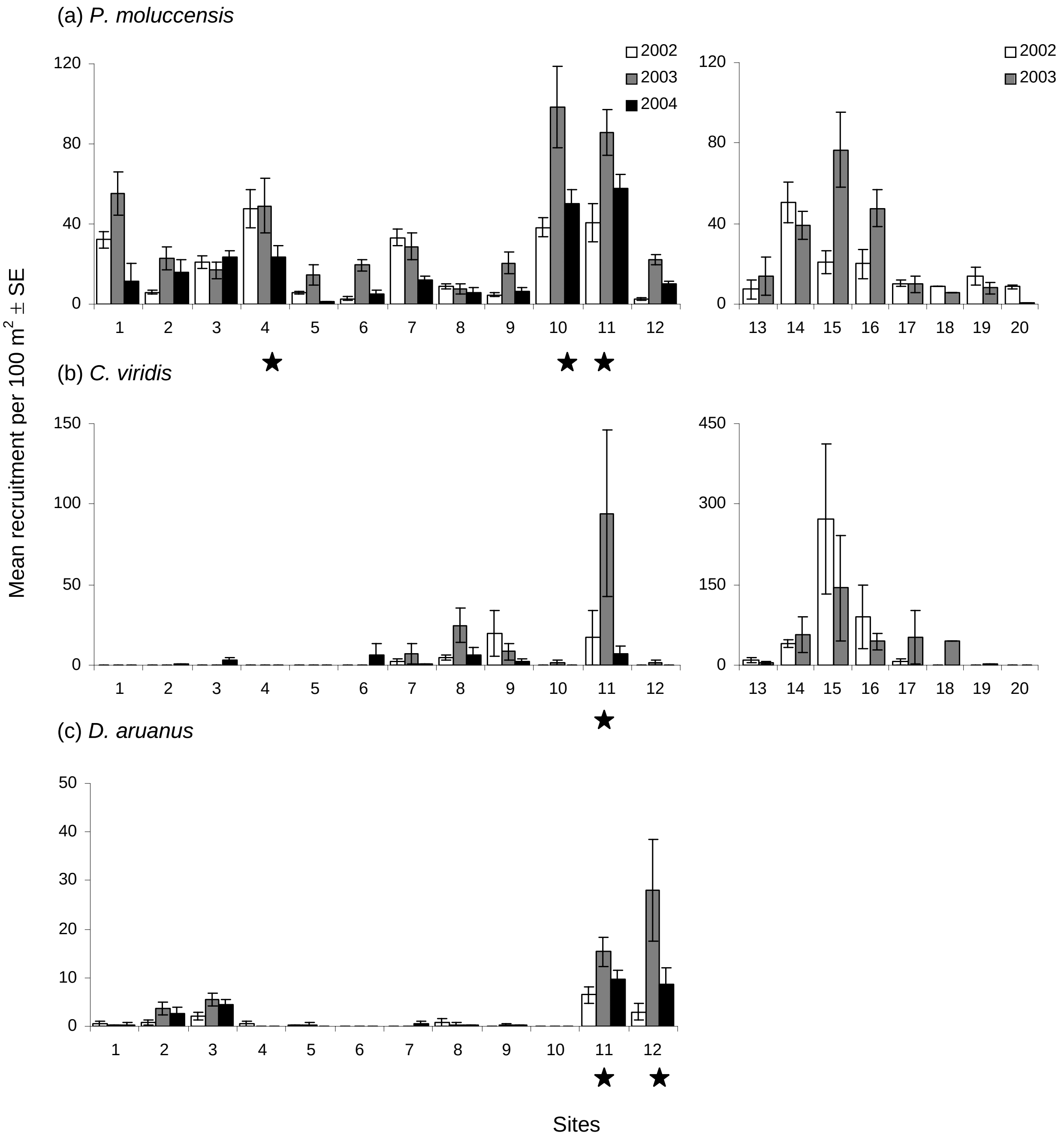


**Figure 2.** Mean recruitment per 100 $m^2$ ± SE for three species at 20 sites in two habitats, the lagoon and reef slope, at One Tree Reef. Data for the lagoon represents the average for January and March surveys in each of three years 2002, 2003 and 2004 while data for the slope represents the average for March surveys in 2002 and 2003. (a) *Pomacentrus moluccensis* (b) *Chromis viridis* (c) *Dascyllus aruanus.*

*Dascyllus aruanus* regularly recruited to only 4 (out of 12) sites in the lagoon, and never recruited to any sites outside of the lagoon. Recruitment of *Dascyllus aruanus* was always greatest at sites 11 and 12. Average recruit densities at these two sites (10 to 13 fish per 100 $m^2$) were two and a half to five and a half times the densities at sites with intermediate levels of recruitment (2 to 4 fish per 100 $m^2$ at sites 2 and 3 in the southern location), which also ranked highly every year, and a magnitude greater than at sites with low levels of recruitment (less than one recruit per 100 $m^2$). Two sites in the lagoon experienced no *D. aruanus* recruitment over the study period, and over the two years that recruitment was monitored on the slope no *D. aruanus* recruits were recorded even though adults were present in transects. Site ranks in the lagoon remained consistent over the three years ($W_c = 0.829$, $(\chi_r^2)_c = 27.4$, $p < 0.005$), however, like the other two species in the lagoon there were differences in relative magnitudes among sites over time (Table 1).

### *Congruence in recruitment hotspots among species*

In the lagoon, site 11 in the western location was a 'recruitment hotspot' for all three species. The two other western lagoon sites were recruitment hotspots for individual species, *Pomacentrus moluccensis* (site 10) and *Dascyllus aruanus* (site 12). For the slope, site 14 in the north western location and sites 15 and 16 in the western location, were recruitment hotspots for both *P. moluccensis* and *C. viridis*.

### *Recruitment and hydrodynamics*

Relationships between the mean abundance of recruits and the mean water flow at each site varied among species, and for one species, between lagoon and slope habitats, however they were always non-linear because low recruitment could occur at sites with any flow levels. Recruitment for *Pomacentrus moluccensis* in the lagoon was highest (40 fish per 100 $m^2$ or greater) at sites with medium flow (0.3 to 0.4 % $d^{-1}$ $m^{-1}$ or 3 to 5 cm $s^{-1}$) and low at both high and low flow sites (Figure 3a). In contrast, on the slope recruitment was inversely related to water flow. The highest recruitment (77 fish per 100 $m^2$) occurred at the site with the lowest flow (1.0 % $d^{-1}$ $m^{-1}$ or 12 cm $s^{-1}$), and low recruitment (on average 10 recruits per 100 $m^2$) occurred at the site with the highest flow (1.5 % $d^{-1}$ $m^{-1}$ or 22 cm $s^{-1}$). Like for *P. moluccensis* on the slope, for *Chromis viridis*, recruitment was highest at sites with low water flows (Figure 3b). This was the case for both the lagoon (94 fish per 100 $m^2$ where flow was 0.3 % $d^{-1}$ $m^{-1}$ or 2.5 cm $s^{-1}$) and on the slope (272 fish per 100 $m^2$ where flow was 1.0 % $d^{-1}$ $m^{-1}$ or 12 cm $s^{-1}$). For *Dascyllus aruanus* in the lagoon, there were no clear patterns between recruitment and water flow (Figure 3c). The highest recruitment (28 fish per 100 $m^2$) occurred at the highest flow site (0.43 % $d^{-1}$ $m^{-1}$ or 7.2 cm $s^{-1}$), but the site with the second highest recruitment (15 fish per 100 $m^2$) had one of the lowest flows (0.28 % $d^{-1}$ $m^{-1}$ or 2.5 cm $s^{-1}$).

### *Recruitment and microhabitats*

Microhabitat use varied among the three species, however, all fishes were found predominantly in branching corals from the families Pocilloporidae, Acroporidae and Poritidae (Figure 4). *Pomacentrus moluccensis* used Pocilloporidae, Acroporidae and Poritidae in approximately equal abundance, but was occasionally seen in to recruit to other corals, including *Merulina*, *Galaxea*, *Pavona* and *Psammacora*. A small number of *P. moluccensis* recruits were also found in non-living habitats of dead coral and rubble. In contrast to *P. moluccensis*, both *C. viridis* and *D. aruanus* recruited exclusively to live corals, and used a much smaller range of different corals.

Approximately half of all *C. viridis* recruits were found in corals from the family Acroporidae, and the other half were found in corals from the family Poritidae. The majority of *D. aruanus* recruits (~ 80 %) were found in pocilloporid corals and the rest were found in acroporid corals (Figure 4).

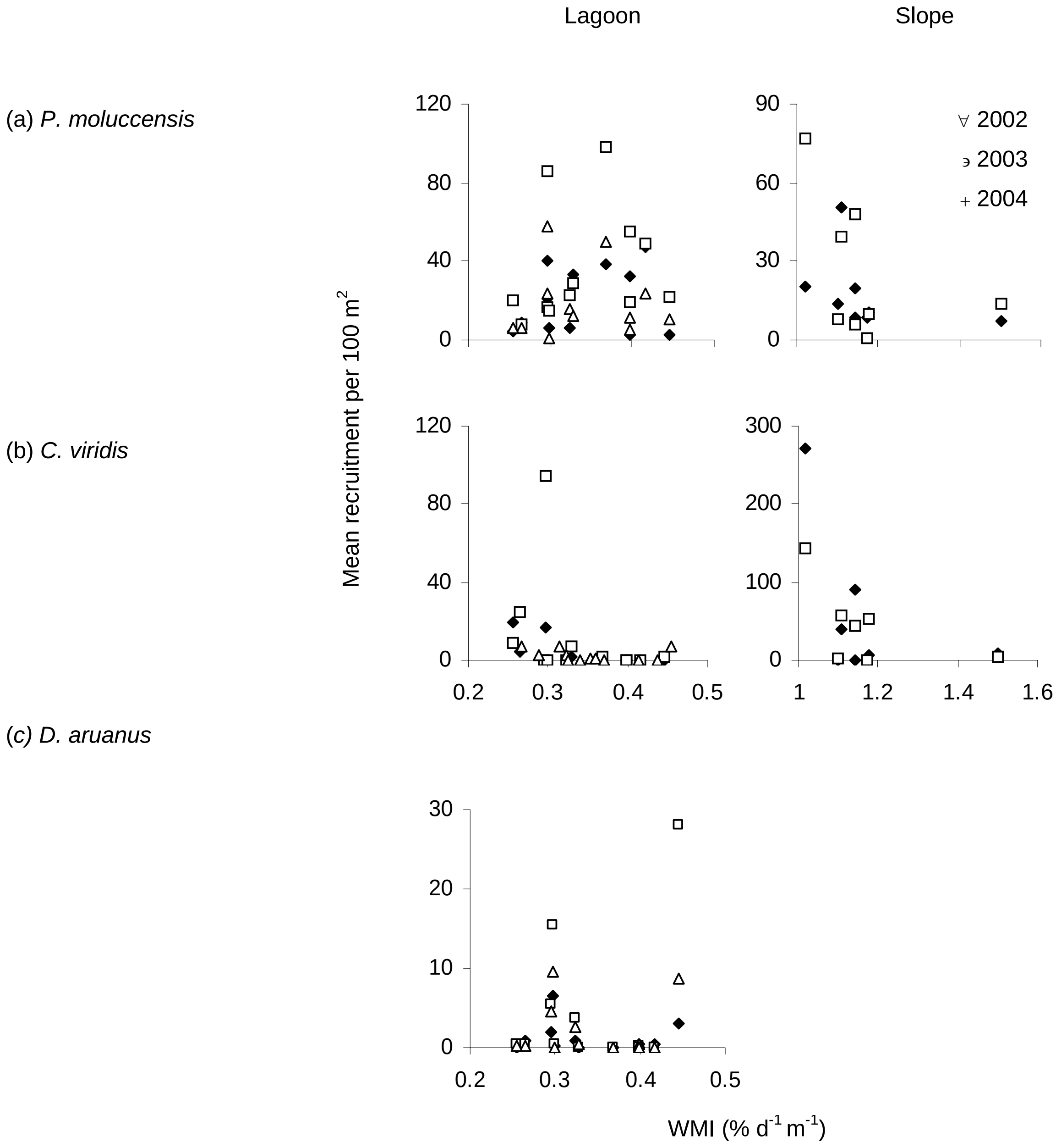


Figure 3: Relationship between time-averaged water flow measured in January 2004 and mean recruitment per site for three years and three species in the lagoon and two years and two species on the slope (a) *Pomacentrus moluccensis* (b) *Chromis viridis* (c) *Dascyllus aruanus*.

