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THE EARLY LIFE HISTORY OF LABROID FISHES AT LIZARD ISLAND, NORTHERN GREAT BARRIER REEF

by

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BSc (Hons.)(UQ)

A thesis submitted for the degree of Doctor of Philosophy in the Department of Marine Biology at James Cook University of North Queensland, in April 1994.

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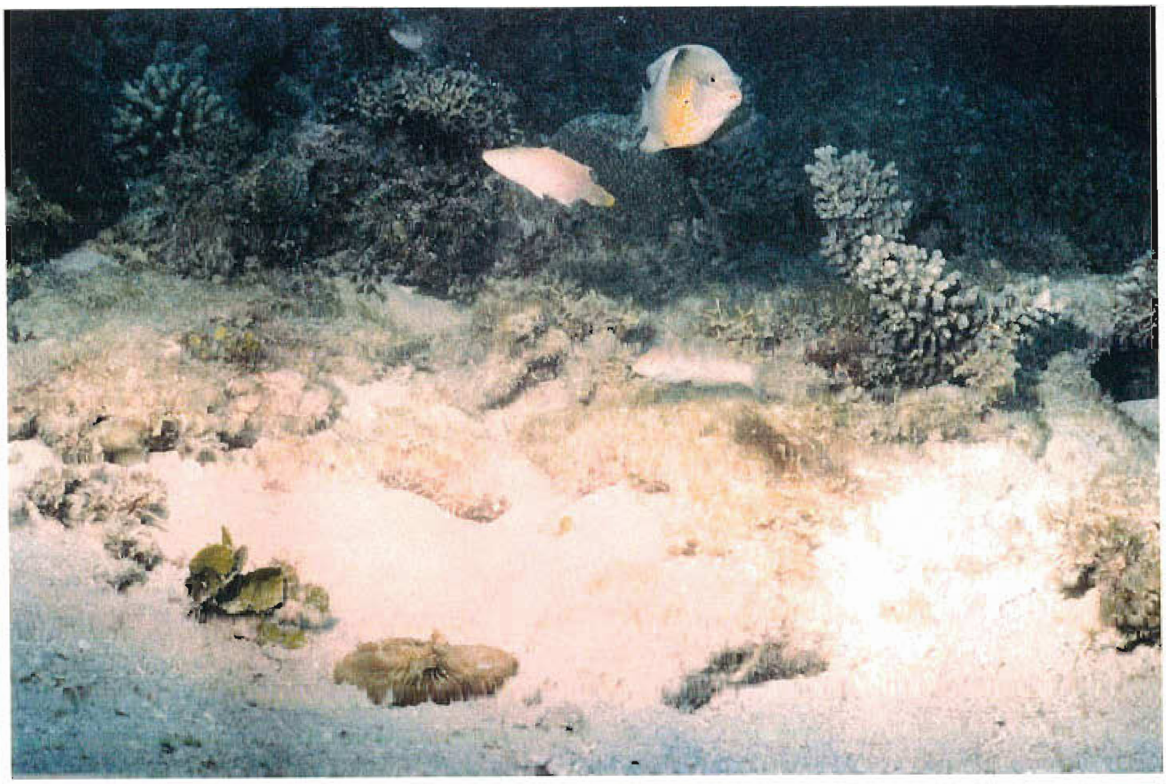

Herbivorous damselfish modify benthic reef assemblages, by facilitating the growth of macroalgae within their territories. Many species of wrasses and parrotfishes use the algae as recruitment sites, and the territories provide an excellent opportunity to study their early life history. This photograph shows a territorial damselfish (*Dischistodus prosopotaenia*; top right) within its territory, along with two of the wrasses (*Coris schroederi* and *Cheilinus diagrammus*) that exploit this resource (Photograph by T. Preen).

ABSTRACT

Adult labrids showed distinctive patterns of distribution and abundance among habitat zones at Lizard Island, which were consistent in space (among sites) and time (annually and seasonally). Patterns of labrid abundance and diversity among habitats were not clearly influenced by substrate characteristics such as percent live cover, substrate diversity and complexity. However depth was an important factor influencing habitat use, with 7 abundant species present in higher densities in either shallow (*Halichoeres* spp., *Stethojulis bandanensis, Thalassoma hardwicke* and *T. jansenii*) or deep habitats (*Coris schroederi*, *H. melanurus*, *T. lunare*). Only one abundant species, *Labroides dimidiatus* was ubiquitous at all depths. Most species used the same habitat zones at different life history stages (adults and recruits), suggesting that patterns of distribution and abundance of adults were determined by recruitment patterns at this scale. In contrast, two species (*Labroides dimidiatus* and *Thalassoma lunare*) showed ontogenetic shifts in habitat use, indicating that their recruitment patterns were modified by post-settlement processes.

Labroid recruits (labrids and scarids) also showed distinctive patterns of distribution and abundance among microhabitats within 2 zones (Reef Base and Sand Flat). Three abundant taxa: 2 labrids (*Coris schroederi* and *Halichoeres melanurus*) and a group of scarids (*Scarus* spp.), were present in significantly higher densities within stands of macroalgae in territories of two herbivorous damselfish (*Dischistodus prosopotaenia* and *D. perspicillatus*) than they were in adjacent microhabitats (reef matrix and rubble/sand patches). The territories provided excellent replicate units of habitat for studying the early life history of these species. Many rare species were also most abundant in the territories.

Each damselfish species facilitated the growth of macroalgae within their territories by excluding trophic competitors and disruptive carnivores. The territories of *D. prosopotaenia* were established on the reef matrix/sand interface at the bottom of the slope, and were characterised by multispecific stands of

green, red and brown algae. *D. perspicillatus* territories were established on sand on the sand flat, and were characterised by a monospecific stand of blue-green algae. In contrast to the territories, adjacent microhabitats were almost devoid of macroalgae. Both damselfish species were abundant and occurred in large aggregations (>20 individuals), where territories covered >20% of large areas (>250m^2). The result was that recruitment of these labroids to large areas with damselfish aggregations, was significantly higher than to adjacent areas without aggregations.

C. schroederi and *Scarus* spp. used both types of territories in high densities, while *H. melanurus* was only present in high densities in *D. prosopotaenia* territories. A manipulative experiment using artificial territories indicated that *H. melanurus* may have discriminated between the territories on the basis of their microhabitat characteristics, rather than their location on the reef profile. However further manipulative studies are required to test this hypothesis.

Labrids which used the territories heavily as recruits did so at different times of the summer. Scarids used them most heavily in the early summer, *C. schroederi* used them in mid-summer and *H. melanurus* used them in late summer. These recruitment patterns were spatially (among sites) and temporally (between years) consistent, and probably decreased the possibility of inter-specific interactions between labroid recruits during the first few weeks of benthic life.

Scarid recruits used the territories for only a few weeks before they were evicted by the resident damselfish. This coincided with the size at which they became herbivores and trophic competitors to the damselfish. In contrast, the carnivorous labrids continued to use territories heavily throughout their lives, with adults of one species (*C. schroederi*) spending >50% of their time within territories. This behaviour appeared to be tolerated by the resident damselfish, which only attacked them on rare occasions.

Living within territories had no negative effects on diet, growth or survivorship of *C. schroederi* and *H. melanurus* recruits during the first 2 months of benthic life, despite their high densities. This was probably because resources (food and shelter) were also much higher in territories than in other microhabitats. The result was that patterns of higher overall recruitment to areas with damselfish aggregations were either reinforced or unchanged by early post-settlement processes, which suggested that sizes of adult populations of these species should have been higher in the vicinity of territories than in adjacent areas without territories. However this was not the case, suggesting that processes operating after the first 2 months of benthic life modified spatial patterns of recruitment. One possibility was that some individuals may have moved out of areas with damselfish aggregations onto adjacent areas where aggregations were absent. These results suggest that damselfish aggregations act as focal sites for labroid recruitment, which may result in higher local abundances of some labroids, both in areas with damselfish aggregations and adjacent reefal areas.

ACKNOWLEDGEMENTS

Many people helped in the production of this thesis, so I will try not to forget anyone! First, thanks to my supervisor Howard Choat, who muttered those immortal words "there's something **** interesting going on in those damselfish territories.....", and who patiently provided guidance and enthusiastic support in all aspects of this project. I also thank my co-supervisor Peter Doherty, for getting me interested in reef fish ecology in the first place, and for generously giving me his time and advice whenever I needed it.

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Preen, Mark Johnston and Mark Burnham took the photographs. Terry Hughes let me use his digitiser, and Liz Dinsdale showed me how to use it. Dirk Zeller helped with the invertebrate sampling, and Ian Price identified the algae. Brett Molony showed me how to process otoliths, and Lynda Axe was a constant source of bits of equipment and usefull advice. Leigh Winsor provided generous and instantaneous advice on matters chemical, while Anne Sharp and Jan Woodley cheerfully helped me steer a course through the minefield of administration. Thanks to you all.

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TABLE OF CONTENTS

Chapter One GENERAL INTRODUCTION

Chapter 2 PATTERNS OF HABITAT USE BY LABRID FISHES AT LIZARD ISLAND

Chapter 3 USE OF DAMSELFISH TERRITORIES BY LABROID FISHES

Chapter 4 RECRUITMENT OF LABROID FISHES TO DAMSELFISH TERRITORIES

Chapter 5 POST-SETTLEMENT ECOLOGY OF LABROID FISHES IN DAMSELFISH TERRITORIES

Chapter One
GENERAL INTRODUCTION

1.1 INTRODUCTION

Most reef fishes have discontinuous distributions at a range of spatial scales from >1000 kilometers to meters (see review in Williams 1991). One of the most striking patterns of habitat association is the distribution of species among physiographic habitat zones on individual coral reefs, although species differ in their degree of habitat specialization (see Williams 1991). In general, habitat zones tend to be characterised by a distinctive suite of physical and biological attributes (Done 1983), and a similarly distinctive fauna of fishes (Goldman & Talbot 1976; Harmelin-Vivien 1989).

On a finer scale, some species display uneven abundances within habitat zones, where they are usually associated with particular structural or biological features, such as substratum type (see review in Williams 1991). This is especially true of juveniles that have recently settled onto the reef (Sale *et al.* 1984a; Eckert 1985a,b).

Patterns at this scale are frequently attributed to "microhabitat selection": the active discrimination among sites by settling larvae. It is presumed that these patterns are established at the time of transition between pelagic and benthic environments (Sale *et al.* 1984; Eckert 1985a,b), by using either visual or olfactory cues (Sweatman 1988). However, the possibility that these patterns may be established by post-settlement processes, such as differential mortality among different microhabitats, has not usually been addressed. This is because the process of settlement is intrinsically difficult to study (Victor 1991), and most cases involve inferences from recruitment data (Doherty & Williams 1988), that by definition, involve older stages (Keough & Downes 1982). For such animals, recruitment patterns are clearly the combined result of settlement and early post-settlement processes of mortality (see Jones 1991) or redistribution (see Robertson 1988a).

Spatial patterns of recruitment by reef fish may have important consequences for their post-settlement ecology. Growth (Jones 1986, 1988; Thresher 1985; Gladstone & Westoby 1988), maturation (see Jones 1991), fecundity (Thresher 1985) and reproductive success (Thresher 1985) have each been shown to vary among habitats, perhaps as a result of food availability (see Jones 1991). Moreover, habitats may vary in the amount of available shelter from predators, which may result in different mortality rates in different habitats (Eckert 1985b; Aldenhoven 1986; Jones 1986, 1988). Strong habitat selection can also produce high densities of juveniles with negative, or compensatory, consequences for growth (Doherty 1982; Victor 1986a; Jones 1987a,b, 1988; Forrester 1990; Booth 1992), reproduction (Ochi 1986; Jones 1987a; Forrester 1990; but see Robertson *et al.* 1981) and mortality (Eckert 1987; Jones 1987b, 1988; Robertson 1988a,b; Forrester 1990). Such differences in post-settlement growth and survival may modify recruitment patterns and be important in determining spatial patterns of distribution and abundance of adults (see reviews in Jones 1991; Williams 1991).

To date, knowledge of these early life history processes has been derived disproportionately from one family: the Pomacentridae or damselfishes, because their life history characteristics facilitate manipulative field experiments (see reviews in Doherty & Williams 1988; Jones 1991). In particular, juveniles are easy to study because they are relatively large, sedentary, abundant and easy to monitor over time. Moreover, many recruit to patch reefs, which offer natural replicates of habitat for ecological studies.

One consequence is that our understanding of the early life history of reef fishes is heavily biased towards this family, and it has been suggested that pomacentrids can be used a model for other taxa (Doherty 1983a, 1991). However, pomacentrids have a distinctive suite of life history characteristics, which influence their patterns of recruitment and early post-settlement ecology. Spawning occurs during a limited period each month, and is often associated with lunar phase (see Doherty 1983b; Robertson *et al.* 1988, 1990; Meekan *et al.*

1993). Larval duration of most species vary among narrow limits (Brothers *et al.* 1983; Robertson *et al.* 1988; Wellington & Victor 1989), and metamorphosis into a pelagic juvenile form occurs prior to settlement (Victor 1983a). Newly settled juveniles are large relative to their adult size (Brothers *et al.* 1983; Wellington & Victor 1989), and at an advanced stage of development (Victor 1991). The result is that most species recruit into adult habitats, where they remain throughout their lives (Doherty 1983a; Williams 1991). Pomacentrids also have a number of distinctive behavioural characteristics associated with their trophic category. Most species studied in detail, are either territorial herbivores or planktivores, many of which live in size-structured dominance hierarchies (Coates 1980; Ochi 1986; Jones 1987a; Booth 1992; Forrester 1991). There is clearly a need for more studies of other families with different life history characteristics, to determine the degree to which pomacentrids can be used as a general model for reef fishes.

Labroid fishes (*sensu* Greenwood *et al.* 1966: wrasses, Family Labridae; and parrotfishes, Family Scaridae) have a suite of life history characteristics that differ to those of pomacentrids, and which have consequences for their early life history. Labroids spawn on a daily basis, with little apparent lunar periodicity (see Robertson & Hoffman 1977; Warner & Robertson 1978; Thresher 1984; Colin & Bell 1991; but see Ross 1983). Planktonic duration may be quite variable, especially for species with long planktonic durations (Brothers *et al.* 1983; Victor 1986b,c; Cowen 1991). Labroid larvae metamorphose into juveniles after settling onto the reef (Victor 1983a), and it has been suggested that at least some species bury in the sand for up to 5 days after settlement (Victor 1983a, 1986a). Most labroid recruits are very small (Brothers *et al.* 1983), and at early developmental stages (Victor 1991). The result is that some species do not recruit into adult habitats, and show ontogenetic shifts in their ecology (Jones 1984a; Eckert 1985b; Victor 1986a; Bellwood 1988; Williams 1991). Furthermore, labrids are benthic carnivores, while scarids are herbivores (scarids). Because of these differences, studies of labroids provide an interesting contrast to those of pomacentrids.

However, many of these characteristics make it difficult to study the early life history of labroids in most situations. For example, newly settled individuals are often hard to locate and monitor over time, because of their small size, colouration and cryptic behaviour (Green *in press*). In addition, most species do not settle in high densities onto patch reefs, and may be difficult to locate among the structural complexity of these reefs (Green *in press*).

One notable exception among the labroids is the genus *Thalassoma*, which settles at a relatively large size and age (Brothers *et al.* 1983; Victor 1986c) and settles onto patch reefs in relatively high densities (Eckert 1985a,b; Victor 1986a). Consequently, the two intensive studies of the early life histories of labroids, focused primarily on this genus (Eckert 1984, 1985a,b; Victor 1983a,b, 1984, 1986a,b,c). Moreover the adult ecology of this genus in now well understood (Eckert 1985b; Warner 1991; Shapiro 1991). However, *Thalassoma* may not be representative of the majority of labroids, which settle at a much smaller size, younger age and earlier stage of development (Brothers *et al.* 1983; Victor 1986b; A. Green *unpubl. data*), and there is now a need for more studies of the early life history of these more "typical" labroids. The problem has been to identify a situation where these species are present in high densities, so they can be reliably located and monitored through time.

Recently it was reported that newly settled labroids were present in high densities within stands of macroalgae in territories of herbivorous damselfish (Bellwood 1986; Bellwood and Choat 1989; Green *in press*), where they were easy to locate and monitor through time (Green *in press*). In this study I used damselfish territories as replicate units of habitat to study the early life history of labroid fishes, in the same way that patch reefs have been used to study pomacentrids.

1.2 THESIS OUTLINE

In Chapter 2, the spatial and temporal patterns of the distribution and abundance of labrid fishes among habitat zones are described, and the processes that may have produced these patterns are discussed. In particular, habitat use by labrids at different life history stages are compared, to examine the degree to which patterns of distribution and abundance of adults appear to be determined by recruitment or post-settlement processes. This study provides the basis for choosing candidate species for a more detailed examination of the importance of these processes in determining spatial patterns of adult abundances.

Finer scale patterns of habitat use by labroid recruits are described in Chapter 3. In particular, the use of damselfish territories and adjacent microhabitats (reef matrix and rubble/sand patches) are described in two habitat zones: Reef Base and Sand Flat. This study confirms that the recruits of some labroids are present in much higher densities in the territories of two damselfish species, *Dischistodus prosopotaenia* and *D. perspicillatus*, than they are in the adjacent microhabitats. Damselfish territories are then used as replicate study units to examine temporal and spatial patterns of labroid recruitment at Lizard Island (Chapter 4), based on three abundant taxa: *Coris schroederi* and *Halichoeres melanurus*, and a group of closely related scarids, *Scarus* spp.

In Chapter 5, damselfish territories and adjacent microhabitats are used to examine the consequences of microhabitat selection by *C. schroederi* and *H. melanurus* recruits on their post-settlement ecology. This involved detailed descriptions of diet, growth and mortality of these species in each microhabitat, as well as descriptions of the resources (food and shelter) available in each situation. This information is then used to examine the degree to which patterns of labroid recruitment to territories are reinforced or modified by post-settlement processes, and translated into spatial patterns of adult abundances.

1.3 GENERAL MATERIALS AND METHODS

Location of study areas

This study took place at Lizard Island (14°38'S, 145°24'E) on the northern Great Barrier Reef (GBR: Figure 1.1). Lizard Island is a mid-shelf continental island, surrounded by fringing reef. It is situated 36 kms from the Queensland coast and 16 kms from the outer barrier reef. All of the work was done at four study sites on the northeast side of the island, described in detail in Section 2.2.

Timing of field work

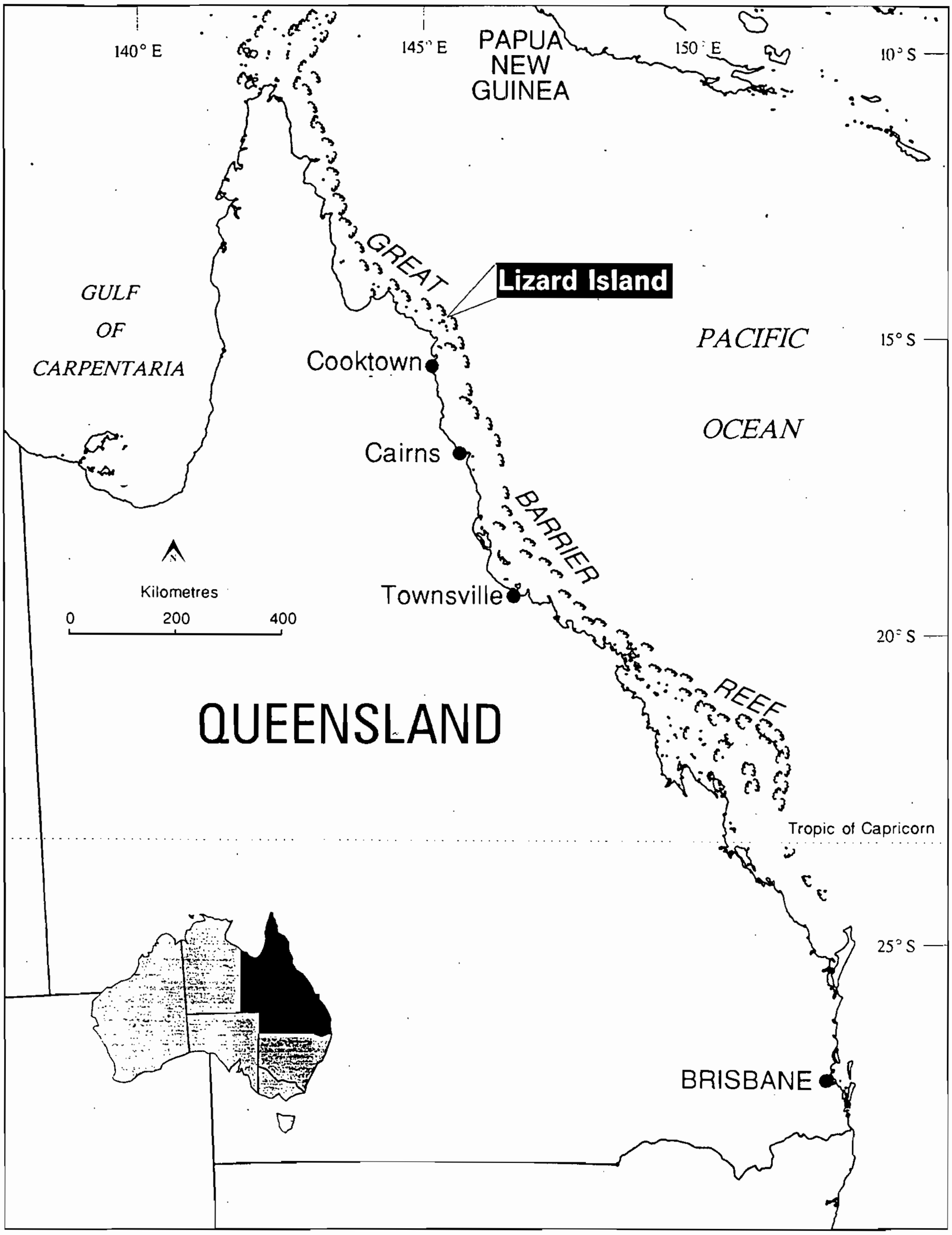
All studies took place between August 1990 and May 1993, with most work conducted during the austral summers (November to February). Three short trips were also done during the austral autumn and winter (May to August) in two years (1990 and 1991).

General statistical procedures

Differences were considered significant at $\alpha < 0.05$. Where multiple tests were performed on the same data set, error rates were adjusted using the Bonferroni method: $\alpha = 0.05/n$, where n=number of tests (Day & Quinn 1989). *A posteriori* multiple comparisons were done using Tukey's test (see Day & Quinn 1989). Data sets were pooled for further analysis only when $p > 0.2$ (see Winer 1971).

Prior to performing univariate or multivariate parametric tests, data was examined for conformation to the assumptions of the analysis, which included testing for homogeneity of variances (using Cochrane's test) or variance-covariance matrices (using a Multivariate Levene's Test), and univariate or multivariate normality (using a graphing procedure). When raw data did not conform with assumptions, data was transformed and retested. Transformed data sets were used if they successfully corrected for violations of the assumptions. Raw data sets were used when data transformations were unsuccessful, and when the design was balanced (see Day & Quinn 1989).

Figure 1.1
Location of Lizard Island on the northern Great Barrier Reef.



Chapter 2

PATTERNS OF HABITAT USE BY LABRID FISHES AT LIZARD ISLAND

2.1 INTRODUCTION

An important goal of reef fish ecology is to determine the processes that are important in structuring reef fish assemblages (see Doherty & Williams 1988; Jones 1991; Hixon 1991). The first step towards understanding these processes is to obtain precise estimates of the distribution and abundance of the assemblages under study (Mapstone & Fowler 1988).

Labrids show discontinuous distributions at a range of spatial scales on the GBR, from among reefs across the continental shelf (Williams 1982; Williams & Hatcher 1983) to among habitats within reefs (Talbot & Goldman 1972; Goldman & Talbot 1976; Eckert 1985b). Eckert (1985b) described the patterns of habitat use by this family at One Tree Reef on the southern GBR. She found that 19 species were restricted to the outside of the lagoon, 11 species were much more abundant inside the lagoon and 10 species showed similar abundances in both habitats.

Patterns of habitat association by labrids may be related to physical and biological characteristics of the habitats (Roberts & Ormond 1987). The first objective of this study was to describe temporal and spatial patterns of distribution and abundance of labrids among habitat zones on the fringing reef at Lizard Island. The second objective was to determine the degree to which these patterns were associated with biological and physical characteristics of the zones.

Processes which establish observed patterns of distribution have been reviewed by Williams (1991), who suggested that adult distributions reflected recruitment events. A case for recruitment driven distribution patterns has also been made for labrids at One Tree Reef by Eckert (1985b). However the extent to which recruitment patterns are modified by ontogenetic shifts in habitat is unclear. The third objective of this study was to examine ontogenetic patterns of habitat use by labrids, to examine the degree to which adult abundances reflected spatial patterns of recruitment.

In this study, visual census techniques were used to describe the distribution and abundance of labrid fishes, based on belt transects. Since previous studies have demonstrated that the precision of this technique is dependent on census methods and study species (Sale & Sharp 1983; Fowler 1987; Bellwood & Alcala 1988; Lincoln Smith 1988, 1989), a pilot study was done to determine the most precise methods for censusing this family (see Appendix I).

The study was divided into two sections. First, habitat zones were described in detail. Second, spatial and temporal patterns of distribution and abundance of labrids among these zones were described, and compared with variations in habitat characteristics. Ontogenetic patterns of habitat use were also examined in the second section.

2.2 MATERIALS & METHODS

Three sites (separated by 0.5 to 1.5km) were chosen on the northeast side of Lizard Island (North Reef, Washing Machine A and North Reef C: see Figure 2.1), because they were areas of well developed continuous reef tracts where exposure to the prevailing southeast winds and tidal currents was moderate. Reef profile, aspect, exposure and topography of these sites have been described by Choat & Bellwood (1985).

2.2.1 Description of habitat zones

The reef at these sites was divided into 6 recognised habitat zones, which differed in their position on the reef profile, depth and degree of wave exposure (Figure 2.1 & Table 2.1). The Inner Reef Flat was located immediately adjacent to the shore of the island, and was littered with large granite boulders. The Crest was defined as the seaward edge of the reef flat where the reef edge drops off into deeper water. The Outer Reef Flat was situated between the Inner Reef Flat and the Crest. The Reef Slope descended from the Crest, at a slope of 50 - 90° (Choat & Bellwood 1985). The Reef Base was situated at the bottom of the Reef Slope, where it joined the Sand Flat which stretched away from the reef towards open water.

Figure 2.1.

Location of study sites at Lizard Island, and the position of six habitat zones on the reef profile at these sites (see inset).

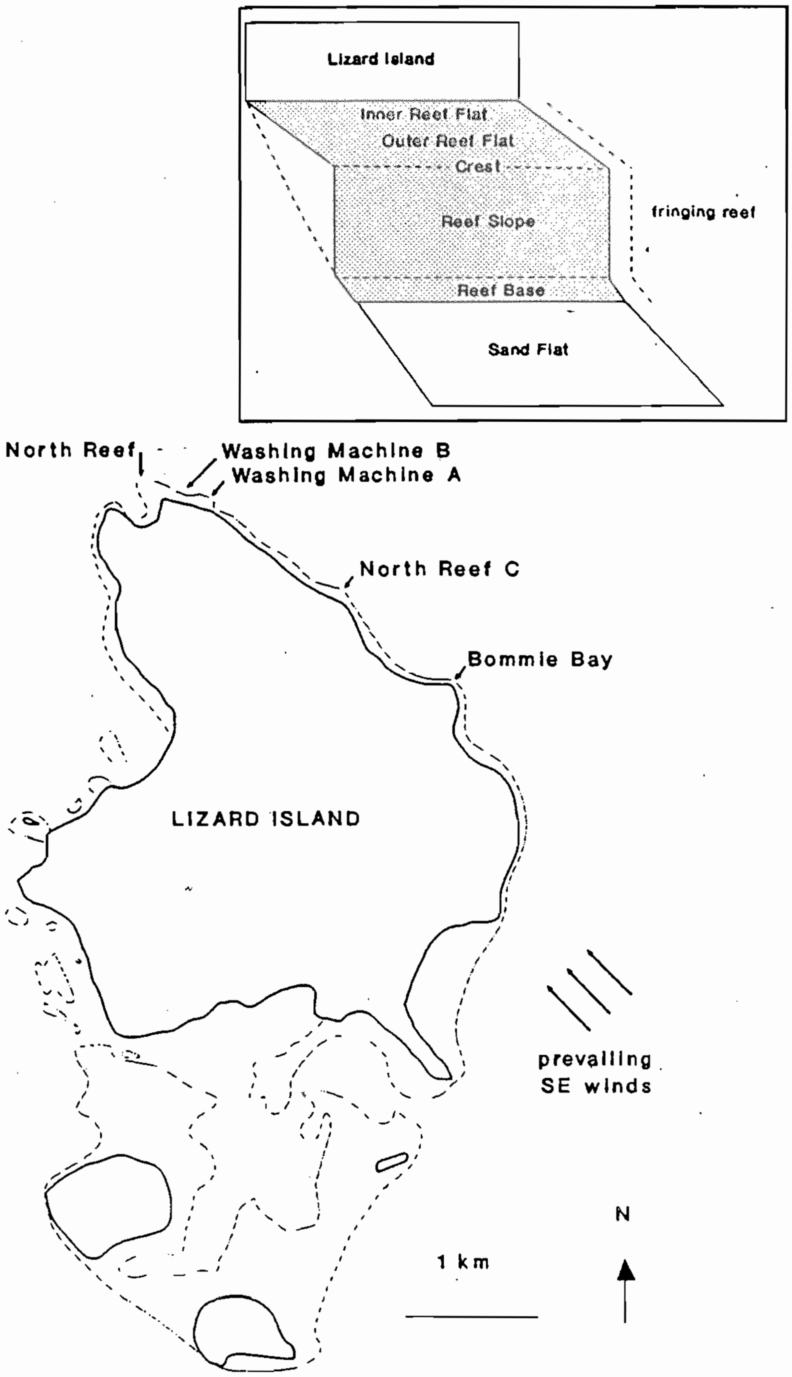


Table 2.1: Physical characteristics of 6 habitat zones at three study sites, in terms of depth and exposure to waves.

habitat zone	depth	wave exposure
Inner Reef Flat	0.0 - 1.5m	low to high
Outer Reef Flat	0.0 - 1.5m	low to high
Crest	0.0 - 3.0m	low to high
Reef Slope	2.0 - 20.0m	low to moderate
Reef Base	5.0 - 20.0m	nil to low
Sand Flat	6.0 - 20.0m	nil to low

Biological characteristics of these zones which may influence habitat use by labrid fishes, were described in January 1991/92, using a modification of a point-based method used by Wiens & Rotenberry (1981) to describe forest habitats for birds. This method was successfully adapted to describe reef fish habitats by Choat & Bellwood (1985), and provides an estimate of biological substratum characteristics (percentage cover of different substrates and substrate diversity) and surface heterogeneity (substrate complexity). Five 50m transects were laid consecutively, in each of the 6 habitat zones at each site. At 1m intervals along each transect, a 2m transect was run perpendicular to the tape. Three sampling points were used along each of the 2m transects (one directly under the 50m tape, and one approximately 1m either side). Fifty 1m intervals along the main transect were sampled in this manner, yielding 150 sample points per transect.

At each point, substrate was recorded as belonging to one of 15 categories: non-living (reef matrix, sand and rubble), crevice (>1m deep), massive coral, digitate coral, plate coral, branching coral, encrusting coral, soft coral, foliaceous coral, free-living coral, gorgonian, hydrozoan, sponge, macroalgae and others (zooanthids, ascidians and clams). The height of the substrate above the reef platform, and the number of contacts or "hits" above the substratum on a vertical line through the object (Wiens & Rotenberry 1981), were also recorded at each point. In combination, these measures enabled me to calculate the biological characteristics of each transect. Total cover of living substrate was calculated as the percentage of all points where living substrate was recorded. Percent cover of each substratum category was calculated as the percentage of the points on each transect that were occupied by each substrate category. Substrate diversity was measured as the diversity of cover of substrate categories, using the formula: $N_1=\exp(-\sum p_i \ln p_i)$ where p_i=proportional coverage of the *i*th substrate category (Weins & Rotenberry 1981). Substrate structural complexity was calculated as the average number of contacts.10 cm^{-1} above the basal substratum.

The influence of site (n=3) and habitat zone (n=6) on percent cover of living substrate, substrate diversity and substrate complexity were each tested using a two way fixed factor analysis of variance. Canonical discriminate analysis was used to test for significant difference between habitat zones at each site, on the basis of the percent cover of each substratum type.

2.2.2 Spatial and Temporal Patterns of Habitat Use by Labrids

Patterns of labrid distribution and abundance among 6 habitat zones at 3 sites were surveyed in January 1991/92, using methods selected in the pilot study (see Appendix I): five 50mx3m transects in each zone per site, done at a speed of 60 seconds.10m^{-2}. The transects were the same as those used to describe habitat features (see Section 2.2.1). Only adults were included in the analysis, which I defined as individuals which were >1/3 of the maximum total length of the species (as recorded in Randall *et al.* 1990: see Appendix II), and were assumed to be mature. Most species could be identified by sight in the field, although one group of closely related species (*Halichoeres margaritaceus*, *H. nebulosus* and *H. miniatus*), were difficult to separate and were lumped as *Halichoeres* spp.

Labrid density and diversity (see Section 2.2.1) were also calculated for each habitat zone at each site, and a two way fixed factor analysis of variance was used to test for the influence of site (n=3) and zone (n=6) on each of these factors. Data were transformed (log [x+1]) for labrid density to homogenise variances. The relationship between each of three substratum characteristics (percent live substrate, substrate diversity and substrate complexity) and labrid density and diversity was examined using Pearson's Correlation Coefficients.

Abundant species that each accounted for >5% of the total number of individuals in the survey (see Section 2.3.2) were chosen for further analysis, because they were present in sufficient numbers to provide powerful estimates of their patterns of distribution and abundant. A canonical discriminate analysis was used to test for a significant difference among habitats at each site, based on the distribution and abundance of these species.

Surveys of habitat use by adult labrids were repeated at two sites (North Reef & Washing Machine A; Figure 2.1) on five occasions over three years, encompassing both summer and winter seasons (August 1990, January 1991, July 1991, February 1992 and February 1993). A correspondence analysis was then used to determine if patterns of habitat use by abundant species were consistent through time. This analysis used Chi-square distances to separate habitat zones by species (see Greenacre 1984), and was used because of the temporal autocorrelation of counts of the same populations through time.

Habitat surveys were also done for recruits at all sites in 1991/93 using narrower transects (50mx1m), because recruits were smaller and more cryptic than adults. Recruits were identified by their appearance (size and colouration) and cryptic behaviour. Patterns of habitat use by adults and recruits were compared for each of the 8 abundant species.

2.3 RESULTS

2.3.1 Description of habitat zones

Percent cover of living substrate and substrate diversity were each found to be significantly different among habitat zones but not among sites (Table 2.2 & Figure 2.2). Both measures were low on the Inner Reef Flat, Reef Base and Sand Flat, and high on the Outer Reef Flat, Crest and Reef Slope. Multiple comparisons revealed each of these characteristics differed among all zones, except the Inner Reef Flat and the Reef Base. In contrast a significant interaction was found between substrate complexity among sites and habitats. This was because substrate complexity was high at the Reef Base at North Reef, and low in this habitat at the other two sites.

Figure 2.2.
Mean (+/− se) percent cover of living substrate, substrate diversity and substrate complexity of each habitat zone at each site (n=5)

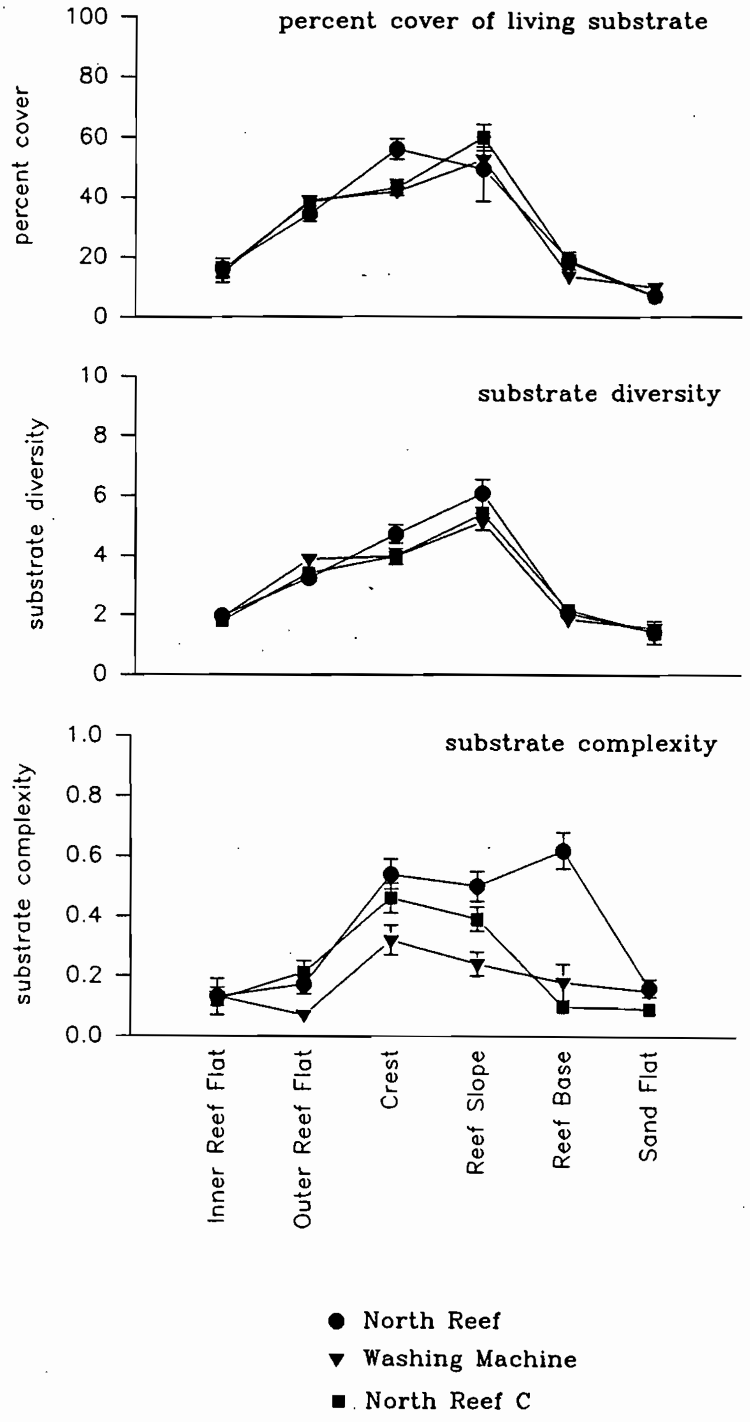


Table 2.2: Results of the two way analysis of variance testing on the influence of site and zone on three habitat characteristics: percent cover of living substrate, substratum diversity and substratum complexity.

		percent cover		
source	df	MS	F	p
site	2	0.0010	2.52	0.0856
habitat zone	5	0.0700	169.58	<0.0001
site*zone	10	0.0007	1.94	0.0525
error	72	0.0004		
total	89			

		diversity		
source	df	MS	F	p
site	2	0.0022	1.00	0.3746
habitat zone	5	0.4175	193.91	<0.0001
site*zone	10	0.0036	1.67	0.1048
error	72	0.0022		
total	89			

		complexity		
source	df	MS	F	p
site	2	0.0182	7.47	0.0013
habitat zone	5	0.0301	12.35	<0.0001
site*zone	10	0.0075	3.09	0.0026
error	72	0.0024		
total	89			

Canonical discriminant analysis found that habitat zones were significantly different (Pillai's Trace=3.3461, Num df=238, Den df=1008, $p<0.0001$), in terms of 13 substratum types which differed among sites (Figures 2.3 & 2.4). Three habitat zones, Crests, Outer Reef Flats and Reef Slopes, each differed significantly from all other zones on the basis of percentage cover of living substratum types (Figure 2.4 also). Crests were characterised by a moderate cover of digitate and branching coral, as well as plate coral at North Reef only. Outer Reef Flats were also characterised by a low cover of digitate, branching, plate and massive coral, except at North Reef C where soft coral was also important. Reef Slopes were characterised by massive coral, encrusting, soft and branching coral. The Inner Reef Flat, Reef Base and Sand Flat, all differed from the other habitat zones, because of their

Figure 2.3.
Results of canonical discriminant analysis of 6 habitat zones at each of 3 sites on the basis of their substratum type. Points are centroid means for each habitat per site, and bars represent 95% confidence limits (n=5). Biplot shows the magnitude and direction of the contribution of each substratum category towards the separation of groups.

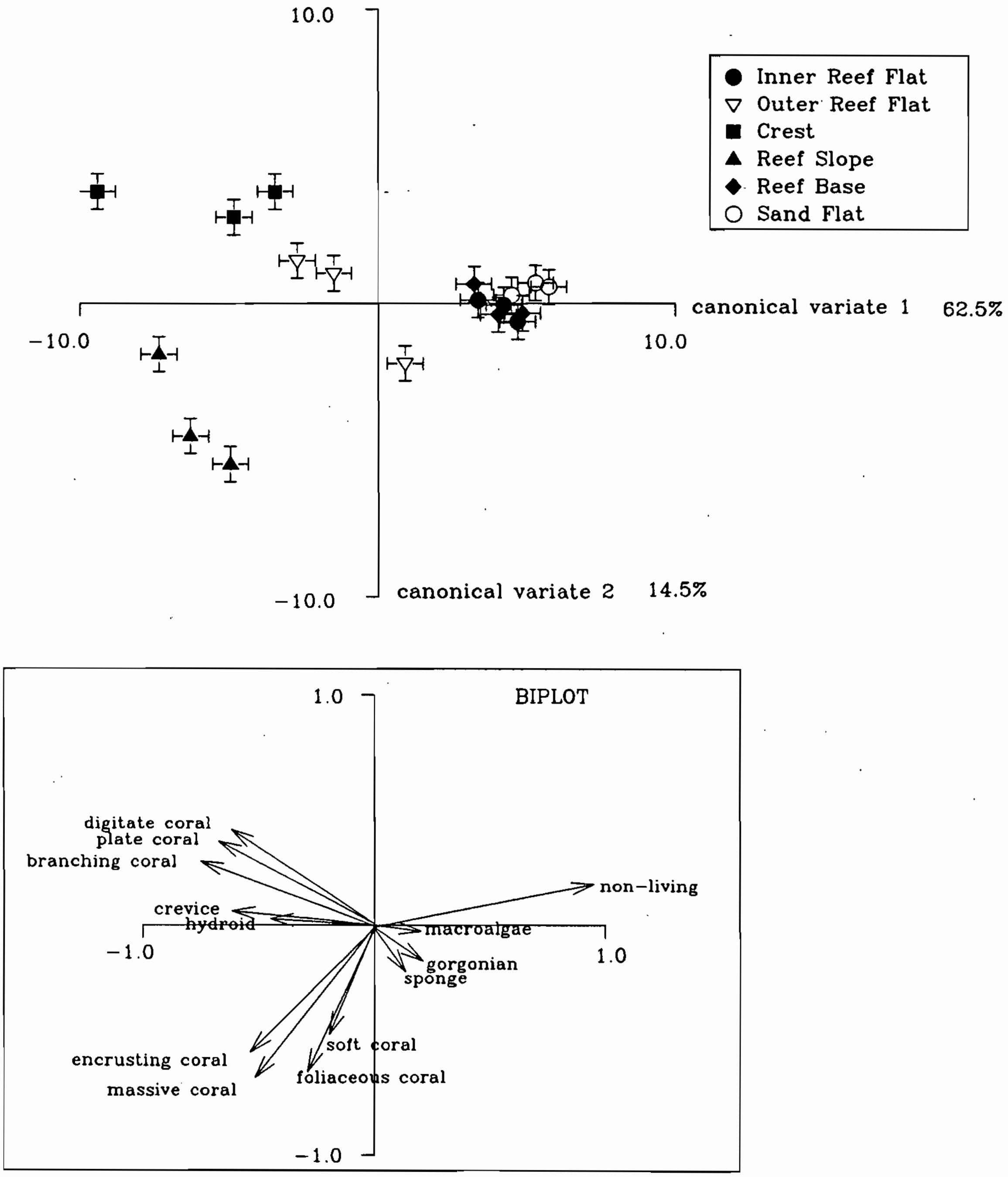
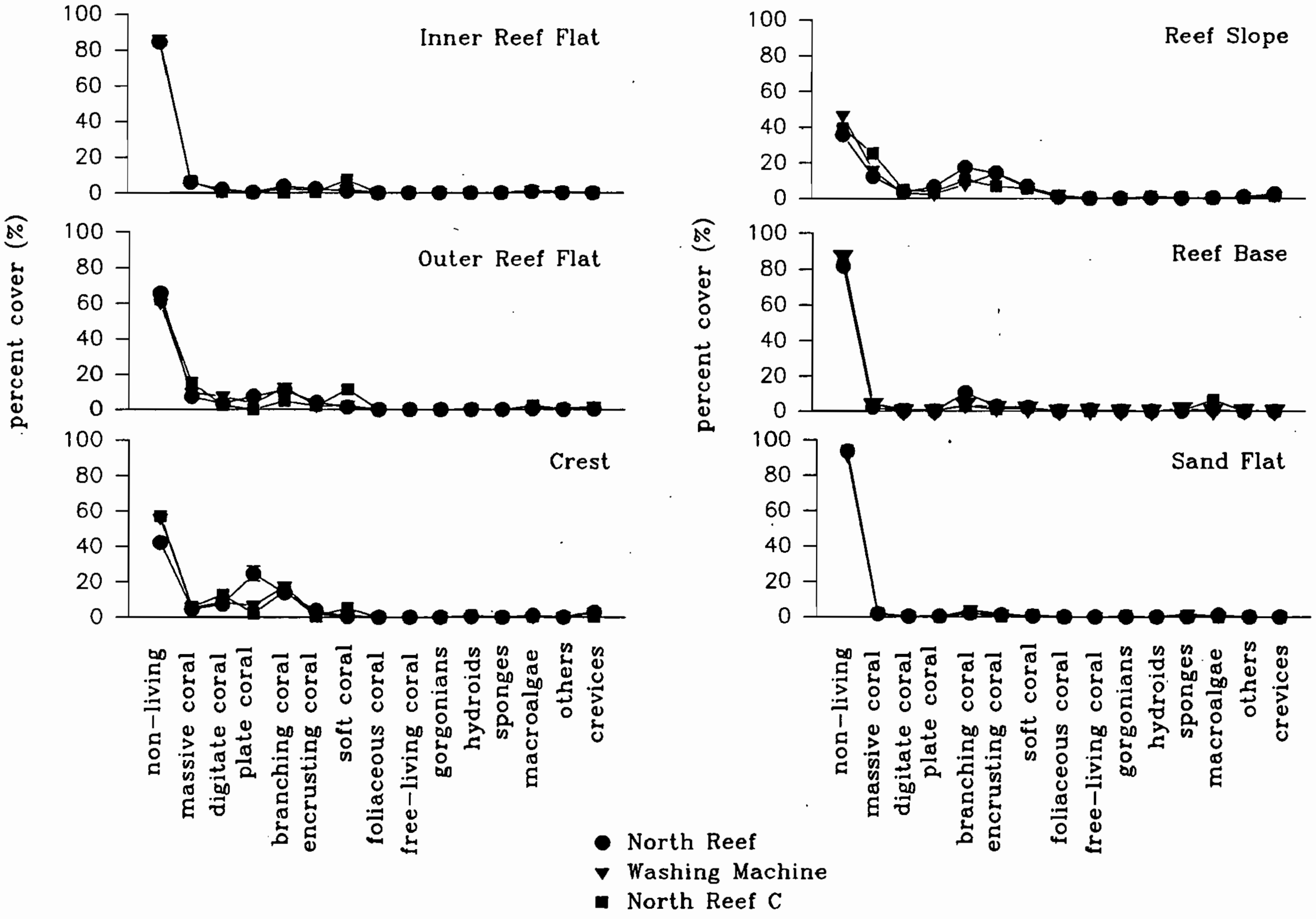


Figure 2.4.
Mean (+/- se) percent cover of each substratum type in each habitat zone at each of three study sites (n=5).



dominance by non-living substrate.

2.3.2 Spatial and Temporal Patterns of Habitat Use by Labrids

Both labrid density and diversity differed significantly among habitat zones (Table 2.3; Figure 2.5). Multiple comparisons revealed that labrid density was significantly lower on the Reef Slope than in either of the other five habitat zones, and significantly lower on the Sand Flat than it was on the Outer Reef Flat, Crest and Reef Base (but not the Inner Reef Flat or the Reef Slope). Multiple comparisons also revealed that labrid diversity was significantly different between the Inner and Outer Reef Flats.

Table 2.3: Results of the two way analysis of variance testing of the influence of site and zone on labrid density and diversity.

		density		
source	df	MS	F	p
site	2	0.01	0.25	0.7838
habitat zone	5	0.53	18.46	<0.0001
site*zone	10	0.05	1.82	0.0727
error	72	0.03		
total	89			

		diversity		
source	df	MS	F	p
site	2	2.04	1.04	0.3608
habitat zone	5	4.75	2.41	0.0438
site*zone	10	2.81	1.43	0.1842
error	72	1.97		
total	89			

Labrid density and diversity each showed no significant correlation with percent living substrate (Table 2.4), substrate complexity (Table 2.4) or with each other ($r^2=0.15$, $n=90$, $p<0.1718$). Similarly labrid diversity was not significantly correlated with substrate diversity (Table 2.4). In contrast labrid density showed a significant, but low, negative correlation with substrate diversity (Table 2.4).

Figure 2.5.
Mean (+/- se) density and diversity of labrids in each of 6 habitat zones at three sites at Lizard Island (n=5).

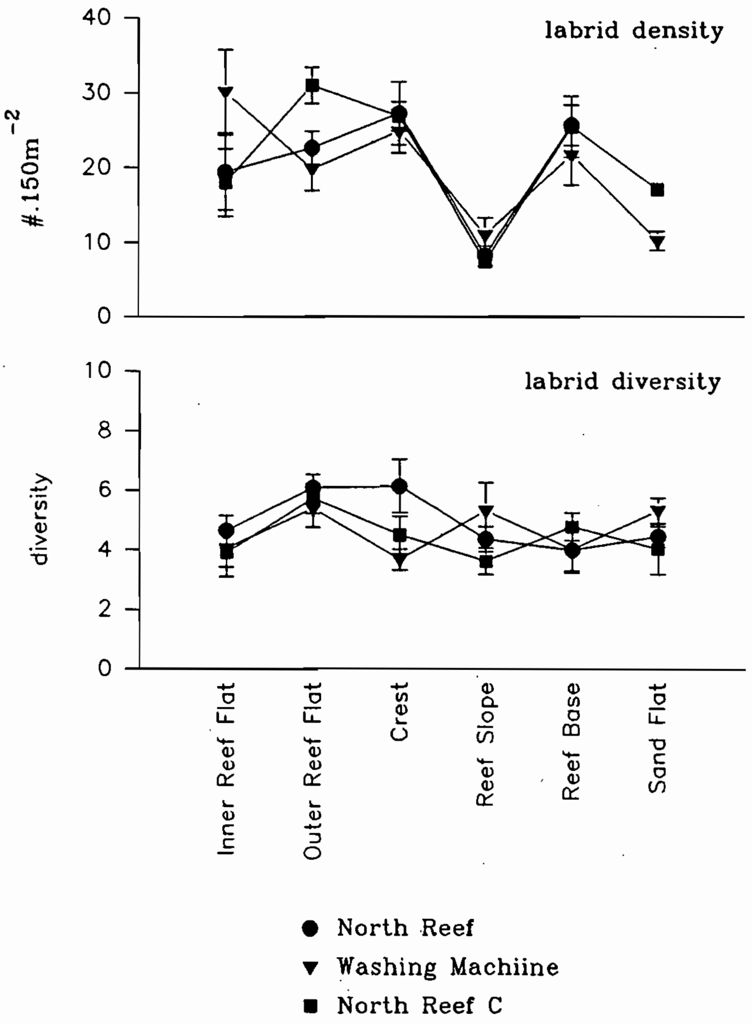


Table 2.4. Results of Pearson's correlation (r^2) between labrid density and diversity and each of 3 substrate characteristics: percent living substrate, substrate diversity and substrate complexity. Where: n=90.

	percent living substrate	substrate diversity	substrate complexity
labrid density	-0.14 ($p<0.1822$)	-0.22 ($p<0.0380$)	0.06 ($p<0.6053$)
labrid diversity	0.13 ($p<0.2100$)	0.10 ($p<0.3503$)	-0.02 ($p<0.8421$)

Sixty-four species were counted in five surveys over 3 years (see Appendix II). Thirty eight species (1804 individuals) were recorded in a single survey (summer 1991/92) of all habitat zones (Figure 2.6), of which 8 were abundant ($n>5\%$ of total), 6 were common ($1\%<n<5\%$ of total) and 24 were rare ($n<1\%$ of total number of individuals). Assemblages of abundant species differed significantly among habitat zones (canonical discriminant analysis: Pillai's Trace=5.07, Num df=136, Den df=576, $p<0.0001$; Figures 2.7 & 2.8). Inner and Outer Reef Flats differed significantly from other habitats but not from each other, because they were both dominated by high densities of *T. jansenii* and *S. bandanensis*, as well as *Halichoeres* spp. (especially the Inner Reef Flat at North Reef C: Figures 2.7, 2.8). However the results for Inner Reef Flats should be interpreted with caution, because they may be of low precision (see Appendix I). Crests differed significantly from other habitats, because of a high density of *T. hardwicke*. In contrast, Reef Slopes differed significantly from other habitats, because of the low densities of all of these species. The Reef Base and Sand Flat differed significantly from other habitats, because of the high densities of *H. melanurus* and *C. schroederi*. These two habitats were also significantly different from each other at two sites, because of the higher and lower densities of *H. melanurus* and *C. schroederi* respectively on the Reef Base than the Sand Flat.

Six abundant species showed similar patterns of habitat use as both adults and recruits (Figure 2.8): *C. schroederi*, *H. melanurus*, *Halichoeres* spp., *S. bandanensis*, *T. hardwicke* and *T. jansenii*. In contrast two species showed

Figure 2.6.
Relative abundance of 38 labrid species on the oblique fringing reef on the northeastern side of Lizard Island (n=1804).

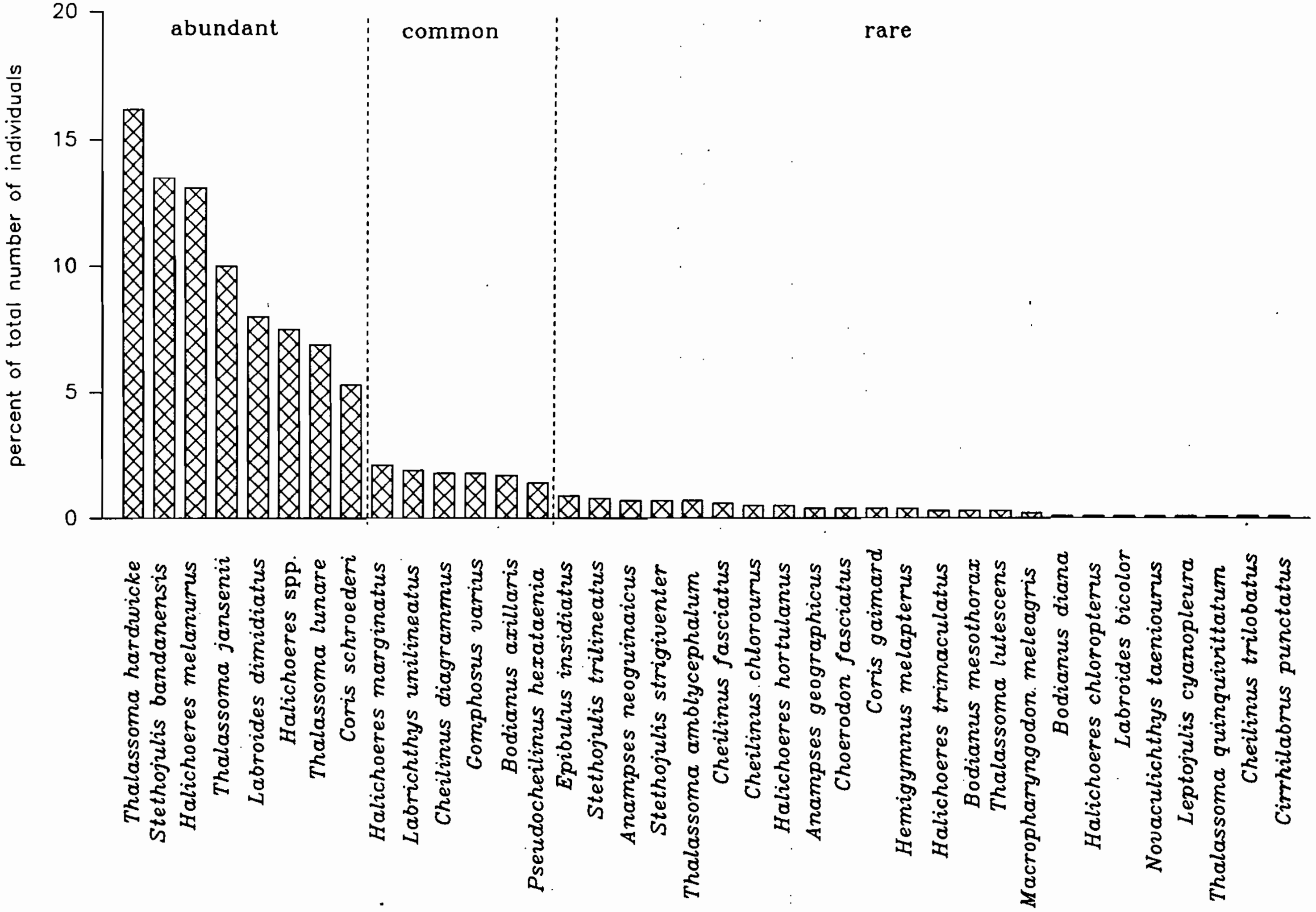


Figure 2.7.
Results of canonical discriminant analysis of 6 habitat zones at each of 3 sites on the basis of their assemblages of abundant labrids. Points are centroid means for each habitat per site, and bars represent 95% confidence limits (n=5). Biplot shows the magnitude and direction of the contribution of each labrid species towards separation of groups.