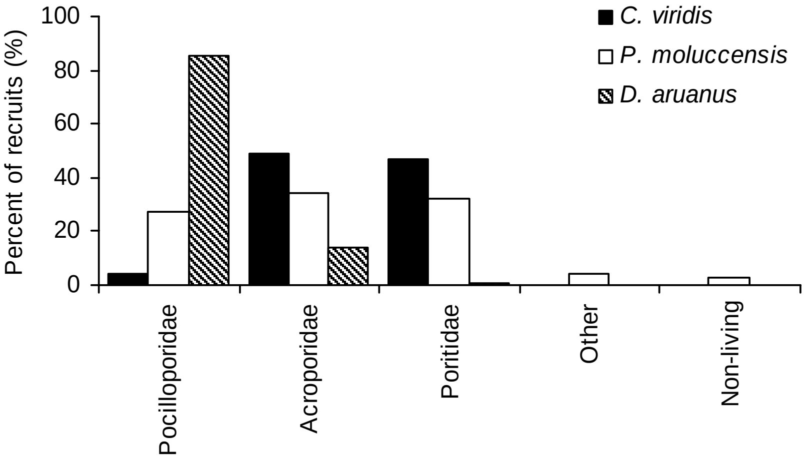


**Figure 4:** The percentage of recruits for three fish species found in each of five habitat categories in the lagoon during surveys in 2003 and 2004. (a) *Pomacentrus moluccensis* n = 3962 (b) *Chromis viridis* n = 980 (c) *Dascyllus aruanus* n = 489

Variation in the availability of suitable microhabitats explained a small but significant proportion of variation in the abundance of fish recruits, at least among lagoonal sites. For *P. moluccensis* in the lagoon, recruitment rate was significantly positively linearly correlated with the overall abundance of the three main coral families they inhabited, Pocilloporidae, Acroporidae and Poritidae (LSR: df = 1, F = 4.92, $R^2$ = 0.126, p = 0.033, Figure 5a). There was no significant relationship on the slope, however, high recruitment only occurred at sites with >50% coverage of the three coral families. For *Chromis viridis*, recruitment rates within the lagoon were positively correlated with percentage cover of Acroporidae (LSR: df = 1, F = 5.55, R2 = 0.140, p = 0.024) but this relationship only described 14 % if the variation in the data (Figure 5b). Again there was no relationship between recruitment and microhabitat availability on the slope, however sites of high recruitment were characterised by having greater than 50 % coverage of Acroporidae. *Dascyllus aruanus* was the most specialized of the three species in terms of microhabitat use, but recruitment rates appeared to be unrelated to the abundance of Pocilloporidae, which was the microhabitat it used most often (Figure 5c).

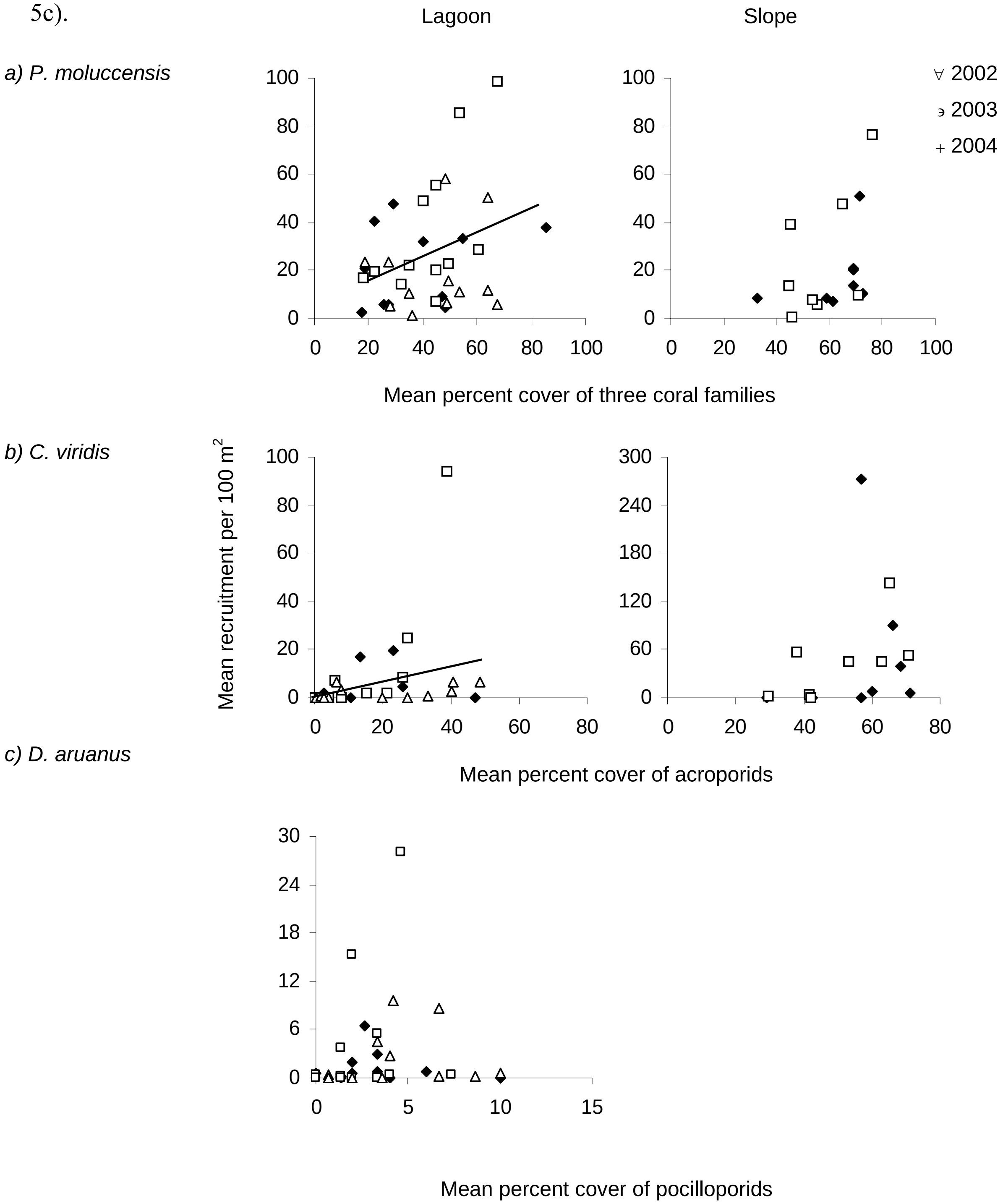


**Figure 5:** Relationship between the mean recruitment per site and the percent cover of coral habitats measured in each of three years in the lagoon (2002, 2003, 2004) and two years on the reef slope (2002, 2003) for (a) *Pomacentrus moluccensis* (b) *Chromis viridis* (c) *Dascyllus aruanus.*

### *Hydrodynamics and microhabitats*

Patterns of habitat selectivity in the field for different types of coral habitats varied in the same way among sites within the northern lagoon for the two species in which this was examined (Figure 6). Patterns of habitat selectivity at site 7 differed from patterns at sites 8 and 9, which were the same. *Pomacentrus moluccensis* and *Dascyllus aruanus* both used pocilloporid and acroporid corals in greater proportions to their abundance at sites 8 and 9. In contrast, at site 7 neither *P. moluccensis* or *D. aruanus* used pocilloporid corals in greater proportions to their abundance, *P. moluccensis* instead inhabited corals from other families (*Merulina* and *Galaxea*) and *D. aruanus* inhabited only acroporid corals in greater proportions to their abundance.

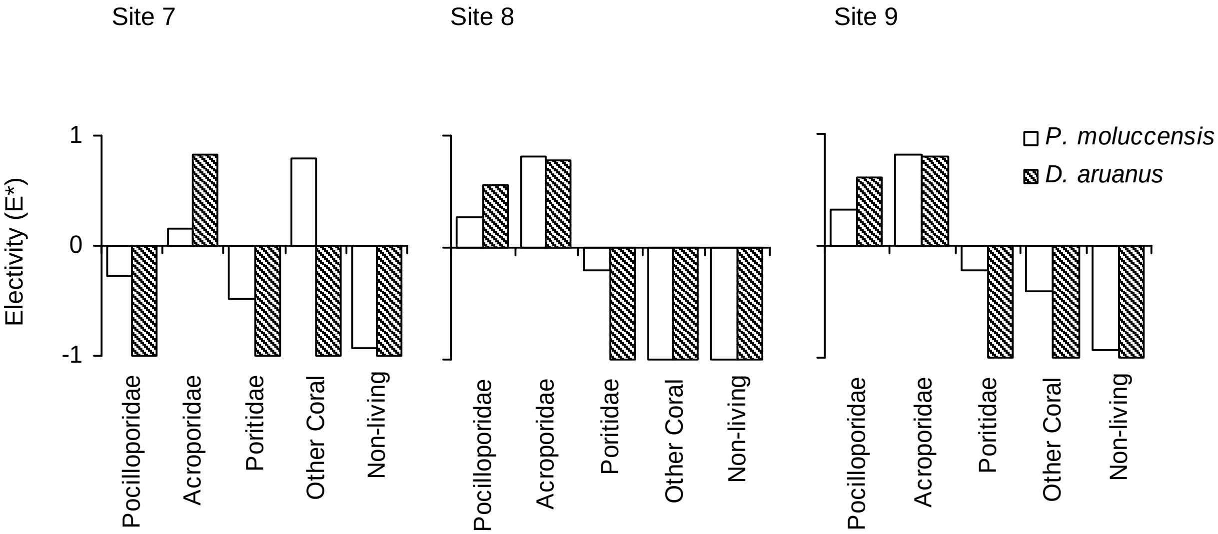


**Figure 6:** Vanderploeg and Scavia (1978) habitat electivity for *Pomacentrus moluccensis* and *Dascyllus aruanus* recruits for five habitat categories at three North lagoon sites. Positive values indicate that habitats are used in greater proportion to their abundances and negative values indicate that habitats are used is lesser proportions than their abundance.

The reason for this variation in the use of coral habitats from different families among sites was likely related to variation in colony morphology of corals between sites. Mean inter-branch spaces for *Pocillopora damicornis* were over one and a half times greater at sites 8 and 9 compared with site 7 (Figure 7a). One way nested ANOVA's found significant differences among sites for both field measured colonies (ANOVA: F = 7.17, df = 2, p = 0.004) and colonies used in the experiment (ANOVA: F = 10.0, df = 2, p = 0.047). There was also a significant difference in inter-branch spacing among colonies within sites for field measured colonies (ANOVA: F = 3.80, df = 21, p < 0.001) but not between the two colonies representing each site that were used in the settlement experiment (ANOVA: F = 1.35, df = 3, p = 0.290). Patterns of inter-branch spacing among sites coincided with a 20 % decrease in water movement at sites 8 and 9 (Figure 7b), which had significantly lower flow compared to site 7 (F = 44.2, df = 2, p < 0.000). Tukey's post-hoc tests showed sites 8 and 9 grouped together and were significantly different from site 7 in all cases.

In tank trials, *Pomacentrus moluccensis* and *Dascyllus aruanus* both had strong and consistent preferences for *P. damicornis* from low-flow sites (sites 8 & 9), which had more open branching (Figure 7c). All (18/ 18 individuals) of the *P. moluccensis* recruits selected *P. damicornis* colonies from either site 8 or site 9, never occupying tightly branching colonies from site 7, and this differed significantly from the hypothesis of a 2:1 ratio of selection for open branching versus tightly branching colonies (Chi-square goodness of fit: $\chi^2 = 9.00$, $p < 0.005$) for the three colonies in the tank. Similarly, 80 % (15/ 18 individuals) of *D. aruanus* selected the open branching morphology, however, this proportion was not significantly different from a 2:1 ratio (Chi-square goodness of fit: $\chi^2 = 2.25$, $0.1 < p < 0.25$). Interestingly, the few fish (3/ 18 individuals) that did select the tightly branching morphology were among the smallest individuals collected.

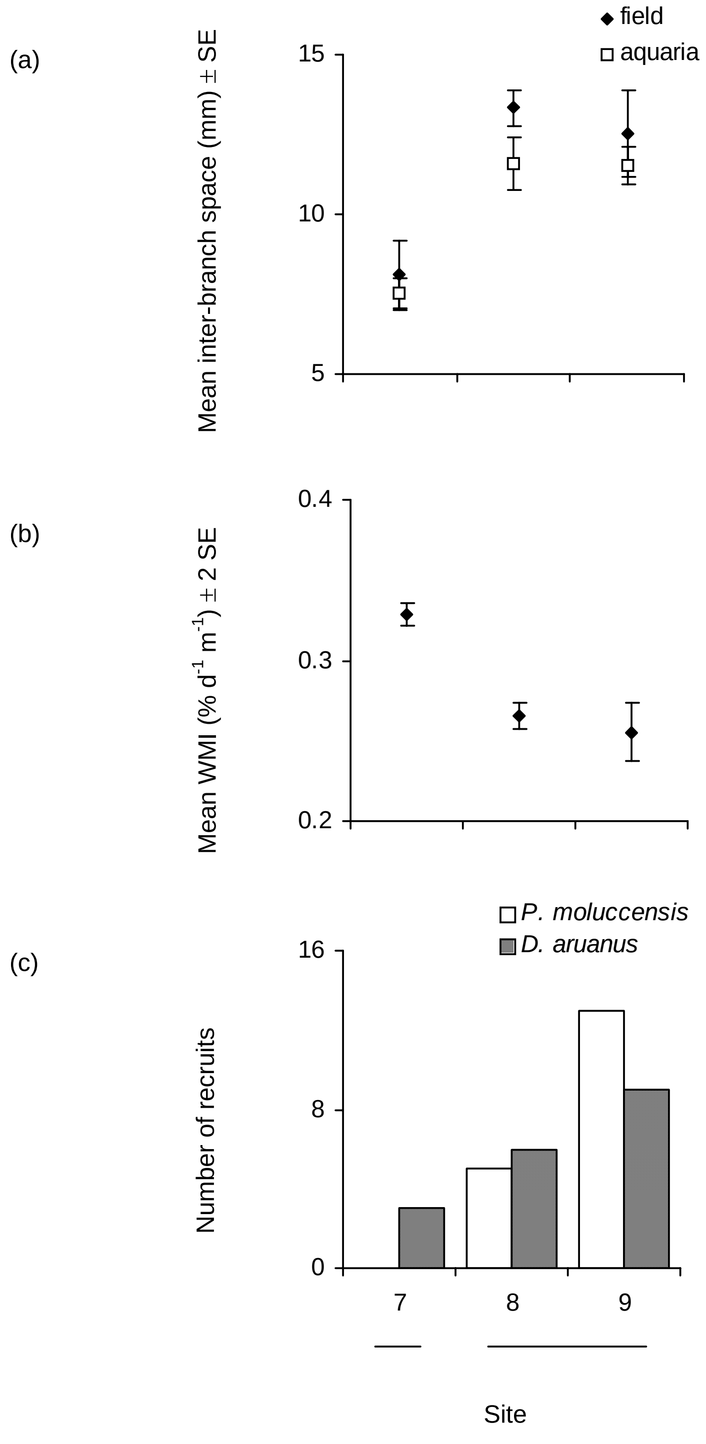


**Figure 7:** Variation among three North lagoon sites in (a) mean inter-branch space of field and experimental colonies of *Pocillopora damicornis* (b) mean time-averaged water flow (WMI) ± SE measured in January 2004 (c) number of recruits of *Pomacentrus moluccensis* and *Dascyllus aruanus* choosing to inhabit *Pocillopora damicornis* colonies collected from three sites in the One Tree lagoon. Lines joining sites show Tukey's groupings in part (a) and (b).