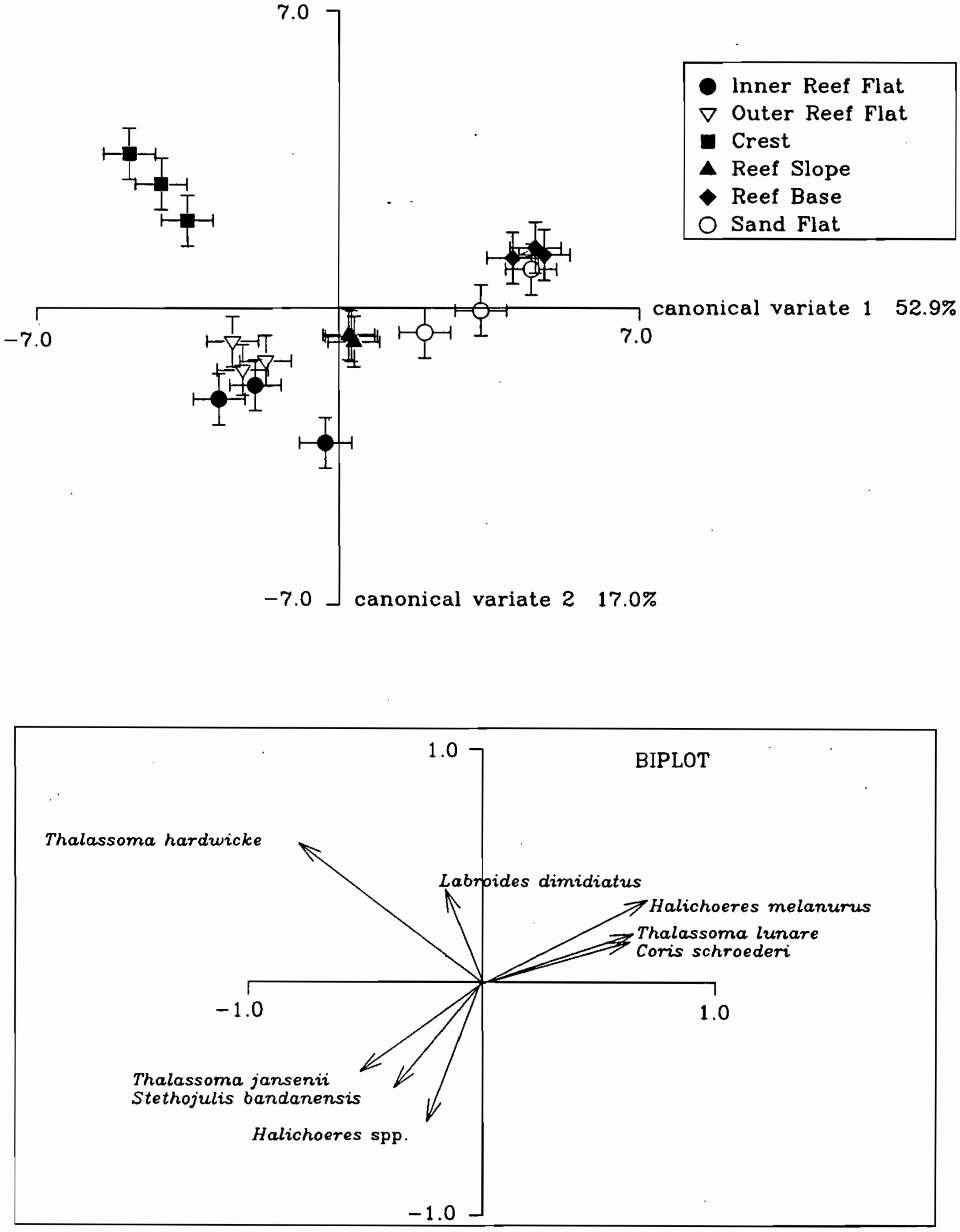


Figure 2.8.
Mean (+/− se) density of adults and recruits of each of 8 labrid species in 6 habitat zones at each of three sites (n=5).

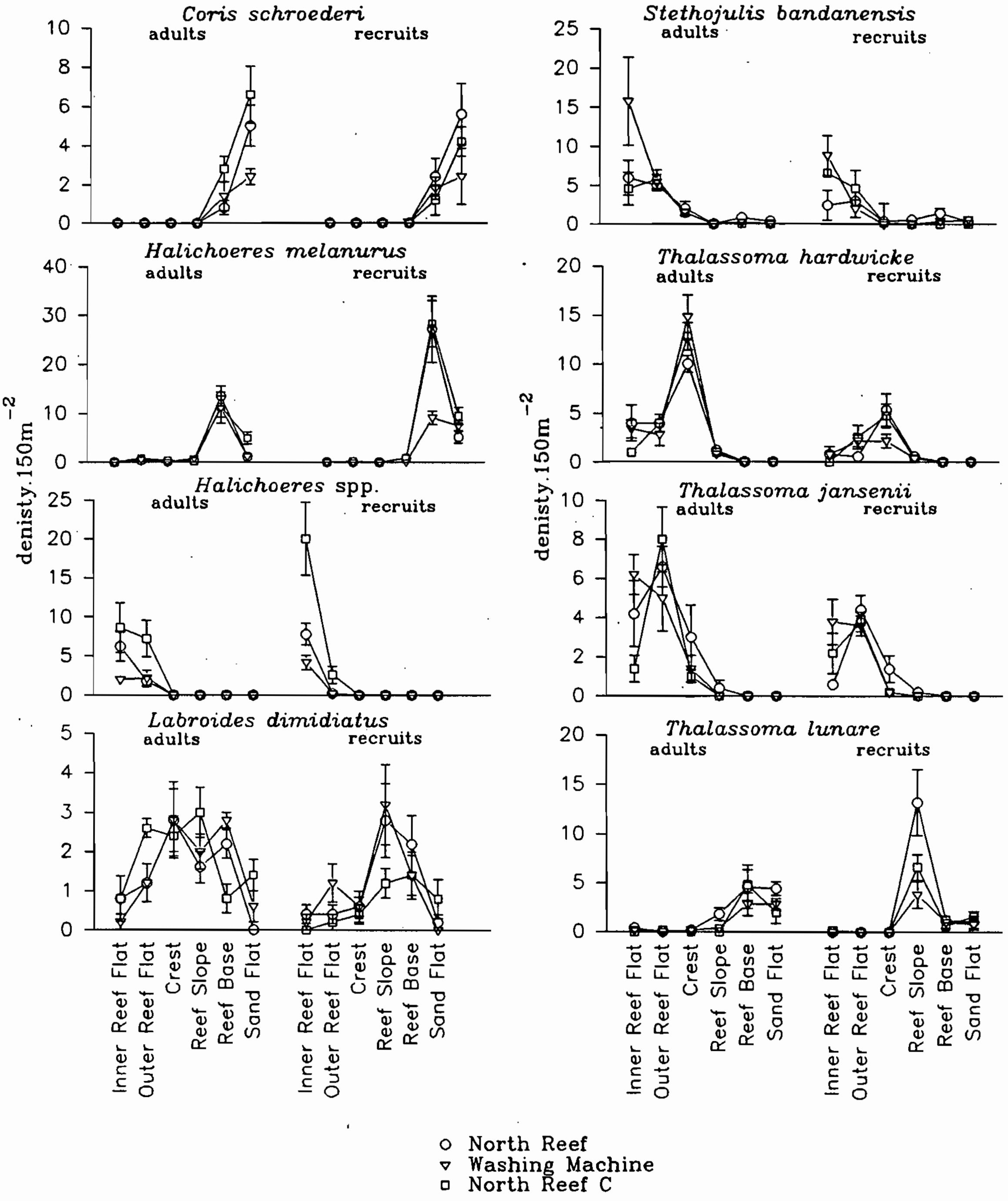
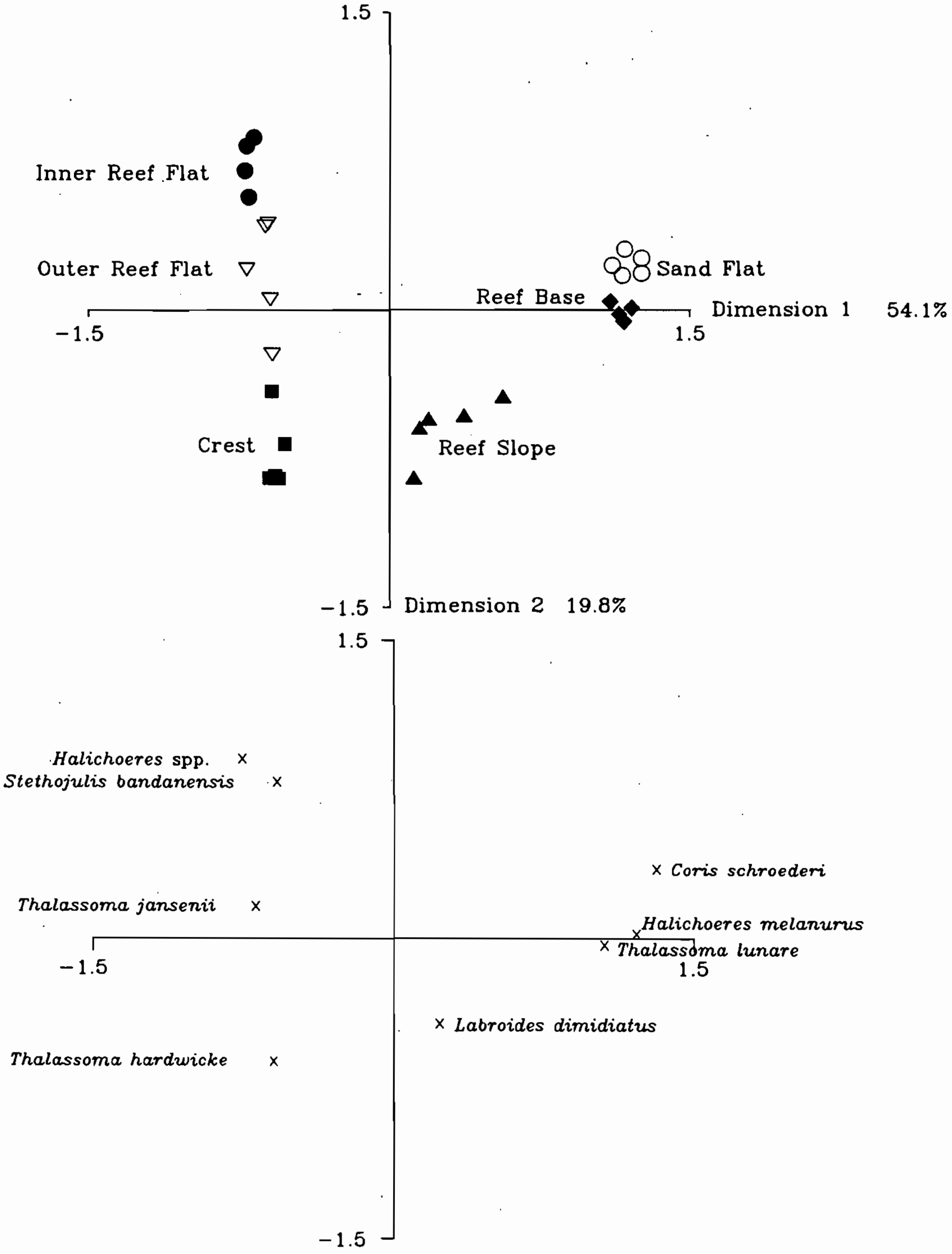


Figure 2.9.
Results of correspondence analysis comparing six habitat zones on five occasions over three consecutive years, in terms of the relative abundance of eight labrid species.



ontogenetic shifts in habitat use. *L. dimidiatus* was most abundant on the two deeper habitats (Reef Slope and Reef Base) as recruits, and used shallower habitats more as adults. *T. lunare* was also most abundant as recruits on the Reef Slope, but used deeper habitats more as adults.

The correspondence analysis established that the labrid assemblages that characterised each habitat zone, where consistent across seasons and years, with counts from the same habitat grouping together through time (Figure 2.9).

2.4 DISCUSSION

Many labrid species (64) were represented on the fringing reef at Lizard Island over 3 years. The relative abundance of species was described by a J shaped curve, which is characteristic of high diversity reef fish assemblages (Sale & Dybdahl 1975; Williams & Hatcher 1983; Clarke 1988). Few species were abundant or common (21.1% and 15.8% respectively), while the majority were rare (63.2%).

Most abundant labrids showed distinctive patterns of distribution and abundance among habitat zones, except for *Labroides dimidiatus* which was relatively ubiquitous. Depth appeared to be of over-riding importance in determining habitat use, with most species occurring either in shallow (Inner Reef Flat, Outer Reef Flat or Crest) or deep (Reef Base and Sand Flat) habitat zones. No abundant species were present in high densities on the Reef Slopes, which may have been because the slopes were very steep in most places (Choat & Bellwood 1985; Section 2.2.1). Within depth ranges, the labrid assemblages associated with habitat zones differed in terms of the relative abundance of species. In contrast, no clear relationship was detected between labrid density or diversity, and other habitat features such as percentage living substrate, substrate diversity and substrate complexity. These results were consistent with those reported for labrids in the Red Sea by Roberts & Ormond (1987). SImilarly, most other previous studies have also failed to find a strong correlation between reef fish habitat association and specific substrate characteristics, except for some obligate corallivorous chaetodontids or small site-attached species (see review in Williams 1991). Consequently, Roberts & Ormond

(1987) have suggested that families such as labrids may be unlikely to show strong association with habitat characteristics because they have large home ranges, which may encompass a range of habitat features. However this remains to be tested experimentally, and it is now clear that large scale habitat manipulations are required to discriminate between the relative importance of habitat features in determining patterns of habitat use by different groups of reef fish.

Patterns of habitat use by labrids appear to be consistent through time at two locations on the GBR (Eckert 1985b; this study). Temporal consistency in habitat association has also been recorded for other tropical and temperate reef fish families (Choat 1982; Fowler 1990). Patterns of habitat use by labrid fishes also appear consistent among sites separated by a few kms (Roberts & Ormond 1987; this study). At a larger scale, Williams (1986) found patterns of distribution of labrids across the continental shelf on the GBR, to be consistent over 8 years (Williams 1986).. As such it appears that instantaneous estimates of distribution and abundance may be adequate for describing patterns of habitat use by these fishes.

The degree to which habitat association by adult labrids reflected recruitment patterns varied among species in this study. Two species, *L. dimidiatus* and *T. lunare*, showed different patterns of habitat use by adults and recruits, with recruits showing greater restriction in distribution than adults. Similar patterns have also been described for labrids in other locations (Eckert 1985b; Victor 1986a; Williams 1991), which suggests that patterns of distribution and abundance of many species cannot be attributed to spatial patterns of recruitment alone. Conversely, most labrid species did use the same habitat zones as adults and recruits, a pattern which has previously been reported for many other labrids (Eckert 1985b). In the past, it has been suggested that these results infer that recruitment patterns may be important in structuring patterns of habitat use by many reef fish (see Williams 1980; Williams & Sale 1981; Eckert 1985b; Williams 1991). However, similar patterns of habitat use by recruits and adults could also occur as a result of differential growth and survival in different habitats, in combination with a subsequent redistribution of individuals among habitats. To date it has not been possible to discriminate between the relative importance of recruitment and post-settlement processes in influencing habitat use by labrids, since little is known of their post-settlement ecology in different habitats. These issues are addressed in subsequent chapters, by using damselfish territories and adjacent microhabitats as replicated habitat units to study the influence of habitat on post-settlement processes such as diet, growth and mortality. The degree to which recruitment patterns are reinforced or modified by these processes will also be examined. This will be done based on two species which were abundant on the Reef Base and Sand Flat at Lizard Island: *C. schroederi* and *H. melanurus*.

Chapter 3

USE OF DAMSELFISH TERRITORIES BY LABROID FISHES

3.1 INTRODUCTION

Labrids show clear patterns of distribution and abundance among habitat zones at each stage of their life history (Eckert 1985b; see Sections 2.1, 2.4). Many species are also associated with specific microhabitat features within habitats, especially as recruits (Doherty & Sale 1985; Eckert 1985a,b; Victor 1986a).

On temperate reefs, labrid recruits are often associated with stands of macroalgae (Jones 1984a,b; Levin 1991). On offshore coral reefs on the GBR, such stands of macroalgae are generally restricted to aggressively defended territories of herbivorous damselfish (Hatcher & Larkum 1983). Recently, it has been reported that labroid recruits on coral reefs are also associated with macroalgae, and are concentrated within the algal gardens of damselfish territories (Bellwood 1986; Bellwood & Choat 1989).

The primary objectives of this study were to:

i. quantify patterns of use of damselfish territories and adjacent microhabitats by labroid recruits; and

ii. determine whether damselfish territories provide appropriate units for studies of the early life histories of labroid fishes.

Two abundant species of damselfish *Dischistodus perspicillatus* (Cuvier, 1830) and *D. prosopotaenia* (Bleeker, 1852) which establish large well defined algal gardens (*pers. obs.*; Potts 1977) were selected for this study, which was done in two parts. First, the behaviour of each damselfish species and the characteristics of their territories were described. Second, the use of the macroalgal assemblages within damselfish territories by microinvertebrates and labroid fishes (recruits and adults) were described.

3.2 MATERIALS AND METHODS

Study sites were selected on the northeastern side of Lizard Island (see Figure 2.1), where large numbers of territories of each species were present: Washing Machine A, Washing Machine B and North Reef C for *D. prosopotaenia*; and Washing Machine B, Bommie Bay and North Reef C for *D. perspicillatus* (see description of sites in Choat & Bellwood 1985; Section 2.2). This study was conducted between 2 December 1992 and 2 February 1993.

3.2.1 Description of damselfish and their territories

Distribution and abundance of damselfish territories

Patterns of distribution and abundance of each damselfish species were quantified among 6 habitat zones at each of three sites (Washing Machine, North Reef C and Bommie Bay). Habitat zones were the same as those described in Chapter 2: Inner Reef Flat, Outer Reef Flat, Crest, Reef Slope, Reef Base and Sand Flat. Both species were counted simultaneously along ten replicate transects within each habitat zone at each site. Relatively wide belt transects (50mx5m) were used, because these damselfish are large (up to 20cm TL), and readily counted at prevailing visibilities ($>$10m). Transects ran parallel to the reef profile.

The relationship between habitat zone and density for each damselfish species was tested using an analysis of variance, with sites (n=3) orthogonal within habitats (n=6). Data was transformed by $\sqrt{(x+1)}$ because of unequal variances. Estimates of overall variation (Error Mean Squares) were also extracted from these analyses (using untransformed data), to indicate the degree to which each species was aggregated.

Damselfish tended to occur together in groups ($\geq$10 individuals.100m^{-2}). The percentage cover by territories within areas with damselfish aggregations was measured by drawing a detailed map of one colony of each species at each of the three sites. Each map was drawn to scale on underwater paper (using a grid of 50mx50m tapes) and showed the cover of each of the major microhabitat types within the areas (damselfish territories, reef matrix and rubble/sand patches). The area of each type of microhabitat within each area was subsequently measured directly from the maps using a Houston Instrument Hipad Plus digitiser with Jandel Scientific Sigmascan 3.92 software. Distance between the edges of territories was also quantified by measuring the distance from the edge of each territory to its nearest neighbour using the same technique.

Territorial behaviour of damselfish

Behaviour of each species of damselfish was quantified during two time periods each day: morning (0800 - 1200hrs) and afternoon (1300 - 1700hrs). Within each time period, ten haphazardly selected individuals of each species were observed for thirty minutes at each of three sites. At the beginning of each observation period, time of day and the identity of the fish were noted (to avoid using the same individual more than once in the study). Observations were made by a stationary SCUBA diver positioned 4 - 5m from the territory.

Two types of information were recorded for each species: i. frequency of attacks by damselfish; and ii. numbers of intruding and resident fish (by family) attacked by the territory holder. Territory edge was defined by the limits of growth of macroalgae, which was defended by the territory holder (see Brawley & Adey 1977). Residents and intruders and residents were defined as individuals that did and did not reside in the damselfish territories respectively. An attack was defined as an act of overt aggression by the damselfish towards the intruder. The relationship between time of day or site on the frequency on attacks on intruders, was tested using a two way fixed factor analysis of variance for each species. Prior to performing the ANOVA, data were transformed by $\sqrt{(x+1)}$ for one species only (*D. perspicillatus*) to homogenise variances.

Description of territories

Area, microhabitat characteristics and substratum type of each damselfish territory was described. Area of each territory was estimated at each site by measuring the dimensions of the territory, and then drawing it to scale onto underwater paper. The area of the territory was later measured directly from the maps using a digister (see above). Territory area of each species was compared using a nested analysis of variance, with sites (n=3) nested within damselfish (n=2).

Five permanent quadrats were established on both reef matrix and rubble/sand patches at each of two depths, (6-9m deep and interspersed with *D. prosopotaenia* territories; and 9-12m deep and interspersed *D. perspicillatus* territories), by marking the edges with metal stakes and cord. Different sized quadrats were used in each depth zone according to the mean size of damselfish territories (2.25m^2 and 6.25m^2 for *D. prosopotaenia* and *D. perspicillatus* respectively). A scaled map was then drawn of each territory and quadrat onto underwater paper, which showed the cover of each substrate type within the sampling unit. Percentage cover of each substratum type was later measured using the digitiser (see above). Microhabitats within territories and on reef matrix and rubble/sand patches were compared in terms of the percentage cover of each of 13 substratum categories (reef matrix, sand, rubble, branching coral, massive coral, encrusting coral foliaceous coral, solitary coral, soft coral, zooanthids, gorgonians, sponges and macroalgae).

Macroalgal assemblages within each territory type were also compared by measuring canopy height and by collecting all of the algae from within 3 haphazardly selected 10cm^2 quadrats in 3 territories of each species at each of three sites. Algae were sorted to genus or species (where possible) and the samples dried at 80° to a constant weight (usually three days), after which each sample was weighed. The dried weight of each type of macroalgae was then compared between the two types of territories.

The type of substrate (reef matrix, rubble or sand) on which the algae was established was estimated by drawing scaled maps onto underwater paper, and determining the percent cover of each substratum using the digitiser (see above).

3.2.2 Use of damselfish territories and adjacent microhabitats by invertebrates and labroid fishes

Abundances of microinvertebrates

The microinvertebrates within territories were sampled using three replicate quadrats ($10cm^2$) within each of three territories of each species at each of three sites. Quadrats were placed haphazardly within the territory, and then the algae and microinvertebrates were removed by enclosing the entire contents of the quadrat within a plastic bag. The sides of the quadrat were 10cm high, which minimised escape of invertebrates from the sample. Invertebrate samples were also collected on reef matrix and rubble/sand patches at each site, using the same procedure.

Invertebrates were stained with 1-2% erthyrosin B in 100ml seawater, and fixed in 10% buffered seawater formalin. They were subsequently counted and identified to order by a systematic search of each sample using a Bogorov tray and a stereo-microscope.

Abundances of labroid recruits

Abundances of labroid recruits in damselfish territories and adjacent microhabitats (reef matrix and rubble/sand patches) were counted. At each of three sites per damselfish species, five territories were haphazardly selected for monitoring. In addition, five permanent quadrats of each of reef matrix and rubble/sand patches, were also monitored at each of two depths (see above).

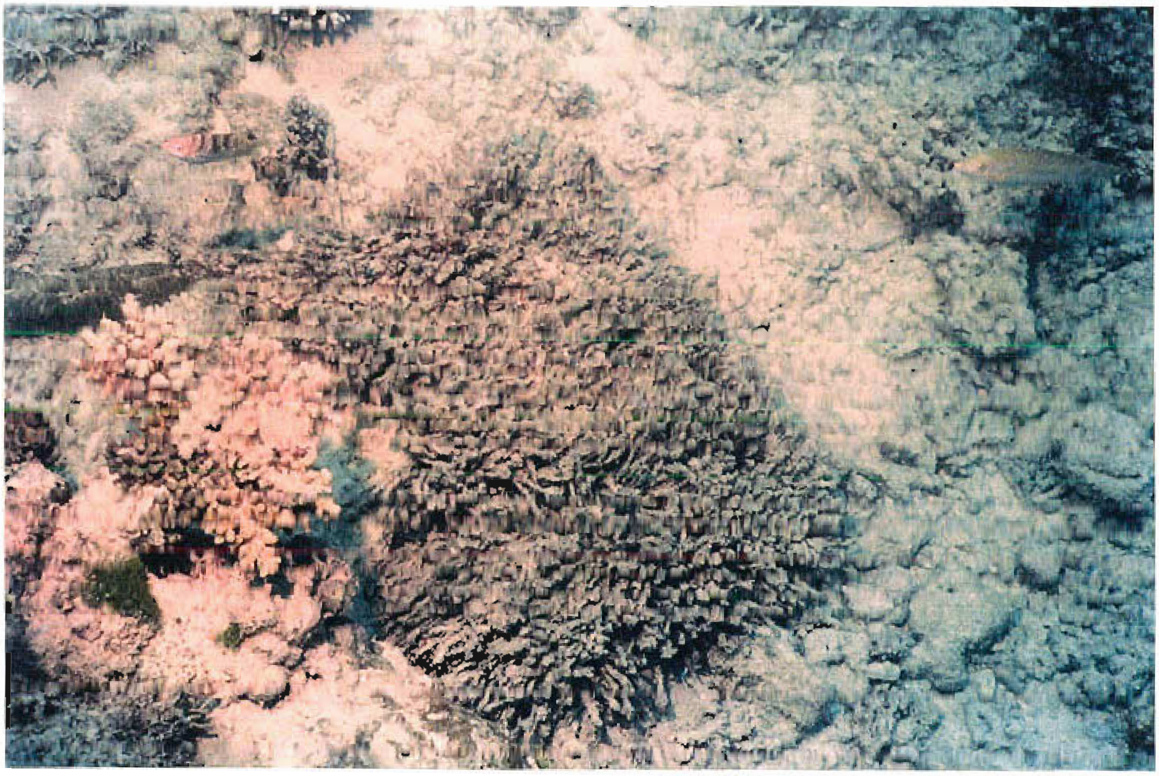
Labroid recruitment to each of these 6 microhabitats was monitored at weekly intervals for 11 weeks throughout the 1992/93 summer, by a slow speed intensive search of each territory or quadrat. The duration of each count was dependent on area, but averaged 5-10mins. Recruits were easily identified by a combination of size (<15mm TL), colouration (transparent to very light colour) and behaviour (recruits behaved more cryptically than older juveniles). Many scarid species including *S. sordidus, S. schlegeli, S. spinus, S. psittacus* and *S. rubroviolaceus* are difficult to distinguish in the field when newly settled (see Bellwood & Choat 1989); these taxa were pooled as *Scarus* spp. Other labrid and scarid recruits could be identified to species, with the exception of one species of *Anampses*. Counts from each microhabitat were converted to density.10m^{-2}, to standardise data for differences in size of the sampling units.

The relationship between microhabitat and recruit density was tested throughout the summer for each of three abundant taxa (*Coris schroederi*, *Halichoeres melanurus* and *Scarus* spp.) using a repeated-measures analyses (see Winer 1971) with sites (n=3) nested within microhabitats (n=6) for each species. Repeated measures were calculated using multivariate analysis of variance procedures (and Pillai's Trace test statistic), to accommodate for autocorrelation of counts among times (see Tabachnick & Fidell 1989). *H. melanurus* data was transformed (log [x+1]) to conform with the assumption of homogeneity of variance-covariance matrices.

A nested analysis of variance with sites (n=3) nested within microhabitats (n=6) was also used to test for the influence of microhabitat on the density of *H. melanurus* at week 8 only, when this species was recorded in the highest densities. Data were transformed (log [x+1]) because of heterogeneity of variances.

A manipulative experiment was also done to determine if labroid species discriminated between the two types of territories on the basis of habitat selection (Reef Base vs Sand Flat) or on the basis of microhabitat (type of macroalgae within the territories). This was done by making artificial territories out of green polyethylene rope (1cm diameter) tied onto rectangular (0.5mx0.4m) pieces of plastic mesh. Each piece of rope was cut to 8cm high and frayed to simulate stands of green macroalgae (see Figure 3.1). Five of these artificial territories were attached to the substrate at the Reef Base (interspersed with *D. prosopotaenia* territories) and on the Sand Flat (interspersed with *D. perspicillatus* territories) at each of the two sites (Washing Machine B and North Reef C). Artificial territories covered an mean area of 0.2m^2 *in situ* (se=0.01, n=20), and were attached using tent pegs in each corner. Labroid recruitment was monitored to these substrates on 10 occasions at approximately weekly intervals throughout the summer.

Figure 3.1.
Artificial territory (0.2 m^2) *in situ* (Photo: M. Burnham).



The influence of habitat (Reef Base and Sand Flat) on the density of each of the three abundant labroids within the artificial territories was tested using an analysis of variance for each labroid species, with sites (n=3) orthogonal within habitat (n=2). Data was transformed by ($\sqrt{[x+1]}$) for *C. schroederi* and *H. melanurus* to satisfy the assumption of equal variances.

Recruitment of labroids to areas with and without damselfish aggregations

At each of three sites, recruitment of *C. schroederi*, *H. melanurus* and *Scarus* spp. was monitored to large adjacent areas (>250m^2) with and without *D. prosopotaenia* aggregations, and to large adjacent areas (>500m^2) with and without *D. perspicillatus* aggregations. Adjacent areas were similar to areas with aggregations in terms of habitat, depth and size, and apparently differed only by the absence of damselfish territories.

Percentage cover of each microhabitat type (damselfish territories, reef matrix and rubble/sand patches) in each area was estimated using scaled maps and a digitiser (see above). Recruitment to each microhabitat in each area was quantified by censusing 5 replicate quadrats or territories of each microhabitat (see above) in areas with and without territories at each site. These counts were done in mid-January 1993, because *H. melanurus* was only observed in high densities at this time. Recruitment to each microhabitat in each area was measured by multiplying the density of recruits.m^{-2} of each microhabitat by the cover (m^2) of each microhabitat within the area. Recruitment to each area was then approximated by summing the estimated total recruitment to each component microhabitat. These measures were then converted to density of recruits of each species.100m^{-2} in areas with and without territories. Overall density of recruits of each species across all microhabitats, was then compared between areas with and without territories, using a two way fixed factor analysis of variance, where the fixed factors were presence of aggregations (n=2) and damselfish species (n=2).

Use of damselfish territories by adult labrids

The degree to which adult ($\geq$8cm TL) *Coris schroederi* used damselfish territories was also quantified, by following individuals for 20 minutes, noting the time spent inside and outside of territories. Bite rates were also recorded inside and outside territories. These observations were repeated for ten fish at two times of the day (morning and afternoon) in areas with aggregations of *D. prosopotaenia* or *D. perspicillatus* at Washing Machine B and North Reef C.