## Discussion

This study adds to a growing body of literature indicating that coral reef fishes exhibit strong and consistent differences in rates of recruitment among sites separated by as little as 100m (Fowler et al. 1992, Caselle & Warner 1996, Sponaugle & Cowen 1997, Tolimieri et al. 1998, Vigliola et al. 1998, Booth et al. 2000, Hamilton et al. 2006). Although it is widely accepted that recruitment is variable, some sites (recruitment hotspots) consistently receive higher recruitment and make a disproportionate contribution to replenishment of open populations. Contrary to many previous studies (Sponaugle & Cowen 1996a, Tolimieri et al. 1998, Danilowicz et al. 2001), this study also shows that recruitment hotspots may receive disproportionate numbers of recruits across several distinct species. Most notably, site 11 in the One Tree lagoon was a recruitment hotspot for all three species studied (see also Booth et al. 2000), while sites 14, 15 and 16 on the outer slope were recruitment hotspots for both *P. moluccensis* and *C. viridis*.

Much of the existing literature on recruitment hotspots comes from the Caribbean (Sponaugle & Cowen 1996b, Tolimieri et al. 1998, Danilowicz et al. 2001) and Hamilton et al. (2006) suggested that reefs in the GBR are less likely to show persistent recruitment patterns compared with the Caribbean reefs because hydrodynamics are much more complex and variable (Caselle & Warner 1996, Hamilton et al. 2006). Accordingly, there are many studies from the GBR region that report considerable temporal (mostly, inter-annual) variation in patterns of recruitment (Eckert 1984, Sale et al. 1984a, Sale et al. 2005). It is clear from this study however, that oceanographic regimes and relative hydrodynamic forces may be highly conserved around GBR reefs, and may contribute to the formation of recruitment hotspots (see also Booth et al. 2000).

We found relationships between recruitment hotspots and hydrodynamics at two spatial scales. At the larger scale, multi-species recruitment hotspots were located at one site in the western lagoon and three sites on the nearby leeward slope, thereby creating a region of high recruitment that spans over a kilometre in the leeward section of the reef (see Figure 1). This area is a known low flow zone (Burgess et al. 2007) and low flow island-wake areas contain high densities of pre-settlement fish larvae (Carleton et al. 2001a). This is the first study, however, to demonstrate that high densities of pre-settlement fish in low flow zones may well translate into areas of high settlement and recruitment. Interestingly, hydrodynamic variability at this scale may have the ability to both enhance and suppress recruitment at different sites. Time-integrated water flow at site 13 was the fastest recorded across all 20 sites (~22 $cms^{-1}$) due to an out-pouring of lagoonal waters during outgoing tides, This site also received lowest rates of recruitment for both *D. aruanus* and *C. viridis*, despite being <500m from a recruitment hotspot. Similarly, in the Caribbean, offshore tidal flows were reported to greatly suppress recruitment by eight species of wrasses (Sponaugle & Cowen 1997).

While hydrodynamics at a larger scale appeared to be important to multi-specific recruitment hotspots, there also existed relationships between the recruitment of each species and hydrodynamics at the smaller ‘site’ scales at which water flux was measured. Species-specific relationships were, however, variable among species and variable between lagoon and slope environments. There were patterns in recruitment and time-integrated water flow at the ‘site’ scale for *Pomacentrus moluccensis* and *Chromis viridis* but not *Dascyllus aruanus*. The lack of relationship between *D. aruanus* and water flow was surprising since the abundance of recruits of this species was found to have a positive but decelerating function with ambient flow in the lagoon at Moorea (Schmitt & Holbrook 2002b), but may have been because maximum flows in One Tree lagoon (~ 7.5 cm $s^{-1}$) were approximately half the maximum recorded in Moorea (~ 15 cm $s^{-1}$).

For *Pomacentrus moluccensis* and *Chromis viridis* on the slope, and for *C. viridis* in the lagoon greatest recruitment occurred at sites with the lowest flows. This suggests that recruitment is not related to water flux, where sites with greater water flow are delivered more larvae, but instead that recruitment occurs due to greater residence times of water over certain reef areas, or due to larvae choosing to settle under low flow conditions. For *Pomacentrus moluccensis* in the lagoon, greatest recruitment in the lagoon occurred at sites with medium levels of water flow. It is unlikely that this pattern is primarily driven by supply, since *Chromis viridis* larvae were effectively supplied to low flow lagoon areas. Suppression of recruitment at higher flows may occur due to an inability of fish to settle in the fast currents likely to be present at the time they are 'delivered' to the reef, however, it is most likely that *P. moluccensis* chooses to settle at medium flow sites, as was the case for *Dascyllus trimaculatus* in Moorea (Schmitt & Holbrook 2002b).

Hydrodynamics may be important in directing larvae to a broader location of reef, but distribution patterns of recruits among and within sites may ultimately be due to factors such as microhabitat abundances (Danilowicz et al. 2001, Hamilton et al. 2006). There were positive relationships between recruit densities and the abundance of preferred microhabitats for *P. moluccensis* and *C. viridis*, but not for *D. aruanus* . In the literature, there are numerous examples of where abundances of coral habitats preferred by fish recruits at small scales predict the recruitment of fish at larger scales (Eggleston 1995, Tolimieri 1998a, Levin & Hay 2002), as well as examples of where they do not (Tolimieri 1995). Clearly, species need to be evaluated on a case-to-case basis in order to assess the importance of microhabitat in determining patterns of recruitment at this scale.

*Pomacentrus moluccensis* and *Chromis viridis* recruitment in the lagoon was positively and significantly linearly correlated with the percentage cover of the major coral families that they inhabited. These patterns were also apparent on the slope, however, relationships were not significantly significant. For *C. viridis* this result was, however, confounded with the fact that *C. viridis* recruitment showed an inverse relationship with water flow, as did the percent cover of acroporids, therefore it is not possible to say whether variation in recruitment among sites of this species was in response to hydrodynamics or microhabitat abundance. In addition, other studies report that the most important deterministic factor affecting settlement in *C. viridis* recruits is the presence of conspecifics (Lecchini 2005, Lecchini et al. 2005). Nevertheless, habitats or flow could be used to predict areas of high recruit density of this species at One Tree Reef.

Densities of *Dascyllus aruanus* recruits in the lagoon were greatest at sites that had intermediate percentage cover of the corals that this species most commonly recruited to (pocilloporids). The greatest abundances of pocilloporids were found at sites of low flow, and at these sites corals would also be of the preferred wide-branching morphology. The lack of a positive relationship between *D. aruanus* and pocilloporid abundances may have been because larval or planktonic food supply is too low at low flow sites where pocilloporids are most abundant (but this did not appear to be the case for *Chromis viridis*) or because the classification of 'suitable' habitat for *D. aruanus* needs to include not only the percentage cover and branching structure of particular coral species, but also variables such as colony size and proximity to sand (Holbrook et al. 2000) or other multivariate measure of microhabitats (Sponaugle & Cowen 1996a, 1997, Wilson & Osenberg 2002). Furthermore, like *C. viridis*, *D. aruanus* is also known to settle in greater abundances where adult conspecifics are present (Sweatman 1983, Schmitt & Holbrook 2002a).

Hydrodynamics are also likely to affect recruitment of coral reef fishes through modifying effects on the structure of microhabitats. Even though pocilloporid corals occur at both low and high flow sites, there are marked differences in the physical structure of these coral under different hydrodynamic regimes, which greatly influences their suitability as microhabitat for coral-dwelling fishes. Strong and consistent microhabitat preferences of new recruits are most likely related to differential of survivorship in different habitats. For example, the survivorship of *Stegastes partitus* recruits differed between two coral habitats, *Montastrea* and *Porites*, according to crevice size (Nemeth 1998). Habitat morphology also affected recruitment of kelp bass, *Paralabrax clathratus*, where recruits was related to the density of *Macrocystis pyrifera* kelp, however, densities of fish recruits saturated at intermediate densities of algae because the structural complexity of kelp blades was inversely related to plant density (Carr 1994). Preferences for particular morphological types within habitat forming species may decouple relationships between microhabitat coverage and recruitment, such as was the case for *Dascyllus aruanus*. Species that are habitat generalists may not be affected in the same way, e.g. *Pomacentrus moluccensis* recruits in this study. Even though *P. moluccensis* also preferred wide-branching *Pocillopora damicornis*, where appropriate pocilloporids were not available, recruits instead inhabited acroporids and poritids.

The existence of common recruitment hotspots has important implications for the replenishment and management of coral reefs and associated fish populations. Knowledge of where recruitment hotspots are can provide information on likely sources of recruitment among reefs, and likely patterns of adult re-distribution within reef systems. Identifying and maintaining the health of recruitment hotspots will be critical to the management of coral reefs. Marine Protected Area's designed to protect the major locations of larval delivery could be achieved relatively simply. Depending on the priorities of conservation, hotspots could be preserved for biodiversity goals or used to enhance fisheries productivity. However, information is needed for other locations, to assess how predictable recruitment hotspots are, and for other species, to assess the degree of congruence in recruitment hotspots in reef fish communities as a whole.

## Conclusions

While the fish species in this study exhibited common recruitment hotspots, many of the particular relationships between patterns of recruitment, hydrodynamics and habitats were complex and species-specific. In some cases they differed between the lagoon and slope habitats. Clear relationships between recruitment and habitats at around reef scales may be obscured by interactions between hydrodynamics and habitats. Hydrodynamics and habitat appear to be deterministic factors that direct where maximum recruitment can occur; however, recruitment can be lower than these potential maxima at any time. Previous studies that have found no relationship between recruitment and microhabitats may have not been assessing recruit habitats at an appropriate resolution. Hydrodynamics regimes and microhabitats will need to be carefully assessed where they are used to predict potential locations for recruitment hotspots for coral reef fishes.

# Chapter 6 – General Discussion

Collectively, the chapters of this thesis strengthen the concept of recruitment hotspots and its potential utility in the management of both corals and fishes – the two key taxa on coral reefs. The identification of recruitment hotspots at One Tree Reef adds to a growing body of literature suggesting that patterns of recruitment variation along reefs that persist over time are the norm for some families of corals (Glassom et al. 2004) and some species of fishes (Tolimieri et al. 1998, Booth et al. 2000, Hamilton et al. 2006). Contrary to a general expectation that recruitment is variable, this study provides further support that at some scales relative patterns of recruitment can be predictable. The existence of recruitment hotspots demonstrates that while the magnitude of recruitment variation may be stochastic, deterministic processes also contribute to patterns of mean recruitment around and across coral reefs.

The persistence of recruitment hotspots for the duration of the study can be explained in part due to persistent patterns in hydrodynamics and in the composition of benthic habitats to which recruitment was related. Relative patterns of flow in the 'free-stream' as defined in Chapter 2, were consistent during the two time periods they were examined. Semi-diurnal ebb and flood tides cause complex alternating circulation patterns, including the formation of eddies and strong convergence zones, which also interact with wind-generated currents (Burgess et al. 2007). Furthermore, the influence of the unidirectional East Australian Current, which causes predictable island-wake zones at other reefs in the GBR (Wolanski 1988, Ayukai 1995, Rissik et al. 1997, Furukawa & Wolanski 1998), is negligible at One Tree because it is deflected eastwards along the continental margin at the Swains group of reefs just north of the Capricorn-Bunker group (Kleypas & Burrage 1994, Burrage et al. 1996). Despite these complexities, relative patterns of flow in near-reef environment were consistent during two time periods and so are likely to be driven by reef topography at a number of scales (Chapter 2).

Relative patterns in the composition of coral reef habitats among sites were also consistent over the time period of the study. Consequently, recruitment hotspots may have persisted in response to an abundance of preferred settlement habitats of larval reef coral and fishes, or in the case of brooding coral families, an abundance of parent colonies. Coral habitats at One Tree Reef may be more stable than other areas of the GBR because of their isolation and southerly location protecting them from disturbances such as crown-of-thorns (*Acanthaster planci*) and *Drupella* outbreaks, coral diseases, cyclones and bleaching. Even after major disturbances such as cyclones, reefs in this group have been found to recover to their previous states (Halford et al. 2004). As a result, benthic compositions were closely related to local scale patterns of hydrodynamics probably because water flow is known to influence patterns of distribution and abundance of coral reef organisms through effects on various aspects of their life history. Using both observations of field patterns and experimental approaches, this study was able to describe complex relationships between hydrodynamic and habitat patterns and recruitment hotspots of reef corals and fishes.

### ***Congruence in recruitment hotspots for corals and fishes***

This study is the first to investigate recruitment hotspots for reef corals and fishes simultaneously, and also the first to document the clustering of recruitment hotspots for coral and fish taxa. Although the positions of recruitment hotspots at One Tree Reef differed between corals and fishes, and among coral families and fish species, the northwestern section of reef contained sites that were recruitment hotspots for all three species of coral-dwelling fishes and two of the three coral families (Figure 1). This cluster of hotspots is on the leeward side of the reef and in the 'island-wake' during incoming tides (Burgess et al. 2007). The hydrodynamic model of circulation around One Tree Reef suggests this area has a relatively low flow, and is similar to areas of high water residence at Helix and Bowden reefs where patches of both coral and fish larvae accumulated (Black 1988, Sammarco & Andrews 1988, Willis & Oliver 1988, Carleton et al. 2001a). Clear relationships between island-wide recruitment patterns and hydrodynamics have also been found for some fish species in the Caribbean (Sponaugle & Cowen 1996b, Sponaugle & Cowen 1996a, Hamilton et al. 2006). Individual sites within this area could, however, have either low or high flows at the 'free-stream' scale described in Chapter 2. Patterns of recruitment at One Tree Reef may be evidence of a two-stage recruitment process (Danilowicz 1997) where larvae 'choose' a general location according to hydrodynamics or gross topography (here the north western corner of the reef) and then a specific site and microhabitat at that location.

### ***Relationships between recruitment, hydrodynamics and habitat***

Although recruitment hotspots were clustered in one location of One Tree Reef, sites of high recruitment differed among taxa in relation to species-specific responses to hydrodynamic and microhabitat preferences (Table 1), though not all of these relationships were statistically significant and so further research is still required. The nature of relationships between recruitment, hydrodynamics and habitat varied not only among the different taxa, but also for individual taxa between lagoon and slope environments. For *P. moluccensis*, pocilloporids and poritids in the lagoon, greatest recruitment occurred at sites with medium flows, though not all medium flow sites were recruitment hotspots. In contrast, greatest recruitment of *C. viridis* in the lagoon occurred at sites of lowest flow, and this was also the case for this species on the reef slope, however recruitment could also be low at these sites at some times. The greatest recruitment, for *P. moluccensis* also occurred at sites on the reef slope with low flow. There were no relationships between recruitment and flow on the reef slope for any coral family, and between recruitment and flow for acroporids in the lagoon. These findings support studies that have found that even closely related taxa have different responses to hydrodynamics and microhabitats (Ohman et al. 1998, Harii & Kayanne 2002, Schmitt & Holbrook 2002b, Baird & Morse 2004) that apparently occur whilst larvae are still in the pelagic environment (Sammarco & Andrews 1988, Doherty et al. 1996, Leis & Carson-Ewart 2000, Carleton et al. 2001a, Leis & Carson-Ewart 2003).

| | Lagoon | | Slope | |
|---|---|---|---|---|
| | Water movement | Benthic composition | Water movement | Benthic composition |
| Pocilloporidae | Medium | High (adults) | 0 | 0 |
| Poritidae | Medium | 0 | 0 | High (adults) |
| Acroporidae | 0 | 0 | 0 | 0 |
| *Pomacentrus moluccensis* | Medium | High (3 families) | Low | High (3 famililes) |
| *Chromis viridis* | Low | High (acroporids) | Low | High (acroporids) |
| *Dascyllus aruanus* | 0 | Medium (pocilloporids) | - | - |

**Table 1:** Summary of relationships between recruitment of six taxa, hydrodynamics and habitat in the lagoon and on the slope at One Tree Reef. 0 denotes no relationship while – denotes species does not occur there

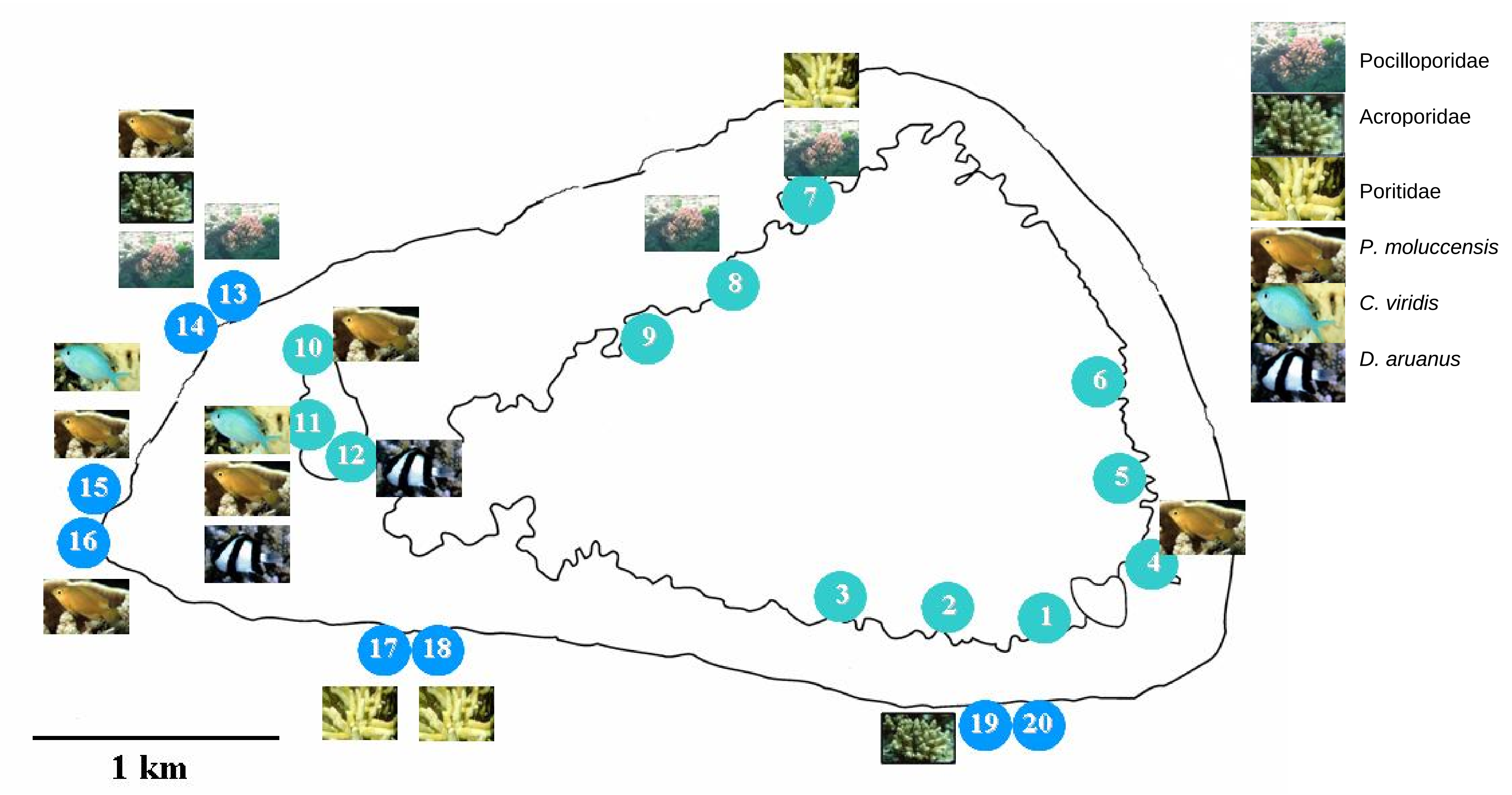


Figure 1: Sites of recruitment hotspots for three coral families and three species of coral-dwelling fishes at One Tree Reef. Numbers are site labels and hotspots are represented by a symbol for each species at sites with persistently high recruitment.

In a flow-limited environment such as the One Tree Reef lagoon, sites with medium flow may represent a compromise between sites with low flow, where few larvae are delivered, and sites with high water flow that have a good potential for larval delivery, but where flows may be too high during certain times for settlement, as demonstrated for *Acropora nasuta* in experimental aquaria (Chapter 3). This pattern may have applied to pocilloporids, poritids and *P. moluccensis,* which were all characterised by greatest recruitment at medium flow sites in the One Tree lagoon. On the reef slope, where flows were two to four times those in the lagoon, only two taxa demonstrated relationships between recruitment and flow. Greatest recruitment for two of the fish species, *P. moluccensis* and *C. viridis* occurred at the sites with the lowest flow. This pattern may have resulted from larval accumulation due to high water residence times (Kingsford 1993, Carleton et al. 2001a), preferences of these species for low flow regimes as has been found in other studies (Schmitt & Holbrook 2002b) or due to greater abilities of larvae to settle at low flow sites.

The lack of relationships between recruitment of any coral taxa and water flow on the reef slope, combined with clear preferences for low flow conditions during settlement in experimental aquaria (Chapter 4), may signify that cumulative flows among sites on the reef slope are too fast for settlement at least in coral larvae. Swimming abilities are much poorer for coral larvae than reef fishes (Harrison & Wallace 1990, Leis & Carson-Ewart 1997, Stobutzki & Bellwood 1997) therefore settlement on the reef slope may only occur when mass spawning events coincide with extremely low flow conditions (Babcock et al. 1986), or at regular low flow times for brooding species that planulate over longer time periods (Harrison & Wallace 1990). Despite extremely low flow conditions in parts of the lagoon, lower recruitment in the lagoon overall, as well as the lack of a relationship between acroporids and flow in the lagoon, was probably related to a scarcity of larvae, which has been predicted for lagoons elsewhere on the GBR (Black & Moran 1991, Harriott & Simpson 1997). Greater recruitment at sites in the lagoon with low flow for *C. viridis* and no relationship between recruitment and flow for *D. aruanus* were likely to have been linked to relationships with benthic composition.

As for relationships with water movement, relationships between recruitment and benthic composition differed among taxa and between the slope and lagoon environments at One Tree Reef. There were positive correlations between recruitment and benthic composition for three of the six taxa both in the lagoon and on the slope. In the lagoon pocilloporid corals recruited in greatest numbers to sites that had high coverage of adult colonies from this family (Chapter 4). In contrast, on the slope only poritids recruited in greatest numbers to sites that had high coverage of adults from this family. For the coral taxa, it is unknown whether recruits were selecting to settle in areas where adults covered more of the reef substratum (Maida et al. 1995a, Baird et al. 2003), or whether recruits were from brooded larvae produced by these colonies that settled extremely close to parents (Harii & Kayanne 2003).

Recruitment for two of the fish species, *P. moluccensis* and *C. viridis,* were also positively correlated with characteristics of the benthic habitat at sites, and relationships for these two species were the same between the lagoon and slope environments. The abundance of *P. moluccensis* recruits was related to the summed percentage cover of the three coral families, to which it recruited in equal proportions. The abundance of *C. viridis* recruits was related to the percentage cover of acroporids, the coral family most commonly used by recruits of this species (Chapter 5), however, there was also a significant negative relationship between water movement and the percentage cover of acroporids (Chapter 3) so it was not clear whether *C. viridis* settled due to low flow, or high coverage of acroporids. There was also a relationship between recruitment of *D. aruanus* and the percentage cover of pocilloporids, the habitat to which it recruited in greatest proportions, however, recruit numbers were highest at sites with medium levels of cover of this family. While low recruitment of this species at high flow sites might be expected, because colonies of *Pocillopora* are less abundant and have a tighter branching morphology less preferred by recruits (Chapter 5), recruitment was also low at the sites at which pocilloporids were most abundant, and where colonies were of the preferred branching morphology for settlement. It is unlikely that this result was due to a limited supply of larvae, since *C. viridis* recruits were most abundant at low flow sites in the lagoon, however, other factors that may have contributed include distribution patterns of adults (Sweatman 1983), variable predation (Connell & Kingsford 1998) and relationships with microhabitat characteristics preferred by this species that were not accounted for (Holbrook et al. 2000).

Strong relationships between hydrodynamics and benthic composition made it difficult to determine whether greater recruitment was in response to water movement or the percentage cover of habitats. Relationships between flow, benthic composition and recruitment were made clearer, however, from the experimental results. In Chapter 4, it was shown that greater numbers of acroporid corals settled under low flow conditions and onto tiles conditioned in the lagoon, and particularly at one site in the lagoon, which was also a field recruitment hotspot for pocilloporid and poritid larvae (site 7). This suggests that recruitment in the lagoon may be driven by the presence of a particular settlement surface, such as a particular species of calcareous algae (Baird & Morse 2004, Harrington et al. 2004), which for some reason was particularly abundant at this site. This would be an interesting area for further research into the causes of recruitment hotspots in scleractinian corals. The experimental results from Chapter 5 demonstrated that not only is water movement correlated with the composition of benthic habitats (Chapter 3), but also with the morphology of coral colonies, and thus their suitability as settlement habitat. This means that to assess relationships between recruitment and benthic habitats, care must be taken to census only habitats used by recruits, which is at a resolution finer than species level.

### ***Implications of recruitment hotspots for future research***

This study showed that there are significant, persistent and correlated patterns of variation in water flow, benthic composition, and coral and fish recruitment among sites on a reef. Variation in ecological patterns at this scale is often examined, however, only rarely is it the focus (Edmunds & Bruno 1996, Hamilton et al. 2006). The results of this study suggest that variation among sites should be an important consideration in the selection of sites for research on coral reef assemblages, since sites can be subject to very different levels of water flow, recruitment and composed of different benthic habitats. Subsequently, the identity of sites chosen for any one study has the potential to affect the outcome of results, as has been found in studies that examined changes in coral cover on the GBR (Ninio et al. 2000) and in the Caribbean (Edmunds & Bruno 1996). At One Tree Reef, local scale populations of fish and corals only hundreds of metres to kilometres apart may be structured by different mechanisms. Populations at recruitment hotspots may be structured by competition and predation, while populations at low recruitment sites may be structured by larval supply (Gaines & Roughgarden

1985, Connolly & Roughgarden 1998, Svensson et al. 2004). This means that the influence of cohabiting species on one another may vary in different reef areas. Where possible, multiple sites should be included in the examination of smaller scale patterns and processes, but may not be necessary in cases where the majority of variation occurs at the within site scale, as was the case for variation of flow in the boundary layer in this study (Chapter 2).