3.3 RESULTS

3.3.1 Description of damselfish and their territories

Distribution and abundance of damselfish territories

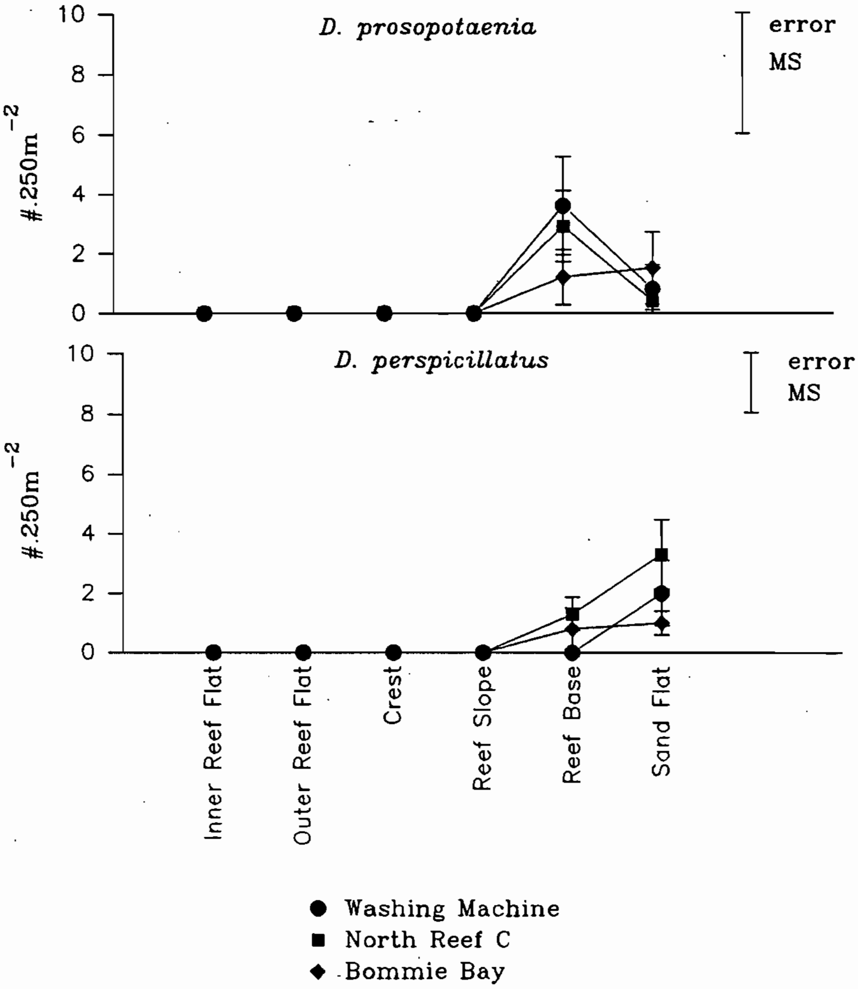
The density of each species of damselfish differed significantly among habitat zones (Table 3.1), with each species clearly associated with deeper habitats (Figure 3.2). The two damselfish showed different patterns of habitat use, with *D. prosopotaenia* significantly more abundant at the Reef Base than it was in the other 5 habitats, while *D. perspicillatus* was significantly more abundant on the Sand Flat than it was in the other 5 habitats (Tukeys multiple comparison test). The relatively high error mean squares in these analyses (Figure 3.2) for both damselfish species (especially for *D. prosopotaenia*) was a result of their aggregated distributions.

Table 3.1: Two way fixed factor analysis of variance testing for the effects of habitat on the density of *Dischistodus prosopotaenia* and *D. perspicillatus*.

	D. prosopotaenia			
source	df	MS	F	p
habitat	5	2.14	11.09	0.0008
site	2	0.07	0.33	0.7240
habitat*site	10	0.19	0.90	0.5354
error	162	0.21		
total	179			

	D. perspicillatus			
source	df	MS	F	p
habitat	5	1.70	10.00	0.0012
site	2	0.30	2.14	0.1186
habitat*site	10	0.17	1.21	0.2877
error	162	0.14		
total	179			

Figure 3.2.
Mean density (+/− se) of territories of *Dischistodus prosopotaenia* and *D. perspicillatus* in six habitat zones at each of three sites.



D. perspicillatus aggregations were larger than those of *D. prosopotaenia*, although the mean number of individuals per colony was similar (Table 3.2). Mean distance between the territories was slightly higher for *D. perspicillatus* than it was for *D. prosopotaenia*. Within *D. prosopotaenia* and *D. perspicillatus* aggregations (Table 3.3), territories occupied 19.6% to 32.1% of the area respectively, while the remaining area was occupied by reef matrix (29.5% to 29.8% respectively) and rubble/sand patches (47.0% to 43.8% respectively).

Table 3.2: Characteristics of damselfish aggregations, including mean (+/-se) area, number of individuals and distance between territories.

	mean area (m^2)	mean number of individuals	mean distance between territories (m)
D. prosopotaenia aggregations	247.9 (55.25) n=3	24.0 (4.04) n=3	0.94 (0.15) n=72
D. perspicillatus aggregations	563.9 (131.05) n=3	21.7 (5.39) n=3	1.32 (0.17) n=64

Table 3.3: Mean (+/- se) percent cover of each of 4 microhabitats within areas with aggregations of *Dischistodus prosopotaenia* and *D. perspicillatus* (n=3).

	D. pros. territories	*D. pers.* territories	reef matrix	rubble/ sand
D. prosopotaenia aggregations	19.4% (2.34)	4.0% (2.83)	29.5% (2.18)	47.0% (0.58)
D.perspicillatus aggregations	0.2 (0.21)	28.1% (6.26)	29.8% (4.42)	43.8% (9.11)

Territorial behaviour of damselfish

Each damselfish species was observed for a total of 30hrs, during which 1519 individuals of 23 families (106 species) were recorded entering *D. prosopotaenia* territories, while 1673 individuals of 27 families (128 species) were recorded entering those of *D. perspicillatus* (see Appendix III). Residents included gobies (including *Amblygobius rainfordi* [Whitley, 1940], *Eviota prasites* Jordan & Seale, 1906 in *D. prosopotaenia* territories; and *Amblygobius decussatus* [Bleeker, 1855], *Macrodontogobius wilburi* Herre, 1936, *Signigobius biocellatus* Hoese & Allen 1977 in *D. perspicillatus* territories) and labrid and scarid recruits (see below).

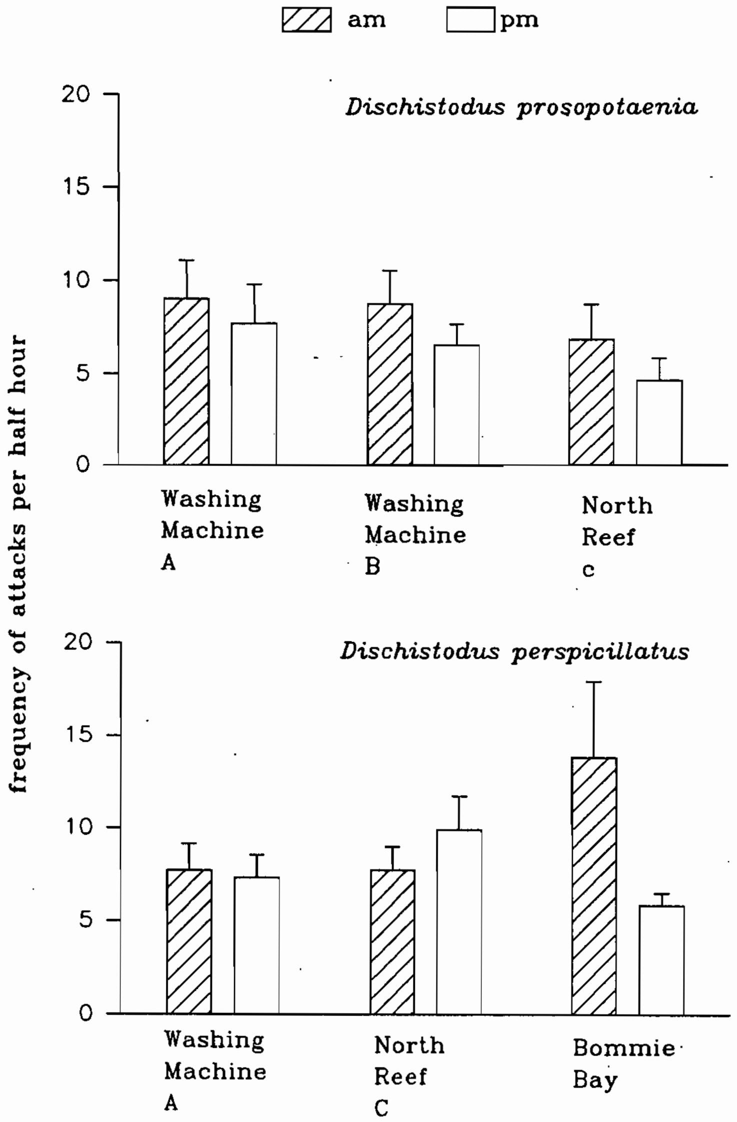
Territory holders attacked other fishes at a frequency of 7.2 (± 0.70) and 8.7 (± 0.88) attacks per half hour observation period by *D. prosopotaenia* and *D.perspicillatus* respectively (Figure 3.3). No significant difference was detected in the frequency of attacks by *D. prosopotaenia* at different times of the day, or at different sites (Table 3.4). However, a significant interaction was detected between these two factors for *D. perspicillatus*, which was probably because they attacked more frequently in the morning than the afternoon at Bommie Bay only.

Table 3.4: Two way analysis of variance testing for the relationship between time of day and site and the frequency of attacks by each of two damselfish species.

	Dischistodus prosopotaenia			
source	df	MS	F	p
time	1	54.15	1.82	0.1824
site	2	37.32	1.26	0.2926
time of day*site	2	1.35	0.05	0.9556
error	54	29.68		
total	59			

	Dischistodus perspicillatus			
source	df	MS	F	p
time of day	1	0.94	1.23	0.2725
site	2	0.40	0.52	0.5963
time of day*site	2	2.49	3.25	0.0463
error	54	0.77		
total	59			

Figure 3.3.
Mean frequency (+/– se) of attacks by each of two damselfish species on other fishes at two times of the day at three sites.



The frequency of attack was not proportional to the frequency of intrusion by a family (Figure 3.4). Many attacks by both damselfish were directed against other pomacentrids, despite the fact that they represented a low percentage of the intruders. Many attacks by *D. perspicillatus* were also directed against scarids and mullids, despite their low rates of intrusion. Both species chased resident gobies (especially *D. perspicillatus*), but they did not chase resident labroid recruits. Adult labrids did not account for many chases, despite the fact that they were the most frequent intruders to the territories. One species, *C. schroederi*, represented 18.3% to 13.4% of all entrants to *D. prosopotaenia* and *D. perspicillatus* territories, but was chased only 0.4% to 0.9% of the times that it appeared. In comparison another labrid, *Thalassoma lunare*, was chased 9.3% to 34.6% of the times that it appeared in *D. prosopotaenia* and *D. perspicillatus* territories respectively. Most other families were chased in relative proportion to their appearance in the territories, except chaetodontids and nemipterids, which were not chased very often by *D. perspicillatus*.

Description of territories

The two species established their territories on different types of substratum: *D. prosopotaenia* used a mixed substratum of reef matrix, sand and rubble (Figure 3.5, 3.6 and Frontispiece), while *D. perspicillatus* used sand (Figures 3.5, 3.7). *D. perspicillatus* territories occupied 6.01m^2 (se=0.63, n=30) , which was significantly larger than the 2.42m^2 (se=0.15, n=30) occupied by territories of *D. prosopotaenia* (Table 3.5).

Table 3.5: Nested analysis of variance testing for the relationship between damselfish species and territory size.

source	df	MS	F	p
damselfish species	1	358.88	98.26	<0.0001
site (damselfish species)	4	8.91	2.44	0.0579
error	54	3.63		
total	59			

Figure 3.4.
Percent of intruders of each family that entered territories (☐) and percent of attacks on each family of intruders and residents (☒) by two damselfish species. Where: r=residents.

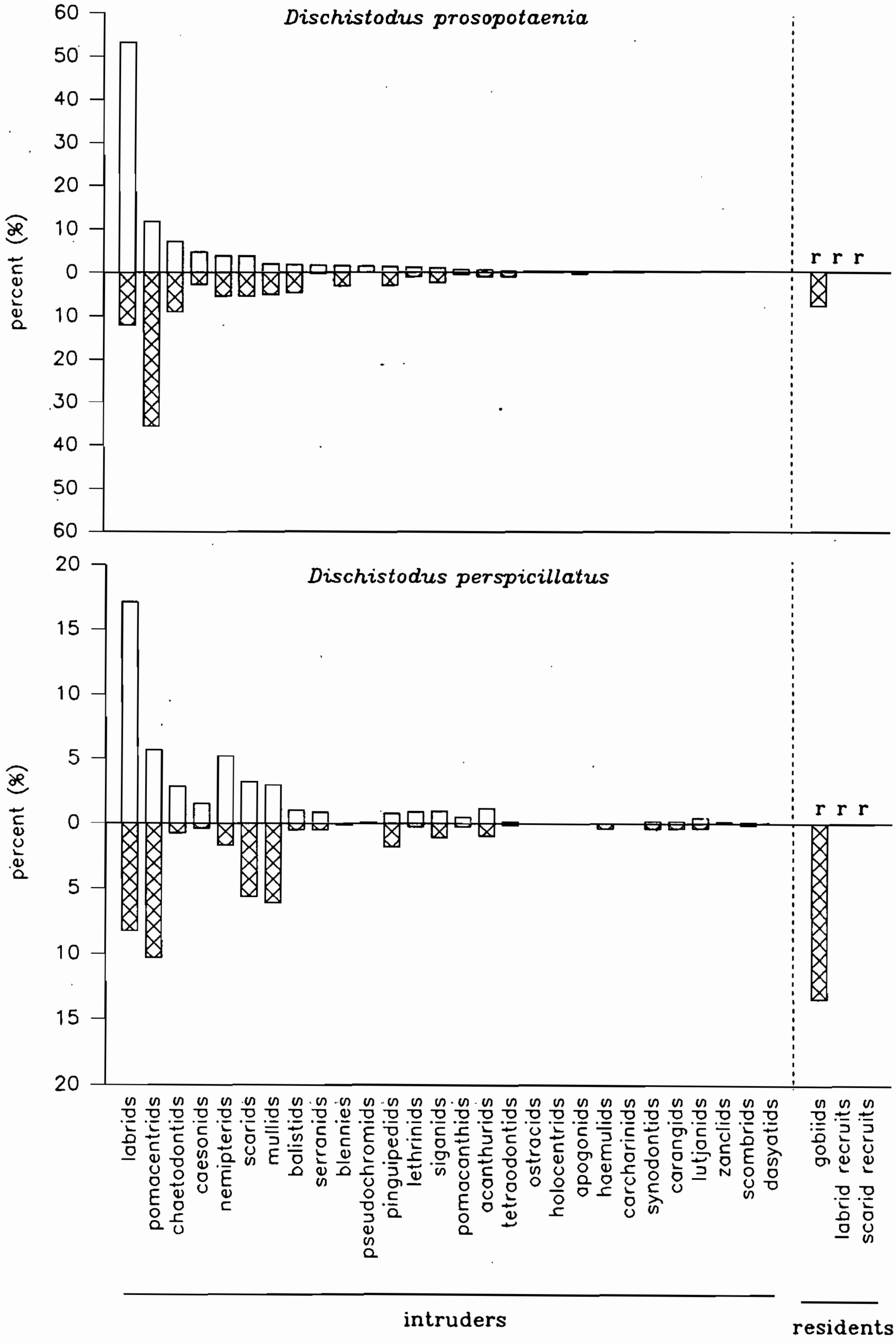


Figure 3.5.
Mean (+/− se) percent cover of each substratum type on which *Dischistodus prosopotaenia* and *Dischistodus perspicillatus* established their territories (n=5).

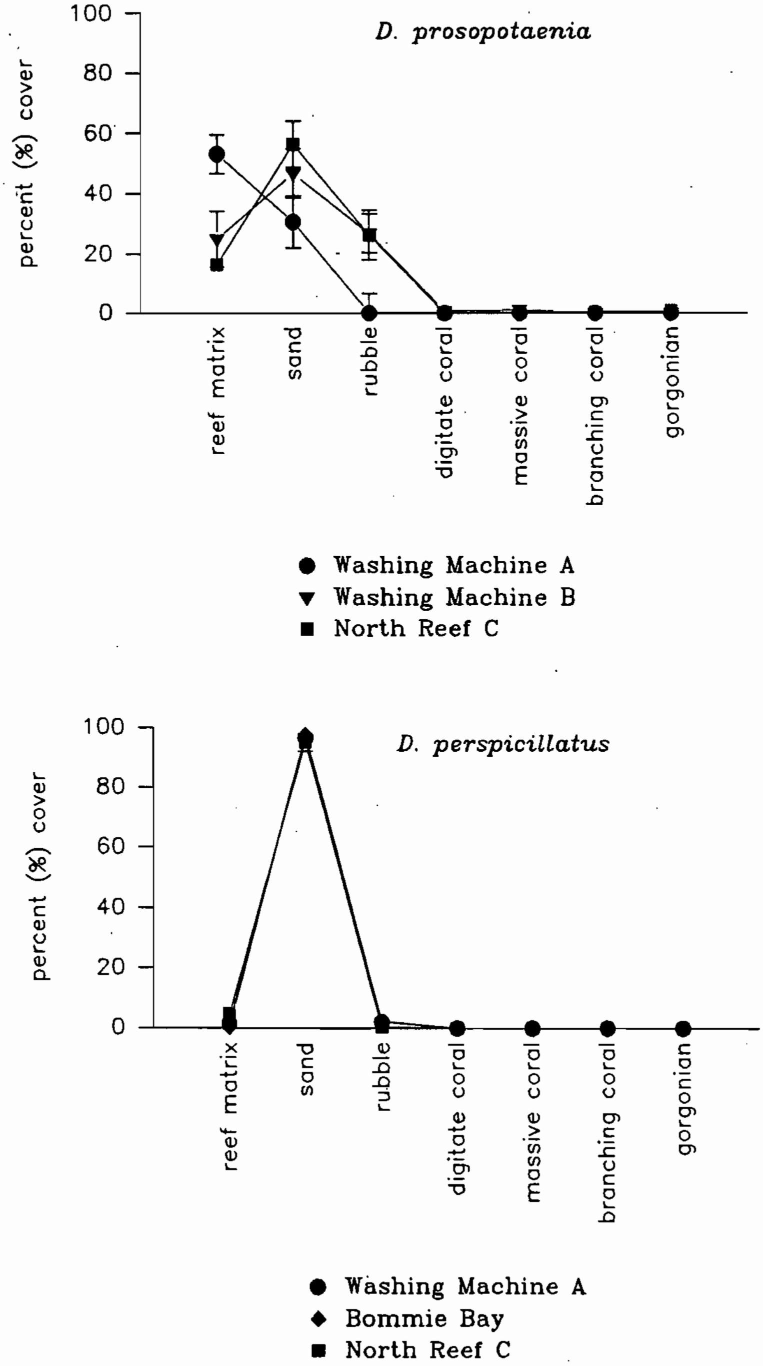


Figure 3.6.

a) Dischistodus prosopotaenia (approx. 16cm TL) on edge of multispecific stand of macroalgae within its territory (Photo: T. Preen).

b) Close up of multispecific stand of macroalgae within a territory of *D. prosopotaenia* (Photo: T. Preen).

Figure 3.7.
Dischistodus perspicillatus (approx. 18cm TL) over monospecific stand of blue green algae (*Lyngbia* spp.) within its territory (Photo: M. Johnson).

The percent cover of each substrate type within territories differed from adjacent microhabitats (Figure 3.8). Territories of both species were dominated by a high percentage cover macroalgae, which was higher in *D. perspicillatus* territories than it was in those of *D. prosopotaenia*. In contrast, adjacent microhabitats were almost completely devoid of macroalgae.

The type of macroalgae also differed between the two types of territories (Figure 3.9). *D. prosopotaenia* territories comprised multispecific algal assemblages (see Figure 3.6) that were dominated by green (*Halimeda* spp. and/or *Caulerpa urvilleana*) and red algae (*Gelidiopsis intricata*). Brown algae (*Padina tenuis*) and blue green algae (*Lyngbia* spp.) were recorded only in very low quantities (Figure 3.9). In contrast, territories of *D. perspicillatus* consisted almost entirely of *Lyngbia* spp. (see Figure 3.7). The height of algae in the territories was variable, but ranged from 0 - 12cm and 0 - 8cm within *D. prosopotaenia* and *D. prosopotaenia* territories respectively.

3.3.2 Use of damselfish territories and adjacent microhabitats by invertebrates and labroid fishes

Abundance of microinvertebrates

Microinvertebrates were present in substantially higher densities within damselfish territories than they were in adjacent microhabitats (Figure 3.10), with the highest densities recorded in *D. perspicillatus* territories.

Microhabitats also differed in the relative abundance of microinvertebrates in each taxonomic category. *D. prosopotaenia* territories were dominated by crustaceans such as copepods and/or tanaids, with lower abundances of other taxa such as gammarids. In contrast, *D. perspicillatus* territories were almost exclusively occupied by copepods. Both reef matrix and rubble/sand patches differed from the territories by having a higher proportion of polychaetes, nematodes and molluscs as well as a mixed assemblage of crustaceans (Figure 3.10).

Figure 3.8.

Mean percent cover (+/− se) of each substratum category in *Dischistodus prosopotaenia* and *D. perspicillatus* territories, and microhabitats adjacent to each at three sites (n=5).

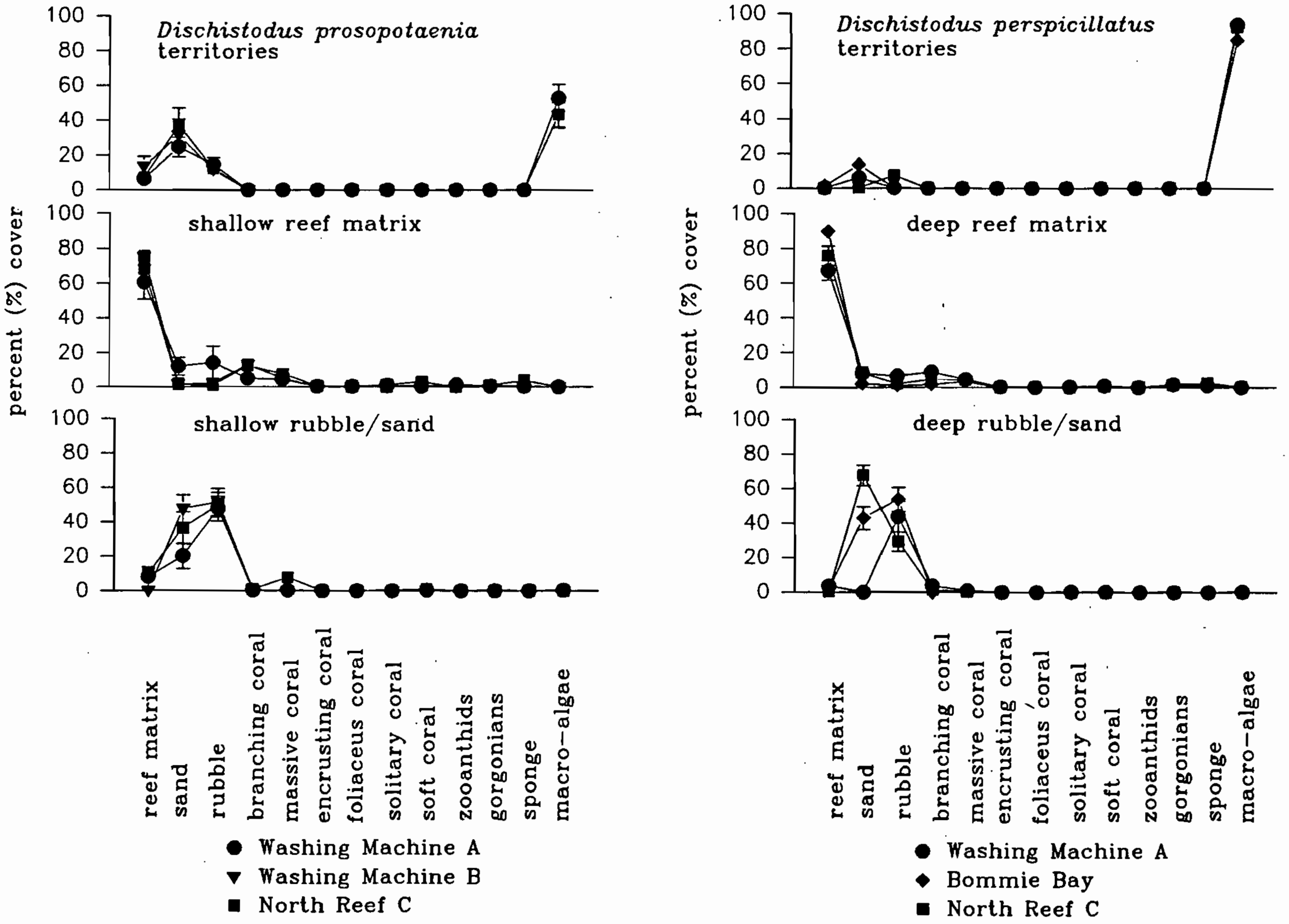


Figure 3.9.
Mean (+/− se) dried weight of algae of each genus in territories of *Dischistodus prosopotaenia* and *Dischistodus perspicillatus* at each of three sites (n=9).

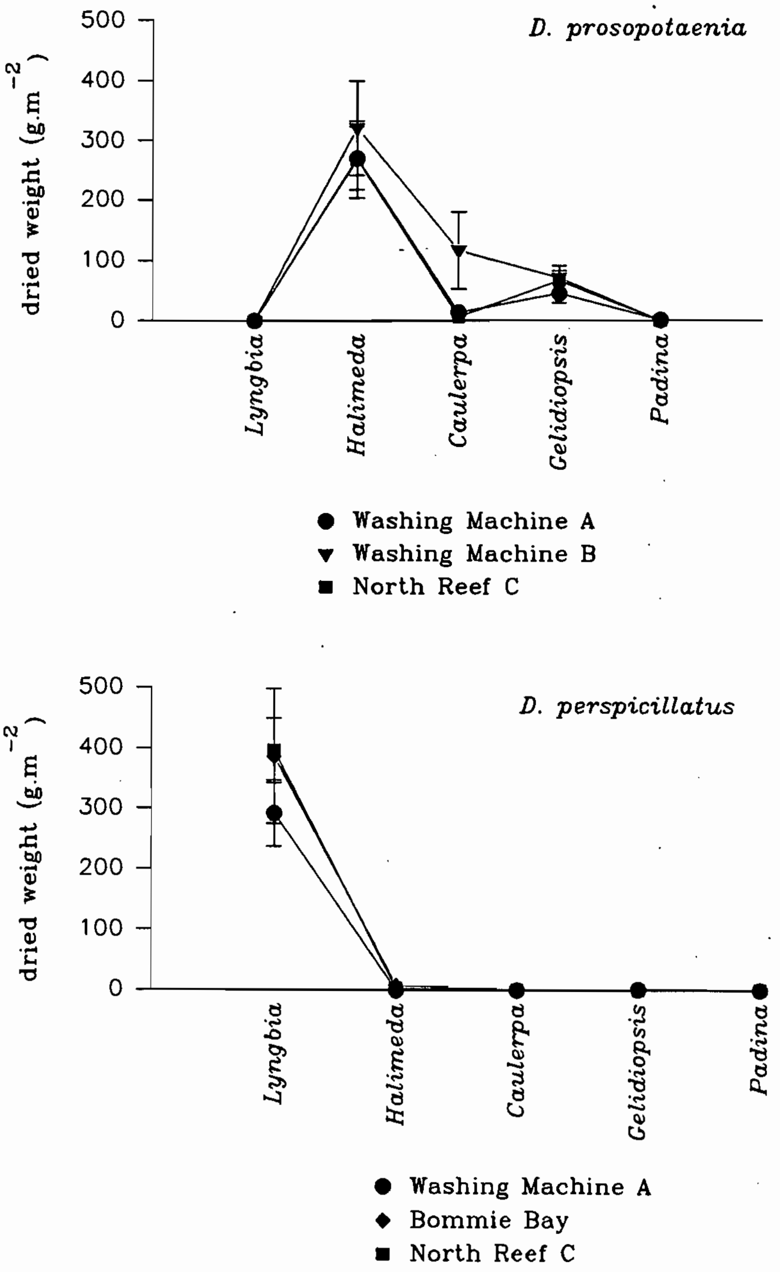
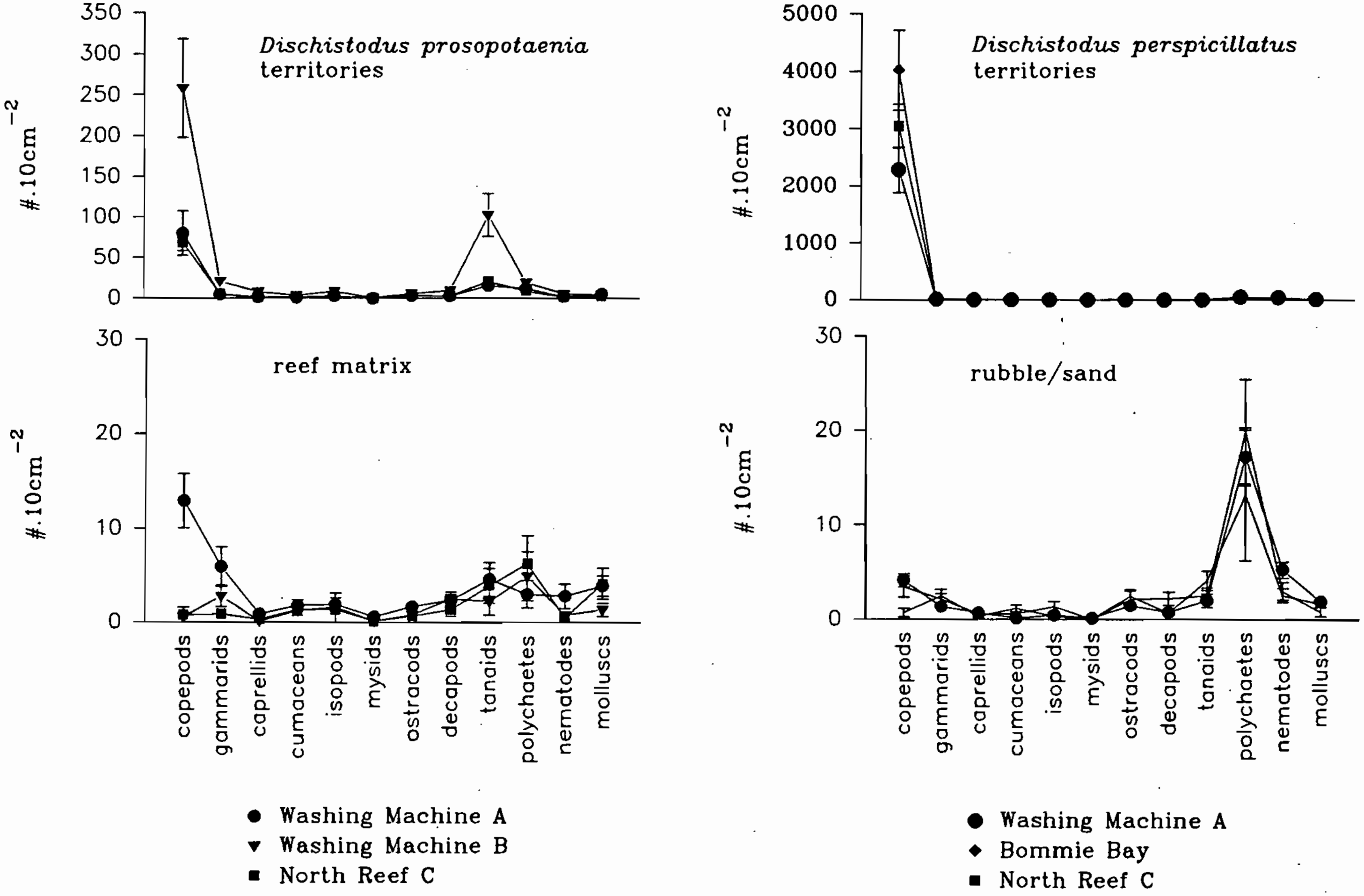


Figure 3.10.
Mean (+/- se) density of microinvertebrates of each taxonomic category, within damselfish territories and adjacent microhabitats at three sites (n=9). Note different y axes.



Abundance of labroid recruits

Recruits of 18 labroid species (13 labrids, 5 scarids) were found in the 6 microhabitats throughout the summer (Tables 3.6, 3.7) Eleven species were rare ($n<10$), 4 species (*H. trimaculatus*, *S. bandanensis*, *T. lunare* and *S. niger*) were common ($10<n<100$), and three (*C. schroederi*, *H. melanurus* and *S.* spp.) were abundant (>300 individuals).

Most common or abundant species showed clear patterns of microhabitat use. *H. melanurus*, *S. bandanensis*, *S. niger* and *Scarus* spp., were all present in their highest densities in *D. prosopotaenia* territories. *C. schroederi* was characteristic of both types of territories, as well as rubble/sand patches. *H. trimaculatus* was most abundant in *D. perspicillatus* territories and rubble/sand patches. Only one species, *T. lunare*, was most abundant outside territories, with most individuals being found on reef matrix, especially at the deeper locations.

Rare species also showed patterns of microhabitat use, with 5 species (*Anampses* spp., *C. chlorourus*, *C. diagrammus*, *H. chloropterus* and *S. frenatus*) primarily found in *D. prosopotaenia* territories, and *M. negrosensis* mostly found in *D. perspicillatus* territories. In contrast, 5 rare species were found outside of territories, either on reef matrix (*A. neoguinaicus*, *C. gaimard*, *L. dimidiatus* and *T. hardwicke*) or rubble/sand patches (*H. longiceps*). However, these patterns should be interpreted cautiously, because of the low numbers of individuals involved.

Table 3.6: Abundance and mean density (+/- se) of labrid and scarid recruits in *D. prosopotaenia* territories and adjacent reef matrix and rubble/sand patches at the Reef Base at three study sites at Lizard Island. Where n=total number of individuals recorded over the 1992/93 summer; mean=mean density.10m^{-2} over 11 weeks; and se=standard error of the mean.

	D. prosopotaenia territories			shallow reef matrix			shallow rubble/sand		
	n	mean	se	n	mean	se	n	mean	se
Anampses spp.	2	0.08	0.08	-	-	-	-	-	-
Cheilinus chlorourus	1	0.04	0.04	-	-	-	-	-	-
Cheilinus diagrammus	5	0.20	0.16	-	-	-	-	-	-
Coris gaimard	-	-	-	-	-	-	1	0.04	0.04
Coris schroederi	119	4.82	1.05	1	0.04	0.04	26	0.85	0.25
Halichoeres melanurus	321	12.90	4.79	70	2.57	0.80	13	0.48	0.19
Halichoeres trimaculatus	9	0.37	0.28	-	-	-	9	0.33	0.17
Labroides dimidiatus	-	-	-	2	0.08	0.05	-	-	-
Stethojulis bandanensis	11	0.41	0.16	-	-	-	-	-	-
Thalassoma hardwicke	-	-	-	1	0.04	0.04	-	-	-
Thalassoma lunare	-	-	-	7	0.26	0.15	-	-	-
LABRIDAE (all species)	468	18.97	4.81	81	2.98	0.78	49	1.8	0.38
Scarus frenatus	1	0.04	0.04	-	-	-	-	-	-
Scarus niger	11	0.45	0.36	1	0.04	0.04	-	-	-
Scarus spp.	230	9.32	0.54	13	0.48	0.29	8	0.30	0.17
SCARIDAE (all species)	242	9.81	2.84	14	0.52	0.20	8	0.30	0.17
LABROIDS (all species)	710	28.78	5.02	95	3.49	0.86	57	2.09	0.48

Table 3.7: Abundance and mean density (+/- se) of labrid and scarid recruits in *Dischistodus perspicillatus* territories and adjacent reef matrix and rubble/sand patches on the Sand Flat at three sites at Lizard Island. Where n=total number of individuals recorded over the 1992/93 summer; mean=mean density.10 m^{-2} over 11 weeks; and se=standard error of the mean.

	D. perspicillatus territories			deep reef matrix			deep rubble/sand		
	n	mean	se	n	mean	se	n	mean	se
Anampses neoguinaicus	-	-	-	1	0.01	0.01	-	-	-
Coris schroederi	191	1.88	0.50	7	0.10	0.04	34	0.45	0.21
Halichoeres chloropterus	1	0.01	0.01	-	-	-	-	-	-
Halichoeres melanurus	27	0.27	0.12	88	1.16	0.55	24	0.32	0.17
Halichoeres trimaculatus	51	0.71	0.32	4	0.05	0.03	18	0.24	0.11
Labroides dimidiatus	-	-	-	4	0.05	0.03	-	-	-
Macropharyngodon negrosensis	6	0.06	0.03	-	-	-	1	0.01	0.01
Stethojulis bandanensis	1	0.01	0.01	-	-	-	-	-	-
Thalassoma lunare	-	-	-	25	0.25	0.12	1	0.01	0.01
LABRIDAE (all species)	277	2.73	0.48	128	1.69	0.65	78	1.03	0.38
Hipposcarus longiceps	6	0.06	0.03	-	-	-	1	0.01	0.01
Scarus niger	7	0.07	0.03	1	0.01	0.01	-	-	-
Scarus spp.	156	1.54	0.48	20	0.26	0.09	11	0.15	0.07
SCARIDAE (all species)	163	1.61	0.49	21	0.29	0.10	12	0.16	0.08
LABROIDS (all species)	440	4.34	1.18	149	1.99	0.66	90	1.19	0.41

Repeated measures analysis showed that the patterns of microhabitat use described for two of the abundant labroid taxa (*C. schroederi* and *Scarus* spp.), were consistent throughout the summer (Figures 3.11, 3.12), with a significant influence of microhabitat on the density of each of these species (Table 3.8). Each species was present in higher densities within territories than within adjacent microhabitats, except at Bommie Bay where there was very little recruitment to either microhabitat.

In contrast to these species, there was no significant difference in the density of *H. melanurus* in the different microhabitats (Table 3.8). This was because this species did not show clear patterns of microhabitat use during weeks of low recruitment (Figure 3.13), but when there was a recruitment peak (in late January), microhabitat did have a significant influence on the density of this species (Table 3.9). Highest densities were recorded from *D. prosopotaenia* territories (Figure 3.13).

All three abundant groups of labroid recruits used the artificial territories throughout the summer (28, 71 and 23 individuals of *C. schroederi*, *H. melanurus* and *S.* spp. respectively). No significant difference was detected in the density of each species in the artificial territories within different habitats (Table 3.10).

Figure 3.11.
Mean (+/− se) density of *Coris schroederi* recruits in each of 6 microhabitats at each of three sites in 1992/93 summer (n=5).

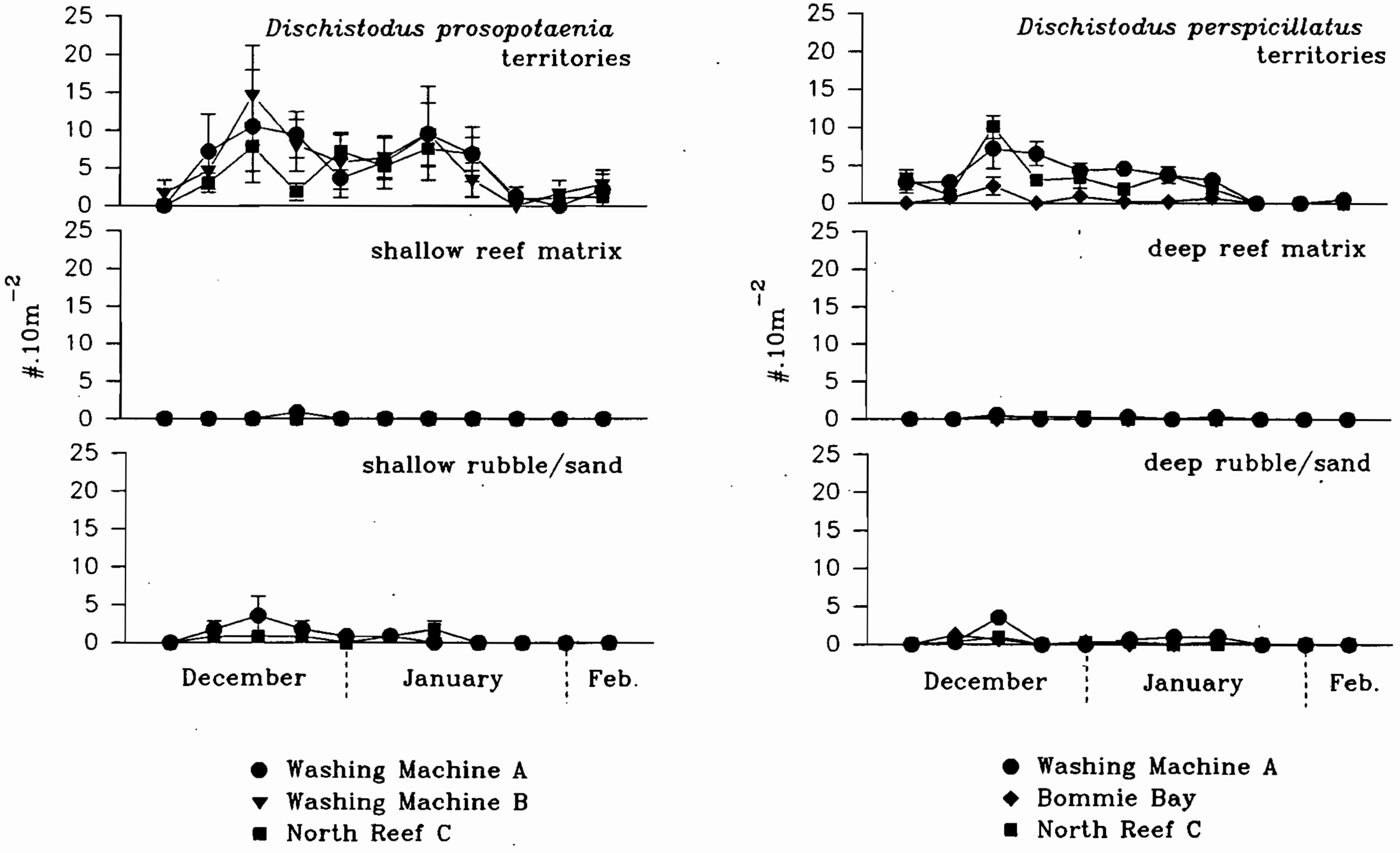


Figure 3.12.
Mean (+/- se) density of *Scarus* spp. recruits in each of 6 microhabitats at each of three sites in 1992/93 summer (n=5).

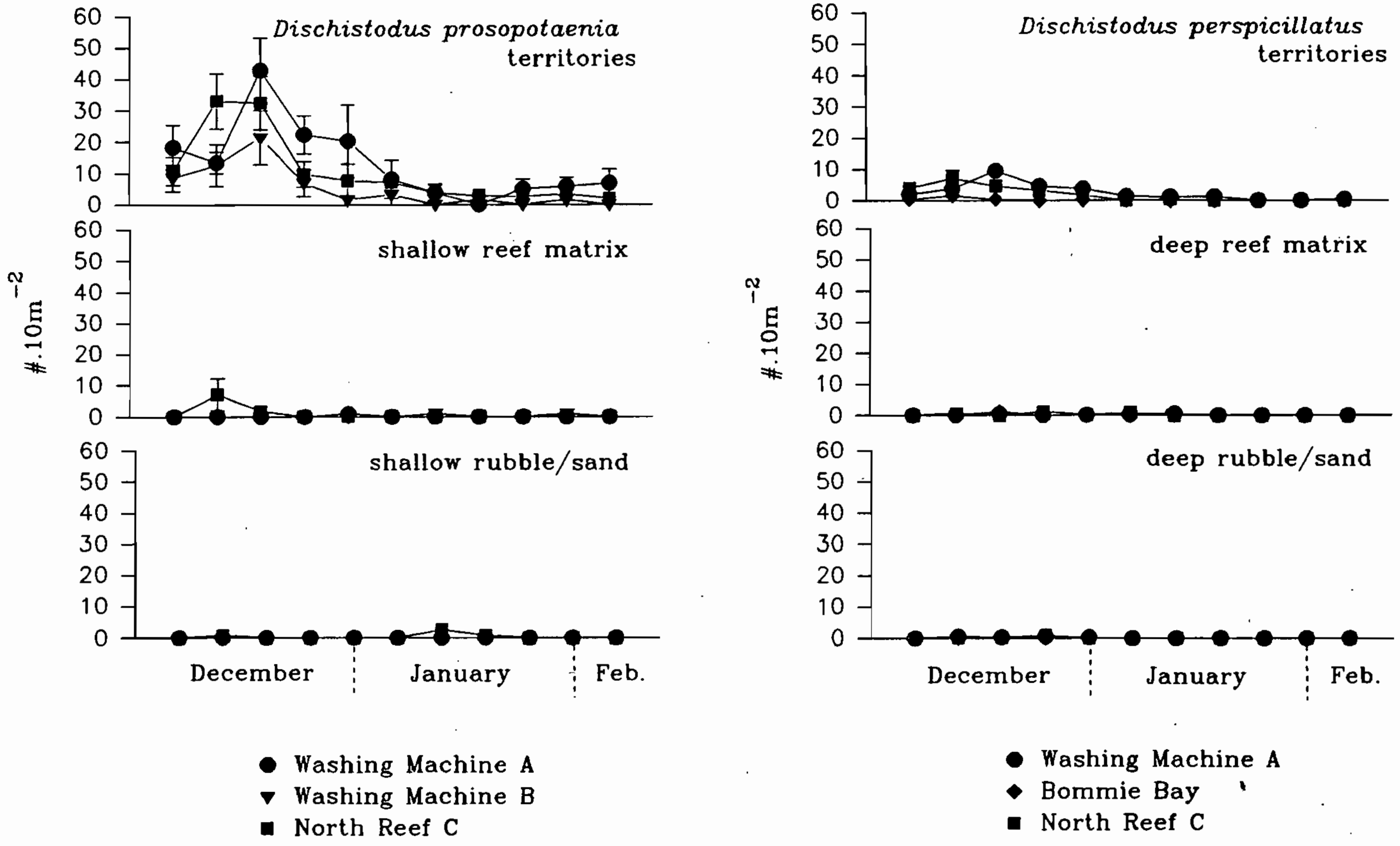


Figure 3.13.
Mean (+/- se) density of *Halichoeres melanurus* recruits in each of 6 microhabitats at each of three sites in 1992/93 summer (n=5).

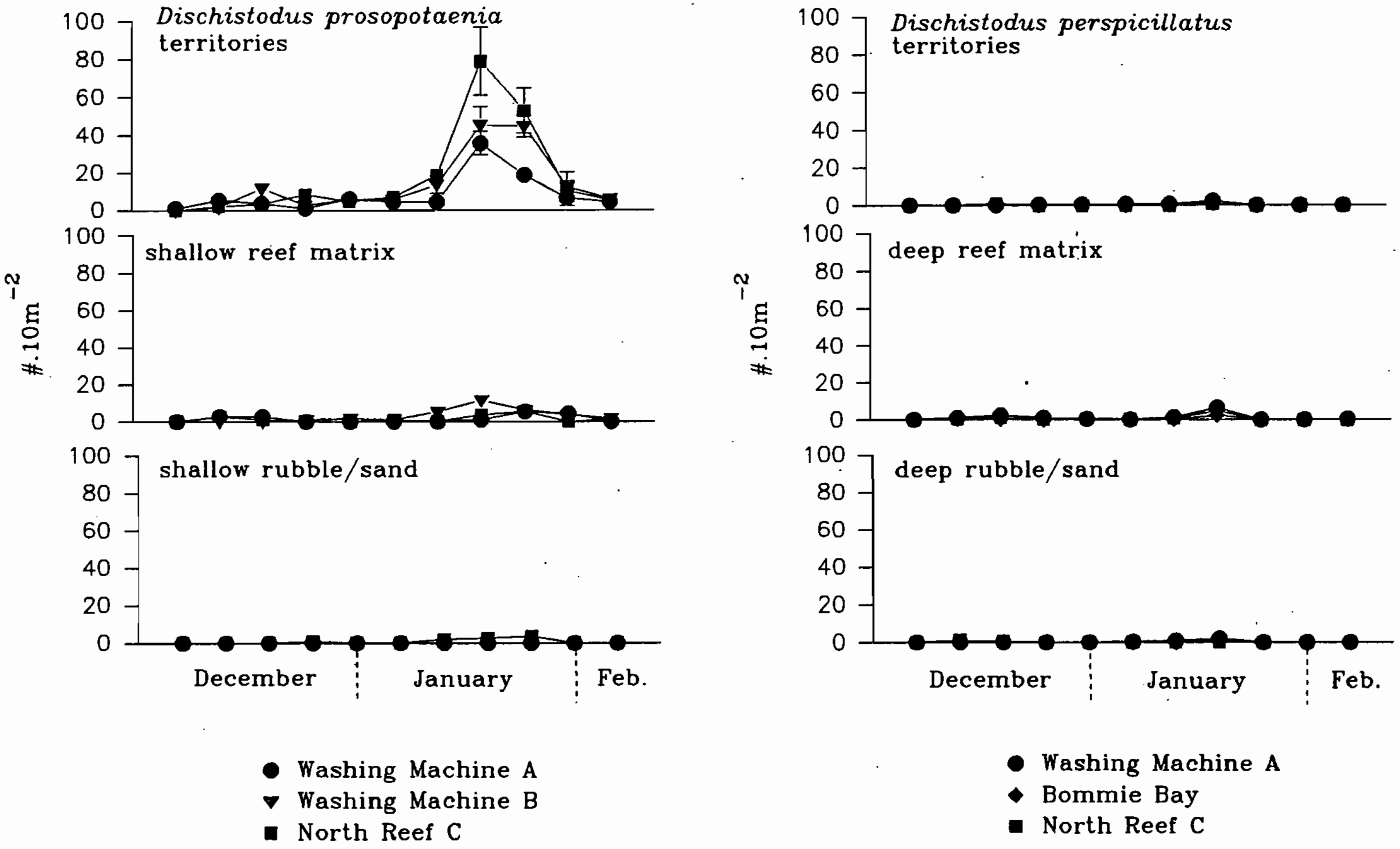


Table 3.8: Repeated-measures nested MANOVA testing the relationship between microhabitat and density of three labroid taxa throughout the summer.

BETWEEN SUBJECTS EFFECTS:	*Coris schroederi*			
source	df	MS	F	p
microhabitat	5	121.73	12.09	0.0044
site (microhabitat)	6	10.07	0.32	0.9270
error	78	31.91		
	Halichoeres melanurus			
source	df	MS	F	p
microhabitat	5	56.55	0.14	0.9748
site (microhabitat)	6	393.38	12.66	0.0001
error	78	31.06		
	Scarus spp.			
source	df	MS	F	p
microhabitat	5	601.43	14.34	0.0028
site (microhabitat)	6	41.94	0.68	0.6648
error	78	61.52		

WITHIN SUBJECTS EFFECTS:	*Coris schroederi*			
source	num df	den df	F	p
date	10	69	2.54	0.0115
date*microhabitat	50	365	0.90	0.6588
date*site (microhabitat)	60	444	0.81	0.8449
	Halichoeres melanurus			
source	num df	den df	F	p
date	10	69	2.31	0.0200
date*microhabitat	50	365	1.09	0.3200
date*site (microhabitat)	60	444	1.28	0.0800
	Scarus spp.			
source	num df	den df	F	p
date	10	69	3.07	0.0028
date*microhabitat	50	365	1.18	0.1994
date*site (microhabitat)	60	444	1.09	0.3107

Table 3.9: Nested analysis of variance testing for the relationship between microhabitat and the density of *H. melanurus* in late January, 1993.

source	df	MS	F	p
microhabitat	5	4.80	41.61	<0.0001
site (microhabitat)	12	0.24	2.09	0.0281
error	72	0.11		
total	89			

Table 3.10: Two way fixed factor analysis of variance testing for the relationship between habitat and site and the density of *Coris schroederi*, *Halichoeres melanurus* and *Scarus* spp. within artificial territories.

	C. schroederi			
source	df	MS	F	p
habitat	1	67.40	3.20	0.3245
site	1	5.13	0.13	0.7232
habitat*site	1	21.03	0.55	0.4691
error	16	38.08		
total	19			
	H. melanurus			
source	df	MS	F	p
habitat	1	236.75	17.64	0.1488
site	1	2.47	0.07	0.7947
habitat*site	1	13.42	0.39	0.5411
error	16	34.54		
total	19			
	Scarus spp.			
source	df	MS	F	p
habitat	1	6.80	15.81	0.1569
site	1	5.39	0.15	0.7036
habitat*site	1	0.43	0.01	0.9216
error	16	35.92		
total	19			

Recruitment of labroids to areas with and without damselfish aggregations

The recruits of *C. schroederi* and the scarids were significantly more abundant in areas with damselfish aggregations, than they were in areas without aggregations (Figure 3.14, Table 3.11). *Scarus* spp. species were also significantly more abundant in *D. prosopotaenia* aggregations than they were in *D. perspicillatus* aggregations.

In contrast, there was a significant interaction between the influence of presence of aggregations and damselfish species on density of *H. melanurus* (Figure 3.14; Table 3.11). This was because *H. melanurus* was significantly more abundant in areas with *D. prosopotaenia* aggregations than it was in areas without these aggregations. However the same pattern was not found for areas with and without *D. perspicillatus* aggregations. This is not surprising, since *H. melanurus* recruits do not use *D. perspicillatus* territories in high densities (see above).

Use of damselfish territories by adult labrids

Adult *C. schroederi* used territories more than other microhabitats, spending 48.3% and 74.6% of their time in territories within *D. prosopotaenia* and *D. perspicillatus* aggregations respectively, although territories occupied only 23.4% and 28.3% of the areas respectively (Figure 3.15 & 3.16; Table 3.3). *C. schroederi* also took a large percentage of its feeding bites from within damselfish territories, with 50.0% (se=4.10) and 50.0% (se=2.93) of bites taken from territories in *D. prosopotaenia* and *D. perspicillatus* aggregations respectively.

Figure 3.14.
Mean (+/− se) recruitment of each of three labroid taxa to areas with and without aggregations of *Dischistodus prosopotaenia* and *D. perspicillatus* (n=3).

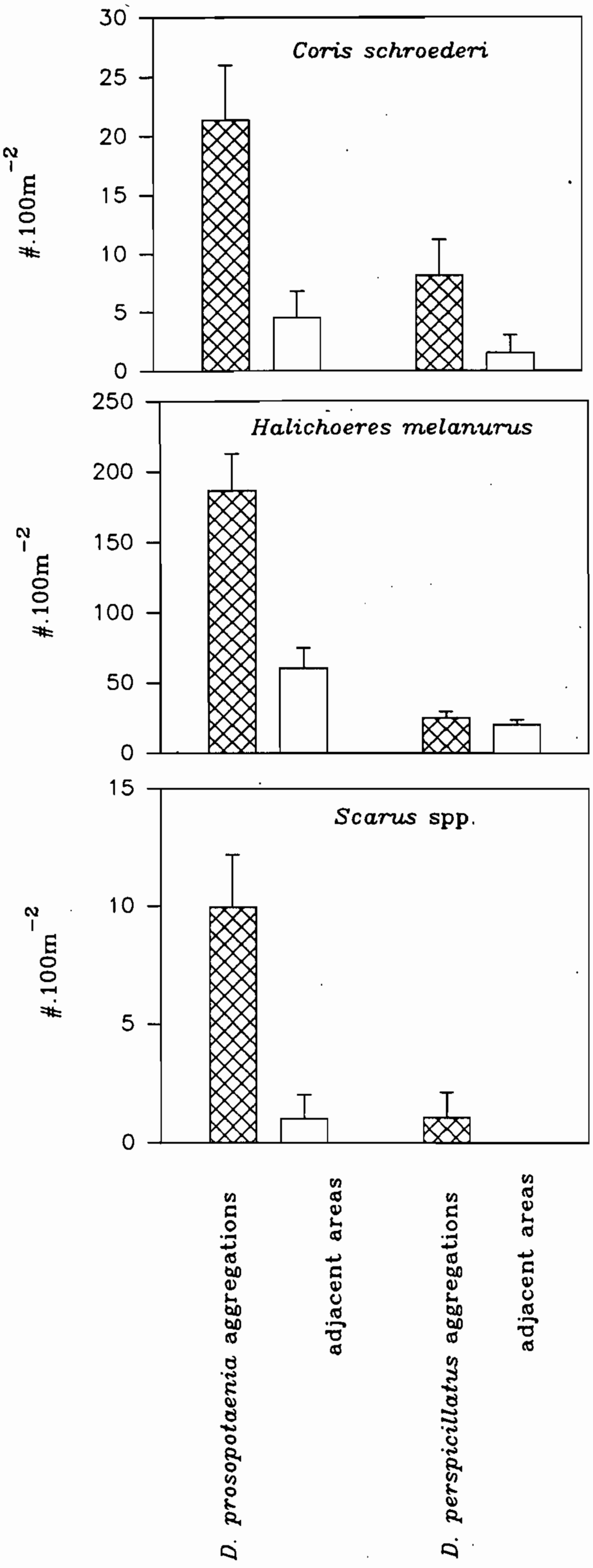


Figure 3.15.
Mean percent (+/– se) time spent by *Coris schroederi* in damselfish territories and adjacent microhabitats (☐; n=40) and cover of each microhabitat (▩; n=3) in aggregations of *Dischistodus prosopotaenia* and *D. perspicillatus*.

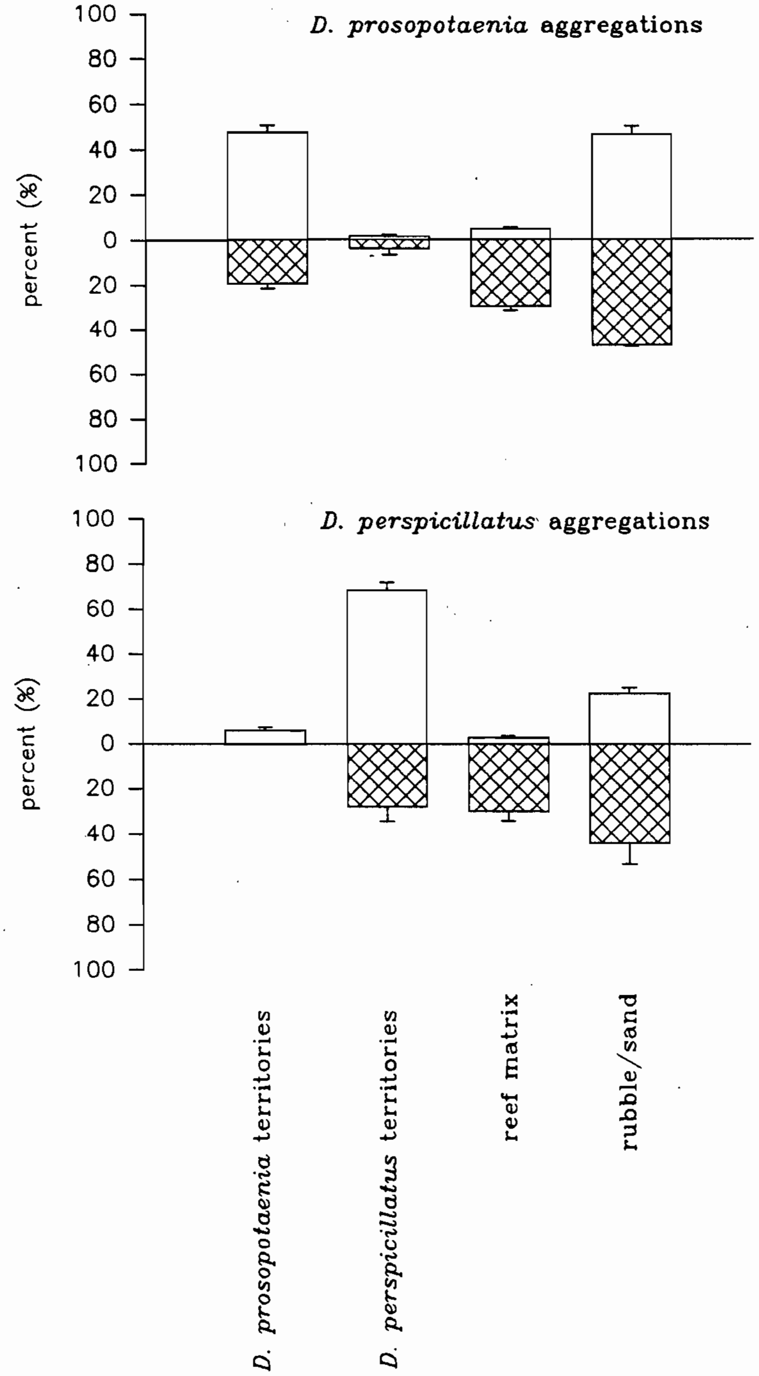


Figure 3.16.
Adult *Coris schroederi* (approx. 12 cm TL) in territory of *Dischistodus prosopotaenia* (Photo: T. Preen).