Whether or not there is important variation among sites may depend on the topographical heterogeneity of reef tracts, as well as the larger scale environment e.g. lagoon versus slope. Where sites are spaced at regular intervals along straight sections of elongated reef with similar exposure gradients, slope and topography, variation in recruitment, hydrodynamics and benthic assemblages may be negligible compared to variation at larger (e.g. reef and regions) or smaller scales (e.g. spur v groove) as has been previously found (Hughes et al. 1999, Murdoch & Aronson 1999, Ninio et al. 2000). In contrast, where reefs are small, rounded or unevenly shaped, around islands or along coasts with convoluted coastline topography, there are likely to be significant differences among sites in biological parameters that may be related to hydrodynamic patterns and persistent over time (e.g. Edmunds & Bruno 1996, Glassom et al. 2004, Hamilton et al. 2006). At these kinds of locations care must be taken in the "scaling up" of outcomes from small-scale studies (Levin & Hay 2002, Chittaro 2004, Steele & Forrester 2005) and homogenous tracts of reef with similar exposures should be monitored at this scale when part of larger scale studies (Ninio et al. 2000, Ninio & Meekan 2002).

### *Implications of recruitment hotspots for reef management*

This research has demonstrated that hydrodynamics, benthic composition and recruitment of reef corals and fishes varied across One Tree Reef, but that this variation was temporally persistent. Subsequently not all parts of a reef will be equally valuable for different reef uses. As coral reefs are often managed at the scale of kilometres (Sobel & Dahlgren 2004), knowledge of these patterns could be incorporated into reef zoning plans. Incorporation of ecological processes to better design protected area networks must be backed, however, by comprehensive and detailed knowledge of patterns and processes in individual taxa. Although the specific sites of recruitment hotspots at One Tree varied among taxa due to differences in relationships with water flow and benthic habitats, a broad area of reef contained a number of sites that predictably received consistently higher levels of recruitment for different taxa. Clearly further work is required to determine whether clusters of recruitment hotspots such occur at predictable places on other platform reefs within the Great Barrier Reef and in other locations for other species, and whether patterns are congruent among a wider range of species.

The existence of common recruitment hotspots has important implications for the replenishment and management of coral reefs and associated fish populations. Depending on the conservation and economic goals impinging on the formation of marine reserves and whether or not recruitment hotspots are ‘sources’ or ‘sinks’, they may be either designated as reserves for conservation purposes and may enhance fisheries productivity through spillover (Russ & Alcala 1996, Russ et al. 2003, Abesamis & Russ 2005, Ashworth & Ormond 2005). Alternatively, they may be designated as ‘open’ areas due to their potentially greater capacity to recover from disturbances and enhance fisheries productivity.

For isolated platform reefs, recruitment hotspots could be critical for recovery and maintenance of reef-wide populations. Knowledge of where recruitment hotspots are can provide information on likely sources of recruitment among reefs, and likely patterns of adult re-distribution within reef systems. Identifying and maintaining the health of recruitment hotspots will be critical to the management of isolated coral reefs. If recruitment hotspots suffer environmental damage as a consequence of being used, then under some circumstances they may cease to be recruitment hotspots. For example, if recruitment hotspots for corals result from a high percentage cover of brooding species, high recruitment and more rapid recovery would not necessarily occur if the coral cover of adult colonies was reduced. Similarly, recruitment hotspots were linked with high cover of recruit habitats for two fish species. If recruit habitats were damaged, even if hydrodynamic regimes continued to 'deliver' greater numbers of larvae, these may not translate in greater numbers of recruits.

This study is one of just a few beginning to explore the location of recruitment hotspots and their causes for a range of important reef organisms. The results show that the existence of recruitment hotspots may be more common than predicted, and occur for both coral and reef fishes. Although three coral and three fish taxa differed in the location of recruitment hotspots according to variable relationships between recruitment, hydrodynamics and habitat, one area of One Tree Reef contained sites that were recruitment hotspots for almost all taxa. The challenge now is to determine whether recruitment hotspots are the norm for other corals and fishes, in other locations, and the factors that cause them. Further information about recruitment hotpots may help to ensure that coral reef habitats are preserved for the future.

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## Appendix of papers published or in review during PhD Candidature

Eagle, J.V., Jones, G.P., Kingsford, M.J., Pratchett, M.S. (in review) Recruitment hotspots for coral reef fishes Oecologia (Chapter 5)

Eagle, J.V., Jones, G.P., Kingsford, M.J. (in review). Hydrodynamics as a potential determinant of the structure of coral assemblages across an isolated platform reef Coral Reefs (Chapter 3)

Eagle, J.V., Kingsford, M.J., Jones, G.P. (in review). Experimental evaluation of spatio-temporal variation in water flow near the substratum of a coral reef Marine Biology (Chapter 2)

Eagle, J.V., Baird, A.H., Jones, G.P. and Kingsford, M.J. (in review). Recruitment hotspots for scleractinian corals: the roles of water flow, adult abundance and substratum selection Marine Ecology Progress Series (Chapter 4)

Pratchett, M.S., Marnane, M.J., Berumen, M. L., Eagle, J.V., Pratchett, D.J. (in review) Ontogenetic habitat shifts relate to dietary versatility for Chaetodon butterflyfishes (Chaetodontidae) Coral Reefs

Moland, E., Eagle, J.V. and Jones G.P. (2005) Ecology and evolution of mimicry in coral reef fishes. Oceanography and Marine Biology: An Annual Review 43: 457-484

Eagle, J.V. and Jones, G.P. (2004) Mimicry in coral reef fishes: ecological and behavioural responses of a mimic to its model. Journal of Zoology (London) 264:33-43

Jones, G.P., McCormick, M.I., Srinivasan, M., Eagle, J.V. (2004) Coral decline threatens fish diversity in marine reserves. Proceedings of the National Academy of Sciences of the United States of America 101(21): 8251-8253

Eagle, J.V., Jones, G.P. and McCormick, M.I. (2001) A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae). Marine Ecology Progress Series 214: 253-265

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# A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae)

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ABSTRACT: The degree to which species partition resources often depends on the spatial scale of the study. To investigate this, we examined the distribution and abundance patterns of 3 relatively rare pygmy angelfishes (family Pomacanthidae: *Centropyge*) among reef locations, depths and microhabitats at Lizard Island on the Great Barrier Reef. A strong association among species and between species and their habitat was found at some scales, but not others. On a broad scale, the abundances of the 3 species were highest at the same 4 sites (kilometres apart). These sites were all located at headlands, suggesting that the patterns of abundance may be in response to the topographic features of the island at this scale. Differences among species occurred at intermediate scales (10s to 100s of metres), where species were associated with different depth zones or reef locations. *Centropyge vroliki* occurred shallower than *C. bicolor*, while the depth distribution of *C. bispinosa* overlapped with both of these species. Laterally along the fringing reef, *C. vroliki* were more abundant in areas where both *C. bicolor* and *C. bispinosa* were also abundant, but these 2 latter species were not correlated with each other. The proportions of substratum types present in home patches differed among species, to some extent reflecting the benthic composition of the reef area where each occurred. However on a fine scale (metres), all 3 species appeared to use the same substratum type, which consisted of dead branching coral covered in algae, and occasionally formed multi-species groups. Species abundances were not correlated with this commonly used microhabitat, but rather the availability of the substrata characterizing the reef areas in which they were most abundant. Here, although *Centropyge* species use the same type of microhabitat, they may be an example of species that partition space on the basis of non-preferred resources. For example, all 3 species used home patches containing high proportions of overgrown corals; however where this habitat was not available, *C. bicolor* used sand and rubble habitat at the reef base, while *C. vroliki* used coral habitat on the reef crest. Most importantly, this study emphasizes that a multi-scale approach is necessary to determine appropriate scales for examining species associations and resource partitioning in reef fishes.

KEY WORDS: *Centropyge* · Pomacanthidae · Great Barrier Reef · Habitat use · Distribution patterns · Multi-scale analysis · Spatial scale · Species associations

## INTRODUCTION

The importance of resource partitioning to the coexistence of ecologically similar coral reef fish species and its relationship to the high diversity that characterizes these assemblages have been the subject of much debate. Early studies on reef fish communities not only found them to be highly speciose assemblages, but also to be relatively generalised in terms of both diet and space requirements (Roughgarden 1974, Sale

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1975, 1977, 1978). This appeared to conflict with competition theory, which argued that coexistence in diverse assemblages results from the partitioning of resources among species (Pianka 1966, MacArthur 1969, Colwell 1973). Early attempts to demonstrate that competition plays a role in habitat partitioning on coral reefs repeatedly failed (Doherty 1983, Roberts 1987, Jones 1988). As an alternative, it has been argued that diversity may be related to the variability in the supply of pelagic larvae and juvenile recruitment, at levels below which space would become saturated (Talbot et al. 1978, Doherty 1983, Victor 1983, Sale et al. 1984, Doherty & Williams 1988). This variability may act to reduce the capacity for a competitively dominant species to eliminate an inferior competitor.

Since the pioneering work on reef fishes, numerous studies have documented distinct patterns of food and habitat utilisation among similar species. Examples can be found in a range of coral reef fish families including surgeonfishes (Robertson 1980, Waldner & Robertson & Gaines 1986, Robertson & Lassig 1980), blennies (Clarke 1994), groupers (Shpigel & Fishelson 1989), sandperch (Sano 1990), damselfishes (Ormond et al. 1996), butterflyfishes (Pitts 1991, McAfee & Morgan 1996) and gobies (Munday et al. 1997). In addition, there is increasing evidence that inter-specific competitive interactions play a role in maintaining species-specific patterns in habitat use (Robertson 1984, 1996, Ebersole 1985, Robertson & Gaines 1986, Clarke 1989).

There are a number of reasons why some studies emphasize ecological similarities among species, while others highlight their differences. Coral reef fishes are found in an environment which is structurally complex on a hierarchy of spatial scales (Sale 1991, 1998) and reef fish appear to respond to the environment at all spatial scales that have been examined (Williams 1991). For example, the species composition of fish assemblages have been found to vary across continental shelves (Williams 1991), along gradients of wave exposure (Talbot 1965, Williams 1982, Victor 1986), and depth (Waldner & Robertson 1980, Eckert 1985, Fowler 1990, McCormick 1994, Green 1996), and among microhabitats (Itzkowitz 1977, Jones 1988, Jennings et al. 1996, Ormond et al. 1996). However, not all species respond to all gradients in habitat structure, and species may partition resources at some scales and not others. Consequently, multi-scale approaches should be used to identify appropriate scales to measure ecological similarity and differences among species.

Different levels of resource partitioning may be characteristic of different taxa. Ecological theories regarding processes which contribute to high diversity in coral reef fish assemblages have been constructed primarily on the results of studies on relatively common and speciose taxa, such as damselfish (Doherty 1983, Sale et al. 1984). However, coral reefs contain a large number of species that are locally rare even though the dispersive larval stage ensures relatively wide geographic distributions (Jones & Kaly 1995). Patterns of resource partitioning in common taxa may not be representative of their rarer counterparts. If rarity results from low availability of preferred resources, then competition for these resources may be more intense among closely related rare species compared with more common ones. Alternatively, if rarity is due to inherent life history characteristics such as low reproductive output, recruitment rates, or mortality rates, then shared resources may be in abundant supply, and thus resource use among rare species may overlap to a greater degree than expected. An examination of patterns of resource use by rare species and their subsequent effects on distribution and abundance may give some indication of whether coexistence in rare species is maintained through resource partitioning. In addition, investigations of rare species may provide further clues as to the causes of diversity in reef fish assemblages as a whole.

Pygmy angelfishes (genus *Centropyge*) are a group of relatively rare but conspicuous reef fishes, with several congeners occurring on almost all tropical coral reefs. These characteristics make the pygmy angelfishes an ideal genus to compare resource utilization traits and determine how they may affect patterns of distribution. Pygmy angelfishes are known to be highly site-attached with the females holding foraging territories, while the males defend females from other males throughout the year (Lobel 1978, Moyer & Nakazono 1978, Bauer & Bauer 1981, Moyer et al. 1983, Aldenhoven 1984, Sakai & Kohda 1997). Although some information has been published on the habitat requirements of particular *Centropyge* species (Moyer & Nakazono 1978, Moyer et al. 1983, Aldenhoven 1984, Sakai & Kohda 1997), there are no quantitative studies to date that compare habitat use among more than 1 species of *Centropyge*.

This study investigated the distribution and abundance patterns of 3 pygmy angelfishes, *Centropyge bicolor*, *C. vroliki* and *C. bispinosa*, at multiple spatial scales. The aim was to determine appropriate scales for examining ecological partitioning among these species. The spatial scales examined were (1) a large spatial scale (≥ 1000 m) encompassing an exposure gradient, (2) a medium spatial scale (10 to 100 m) along a depth gradient, and (3) fine-scale (1 to 10 m) patterns of dispersion within habitats. The first 2 scales relate to environmental gradients which reef fish are known to respond to, while the smallest scale relates to the extent of movement of *Centropyge* individuals based on the behavioural observations of a previous study (Aldenhoven 1986). Using this sampling hierarchy, we were able to identify scales at which habitat resources appear to influence patterns of angelfish abundance and distribution.

## METHODS

**Study location and species.** This study was carried out at Lizard Island, a continental island located approximately 35 km off the coast of Australia in the northern sector of the Great Barrier Reef (14° 40' S, 145° 28' E). The fringing reefs surrounding the island were divided into 3 sites according to their exposure to the prevailing southeasterly trade winds (Fig. 1a): sheltered (S), moderately exposed or oblique to the prevailing wind (M) and directly exposed (D) (Choat & Bellwood 1985). At Lizard Island, pygmy angelfishes (genus *Centropyge*) are rare in terms of local abundance (*sensu* Gaston 1994) comprising less than half a percent of the demersal reef fish community (Syms & Jones unpubl.). They are, however, easily identifiable by their small size and distinct colour patterns. Three species, *C. bicolor*, *C. vroliki* and *C. bispinosa*, were found in the sites surveyed for this study.

**Sampling design.** A total of 9 sites, 3 within each of the 3 exposures at Lizard Island (i.e. S1–S3, M1–M3 and D1–D3) were censused visually for *Centropyge*. Four replicate 100 × 10 m transects were conducted at each of the 9 sites surveyed, except for one site (D3), where only 3 transects were censused due to adverse weather conditions. For each transect, a 100 m long tape was placed approximately 3 m below and parallel to the reef crest, and pygmy angelfish occurring within 5 m either side of the tape were counted (Fig. 1b). Such a large sampling unit was required due to the rarity of *Centropyge* species. Along each transect, the depth of each *Centropyge* was recorded, and their locations within the transect were mapped to provide comparative information on the degree of dispersion for each species. Data from 2 additional sites, 1 sheltered (Mermaid Cove) and 1 exposed (Bird Islet), were included in the analysis of the smaller scale distribution patterns.

The availability of microhabitats at 7 of the 9 sites used in the fish censuses were quantified by sampling in 3 reef zones: crest, slope and base. Two sites (D2 and D3) were excluded from the data collections due to adverse weather conditions. The same sampling design was used to survey the available habitat as was used for the visual censuses. Four transects 100 m long were carried out at each site, and within these transects the habitat was surveyed separately for each of 3 reef zones, the crest, slope and base (Fig. 1b). Ten ran-

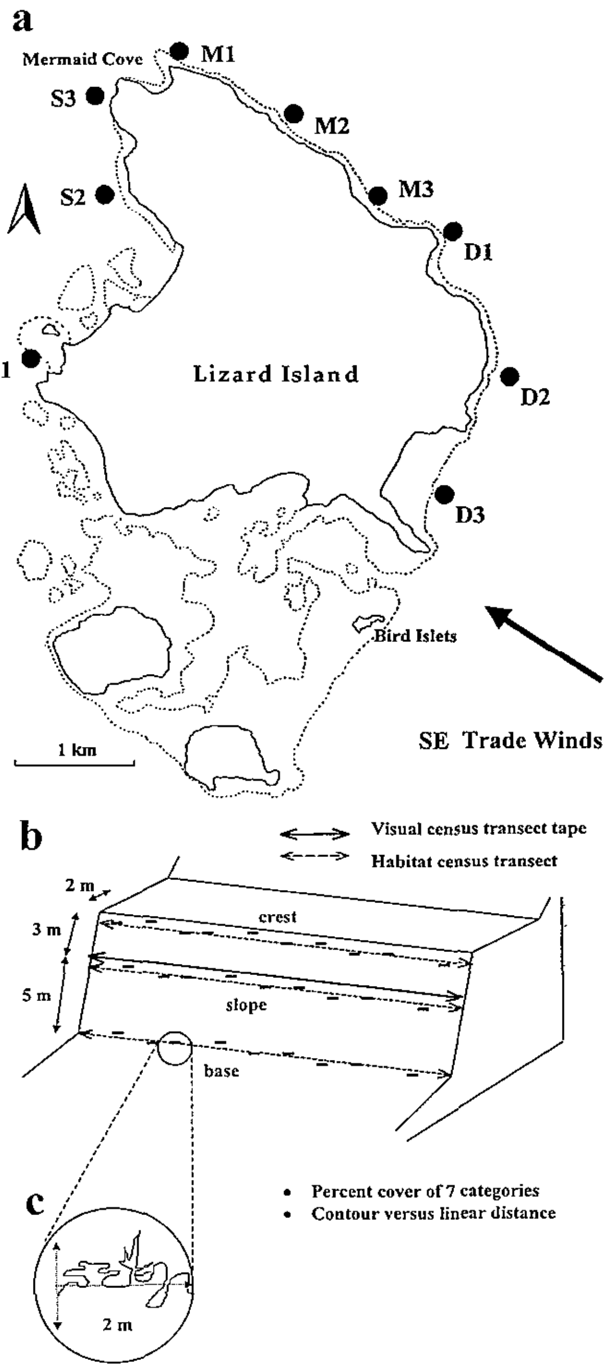

Fig. 1. (a) Map of Lizard Island (14° 40' S, 145° 28' E), showing the main sites used in this study and the direction of the prevailing wind. Codes refer to the relative degree of exposure: S = sheltered, M = moderately exposed, D = directly exposed. (b) Overlay of fish census and habitat availability transects. Within each 'fish' transect, 3 'habitat' transects were laid out along the reef crest, slope and base, in which 10 discrete 2 m sections were surveyed. (c) Data recorded for each 2 m section of habitat surveyed included the topographical complexity (contour vs linear distance) and percentage cover of 7 substratum categories (see Table 1)

domly selected 2 m sections were surveyed along each of these zones. For each 2 m section, the topographic complexity (ratio of contoured length to 2 m) was measured and the intercept lengths of 7 substratum categories (Table 1) along the 2 m section were quantified to estimate percentage composition (Fig. 1c).

To determine the characteristics of the reef substrata used by each of the 3 species of *Centropyge*, 2 m line transects laid parallel to the reef crest were surveyed over the home patches of 45 groups of *Centropyge vroliki*, 43 of *C. bicolor* and 22 of *C. bispinosa*. The home patch was defined as the area of reef into which members of a particular social group would retreat most often when disturbed, and around which most of their foraging was based. Home patches were usually based around an outcrop of rock or coral and contained portions of territories of individual fish. In addition, 13 home patches were surveyed which were occupied by 2 or more species of *Centropyge*.

**Analysis of distribution and abundance.** Total abundance estimates of the 3 species of *Centropyge* were compared among exposures and sites (nested in exposures) using MANOVA followed by a non-metric multidimensional scaling (MDS). To examine the relative abundances of each species of *Centropyge* among sites, an MDS was carried out using a Quantitative Symmetric Kulezynski (QSK) matrix to preserve the rank order of dissimilarities. A complete linkage cluster analysis using Ward's method on the dissimilarities from the matrix was used to group sites according to their similarity in relative abundance of the 3 species, and this was superimposed on the first 2 dimension axes.

Pairwise Pearson's correlations were used to test for associations between species of *Centropyge* at the transect level. Data were $\log_{10}(x+1)$ transformed to reduce the variation resulting from low numbers. To assess patterns in inter-specific associations at an even smaller spatial scale (within 10 × 10 m sections of reef), the presence of each species relative to the presence of the others were compared using chi-square test of independence with an adjusted alpha value (Bonferroni method) for multiple comparisons. At this fine scale, the presence and absence of each species were compared rather than absolute numbers to overcome the bias of different group sizes among the species. Distributions which were found not to be independent were tested for the nature of their association (positive or negative) using the phi coefficient of association (Sokal & Rohlf 1995). These data were obtained from the mapped distributions of fish within each transect using the co-ordinates recorded during visual censuses.

To compare the relative depth distributions among the 3 species of *Centropyge*, the depths recorded for each individual were standardised to mean low water tide. The depth frequency distributions across all sites were then compared among species using Kolmogorov-Smirnov tests with an adjusted alpha value (Bonferroni method) for multiple comparisons (Sokal & Rohlf 1995).

**Analysis of habitat use.** Similarities in the habitat occurring in home patches among *Centropyge* species were examined by comparing the relative proportion of substratum categories, and the variability in the micro-topographic reef profiles. Out of the 13 shared patches censused, 6 were occupied by groups of both *Centropyge bicolor* and *C. vroliki*, 3 by all 3 species, and 2 each by *C. bispinosa* with *C. bicolor*, and *C. bispinosa* with *C. vroliki*. To determine whether the 3 species differed significantly in their habitat use, data were analysed using a 1-way MANOVA. Pillais Trace statistic was used to determine significance. A canonical discriminant analysis (CDA) was used to display similarities in habitat use by plotting each of the 3 species in a 2-dimensional space. Confidence ellipses (95 %) were calculated for all the group mean centroids using the formula:

$$95\%\ \mathrm{CL} = \sqrt{(\chi^2_2, 0.05/n)}$$

where $n$ = the number of replicates (Seber 1984).

Table 1. Seven broad substratum categories used to define reef microhabitat

| | |
|---|---|
| Algae | 1. **Algae (flat)**: Non-complex reef substrata (e.g. massive corals, reef base) overgrown with epilithic algae or macroalgae<br>2. **Algae (compl)**: Complex reef substrata (e.g. branching corals) overgrown with epilithic algae or macroalgae |
| **Sand & rubble** | 3. Calcareous or silicious sediment, live and dead coral rubble |
| **Encrusting** organisms | 4. Benthic categories with an encrusting morphology, including scleractinian corals, algae and sponges |
| Alcyonarians | 5. Includes all **soft corals** |
| Scleractinians | 6. **Complex corals**: Corals with complex morphologies, including branching, corymbose, digitate, foliose and tabular forms<br>7. **Massive corals**: Corals with a massive morphology, or solitary forms |

Electivity indices were used to determine if *Centropyge* species incorporated particular substratum categories into their home patches disproportionately to their availability in the environment. The Vanderploeg & Scavia (1978) electivity index ($E^*$) was used because it is considered to be one of the most robust electivity indices (Lechowicz 1982). Positive values indicate that a particular category is used in greater proportions than expected from its availability. Negative values indicate that categories are used less than expected.

An electivity coefficient ($E^*$) was calculated separately for each species of *Centropyge* for every substratum category using the formula

$$E^* = [W_i - (1/n)]/[W_i + (1/n)]$$

where $n$ = the number of resource types (substratum categories), $W_i = (r_i/p_i)/\Sigma(r_i/p_i)$, $r$ = the proportion of resource utilised, and $p$ = the proportion of resources available (Vanderploeg & Scavia 1978). To compensate for potential variability in the habitat associations exhibited by *Centropyge* across reef zones, electivities were calculated for the average composition of available habitat types for the reef zone in which the territory occurred. Therefore, mean electivities and standard errors could be calculated for each species.

Finally, canonical correlations were calculated to detect any relationships between the abundance estimates $[\log_{10}(x+1)]$ of the 3 species of pygmy angelfish and the availability of habitat types in each site/zone across all exposures. No relationship was detected between the abundance of any species with the habitat available at the site level. Therefore, both abundance and habitat were separated into the 3 reef zones at each site to incorporate the effect of depth into the analysis. Canonical coefficients of the species (interset) were then plotted into the space defined by the canonical coefficients of the habitat variables (intraset).

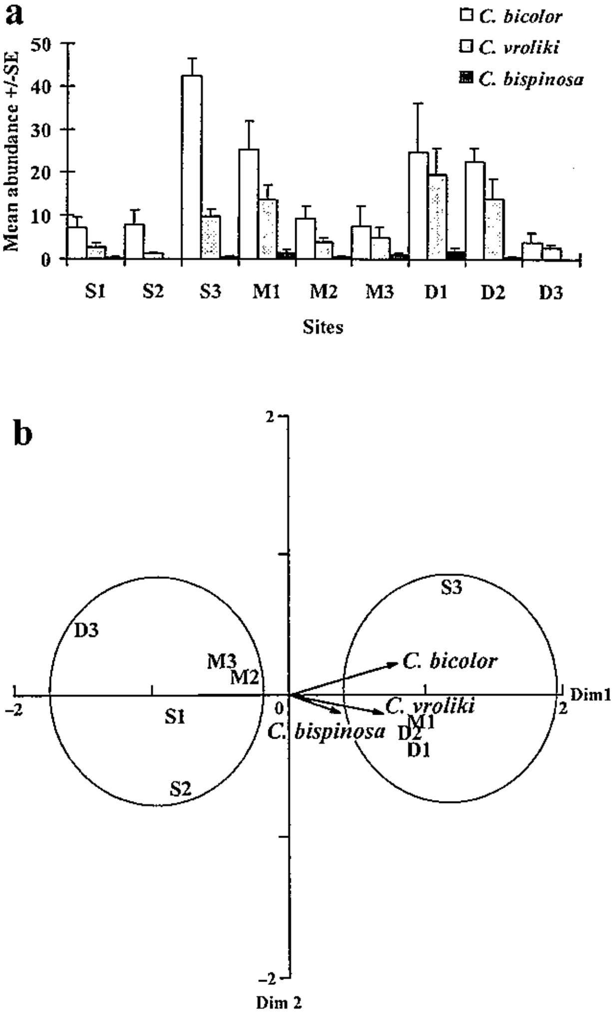

Fig. 2. (a) Mean abundances (±SE) 1000 $m^{-2}$ of the 3 *Centropyge* species at 9 sites including 3 sheltered sites (S1–S3), 3 moderately exposed sites (M1–M3) and 3 directly exposed sites (D1–D3). (b) Non-metric multidimensional scaling of *Centropyge* mean abundances. Sites are represented by their exposure codes and plotted on a dissimilarity matrix described by the 3 species vectors. The 2 clusters show the results of a complete linkage cluster analysis using Ward's method on the dissimilarities from the matrix

## RESULTS

### Distribution and abundance patterns

Over the 9 sites censused, a total of 910 individuals from the genus *Centropyge* were recorded around Lizard Island. Relative abundance patterns of the 3 species found were extremely consistent, with *Centropyge bicolor* always being the most abundant, and *C. bispinosa* the least abundant (Fig. 2a). There were significant differences in the abundances of *Centropyge* among exposed, oblique and sheltered sites, and also in the abundances of *Centropyge* among sites within each exposure (Table 2). Within each exposure type, 2 out of 3 sites tended to be similar in their abundance and composition of the 3 angelfish species while the third site differed markedly in each case (Fig. 2b). Furthermore, 2 main groups within the 9 sites, separated along dimension 1 of the MDS, were identified by the cluster analysis which do not correspond to exposures (Fig. 2b). Sites S3, M1, D1 and D2 were characterized by high abundances of all 3 species of *Centropyge*, while sites S2, S3, M2, M3 and D3 exhibited relatively low abundances (see also Fig. 2a). Interestingly, sites with high abundances of *Centropyge* correspond to reefs that are adjacent to headlands

Table 2. MANOVA result comparing distribution patterns of *Centropyge* species among exposure regimes and sites nested within exposures. $\alpha = 0.05$, *significant effects

| Source of variation | Pillais trace | Hypoth. df | Error df | *F* | Significance of *F* |
|---|---|---|---|---|---|
| Exposure | 1.360 | 6 | 10 | 3.544 | 0.038* |
| Site(Exposure) | 0.887 | 18 | 78 | 1.8194 | 0.037* |

around Lizard Island and sites of low abundance corresponded to reefs located in bays (Fig. 1a).