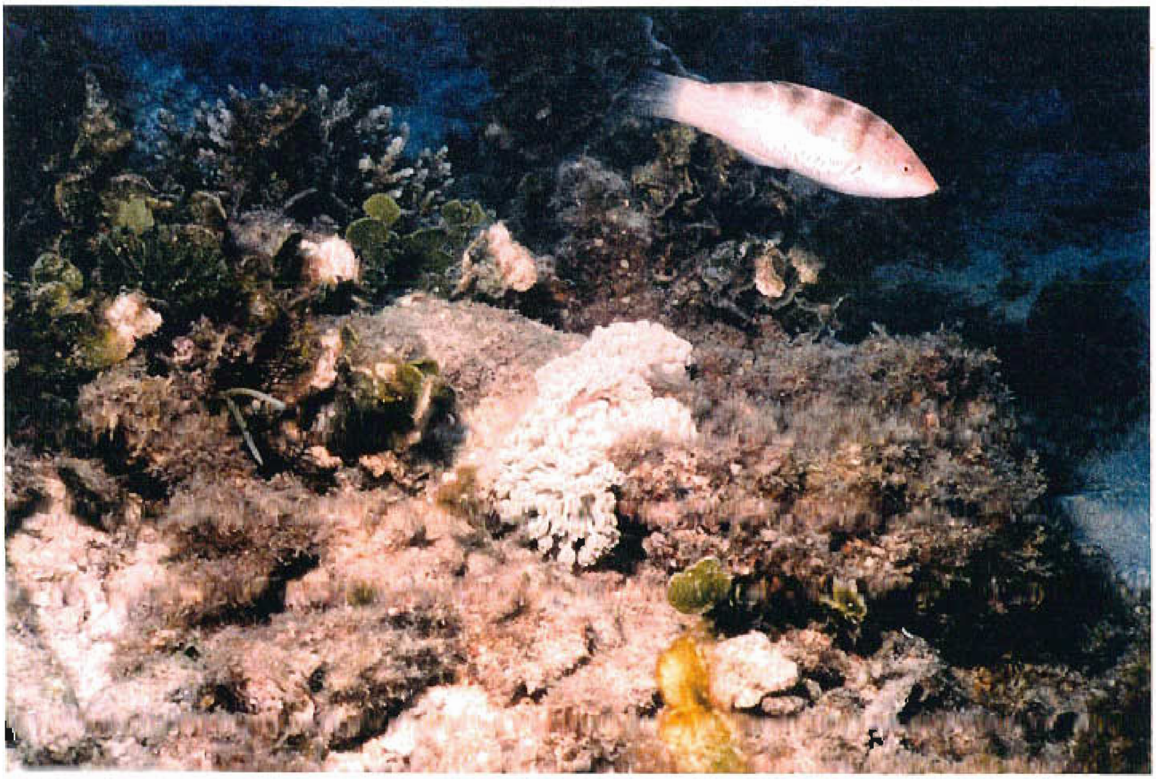


Table 3.11: Two way analysis of variance testing for the relationship between the presence of damselfish aggregations and damselfish species and the recruitment *Coris schroederi*, *Halichoeres melanurus* and *Scarus* spp.

	C. schroederi			
source	df	MS	F	p
presence of aggregations	1	1.45	10.32	0.0124
damselfish species	1	0.45	3.24	0.1095
aggregations*species	1	0.01	0.05	0.8371
error	8	0.14		
total	11			

	H. melanurus			
source	df	MS	F	p
presence of aggregations damselfish	1	0.26	14.10	0.0056
species	1	1.29	69.57	<0.0001
aggregations*species	1	0.12	6.66	0.0326
error	8	0.02		
total	11			

	Scarus spp.			
source	df	MS	F	p
presence of aggregations	1	0.78	11.00	0.0106
damselfish species	1	0.77	10.76	0.0112
aggregations*species	1	0.28	3.86	0.0849
error	8	0.07		
total	11			

3.4 DISCUSSION

Both *D. prosopotaenia* and *D. perspicillatus* modified benthic assemblages in two habitat zones at Lizard Island, by facilitating the growth of high density stands of macroscopic algae within their territories (see Hixon 1983; Russ 1987). This was achieved by vigorously defending their territories from trophic competitors (omnivores and herbivores) which may feed on the algae (Low 1971; Myrberg & Thresher 1974; Thresher 1976; Mahoney 1981; Hourigan 1986; this study), or by excluding destructive carnivores (eg. mullids) which may dislodge the algae while they are searching for prey (Low 1971; this study). In addition, these species chased carnivores (eg. gobies), which may be potential egg predators (see Clark 1970; Fishelson 1970; Myrberg & Thresher 1974).

Different damselfish species promote the growth of different types of algal assemblages within their territories, which may vary between geographic regions (see review in Kamura & Choonhabandit 1986). At Lizard Island, *D. prosopotaenia* territories comprised multispecific assemblages of green, red and brown algae. This assemblage differs from the territories of most other species by the dominance of the green algae, *Halimeda* and *Caulerpa* (see Lassuy 1980; Kamura & Choonhabandit 1986; Hinds & Ballantine 1987; Klumpp & Polunin 1989). *D. perspicillatus* territories were even more distinctive, comprising a monoculture of the blue-green algae *Lyngbia* sp. Monocultures have previously been described for damselfish territories (Vine 1974; Montgomery 1980a,b), but this is the first report of a monoculture of a blue-green algae. These results support the suggestion that some territorial damselfish make an important contribution to rates of nitrogen fixation of reefs, by increasing the biomass of nitrogen fixing blue-green algae within their territories (see reviews in Hixon 1983; Horn 1989).

Previous studies have also suggested that the dense stands of macroalgae within damselfish territories may have indirect effects on other reef organisms and processes (see reviews Hixon 1983; Sammarco *et al.* 1986; Russ 1987; Horn 1989). At Lizard Island I have demonstrated that by establishing algal gardens, two damselfish species influence patterns of distribution and abundance of reef invertebrates (especially copepods) and labroid fishes, which use the territories in high densities (see also Lobel 1980; Hixon & Brostoff 1982; Zeller 1988; Klumpp & Polunin 1989; Green *in press*).

Recruits of three abundant labroids, *C. schroederi*, *H. melanurus* and *Scarus* spp, showed strong patterns of microhabitat use of macroalgal stands within *D. prosopotaenia* and *D. perspicillatus* territories. These results confirm observations that some labroids appear concentrated within damselfish territories during the first few weeks of benthic life (Bellwood 1986; Bellwood & Choat 1989; Green *in press*). However they contrast with previous studies of microhabitat use by two of these taxa (*C. schroederi* and *Scarus* spp.), which reported that they each showed "preferences" for other substratum types such as live or dead corals (Williams & Sale 1981; Sale *et al.* 1984a; Eckert 1985a,b). However these studies did not consider macroalgae as an alternative substratum type, although Sale *et al.* (1984a) and Eckert (1985a) did notice that *Scarus* spp. appeared to show a "preference" for filamentous algae at the base of corals.

Scarids were not identified to species, and the microhabitat use demonstrated for *Scarus* spp was the combined pattern of several species. Therefore, it is possible that one abundant species within the complex may be overriding the pattern of other less abundant species, so these results should be interpreted with caution. It is also necessary to remember that scarids are schooling species (Bellwood 1986), and as such they are likely to show aggregated settlement (Doherty & Sale 1985; Breitburg 1991). Therefore microhabitat selection by individuals cannot be viewed as independent events.

H. melanurus showed strong patterns of microhabitat use between damselfish territories, reaching high densities only in those of *D. prosopotaenia*. A manipulative experiment using artificial territories indicated that this pattern was not due to the difference in the location of the territories on the reef profile, despite the fact that the general surveys found that this species was most abundant on the Reef Base where the *D. prosopotaenia* territories were located (Figure 2.8). These results suggest that *H. melanurus* may have discriminated between the two types of territories on the basis of their microhabitat characteristics (see Figures 3.5, 3.8 & 3.9). Further manipulative studies are now required using different types of artificial microhabitats in both habitat zones to test this hypothesis.

In addition to using the territories as recruitment sites, some labrids, especially *C. schroederi*, continued to use them as feeding sites as adults (see also Klumpp & Polunin 1989), and the damselfish appeared to tolerate this behaviour. For example, *C. schroederi* were observed to spend half of their time in territories, yet they were rarely chased by the resident damselfish. This may be because *C. schroederi* are neither trophic competitors (feeding on benthic invertebrates: Myers 1989), disruptive feeders nor a threat to egg clutches (see above). This is in contrast to another labrid, *Thalassoma lunare*, which is a known egg predator (Myers 1989) and which was chased more frequently by both species of damselfish.

Scarids also used the territories as recruitment sites, but they left the territories when they were quite small (no individuals >20mm were recorded within territories during censuses). Circumstantial evidence suggests that scarids are actively excluded by the resident damselfish at this size. Damselfish did not chase small scarid recruits (<20mm TL: see also Bellwood 1986), but both *D. prosopotaenia* and *D. perspicillatus* chased juvenile scarid intruders (20mm to 40mm TL; *pers. obs.*). This change in damselfish behaviour coincides with the scarids' transition from carnivory to herbivory (Bellwood 1986, 1988) when they become trophic competitors with the damselfish. Alternatively, it may not be energetically rewarding to try to exclude smaller recruits, because they may be able to avoid the damselfish, because of their small size and cryptic behaviour (see Sale *et al.* 1980; Robertson & Polunin 1981).

Labroid recruits may benefit from living within damselfish territories in a number of ways. Firstly, the territories harbour a rich and abundant source of potential prey, in the form of microinvertebrates which are much less abundant on the adjacent substratum. Secondly, recruits in territories may benefit from the protection from predators afforded by the cover of macroalgae (Jones 1984a), or the aggressive behaviour of the damselfish. Alternatively the recruits may not benefit from this behaviour, because their densities are much higher in these "preferred" microhabitats (see Section 1.1). The costs and benefits of living within damselfish territories will be further examined in Chapter 5.

Use of damselfish territories by labroid recruits results in an overall higher recruitment to areas that have aggregations of these species. It is therefore interesting to ask whether these patterns are translated into local differences in adult abundances, or whether they are modified by post-settlement processes (growth, mortality or movement) to another form. This question will also be examined in Chapter 5.

As suggested by Green (*in press*), the territories provide an excellent opportunity for such studies because recruits of some species are present in high densities, where they are easy to locate and monitor over time. Moreover, the territories have a number of attributes in common with patch reefs, which make them ideal as replicated units of habitat for ecological studies. They are discrete, and separated by patches of bare substratum. They are also abundant both within and among sites, so it is possible to have access to replicated study populations using territories at a number of spatial scales. The territories also provide a good opportunity for manipulative field experiments, by either manipulating the algae or resident damselfish, or by using artificial territories. Finally the territories occur in such a wide range of habitats (exposures and depths), that they can be used by a range of ecological studies.

Territories will be particularly useful for studies of recruitment of these species because the recruits are present in high densities. This was clearly demonstrated by the repeated measures analysis which detected significant differences in recruitment rates throughout the summer. As a result, power of statistical analyses will be greater in territories than it is in other microhabitats where low densities have resulted in low power in the past (see Eckert 1984, 1985a,b). One of the problems of low power is the lack of ability to discriminate between patterns. For example, labroid recruitment showed a pronounced peak in *D. prosopotaenia* territories, which was less pronounced in other microhabitats which have been used to monitor labroid recruitment in previous studies (eg. Eckert 1984, 1985a,b).

Territories also provide a source of species which are rare as recruits. In some cases the only reliable source of newly settled individuals of some species are damselfish territories (see also Green *in press*). Thus the territories provide not only discrete study populations of abundant species, they are also valuable source of individuals of rare species, for studies of their early post-settlement biology.

Chapter 4

PATTERNS OF RECRUITMENT OF LABROID FISHES TO DAMSELFISH TERRITORIES.

4.1 INTRODUCTION

Recruitment of coral reef fish is characterised by a high degree of temporal and spatial variability (see Richards & Lindeman 1987; Doherty & Williams 1988). Previous studies have demonstrated that patterns of recruitment variability may not be disrupted by post-settlement processes, such as density-dependent mortality, and may be an important determinant of adult population size (see review in Doherty & Williams 1988; Doherty & Fowler 1994; but see Jones 1991).

To date the majority of recruitment studies have concentrated on species of a single family, the Pomacentridae (Doherty & Williams 1988), and it has been suggested that this family can be used as a model for studies of reef fish recruitment (Doherty 1983a, 1991). However, pomacentrids have a distinctive suite of reproductive characteristics, which may influence their recruitment patterns (see Section 1.1). For example, spawning occurs during a limited period each month, which is strongly associated with lunar phase (see Doherty 1983b; Robertson *et al.* 1990; Meekan *et al.* 1993). The larvae of many species remain in the plankton for a relatively invariant number of days before settling onto the reef (Brothers *et al.* 1983; Robertson *et al.* 1988; Wellington & Victor 1989; but see Thorrold & Milicich 1990). The result is that pomacentrid recruitment is characterised by high magnitude pulses of short duration, which are strongly associated with lunar phase (Robertson *et al.* 1988; Doherty & Williams 1988; Meekan *et al.* 1993; Milicich *in press*).

Labroids have a different set of reproductive characteristics, which may influence their recruitment patterns. Most labroids don't show strong lunar periodicity in spawning (see Robertson & Hoffman 1977; Warner & Robertson 1978; Hunte von Herbing & Hunte 1991; Colin & Bell 1991), and some have extremely variable planktonic larval durations (Brothers *et al.* 1983; Victor 1986b,c; Cowen

1991). The result is that labroid recruitment is characterised by low to moderate recruitment rates over many weeks and lunar phases (Eckert 1985b; Victor 1986a, *in press*; Hunte von Herbing & Hunte 1991; Robertson 1992).

To date only two major recruitment studies have focused exclusively on labroid fishes (Eckert 1984, 1985a,b; Victor 1983b, 1984, 1986a, *in press*), although others have also made important contributions (Williams & Sale 1981; Sale 1985; Hunte von Herbing & Hunte 1991; Robertson 1992; Planes *et al.* 1993). It is now apparent that labroid recruitment is characterised by a high degree of temporal variability at a range of scales (among years and months) for both tropical (Doherty & Williams 1988) and temperate species (Jones 1984b; Kishiro & Nakazono 1991). Despite this variability, some predictable temporal patterns are apparent.

Labroid recruitment is seasonal on the GBR, with the majority of species recruiting during the austral summer (Russell *et al.* 1974; Talbot *et al.* 1978; Williams & Sale 1981; Eckert 1985b). However at least one labrid, *Pseudolabrus guentheri* (=*P. guntheri*), is known to recruit during winter (Talbot *et. al.* 1978). Recruitment seasonality appears to be less pronounced in the Caribbean (Victor 1986a), with some species recruiting throughout the year, although most show peaks in either the wet or dry seasons (Victor 1986a, *in press*).

Within recruitment seasons, labroid recruits appear sporadically with peaks separated by periods of no recruitment, although the calendric timing of these pulses differs from year to year (see Eckert 1985b; Sale 1985; Victor 1986a). Species also differ in the timing, magnitude and duration of pulses (Eckert 1985b; Victor *in press*). Temporal recruitment patterns of only one labrid (*T. bifasciatum*) have been examined in sufficient detail to detect lunar periodicity, and this species shows only a loose association with lunar phase, recruiting throughout most of the lunar cycle with highs around new moon and lows around full moon (Victor 1986a; Hunte von Herbing & Hunte 1991; Robertson 1992).

Variation in labroid recruitment is also evident at a range of spatial scales (see Doherty & Williams 1988), showing high variability among reefs in the same geographic areas, among habitats within the same reef, and among microhabitats within the same habitat for both tropical (Williams & Sale 1981; Eckert 1984, 1985a,b; Victor 1986a; Planes *et al.* 1993; Sections 2.4, 3.4) and temperate species (Jones 1984b).

This picture of labroid recruitment is based on only a few species at a few geographic locations, and is heavily biased towards the labrid genus *Thalassoma* (see Section 1.1). There is now a need to determine if these recruitment patterns are representative of labroid recruitment in general, by studying recruitment of more species at more locations. This has proved difficult, because the recruits are very small and cryptic, and hard to locate in many microhabitats (Green *in press*). Recruits of many species are also difficult to study because they are present in such low densities in most microhabitats, that monitoring studies are not cost-effective.

In Chapter 3, I described how the territories of damselfish belonging to the genus *Dischistodus*, provide a valuable opportunity for studying the recruitment of three abundant labroids: two labrid species (*C. schroederi* and *H. melanurus*) and a group of five closely related scarid species (*Scarus* spp.). The objectives of the current study are two-fold. First, to demonstrate that these territories can be used for intensive studies of labroid recruitment. Second to describe the temporal and spatial patterns of recruitment of these three taxa. Particular attention will be given to the following questions:

i. Do these labroids show distinct recruitment pulses during the summer recruitment season at Lizard Island?

ii. If so, how does the timing, duration and magnitude of these pulses vary temporally (during 2 consecutive summers) and spatially (among sites along 2km of reef edge)?

iii. Is there any evidence of lunar entrainment of temporal recruitment patterns of these species?

iv. Do different species show similar temporal patterns of recruitment?

Results will be discussed in the context of temporal patterns of use of damselfish territories by these fishes, which may have important consequences for their early post-settlement ecology.

4.2 MATERIALS AND METHODS

Labroid recruitment was monitored during two recruitment seasons (summers of 1991/92 and 1992/93). Each summer ten territories were haphazardly selected, labelled and measured at each of three sites for each damselfish species (Washing Machine A, Washing Machine B and North Reef C for *D. prosopotaenia*; and Washing Machine B, North Reef C and Bommie Bay for *D. perspicillatus*: see Figure 2.1, Section 3.2). Each territory was discrete and had a well developed stand of macroalgae (Figures 3.6, 3.7, 3.9). Territories were marked with numbered metal stakes, and their size and shape mapped onto underwater paper. The area of each territory was later estimated using a digitiser (see Section 3.2). Labroid recruitment was monitored to each territory (see Section 3.2.2) during 8 weekly counts from November 1991 to January 1992, and 11 weekly counts from November 1992 to February 1993. Counts were ended prematurely in mid-January 1991/92, because of storm damage to the territories. Counts were standardised to a common density of fish.10m^{-2}.

Temporal recruitment patterns were analysed using time-series analysis (see Chatfield 1979). Data from the two years were concatenated according to the lunar calendar, to produce a contiguous time series which increased the power of the analyses (Milicich *in press*). Two counts (new moon and first quarter in December 1992/93) were excluded from the period of overlap. The result was a single time series of 17 consecutive weeks (by lunar phase) for each species, which was analysed using the Mesosaur Time Series Analysis Package (Kuznetsov & Khalileev 1991).

4.2.1 Temporal recruitment patterns

Temporal recruitment patterns in each type of damselfish territory were compared using cross-correlation analysis for each taxa, after filtering to remove autocorrelations (see Chatfield 1979; Meekan *et al.* 1993; Milicich *in press*). Autocorrelations were inspected using an autocorrelation function (ACF), which was calculated based on successive Pearson's correlation coefficients as the time-series is lagged across itself. A series of strong positive autocorrelation coefficients detected at low lags, implied that neighbouring points were autocorrelated. Ninety-five percent confidence intervals were calculated using the formulae recommended by Chatfield (1979). An autocorrelation was removed from one time series (*C. schroederi*) by fitting a (1,1,0) ARIMA (integrated auto-regressive moving-average) model to the data, since recruitment patterns tend to be auto-regressive in nature (M. Milicich *pers. comm.*) and the model was a good fit to the data set. After the model had been fitted, the ACF of the residuals was inspected to confirm that all significant autocorrelations had been removed. Temporal recruitment patterns detected using the two types of damselfish territories were then examined using a cross-correlation function (CCF; Chatfield 1979) for each taxa, based on methods used by Milicich *et al.* (1992) and Milicich (*in press*). This function is analogous to the ACF, except that correlation values are computed between two separate data sets as one is lagged across the other. Positive and significant correlations at some lag give a measure of how much the peaks in the two data sets are offset from each other. For example, if a significant correlation was found at a lag of 2, then the recruitment peaks detected within the two types of territories occurred two weeks apart. Confidence intervals (95%) were approximated as for the ACF. Cross-correlations were made using the raw data for time series in which no significant autocorrelation was detected, and using the model residuals from the time series in which autocorrelations were removed. Calculated ACF or CCF values that fell outside of 95% confidence intervals were considered significantly different.

Temporal recruitment patterns of three taxa was also compared using cross-correlation analysis, by comparing the time series for each pair of species. Prior to this analysis, an autocorrelation was removed from one time series (*C. schroederi*: see above).

Lunar entrainment of recruitment was also tested by fitting a four-weekly seasonal model to the time series for each taxa. Prior to analysis, time sequences were transformed using (log [x+1]), since large fluctuations in the magnitude of recruitment may override the ability to detect deterministic lunar cycles (see Milicich *in press*). However while this transformation does elevate the magnitude of minor pulses, it may also have the side-effect of elevating the level of background noise in the data (Milicich *in press*). As such, significant leakage away from a lunar signal may be due more to the elevated noise level than to the timing of replenishment events. For this reason it was necessary to examine the raw data time-series while interpreting the results of these analyses.

4.2.2 Spatial recruitment patterns

Spatial patterns in the timing of recruitment of each species between pairs of sites were examined using cross-correlation analysis with 95% confidence intervals. Autocorrelations were removed from three time series (*C. schroederi* at Washing Machine B; *S.* spp. at Washing Machine A; and *S.* spp. at North Reef C), by fitting the ARIMA models (1,1,0), (1,0,0) and (1,0,0) to the data sets respectively.

Spatial patterns in the magnitude of recruitment at each site, were analysed using a repeated measures multivariate analysis of variance (MANOVA) for each species in each recruitment season (1991/92 and 1992/93). This method was used because the analysis treats dates as separate dependent variables, which best accommodates for the likelihood of autocorrelation between counts from the same territories through time (Tabachnick & Fidell 1989). Pillai's Trace test statistic was used, and one data set (*Coris schroederi* in 1991/92) was transformed by log (x+1), because of unequal variances.

4.3 RESULTS

4.3.1 Temporal recruitment patterns

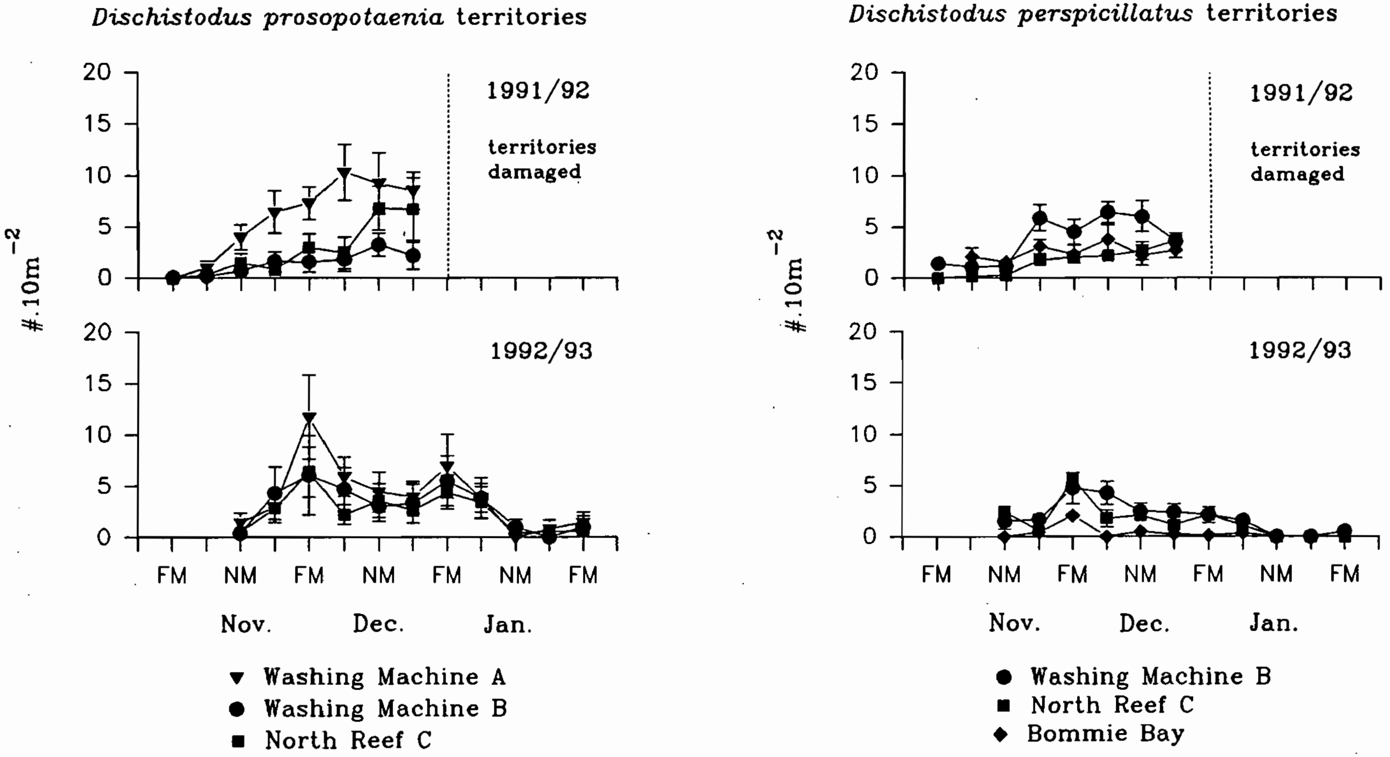
Similar temporal recruitment patterns were detected in the two types of territories for each of two taxa, *C. schroederi* and *Scarus* spp. (Figures 4.1 & 4.2), with significant cross-correlations detected at lag 0. No significant correlation was detected between the temporal recruitment patterns of *H. melanurus* from the two types of territories, because of the extremely low recruitment of this species to *D. perspicillatus* territories (Figure 4.3, Section 3.4). Hence I decided to restrict all further analyses of temporal recruitment patterns to results from the *D. prosopotaenia* territories only.

Two labrids, *C. schroederi* and *H. melanurus*, showed significantly different temporal recruitment patterns (Figures 4.1 & 4.3), which was confirmed by the lack of a significant correlation between the time series for these species. *C. schroederi* recruited in low to moderate levels for many weeks each summer from December to January (Figure 4.1). In contrast, *H. melanurus* arrived in a single pulse of high magnitude and short duration in late January each year (Figure 4.3).

C. schroederi and the scarids (*Scarus* spp.) showed similar temporal patterns of recruitment in both years (Figures 4.1 & 4.2), with a significant cross-correlation detected between their time series at a time lag of 0. In 1991/92, both species showed low to moderate levels of recruitment throughout the recruitment season, while in 1992/93 they both showed a moderate pulse in mid-December. *C. schroederi* also showed a second peak in mid-January 1992/93.

Scarus spp. and *H. melanurus* displayed a similar type of recruitment pattern in 1992/93, with both species showing a distinct, short duration recruitment pulse (Figures 4.2, 4.3). This was confirmed by the cross-correlation analyses, which found a significant correlation between the time series for these two species at a time lag of 5, indicating that the scarid pulse occurred 5 weeks prior to that of *H. melanurus* (Figures 4.2, 4.3). However they showed different patterns in

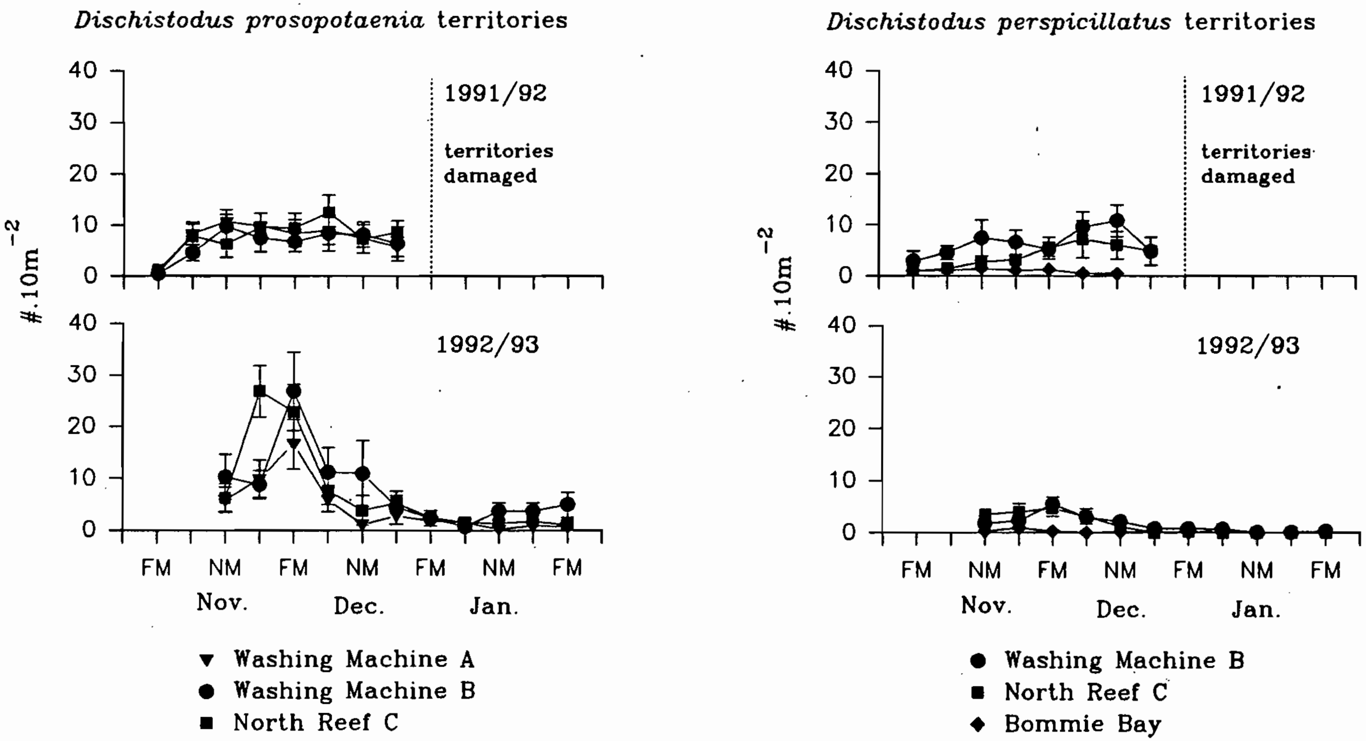
Figure 4.1.
Mean (+/- se) density of recruits of *Coris schroederi* within territories of two damselfish species during two consecutive summers at Lizard Island, with counts aligned by lunar phase. Where: NM=new moon; and FM=full moon.