Although all 3 species of *Centropyge* were most abundant at the same sites, a similar pattern was not observed at the 2 smaller scales examined. At the scale of transects (100 × 10 m), high abundances of *Centropyge vroliki* coincided with high abundances of *C. bicolor* and also *C. bispinosa*, but the abundance estimates of the latter 2 species were not correlated (Table 3). Similarly, *C. vroliki* were more often seen in 100 $m^2$ quadrats, where either *C. bicolor* and *C. bispinosa* were also found, than would have been expected if the species were distributed independently (Table 3), while the occurrences of the latter 2 species were independent.

The 3 species of *Centropyge* largely overlapped in their depth distributions over the range surveyed in this study (Fig. 3). All 3 species were found between depths of 1 and 6 m; however *Centropyge vroliki* and *C. bicolor* were also found as deep as 9 and 10 m respectively. Kolmogorov-Smirnov tests using the total frequency of counts for each depth found that there was a significant difference in the depth distribution between *C. bicolor* and *C. vroliki* ($D = 0.369$, $\alpha = 0.017$, $p < 0.001$), but not between *C. bispinosa* and *C. bicolor* ($D = 0.200$, $\alpha = 0.017$, $p < 0.025$), or *C. bispinosa* and *C. vroliki* ($D = 0.197$, $\alpha = 0.017$, $p < 0.05$). *C. vroliki* was generally found in shallower sections of the reef, with over a quarter of individuals (26%) between 0 and 1 m (around the crest) and with the frequency of observation generally declining with depth. In contrast, the depth distribution of *C. bicolor* approximates a normal distribution, with the greatest frequency of observation between 4 and 5 m, and 31% seen below 6 m.

### Habitat availability and use

The characteristics of the habitat found in home patches varied significantly among species of *Centropyge* (Table 4). These results reflect the depth distribution of each species and corresponding depth-related changes in the benthic cover. In a CDA of home patch habitat composition (Fig. 4) the first 2 canonical axes explained 84% of the variation among habitat characteristics. Differences in depth and the cover of living complex corals accounted for approximately 46% of the variation among home patches (Can 1, Fig. 4). Complex overgrown corals and topographical complexity of habitats accounted for approximately 38% of the variation among home patches (Can 2, Fig. 4). In general *Centropyge bicolor* home patches differed significantly from those of *C. vroliki*, in that they occurred at greater depths and contained proportionately less amounts of live complex corals. *C. bispinosa* territories occurred in areas

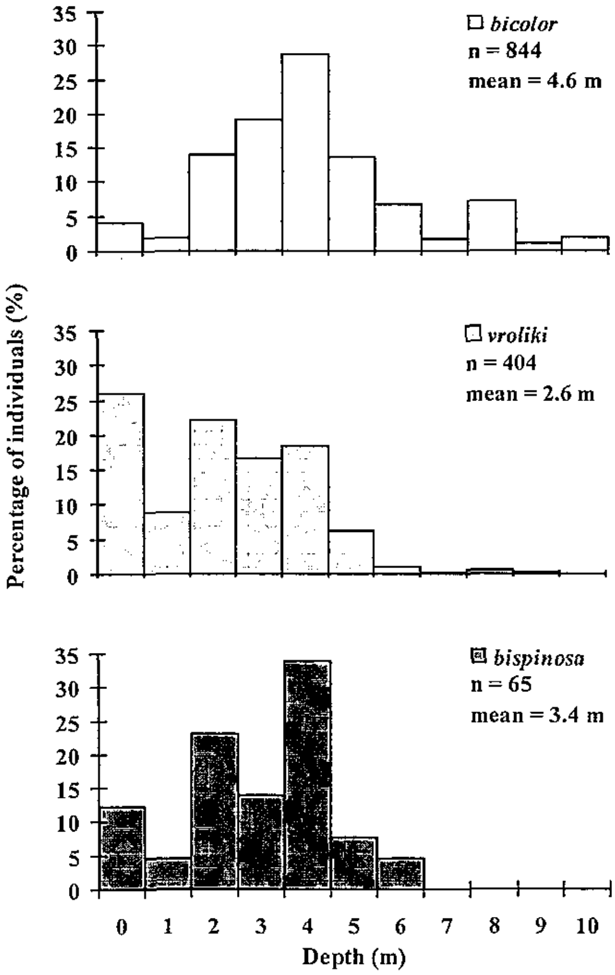

Fig. 3. Depth frequency distributions for the 3 *Centropyge* species across all sites

that were intermediate between the other 2 species in depth and the percent cover of living complex corals. However territories were topographically more complex and contained higher proportions of overgrown complex corals than either *C. vroliki* or *C. bicolor* sites. Shelter sites shared by more than 1 species of *Centropyge* similarly consisted of a higher percentage cover of complex corals overgrown with algae than *C. bicolor* and *C. vroliki* territories.

A comparison of microhabitat use and availability showed that all 3 species appeared to use the same microhabitat (Fig. 5). Overall, home patches for all of the species contained a higher percentage cover of overgrown complex corals than would be expected from the proportion available. Interestingly, there is strong use of overgrown rather than living complex coral substrata, which was not used by any species. Furthermore, all 3 species used non-complex substrata overgrown with algae in approximately the same proportions to which it was available, while most other categories were present in lower proportions in home patches than available.

### Correlations between abundance and habitat

While all 3 *Centropyge* species appeared to associate with reef patches which had high proportions of complex reef substrata covered in algae, only the abundance of *Centropyge bispinosa* correlated with the availability of this habitat type (Fig. 6) The canonical correlation indicates that higher numbers of *C. bispinosa* occur where this type of habitat occurs, regardless of the site or reef zone. In contrast, the abundances of *C. bicolor* and *C. vroliki* were not correlated with this commonly used microhabitat. Instead, their abundances were related to the features of depth strata with which each were related (Fig. 4). *C. bicolor* was more abundant at site/zones where there were increased amounts of sand and rubble, while *C. vroliki* was more abundant in site/zones where there were more complex corals. On a fine scale, these species did not appear to be closely associated with these substrata and used them in lower proportions than expected on the basis of their availability (Fig. 5).

Table 3. Analysis of intermediate and small-scale dispersion patterns of *Centropyge* species. Values in the top right section are correlation coefficients and p-values (parentheses) between the log abundance at the transect level (1000 $m^{-2}$). *Significant correlations. Values in the bottom left section are chi-square values for the within transect distribution of *Centropyge* species (100 $m^{-2}$). *Significant non-independence at $\alpha = 0.013$. The values in parentheses are phi coefficients of association ($-1 < \phi < +1$), where a positive value indicates a positive association, and a negative value would indicate negative association

| | *C. bicolor* | *C. vroliki* | *C. bispinosa* |
|---|---|---|---|
| *C. bicolor* | | 0.56 (0.001)* | 0.31 (0.070) |
| *C. vroliki* | 10.64* (+0.17) | | 0.44 (0.008)* |
| *C. bispinosa* | 0.92 | 17.87* (+0.31) | |

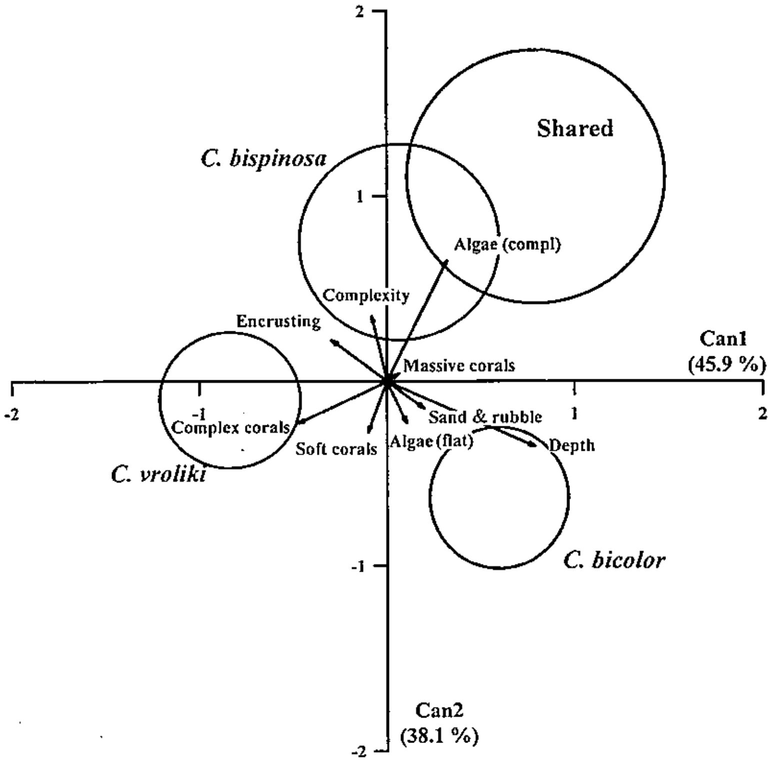

Fig. 4. CDA of the characteristics of shelter sites used by each species of *Centropyge*. Circles are plotted around the means and the size corresponds to the 95 % confidence ellipses of the canonical scores for the substratum composition and profile characteristics of each species. The proximity of circles indicates the similarity in the habitat used. Vectors are structural coefficients of response variables. Axis labels show the proportion of the variation explained by the plot. Can1 and Can 2 = canonical variates 1 and 2

## DISCUSSION

The numerical relationships among the 3 *Centropyge* species, and their patterns of association with features of the habitat, varied depending on the spatial scale examined. Species were positively associated

Table 4. MANOVA results for differences in percentage composition of benthic categories, complexity and depth of shelter sites inhabited by *Centropyge* species. n = 43, 45, 22 for *C. bicolor*, *C. vroliki* and *C. bispinosa* respectively, and n = 13 for shared sites. $\alpha = 0.05$, *denotes significant effects

| Source of variation | Pillais trace | Hypoth. df | Error df | *F* | Significance of *F* |
|---|---|---|---|---|---|
| Species | 0.733 | 27 | 339 | 4.061 | 0.0001* |

with each other at some scales but abundances were inversely related at others. Likewise, each species could be positively associated with particular habitat variables at one scale, but appeared not to associate with these habitats at others. Hence studies of these species carried out at different spatial scales could lead to opposite conclusions.

At the largest scale examined, the 3 species of *Centropyge* recorded the greatest abundance at the same sites around Lizard Island. This suggests that they were responding to the same features of the environment and that there is no partitioning of resources among species at this scale. The factors affecting the distribution and abundance around whole reefs may be phylogenetically conservative in this group. While the species composition for other fish groups has been found to vary at the scale of wind exposures around Lizard Island (Choat & Bellwood 1985, Kingsford 1992, Meekan et al. 1995, Munday et al. 1997), this was not the case for *Centropyge*, which appeared to be associated with headlands. The increased abundance of *Centropyge* at these sites may be the result of preferential settlement by larvae (Victor 1986, Milicich et al. 1992, Tolimieri 1995, Doherty et al. 1996, Light & Jones 1997) or post-settlement survival (Doherty & Sale 1985, Shulman & Ogden 1987, Robertson 1988, Tupper & Hunte 1994), both of which may result in higher population abundances in more favourable habitats.