Dischistodus prosopotaenia territories

Dischistodus perspicillatus territories

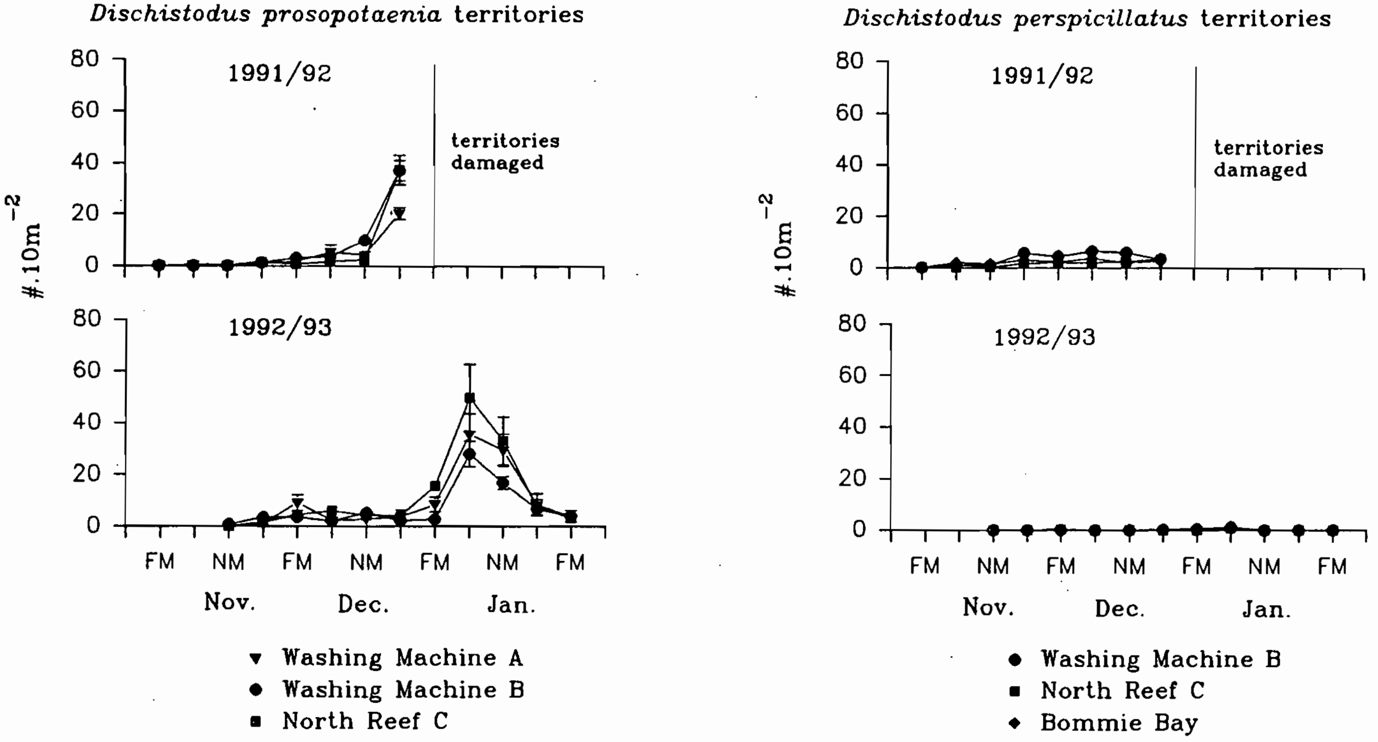
Figure 4.2.
Mean (+/− se) density of recruits of *Scarus* spp. within territories of two damselfish species during two consecutive summers at Lizard Island, with counts aligned by lunar phase. Where: NM=ne moon; and FM=full moon.



Dischistodus prosopotaenia territories

Dischistodus perspicillatus territories

Figure 4.3.
Mean (+/− se) density of recruits of *Halichoeres melanurus* within territories of two damselfish species during two consecutive summers at Lizard Island, with counts aligned by lunar phase. Where: NM=new moon; and FM=full moon.



Dischistodus prosopotaenia territories

Dischistodus perspicillatus territories

1991/92 when the scarids did not show a pronounced recruitment pulse.

No clear pattern of lunar entrainment of recruitment was detected for each labroid taxa, with no significant fit by the lunar model for *C. schroederi* ($r^2=0.0021$, $p=0.9888$), *H. melanurus* ($r^2=0.0463$, $p=0.4620$) or *Scarus* spp. ($r^2=0.0023$, $p=0.9873$). *C. schroederi* recruitment occurred in low to moderate rates throughout the lunar cycle, but was highest from last to first quarter in 1991/92, and showed two peaks around full moon in 1992/93. *H. melanurus* peaks started at first quarter moon in 1991/92, and last quarter moon in 1992/93. *Scarus* spp. recruited in low to moderate rates throughout the lunar cycle, with a peak occurring around the first quarter and full moon in 1992/93.

4.3.2 Spatial recruitment patterns

Recruitment pulses of the *C. schroederi* occurred at all three sites within a period of one week of each other (Figure 4.1), which was confirmed by significant cross-correlations among sites at lags of -1, 0 or 1 (Table 4.1). The differences between sites may have been due to 1991/92, where recruitment increased at Washing Machine A earlier than it did at the other sites. In contrast, *H. melanurus* pulses occurred simultaneously at all three sites in each year (Figure 4.3), which was confirmed by a significant correlation among all pairs of sites at time lag 0 (Table 4.1). Scarid recruitment pulses occurred at all three sites within one week of each other (Figure 4.2), as evidenced by a significant correlation between pairs of sites at time lags of 0 and 1 week (Table 4.1). The lag of 1 week was probably because the scarid pulse occurred one week earlier at North Reef C than it did at the other two sites in 1991/92.

Table 4.1. Cross-correlation analyses comparing temporal patterns of recruitment of each of the three labroid species, *C. schroederi*, *H. melanurus* and *Scarus* spp., to *D. prosopotaenia* territories at three study sites. Lag (in weeks) at which any 2 data sets correlate are given for different site combinations per species. Where: WMA=Washing Machine A, WMB=Washing Machine B and NRC=North Reef C.

site combination	lag of significant correlation		
	C. schroederi	*H. melanurus*	*Scarus* spp.
WMA X WMB	0 1	0	0
WMB X NRC	0	0	0 1
WMA X NRC	-1 0	0	0 1

Magnitude of recruitment of *C. schroederi* was significantly different among sites in the 1991/92 (Table 4.2), because recruitment was higher at Washing Machine A and North Reef C than it was at Washing Machine B in that year (Figure 4.1). In contrast, there was no significant difference in the magnitude of *C. schroederi* recruitment among the three sites in 1992/93 (Figure 4.1).

No significant difference was found in the magnitude of recruitment of *H. melanurus* among the three sites in 1992/93 (Table 4.3). However, a significant interaction was detected between the magnitude of recruitment at a site and the date of the census in 1991/92, because the relative recruitment rates to the three sites differed throughout the summer (Figure 4.3), especially among the weeks of low recruitment.

No significant difference was found in the magnitude of scarid recruitment to the three sites throughout the 1991/92 summer (Table 4.4). However, a significant interaction was detected between the magnitude of recruitment at the three sites and the date of the census in one year only (1992/93), because recruitment occurred one week earlier at North Reef C than at the other two sites (Figure 4.2).

The results of these MANOVAs confirmed that the magnitude of recruitment of each of the three labroid species, was significantly different at different dates throughout each summer (Tables 4.2, 4.3 and 4.4).

Table 4.2: Two repeated measures MANOVAs for determining the relationship between site and the magnitude of recruitment of *C. schroederi* within *D. prosopotaenia* territories at Lizard Island, during each of two recruitment seasons (1991/92 and 1992/93 respectively).

source in 1991/92:	df		F	p
between-subjects effects:				
site	2		6.74	0.0042
error	27			
	Num df	Den df	F	Pillai's Trace
within-subjects effects:				
date	7	21	8.86	0.0001
date*site	14	44	1.57	0.1273

source in 1992/93:	df		F	p
between-subjects effects:				
site	2		0.49	0.6152
error	27			
	Num df	Den df	F	Pillai's Trace
within-subjects effects:				
date	10	18	3.76	0.0071
date*site	20	38	0.63	0.8664

Table 4.3: Two repeated measures MANOVAs for determining the relationship between site and the magnitude of recruitment of *H. melanurus* within *D. prosopotaenia* territories at Lizard Island, during each of two recruitment seasons (1991/92 and 1992/93 respectively).

source in 1991/92:	df		F	p
between-subjects effects:				
site	2		3.32	0.0514
error	27			
	Num df	Den df	F	Pillai's Trace
within-subjects effects:				
date	6	22	28.16	0.0001
date*site	12	46	2.12	0.0339

source in 1992/93:	df		F	p
between-subjects effects:				
site	2		1.92	0.1668
error	27			
	Num df	Den df	F	Pillai's Trace
within-subjects effects:				
date	10	18	5.82	0.0006
date*site	20	38	1.79	0.0600

Table 4.4: Two repeated measures MANOVAs for determining the relationship between site and the magnitude of recruitment of *S.* spp. within *D. prosopotaenia* territories at Lizard Island, during each of two recruitment seasons (1991/92 and 1992/93 respectively).

source 1991/92:	df		F	p
between-subjects effects:				
site	2		0.26	0.7720
error	27			
	Num df	Den df	F	Pillai's Trace
within-subjects effects:				
date	7	21	4.35	0.0040
date*site	14	44	0.77	0.6928

source 1992/93:	df		F	p
between-subjects effects:				
site	2		1.46	0.2506
error	27			
	Num df	Den df	F	Pillai's Trace
within-subjects effects:				
date	10	18	3.71	0.0076
date*site	20	38	1.96	0.0363

4.4 DISCUSSION

This study demonstrates that damselfish territories provide the means to monitor the recruitment of some labroids, which have been difficult to study in the past (see Section 1.1, 3.4). Previous studies of labroid recruitment have been based on monitoring patches of reef or rubble (Williams & Sale 1981; Sale *et al.* 1984b; Sale 1985; Eckert 1984, 1985a,b; Victor 1986a). These patches serve the same purpose as territories in the present study, as some species (*T. bifasciatum*) recruit to them in high densities (Victor 1986a). However, most labroids show no such specificity, and recruit in very low numbers to these areas. By using patch reefs and rubble/sand areas as study units, previous studies may have had inadequate power to describe recruitment variability of some labrids such as *C.*

schroederi (eg. Eckert 1984, 1985a,b: Williams & Sale 1981; see Section 3.4). In contrast, high densities of recruits of *C. schroederi, H. melanurus and Scarus* spp were recorded in this study (see Figures 4.1, 4.2, 4.3)., which provided good power to discriminate between temporal and spatial recruitment patterns.

Temporal recruitment patterns

Each of the three labroids showed distinctive temporal patterns of recruitment throughout the study. *C. schroederi* recruited in low to moderate densities throughout most of the summer, with peaks occurring in mid-summer (December/January). Similar temporal patterns of recruitment have also been described for this species on One Tree Island on the southern GBR (Eckert 1985b).

Scarids also recruited in low to moderate densities for many weeks each year at Lizard Island. However, they also showed a distinct peak in early summer (late November - early December) in 1992/93. Similar patterns of scarid recruitment have also been recorded for the southern GBR (Sale 1985). However caution should be exercised when comparing these patterns, since more than one species is involved, and it is unclear whether the pulses detected in both areas are produced by the same species (see Section 3.4).

In contrast to the two other taxa, most *H. melanurus* recruited during a single, distinct pulse of high magnitude and short duration, which occurred in late summer (mid to late January) each year. This peak in late January was also evident in 1990/91 summer (A. Green *unpubl. data*). These pulses were more similar to those described for pomacentrids, than they are to most labroids (see Eckert 1985b; this study). No comparative data is available on the temporal patterns of recruitment of this species elsewhere on the GBR, although some information is available on the recruitment of a temperate congeneric species (*H. tenuispinus*) in Japan, which also recruits in a single, high magnitude pulse each year (Kishiro & Nakazono 1991).

No clear pattern of lunar entrainment was detected in labroid recruitment patterns at Lizard Island. These results were consistent with those of other workers on the southern GBR, French Polynesia and in the Caribbean (see Eckert 1985b; Sale 1985; Planes *et al.* 1993; Victor *in press*), who also reported no obvious patterns of lunar entrainment. However these studies, including the present one, may lack the temporal precision (ie. weekly counts over few seasons) necessary to detect a lunar pattern, unless it is strong (see Robertson 1992; Milicich *in press*). Only three studies have monitored labrid recruitment with high temporal precision (ie. daily counts of *T. bifasciatum*), of which two found that recruitment peaks were loosely associated with lunar phase (Victor 1986a; Robertson 1992) and one did not (Hunte von Herbing & Hunte 1991).

At present, little is known about spawning periodicity and larval duration of species used in this study. However, limited data from other locations indicate that these species show non-lunar patterns of larval production (Colin & Bell 1991), and have less variable planktonic durations than other labroids such as *Thalassoma* (Brothers *et al.* 1983; Victor 1986b,c). Therefore, it is likely that the lack of lunar periodicity in labroid recruitment detected in this study, may be a reflection of the lack of lunar periodicity in larval supply (see also Hunte von Herbing & Hunte 1991). More intensive concurrent studies of larval production, planktonic larval duration and recruitment of labroids are clearly required, to determine the processes that are important in determining their temporal patterns of recruitment.

The temporal recruitment patterns of the three labroid taxa in this study resulted in their being present in their highest densities in territories at different times, although there was some overlap between species. This may have important consequences for their early life history, since all three taxa are ecologically similar during the first few weeks of benthic life when they all feed on microcrustaceans (Bellwood 1988; see Section 5.4), and many studies have shown the importance of competition to reef fish recruits (see review in Jones 1991; Section 1.1). Similarly, the low to moderate recruitment of two of the species may have also decreased the potential for intra-specific competition in territories. The relationship between recruit density and early post-settlement ecology will be discussed further in Chapter 5.

Spatial recruitment patterns

Differences in the magnitude of recruitment to three sites within a distance of 2km was apparent for only one species, *C. schroederi*. It is possible that territories at one site were in a better position to receive incoming larvae than were the other two sites. However this is unlikely, since the other two species did not show similar patterns. Alternatively, larvae may have actively selected for some characteristic of the territories at Washing Machine A, which differed to those at the other two sites. This is possible since the territories at this site were located on bommies on the Sand Flat, while those at the other two sites were established at the Reef Base. Selection for territories at Washing Machine A by *C. schroederi* may have been due to an over-riding influence of habitat selection by this species for the Sand Flat. This suggestion is supported by the results of Chapter 2 (see Figure 2.8), which showed that this species was more abundant on the Sand Flat than Reef Base. In contrast to *C. schroederi*, *H. melanurus* and *Scarus* spp. showed no difference in the magnitude of recruitment among sites.

Minor differences were detected in the timing of *C. schroederi* and *Scarus* spp. recruitment pulses among sites. Victor (1986a) also recorded similar differences in the timing of labrid recruitment pulses to sites within a small area, which he suggested was the product of random processes operating at that scale. Similarly, it is likely that random processes were responsible for the minor differences detected in the timing of recruitment in this study.

In addition to variation in recruitment among sites, labroids also showed a relatively high degree of variation among replicate territories within a site (over a distance of 30 meters). This may be because some territories were colonised by larvae settling in small groups (particularly the scarids), as has been suggested for some schooling species (Shulman 1984; Doherty & Sale 1985; Breitburg 1991).

Alternatively, the differences may have been the result of microhabitat selection by the larvae at the time of settlement (Victor 1986a) for small-scale differences in microhabitat among individual territories. Another alternative is that, these differences may have been caused by the influence of the prior residents on the rate of settlement by larvae (Sweatman 1985; Jones 1987b, 1991; Sweatman & St. John 1990). The territories offer an excellent opportunity for future manipulative experiments to test such hypotheses.

Chapter 5

POST-SETTLEMENT ECOLOGY OF LABROID FISHES IN DAMSELFISH TERRITORIES

5.1 INTRODUCTION

Many species of reef fish show pronounced patterns of microhabitat use after settlement (Williams 1980; Sale *et al.* 1980, 1984a; Shulman 1984). Labrids are no exception, with many tropical species showing strong association with microhabitat features such as topography (Doherty & Sale 1985), or substratum type (Eckert 1985a,b; Victor 1986a; Chapter 3 this study). In Chapter 3, I demonstrated that some labrids were present in significantly higher densities within stands of macroalgae in damselfish territories than they were in adjacent microhabitats (Figures 3.11, 3.12, 3.13). Similar patterns have also been described for temperate labrids, where juveniles were present in their highest densities within stands of kelp (Jones 1984a,b; Levin 1991).

Patterns of microhabitat use by juveniles may have important consequences for their post-settlement ecology (see review in Jones 1991), which may have three possible outcomes:

1. Patterns of microhabitat use are reinforced by post-settlement processes.

Individuals which live in damselfish territories may benefit in terms of their early post-settlement diet, growth and survivorship. Damselfish territories harbour a rich and abundant source of food for juveniles, which is much less abundant in adjacent microhabitats (see Table 5.1). Juvenile labrids in territories may benefit from increased prey abundances by spending less time searching for food, consuming more prey or by eating a higher proportion of preferred prey species (see Ivlev 1961; Kislalioglu & Gibson 1976; Stoner 1979). Dietary benefits may then be translated into enhanced growth of juveniles within territories, which may ultimately result in higher survivorship because fishes which grow at faster rates may be vulnerable to predators for shorter time periods (see Jones 1984c; Forrester 1990; Sweatman & St. John 1990).

Juveniles may also benefit from living in territories by increased survivorship, as a result of increased protection from predators by the shelter provided by the macroalgae (Jones 1984a), or by the aggressive behaviour of the damselfish (who may chase away potential predators). In this scenario, positive benefits of microhabitat use may serve to reinforce spatial patterns of distribution of juveniles, and ultimately result in higher local abundances of adult labrids in the vicinity of damselfish territories. A similar situation has previously been demonstrated for a pomacentrid by Jones (1986), who showed that growth and survival of *Pomacentrus amboinensis* juveniles were higher in their "preferred" microhabitat.

Table 5.1. Summary of the density of *Coris schroederi* and *Halichoeres melanurus* recruits (see Figures 3.11, 3.13), and the availability of food (copepod density: Figure 3.10) and shelter (algal biomass: Figure 3.8) in four microhabitats: *Dischistodus prosopotaenia* territories, *D. perspicillatus* territories, reef matrix and rubble/sand patches.

	D. pros.	*D. pers.*	reef matrix	rubble/ sand
C. schroederi (#.10m^{-2})	moderate (<4)	moderate (>1.5)	low (<0.5)	low (<0.5)
H. melanurus (#.10m^{-2})	high (>12)	low (<0.5)	low (<0.5)	low (<0.5)
copepods (#.10cm^{-2})	moderate (>70)	very high (>2000)	low (<5)	low (<5)
algae (g.10cm^{-2})	high (>250)	high (>250)	low (<1)	low (<1)

2. Patterns of microhabitat use are modified by post-settlement processes.

A second scenario is that the use of damselfish territories by juveniles may have a negative effect on their early post-settlement ecology, because of increased intra-specific competition at higher densities (see review in Jones 1991). This is likely, since many studies have found an inverse relationship between density and growth (and maturation) for reef fish including labrids (see Victor 1986a; Hunte & Cote

1989; Jones 1991; Booth 1992). Similarly, an inverse relationship has also been recorded between juvenile density and survivorship for some species (see Jones 1991), including labrids (Eckert 1987; Hunte & Cote 1989; but see Victor 1986a). In this situation, negative density-dependent effects may act to modify patterns of microhabitat use by juveniles, resulting in lower abundances of adult labrids in the vicinity of damselfish territories. Such a scenario has been described for a pomacentrid, here initial patterns of juvenile densities were found to be modified by negative density-dependent growth (Jones 1987a). Spatial patterns of microhabitat use by juveniles can also be modified by other post-settlement processes, such as movement (Jones 1984a; Robertson 1988a,c).

3. Patterns of microhabitat use are unchanged by post-settlement processes.
In contrast to the first two scenarios, microhabitat use by juvenile labrids may have no consistent effect on their post-settlement growth or survivorship. In this situation, patterns of adult abundances would be unaffected by post-settlement processes and be a direct reflection of recruitment patterns, which has previously been recorded for both labrids (Victor 1986a) and pomacentrids (Doherty 1983a; Doherty & Williams 1988; Doherty & Fowler 1994).

The primary objective of this study is to determine which of these scenarios best describes the post-settlement ecology of two labrids, *Coris schroederi* and *Halichoeres melanurus*, at Lizard Island. Particular attention was will be given to the following questions:

i. Is early growth and survivorship of *C. schroederi* and *H. melanurus* similar in damselfish territories and other microhabitats?

ii. Is the diet of *H. melanurus* similar inside and outside of damselfish territories?

iii. Are patterns of higher recruitment to areas with damselfish aggregations translated into higher local abundances of adults, or are they modified by post-settlement processes?

5.2 MATERIALS & METHODS

This study was done at four study sites on the northeastern side of Lizard Island (see Section 3.2), during the summer of 1992/93.

5.2.1 Comparison between juvenile diet, growth and survivorship in damselfish territories and adjacent microhabitats

Diet

Diet of *H. melanurus* recruits <15mm in standard length (SL) was quantified within each of two microhabitats: *D. prosopotaenia* territories and reef matrix (see Section 3.3.1). Ten individuals were collected from each of 3 territories and 3 areas of reef matrix, at each of two sites (Washing Machine B and North Reef C) in January 1993. These individuals were fixed in 50% saltwater (s/w) formalin immediately after capture, and then preserved in 10% buffered s/w formalin. Specimens were later returned to the laboratory, where they were dissected and their intestines removed. Intestinal contents were examined microscopically following methods detailed in Bellwood (1988). Prey items were identified to the lowest known taxa (usually order), after which they were counted and measured using a calibrated eye-piece graticule. Uncommon taxa such as anemones and echinoderms were lumped as "others". Prey items were later assigned to one of eleven size length classes, with 10 size classes with intervals of 0.4mm from 0mm to 4.00mm, and then >4.00mm.

Prey densities were also quantified in each microhabitat by collecting samples from three replicate 10cm^2 quadrats within each of three territories and three patches of reef matrix (quadrats) where fish were collected, at each of the two sites (see Section 3.2.2 for methods). Invertebrates within each sample were also identified, counted, measured and assigned to size categories as described above.

Patterns of selectivity for prey taxa by juveniles of *H. melanurus* were examined by comparing the relative abundance of each prey taxa within each microhabitat (*D. prosopotaenia* territories and reef matrix) with their relative abundance within the stomachs of resident juveniles. Selectivity for prey size was also tested by comparing the relative proportion of "preferred" prey (copepods) in each size category in both types of microhabitat, and within stomachs of the resident juvenile.

The diet of *H. melanurus* juveniles was then compared between microhabitats based on stomach contents. First the proportion of prey in each taxa or size class was compared using a Chi-square test for heterogeneity. Second, the number of prey items was compared using a nested analysis of variance, with sites (n=2) nested within microhabitats (n=2).

Growth

Estimates of growth of *C. schroederi* and *H. melanurus* were based on otolith microstructure. Otolith increment formation was validated for each species by capturing 101 *C. schroederi* and 68 *H. melanurus* recruits (<15mm SL) and retaining them in aquaria for 24 hrs. Otoliths were then marked by immersing the fish in an aerated antibiotic/seawater solution (see Schmitt 1984) in complete darkness for 24hrs (see Fowler 1989). Relatively low doses of the antibiotic (tetracycline) were used (125 mg/l and 154 mg/l for *C. schroederi* and *H. melanurus* respectively), because these species were intolerant of higher doses. They were then retained in outside aquaria for 8 days under a natural regime of water temperatures and light cycles, before the treatment was repeated.

Twenty-four hours after the second treatment, fish were killed and preserved in 70% ethanol. Specimens were dissected and the second largest pair of otoliths, the lapilli, were removed (see Victor 1982, 1986a). Lapilli were used because previous studies found that they were most suitable for counting daily otolith increments of labrids (Victor 1982; 1986a,b,c). Otoliths were cleaned then "roasted" on a hot plate for 2 minutes to darken the protein component of the increments before being permanently mounted on microscope slides using a polystyrene based, non-fluorescent medium (D.P.X.: British Drug Houses). Exposure to light was minimised during the procedure. Lapilli were later examined under a high power fluorescence microscope for a fluorescent mark deposited by the antibiotic treatments (Schmitt 1984; Pitcher 1988), and under a high power tungsten light for a dark band caused by the associated 24hrs of darkness (Victor 1982; Fowler 1989). The number of increments between the marks denoting the two treatments were then counted using high magnifications (400-1000x) and a polarising light source (see Victor 1982). The number of increments counted between the marks and the number of days elapsed were then compared.

Spatial and temporal patterns of growth of each species was described by collecting a size range of juveniles ($\leq$30m SL) from each of two sites (Washing Machine B and North Reef C) in February 1993. Within each site, juveniles were collected from each of three microhabitats for *C. schroederi* (*D. prosopotaenia* territories, *D. perspicillatus* territories and rubble/sand patches) and two microhabitats for *H. melanurus* (*D. prosopotaenia* territories and reef matrix). A similar size range was also collected for each species from *D. prosopotaenia* territories at each of these sites in 1991/92.

Each specimen was measured (SL to nearest 0.1mm) and preserved in 70% ethyl alcohol. Lapilli were removed and processed as described above, except that they were mounted using Euparol (see Fowler 1989). Age since settlement was determined by counting the number of daily increments on the lapilli between the settlement mark and the edge of the otolith (see Victor 1982).

Analysis of covariance was used to test for the influence of microhabitat on the early post-settlement growth of each species at each site. When slopes were not found to be significantly different, differences in elevation were tested by comparing mean size at age of juveniles, adjusted for microhabitat (see Underwood 1981). Since a significant influence of microhabitat on growth was found (see Section 5.3), growth was compared between sites for each microhabitat separately. Growth was also compared between two years based on *D. prosopotaenia* territories only.

Survivorship

Survivorship was estimated by censusing *C. schroederi* and *H. melanurus* recruits and juveniles within replicate territories or quadrats of each of 6 microhabitats (*D. prosopotaenia* territories and adjacent shallow reef matrix and rubble/sand patches; *D. perspicillatus* territories and adjacent deep reef matrix and rubble/sand patches) at each of three sites at 11 weekly intervals throughout 1992/93 (see Section 3.2.2). Similar estimates from the same *D. prosopotaenia* territories were made in 1991/92.

The number and size of all juveniles were estimated during each census. My ability to estimate size was continually calibrated by catching juveniles and measuring them *in situ* (by restraining them in a plastic bag). Recruits grew quickly (see this study), so it was possible to use size, as well as colouration, to differentiate between individuals that were only a few days apart in age. Therefore, residents within each study unit could be identified by their estimated size (see Victor 1986a) and their survivorship monitored through time.

Since study units were censused at weekly intervals, each fish was first recorded as a recruit, which had arrived in the last one to seven days. Therefore, survivorship during the first week of benthic life is overestimated (see Eckert 1987). Older individuals present at the start of the study were ignored.

I assumed that a juvenile of a given species seen at the same location over several weeks was the same juvenile (see Sale & Ferrell 1988). If it ceased to be present at that site, it was assumed to have died. This approach assumed that each individual being monitored remained sedentary after settlement, and that it had a high chance of being seen if present. Therefore, my measure of survivorship may include some migration.

The confounding influence of emigration was not monitored directly, because recruits were too small to tag (<10mm SL). However an estimate of the movement of recruits was attained by monitoring the number of known emigrants to the study units throughout the 1991/92 summer. Emigrants were identified as individuals that were present in the territory during a census, that had not been detected as recruits in previous censuses.

Low numbers of emigrants were detected (9.5% for *C. schroederi* and 5.0% for *H. melanurus*). Emigrants were older recruits (>25mm SL), with those of *C. schroederi* larger (mean=32.3mm, se=0.14, n=39) than those of the *H. melanurus* (mean=27.0 mm, se=0.17, n=34). The size of emigrants indicated that both species started to move between study units >60 days after settlement (see results), which suggested that comparisons of survivorship of these species using these methods should be restricted to the first 60 days of benthic life. This result was supported by observations of known individuals, which remained in the same location for >3 months throughout the study (*pers. obs.*).

Since individual fish settled at various times during a summer, data obtained for any given census represented information on the survival to different ages of each fish present (see Sale & Ferrell 1988). Therefore, the data was rearranged to generate a cohort of equal-aged individuals (irrespective of arrival time) to determine the pattern of survivorship (see Cox & Oakes 1984; Sale & Ferrell 1988).

Survivorship (survival distribution function) was calculated using the Life Table Method for monitoring the same individuals through time using discrete time intervals (when the actual time of death is unavailable: see Kalbfleisch & Prentice 1980). This technique includes right-censored data (individuals that are still alive at the end of the study period: see Kalbfleisch & Prentice 1980; Cox & Oakes 1984), because longer-lived individuals are generally more likely to be censored and could not be ignored (see SAS 1985).

Survivorship was compared among microhabitats, sites, years and species using a nonparametric Log Rank Test (Savage exponential scores test), which determines if survivorship distributions could have arisen from identical survival functions (see Kalbfleisch & Prentice 1980). This test was used because it does not assume an underlying exponential survivorship distribution (SAS 1985). Tests were done using SAS statistical package (SAS 1985). Where a significant difference was detected between survival functions, multiple pairwise comparisons were done to detect which functions were significantly different using an adjusted error rate (see Section 1.1).