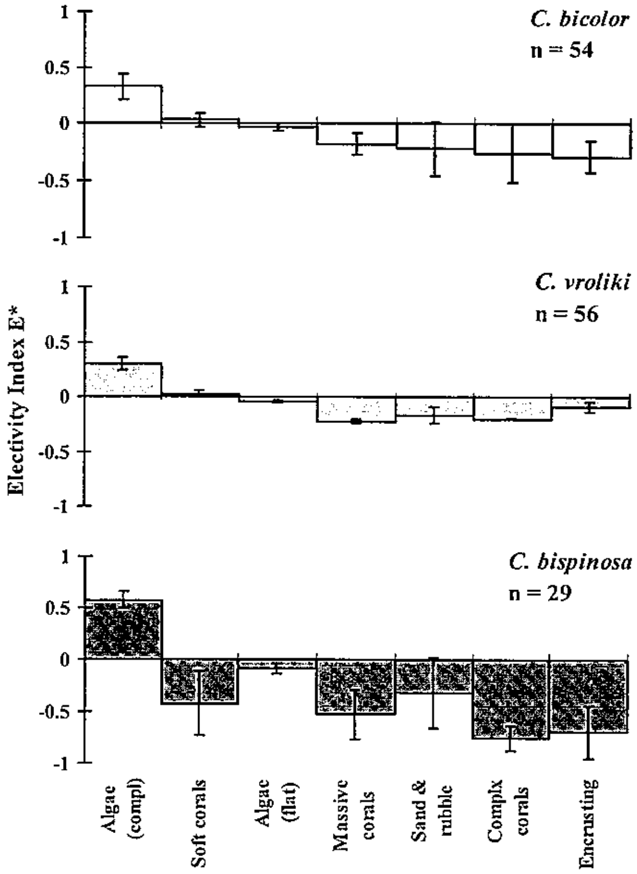

Fig. 5. Patterns of habitat selectivity for *Centropyge* species. Values are mean electivities (Vanderploeg & Scavia's $E^*$) and standard errors. Positive values represent greater use of a habitat type than was available. Negative values represent use of a habitat category less than would be expected from its availability

There could be several reasons why abundances are greater at headlands. Studies of the distribution of fish larvae around reefs have found that specific wind and current regimes can result in larval retention in particular reef areas (Leis 1986, Kingsford et al. 1991, Sponaugle & Cowen 1996). Wave refraction and the formation of slicks and eddies may be concentrating larvae at headlands, and densities of *Centropyge* may be reflecting these differential levels of passive larval supply. Alternatively, high abundances of *Centropyge* at headlands could be due to the preferential settlement of larvae. However, there is currently no information available on large-scale habitat preferences in *Centropyge*.

The headlands at Lizard Island may have upwellings or greater current speeds that are known to sustain higher densities of planktivorous fish (Kingsford & MacDiarmid 1988). It has been observed that populations of *Centropyge interrupta* at Miyake-jima (Japan) are greater in density along cliff areas where upwelling currents attract aggregations of plankton feeders (Moyer & Nakazono 1978). It was suggested that this may be due to the faecal materials of planktivores providing an important percentage of the diet of *C. interrupta*. *C. bicolor*, *C. vroliki* and *C. bispinosa* may be more abundant here because they consume detritus directly, however there is no evidence to sug-

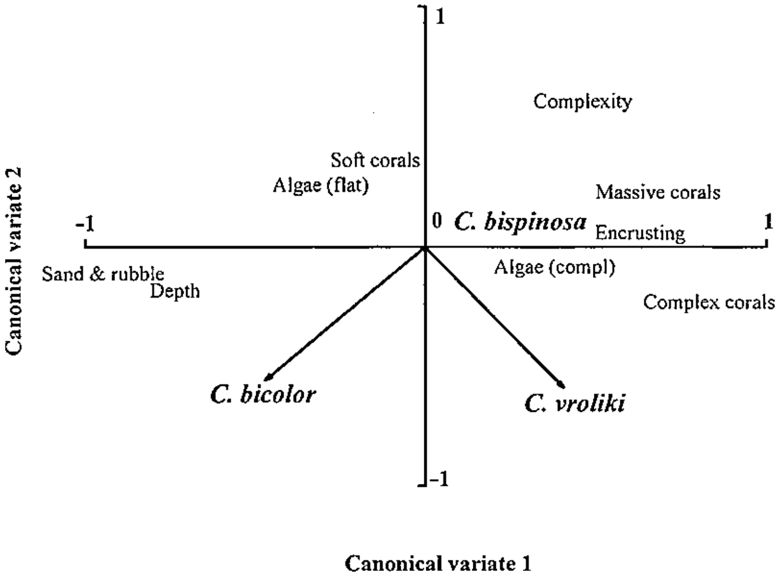

Fig. 6. Canonical correlation of *Centropyge* species abundances and availability of habitat types. Species and habitat projection biplots are shown in the space defined by the canonical variates of the habitat variables. See Table 1 for habitat codes

gest this at present. Alternatively, densities may be higher because increased levels of detritus may enhance the productivity of turf algae that they are known to consume (Moyer & Nakazono 1978, Aldenhoven 1984, Sakai & Kohda 1997, Eagle unpubl. data). However, no relationship was found between the abundance of species at headland sites and the presence of turf algae in this study.

It is possible that site-specific differences in mortality, if correlated among species, may also contribute to the distribution patterns observed. Mortality rates have been estimated to vary 10-fold among sites for *Centropyge bicolor* at Lizard Island (Aldenhoven 1986); however, further investigation is required, with a direct comparison between headland and bay sites.

The greatest species-specific differences in patterns of abundance and habitat-use occurred at the intermediate spatial scale examined. It appears that the species may be partitioning reef areas at scales of 10s to 100s of metres by depth and lateral location. *Centropyge vroliki* was most abundant on the reef crest, and *C. bicolor* was found deeper. There was no significant difference in the depth distribution between *C. bispinosa* and either of these 2 species. This may have been due to the relatively small number of observations of this rarer species obscuring patterns, or its relatively low abundance reducing the need for ecological partitioning. However laterally along the reef margin, *C. bispinosa* was not found in the same areas as *C. bicolor* at either the 1000 or 100 $m^2$ scale, even though *C. vroliki* was found where either *C. bicolor* or *C. bispinosa* were present. Depth partitioning has been reported for 2 cohabiting *Centropyge* species in Guam, where *C. shepardi* replaces *C. flavissimus* at depths greater than 20 m, with a zone of overlap from 20 to 24 m (Moyer 1981). Similar depth segregation has been reported for congeners of many other coral reef fishes, such as *Chaetodon* spp. (Bouchon-Navaro 1986, Fowler 1990), *Cephalopholis* spp. (Shpigel & Fishelson 1989), *Acanthemblemaria* (Clarke 1989), *Stegastes* spp. (Wellington 1992) and *Gobiodon* spp. (Munday et al. 1997).

The patterns of abundance of adult *Centropyge* in these reef zones may reflect differential recruitment to particular reef areas as a result of larval habitat selection. Distribution patterns may correspond with the availability of the reef substrata from which recruits emerge, as found for a number of other reef fishes (Tolimieri 1995, Booth & Wellington 1998, Gutierrez 1998). Previous studies have found that adult densities of some reef fish are correlated with recruit densities (Victor 1986) and also that abundances of recruits are correlated with the availability of preferred shelter sites (Shulman 1984, 1985, Victor 1986, Jones 1987, Light & Jones 1997, Nemeth 1998, Booth & Wellington 1998). It is thought that *Centropyge bicolor* individuals recruit to deeper rubble substrata, whereas *C. vroliki* recruit to the reef flat (D. R. Bellwood pers. comm.). This suggests that *Centropyge* may have subtle ontogenetic shifts in resource use after settlement, in particular a habitat shift towards the reef proper from the reef edges. Post-settlement events such as niche shifts are not uncommon for coral reef fishes (McCormick & Makey 1997, Munday & Jones 1998, St. John 1999).

Depth distributions may also be maintained by preferential settlement of larvae to areas where adult conspecifics are already located (Sweatman 1983, 1985, Wellington 1992, but see Forrester 1995, 1999, Schmitt & Holbrook 1999). Or similarly, juvenile persistence may be confined to adult habitats, as has been found for cohabiting *Stegastes* congeners with complementary depth distributions (Wellington 1992). Thus adult distribution patterns may be driven by a combination of patterns of recruitment, subsequent habitat selection by juveniles and patterns of post-settlement mortality.

On the finest scale examined, all 3 species of *Centropyge* shared the same pattern of high use of algal-covered substratum with a complex morphology, presumably because this type of habitat provides both food and shelter. Aldenhoven (1984) has previously noted that *Centropyge bicolor* at Lizard Island tended to use patches of habitat which contained both food (algae and detritus) and shelter (corals and crevices). Specific habitat associations have been noted for a number of other species of *Centropyge*. *C. interrupta* reportedly prefers areas such as tunnels and caves lacking in *Acropora* cover (Moyer & Nakazono 1978). In contrast, *C. argi* territories were found primarily in areas of 'lush coral growth' (Moyer et al. 1983), and similarly, *C. ferrugata* territories were found to contain higher coral coverage than the surrounding reef (Sakai & Kohda 1997).

It is as yet unknown whether species actively select particular patches of microhabitat, or simply survive and persist in these areas. One study has quantified *Centropyge* abundance in a comparison between reefs infested with *Acanthaster planci* and reefs that were unaffected (Sano et al. 1987). The feeding activities of these coral predators result in reefs retaining their structural complexity but becoming overgrown with turf algae. Interestingly, on living reefs means of 20 individuals (all *Centropyge vroliki*) 1000 $m^{-2}$ were recorded, while on affected reefs 30 individuals (of 2 species *C. vroliki* and *C. heraldi*) 1000 $m^{-2}$ were recorded. The same dead reefs were surveyed again after 2 yr, by which time they had been reduced to rubble with 0 fish 1000 $m^{-2}$ recorded. Notably, the living and affected reefs may have had naturally varying abundances of *Centropyge* which were not due to the effects of *A. planci*. However, it appears possible that overgrown complex habitat is desirable to species of *Centropyge* elsewhere, and that the availability of this type habitat may affect patterns of distribution and abundance.

In our study, however, no significant correlations were found between abundances of 2 of the *Centropyge* species and their commonly used micro-habitat, as has been found for other coral reef species (Tolimieri 1998, but see Robertson & Sheldon 1979). Instead, *Centropyge bicolor* abundances were correlated with the percentage cover of sand and rubble, a substratum category found in lower proportions in home patches than elsewhere. Similarly, *C. vroliki* abundances were positively correlated with the percentage cover of complex living corals, which was also present in lower proportions within home patches than elsewhere. Only abundances of *C. bispinosa* were correlated with the micro-habitat type all species were associated with. These patterns of abundance appear to reflect the species' differing broader-scale habitat use patterns rather than their common microhabitat use patterns.

If competition is involved in the determination of patterns of resource use, then it may involve both phylogenetic constraints in the use of some habitat features and partitioning of others. Competition theory predicts greater specialization and partitioning of resource use among species as competition becomes more intense. Conversely, optimal foraging theory predicts that species will become more generalized in their use of resources when competition becomes more intense and resource availability declines (Stephens & Krebs 1986). This contradiction between competition theory and optimal foraging theory in the role that competition plays in ecological specialization, and thus resource partitioning, has been termed Liem's Paradox. Robinson & Wilson (1998) proposed that because some resources are easy to use and widely preferred, while others require specialized traits by the consumer, optimally foraging consumers evolve specializations to use non-preferred resources without compromising their abilities to use preferred resources. Therefore, the evolution of specializations to use non-preferred resources can be driven by competition, but the specialists act as generalists whenever their preferred resources are available. It is possible that studies so far have not distinguished between preferred and non-preferred resources, which may be partitioned differently, in their examination of resource partitioning and its subsequent effects on distribution and abundance.

Patterns observed for *Centropyge* are consistent with Robinson & Wilson's (1998) proposed solution to Liem's Paradox. For pygmy angelfishes at Lizard Island, the commonly used and possibly preferred microhabitat for all species, overgrown corals, provides both food and shelter and may be easy to use by all species. However, because species tend to be abundant at the same sites, it is possible that this resource is limited in supply and, subsequently, *Centropyge vroliki* and *C. bicolor* have diverged to specialize on the reef top and base respectively. Additionally, these 2 species are more abundant in areas with higher proportions of usable habitat, (i.e. complex corals, and sand and rubble respectively) rather than the most used microhabitat. *C. bispinosa* does not appear to use alternative habitats, which may explain why it is extremely rare at this location, as ecological factors which correlate with rarity include specialised habitat requirements and their availability (Brown et al. 1995) and a poor ability to establish in new areas (Glazier 1980, Rabinowitz 1981).

At some sites, individuals of more than 1 species of *Centropyge* were observed to share the same home patches and to forage together. This has also been observed for cohabiting *Centropyge* species elsewhere (Moyer & Nakazono 1978, Thresher 1982). Significantly, these shared home patches also contained greater proportions of the most used habitat type than the single species patches inhabited by groups of *C. bicolor* or *C. vroliki*. Very little aggression among cohabiting species was observed and this suggests that the intermediate-scale resource partitioning apparent among the species of *Centropyge* at Lizard Island may not be due to direct competitive displacement among individuals. Instead, it may be the result of the so-called 'ghost of competition past' (Connell 1980) or simply 'individualistic responses' to resources (Ebeling & Laur 1986).

The results from our study demonstrate that patterns of distribution and abundance among closely related coral reef fishes vary among spatial scales. Species tended to be positively associated and ecologically similar at the largest and smallest spatial scales examined, but divergent at an intermediate scale. Although all species are relatively rare, they tend to be concentrated at a small number of sites and are virtually absent elsewhere. Because they have similar fine-scale habitat use patterns, they are often found sharing the same territorial sites. It is only at an intermediate scale that the species have complementary distribution and abundance patterns. The role of inter-specific competition in the formation of these patterns needs further investigation. While it is unclear exactly how much habitat partitioning is necessary before competitive interactions are reduced enough to allow coexistence, the partitioning of *Centropyge* species on intermediate scales might enable all 3 species to coexist in relatively small areas of reef where they reach their greatest abundance.

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