Survivorship of each taxon was compared among sites (n=3) based on *D. prosopotaenia* territories, because it was the only microhabitat where the survivorship of >25 individuals per species was monitored at each site (see Sale & Ferrell 1988). Survivorship of *C. schroederi* was also compared between years using *D. prosopotaenia* territories. Comparisons were not made between years for *H. melanurus*, because censusing of this species was discontinued in January 1991/92 because of storm damage to the territories (Figure 4.3; see Section 4.2).

Survivorship was compared among microhabitats used by each species. Microhabitats used by *C. schroederi* were *D. prosopotaenia* and *D. perspicillatus* territories and shallow and deep rubble/sand patches (Figure 3.11), and those use by *H. melanurus* were *D. prosopotaenia* territories and shallow reef matrix (Figure 3.13).

Since no significant difference was detected between survivorship of *C. schroederi* in the same microhabitat at different sites (see results), data from all three sites were combined to compare survivorship of this species among microhabitats. However, since a significant difference was detected between survivorship of *H. melanurus* at each of the three sites, survivorship was compared between microhabitats at each site separately. Survivorship of the two species was also compared in *D. prosopotaenia* territories, at each of the three sites.

5.2.2 Comparison between local adult abundances in areas with and without damselfish territories

Density (#.100m^{-2}) of adult *C. schroederi* and *H. melanurus* were quantified within large areas (>250m^2) with and without aggregations of each damselfish species at three sites (see Section 3.2), by mapping the size and position of each adult onto scaled maps of each area (maps drawn as described in Section 3.2.1). Size of the area was later estimated using a digitiser (see Section 3.2.1), and the density of adults.100m^{-2} was calculated for each area. Density of adults of each species was compared between areas with and without aggregations of each damselfish species, using a nested analysis of variance, with sites (n=3) nested within type of area (n=4).

5.3 RESULTS

5.3.1 Comparison between juvenile diet, growth and survivorship in damselfish territories and adjacent microhabitats

Diet

The selection of prey taxa by juvenile *H. melanurus* was not significantly different between *D. prosopotaenia* territories and reef matrix ($\chi^2 < 0.00$, df=1, p<1.000; Figure 5.1). However, they showed a high degree of "selectivity" for prey taxa (Figure 5.1), with the proportion of microinvertebrates belonging to each taxa significantly different between the substrate samples and the stomach contents of resident juveniles in each microhabitat (χ^2=48.37, df=2, p<0.0001 for *D. prosopotaenia* territories; and χ^2=136.10, df=1, p<0.0001 for reef matrix). Copepods comprised 98.3% and 98.8% of their diet in *D. prosopotaenia* territories and reef matrix respectively, despite the fact that they only represented 58.3% and 17.2% of the microinvertebrates in territories and reef matrix respectively. Other taxa such as tanaids, gammarids, polychaetes and molluscs were consumed in much lower proportions than their relative abundances in each microhabitat.

Juveniles also showed strong patterns of "selectivity" for size of their "preferred" prey (Figure 5.2). In each microhabitat, a higher percentage of copepods in the

Figure 5.1.
Percentage (%) of micro–invertebrates represented by each taxonomic category in *Dischistodus prosopotaenia* territories and adjacent reef matrix, and within the stomachs of juvenile *Halichoeres melanurus* resident in each of these two microhabitats.

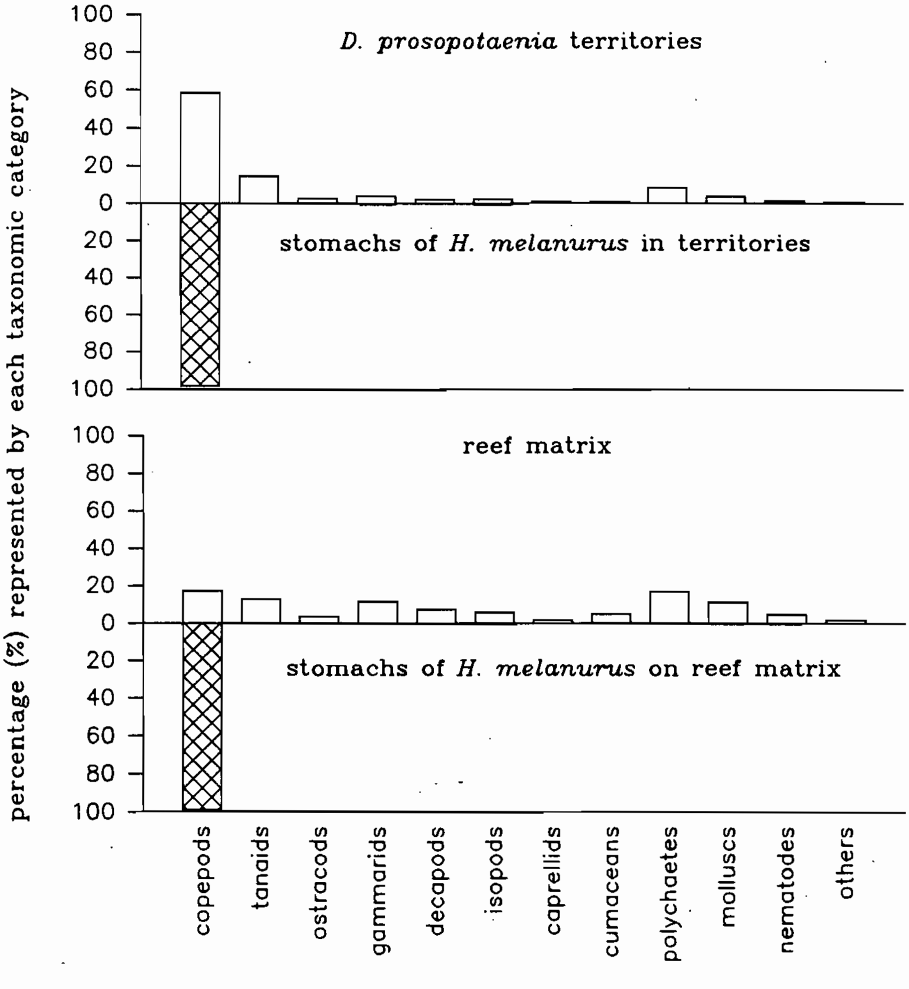


Figure 5.2.
Percentage (%) of copepods in each size class within *Dischistodus prosopotaenia* territories and adjacent reef matrix, and within the stomachs of juvenile *Halichoeres melanurus* resident in each of these two microhabitats.

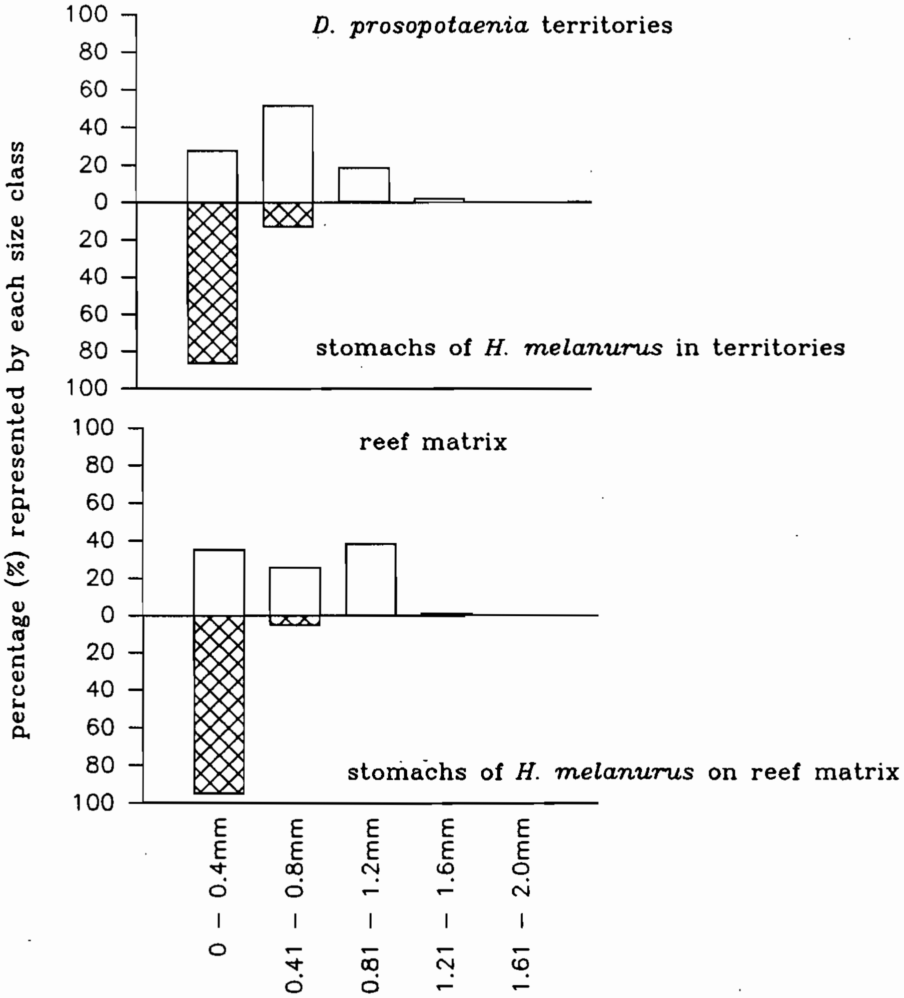
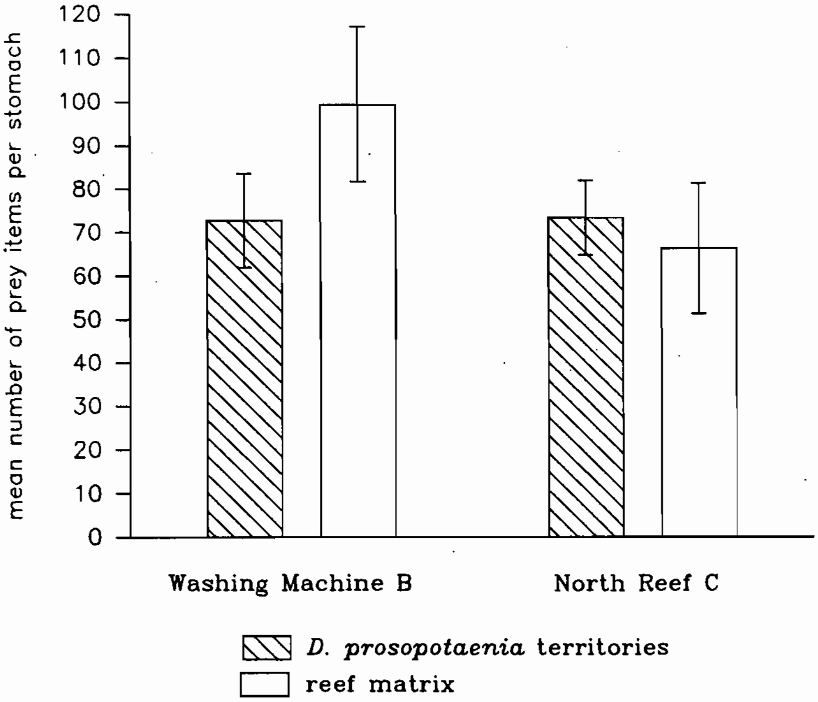


Figure 5.3.
Mean (+/− se) number of prey items in the stomachs of *Halichoeres melanurus* recruits in each of two microhabitats, *Dischistodus prosopotaenia* territories and reef matrix, at each of two sites.



smallest size category (<0.4mm) were present in *H. melanurus* stomachs (86.5% and 94.7% for territories and reef matrix respectively), than they were on the substratum itself (27.8% and 25.1% respectively). Prey size was also significantly different between fishes in different microhabitats ($\chi^2=3.91$, df=1, $p<0.0480$), with individuals from territories eating a higher proportion of larger copepods (0.41 to 0.8mm) than were present on the reef matrix (13.0% and 5.2% respectively). This may have been because there was a significantly higher proportion of microinvertebrates in the second size class in territories than there was on reef matrix ($\chi^2=16.04$, df=2, $p<0.0003$).

In contrast, no significant difference was detected in the number of prey items in stomachs of *H. melanurus* recruits in different microhabitats (Table 5.2 & Figure 5.3). However this result should be interpreted with caution, since the analysis did detect a significant nested effect (site), which was probably because the number of prey items in stomachs was higher on the reef matrix than in the territories at Washing Machine B, while the opposite pattern occurred at North Reef C.

Table 5.2. Nested analysis of variance testing for the influence of microhabitat (*D. prosopotaenia* territories and reef matrix) on the number of prey items in the stomachs of juvenile *H. melanurus*.

source	df	MS	F	p
microhabitat	1	2832.41	2.17	0.1432
site(microhabitat)	2	8236.04	6.32	0.0027
error	116	1303.69		
total	119			

Growth

Twenty-three *C. schroederi* and 43 *H. melanurus* survived the validation experiment, which deposited two marks on the otoliths at the time of treatment: one fluorescent mark produced by the tetracycline (visible under ultraviolet light); and one dark increment which was probably associated with the period of darkness (visible under tungsten light: see Victor 1982; Schmitt 1984; Pitcher

1988; Fowler 1989). The mean number of otolith increments between the two tetracycline marks ranged from 6-9 for *C. schroederi*, with a mean of 7.5 (95% confidence limits: 7.07 - 7.93). Similarly, the mean number of increments between the two marks ranged from 6-9 for *H. melanurus*, with a mean of 7.4 (95% confidence limits: 7.13 -7.67). As such, the number of increments deposited on otoliths of each species, was slightly lower than the number of days (8) that had elapsed between treatments.

Patterns of spatial and temporal growth of labrid juveniles were complex. No significant difference was detected in the slope of growth curves of *C. schroederi* in different microhabitats at either site (Figure 5.4: Table 5.3). However there was a significant difference in the mean size at age of this species, adjusted for microhabitat (intercept) at each site. Multiple comparisons revealed that *C. schroederi* grew at a significantly faster rate within *D. prosopotaenia* territories than within territories of *D. perspicillatus* at each site. *C. schroederi* also grew significantly faster within each type of territory than it did on rubble/sand patches at Washing Machine A, but not at North Reef C. In contrast, *H. melanurus* did not grow at a significantly different rate in the two microhabitats studied at either site (Figure 5.5: Table 5.3).

No significant difference was detected in growth of *C. schroederi* or *H. melanurus* at different sites in either of the three microhabitats (Figures 5.4 & 5.5: Table 5.4). *H. melanurus* grew significantly faster in 1991/92 than it did in 1992/93, but *C. schroederi* grew at the same rate each year (Figure 5.6; Table 5.5).

C. schroederi and *H. melanurus* also grew at significantly different rates in each year, although the species which grew faster differed between years (Figure 5.6; Table 5.6). *H. melanurus* grew faster than *C. schroederi* in 1991/92, while the opposite occurred in 1992/93.

Figure 5.4.
Comparison of growth by *Coris schroederi* juveniles in *Dischistodus prosopotaenia* territories, *Dischistodus perspicillatus* territories and rubble/sand patches at each of two sites.

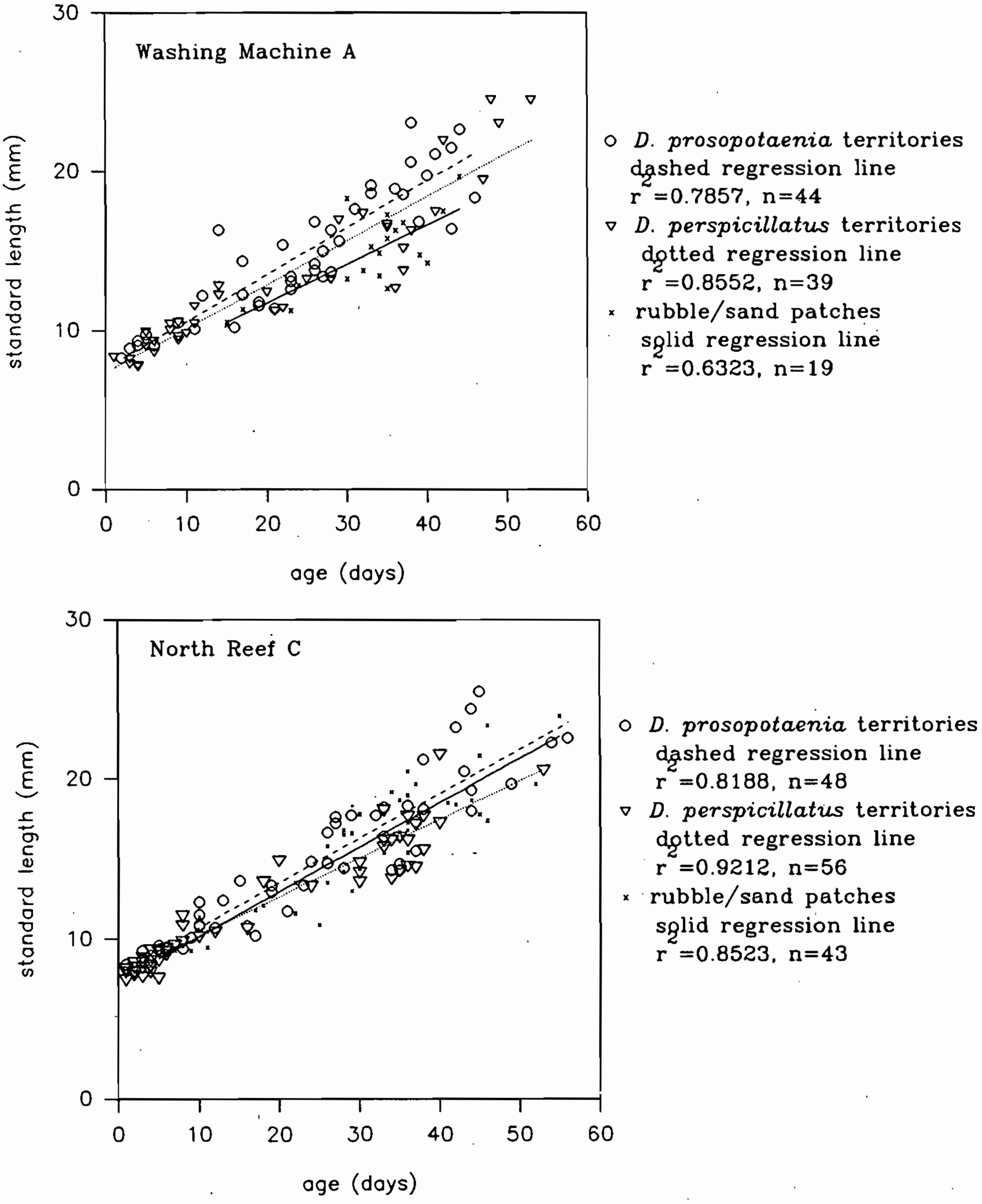


Figure 5.5.
Comparison of growth by *Halichoeres melanurus* juveniles in *Dischistodus prosopotaenia* territories and on reef matrix at each of two sites.

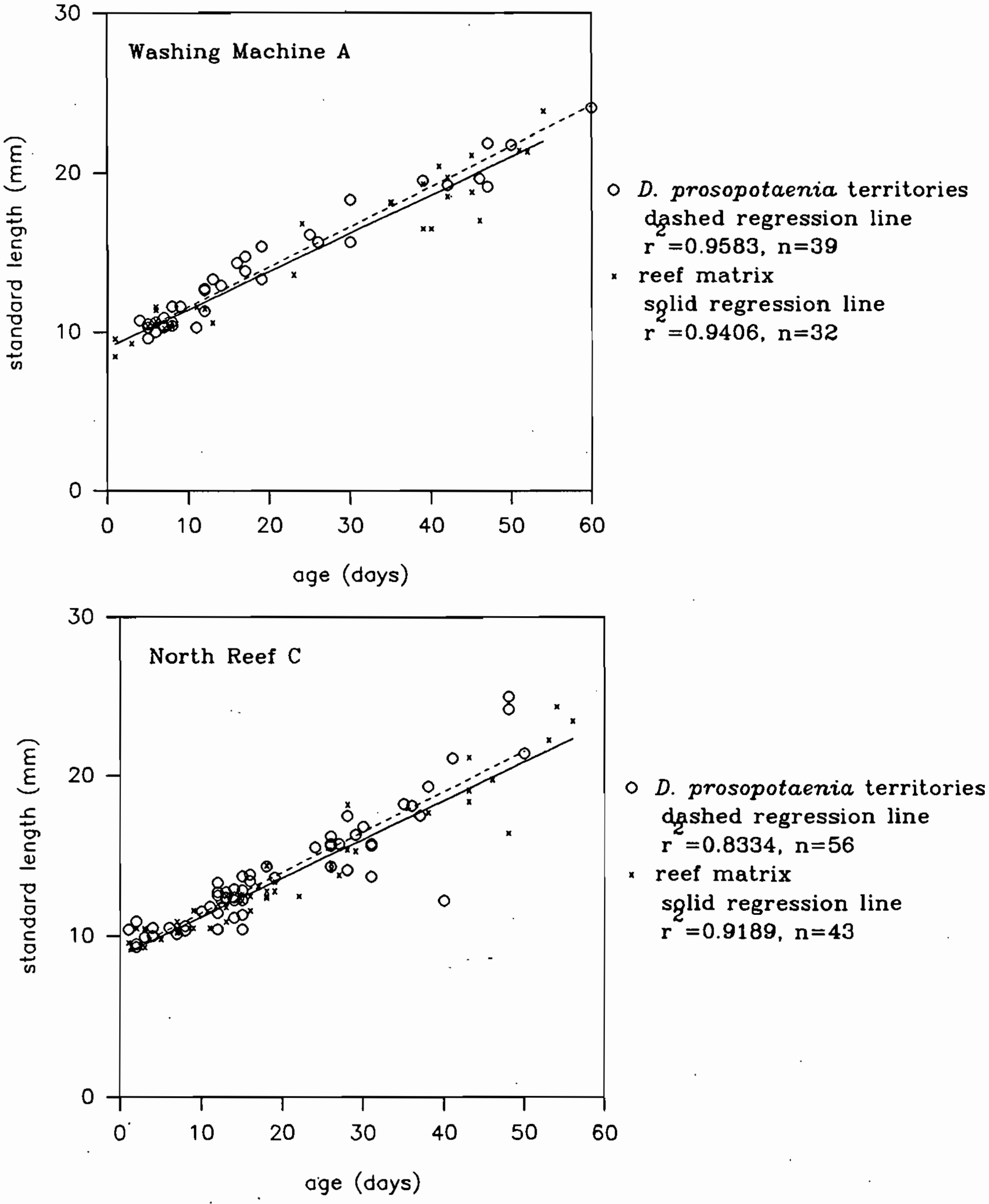


Figure 5.6.
Comparison of growth of juveniles of each of two labrid species in each of two years.

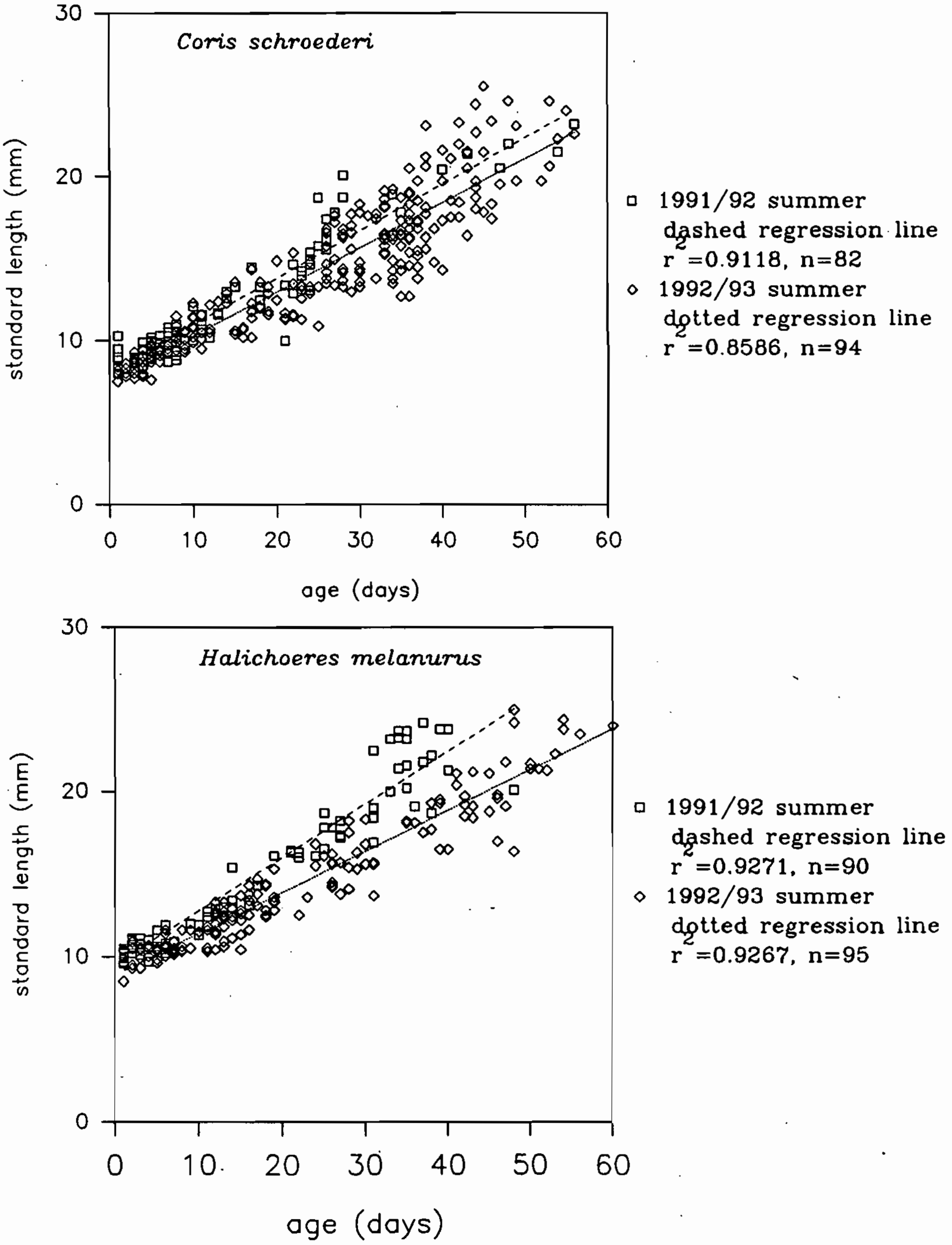


Table 5.3. Analysis of covariance of growth of *Coris schroederi* and *Halichoeres melanurus* in different microhabitats at each of two sites.

	C. schroederi			
	F	Num df	Den df	p
Washing Machine A				
slope	0.72	2	104	0.4935
intercept	12.59	2	104	0.0002
North Reef C				
slope	0.09	2	148	0.9091
intercept	7.04	2	148	0.0088
	H. melanurus			
	F	Num df	Den df	p
Washing Machine A				
slope	0.05	1	72	0.8264
intercept	0.77	1	72	0.3801
North Reef C				
slope	0.76	1	100	0.3840
intercept	0.06	1	100	0.7998

Table 5.4. Analysis of covariance of growth of *Coris schroederi* and *Halichoeres melanurus* at different sites in each microhabitats.

	C. schroederi			
	F	Num df	Den df	p
Dischistodus prosopotaenia territories				
slope	0.03	1	93	0.1838
intercept	0.53	1	93	0.4645
Dischistodus perspicillatus territories				
slope	0.32	1	95	0.5680
intercept	0.04	1	95	0.8444
rubble/sand patches				
slope	0.35	1	63	0.5602
intercept	0.12	1	63	0.7300
	H. melanurus			
	F	Num df	Den df	p
Dischistodus prosopotaenia territories				
slope	0.13	1	96	0.7228
intercept	0.10	1	96	0.7538
reef matrix				
slope	0.01	1	173	0.9071
intercept	0.01	1	173	0.9315

Table 5.5. Analysis of covariance of growth of *Coris schroederi* and *Halichoeres melanurus* in two years.

	F	Num df	Den df	p
C. schroederi				
slope	0.10	1	177	0.7579
intercept	0.49	1	177	0.4859
H. melanurus				
slope	26.10	1	186	0.0198
intercept	-	-	-	-

Table 5.6. Analysis of covariance of growth of *Coris schroederi* and *Halichoeres melanurus* in each of two years.

	F	Num df	Den df	p
1991/92				
slope	0.56	1	173	0.4524
intercept	49.28	1	173	<0.0001
1992/93				
slope	9.24	1	424	0.0270
intercept	-	-	-	-

Survivorship

Survivorship of *C. schroederi* did not differ significantly between sites (Figure 5.7: $x^2=4.12$, df=2, $p<0.1276$) or years (Figure 5.8: $x^2=2.21$, df=1, $p<0.1374$). In contrast, there was a significant difference between survivorship of *H. melanurus* at the three sites (Figure 5.7: $x^2=13.10$, df=2, $p<0.0014$). Multiple comparisons revealed that this was because survivorship of this species was significantly higher in Washing Machine A than it was at North Reef C ($x^2=13.33$, df=1, $p<0.0003$).

C. schroederi survivorship was not significantly different in *D. prosopotaenia* territories than it was on the adjacent shallow rubble/sand patches (Figure 5.9: $x^2=1.11$, df=1, $p<0.2913$). In contrast, survivorship of this species was significantly higher in *D. perspicillatus* territories than it was on the adjacent deep rubble/sand patches during the first three weeks of benthic life (Figure 5.9: $x^2=4.27$, df=1, $p<0.0389$), although a similar percentage of individuals were alive after 5 to 6 weeks (Figure 5.9). Multiple comparisons of all combinations of microhabitats revealed that survivorship of this species was also significantly higher in *D. prosopotaenia* territories than it was in either *D. perspicillatus* territories ($x^2=16.14$, df=1, $p<0.0001$) or deep rubble/sand patches ($x^2=17.18$, df=1, $p<0.0001$).

No consistent pattern was detected for survivorship of *H. melanurus* in different microhabitats at each of the three sites (Figure 5.10). Survivorship of this species was significantly higher in *D. prosopotaenia* territories than on the adjacent

Figure 5.7.
Survivorship of *Coris schroederi* and *Halichoeres melanurus* recruits in *Dischistodus prosopotaenia* territories at each of three sites.

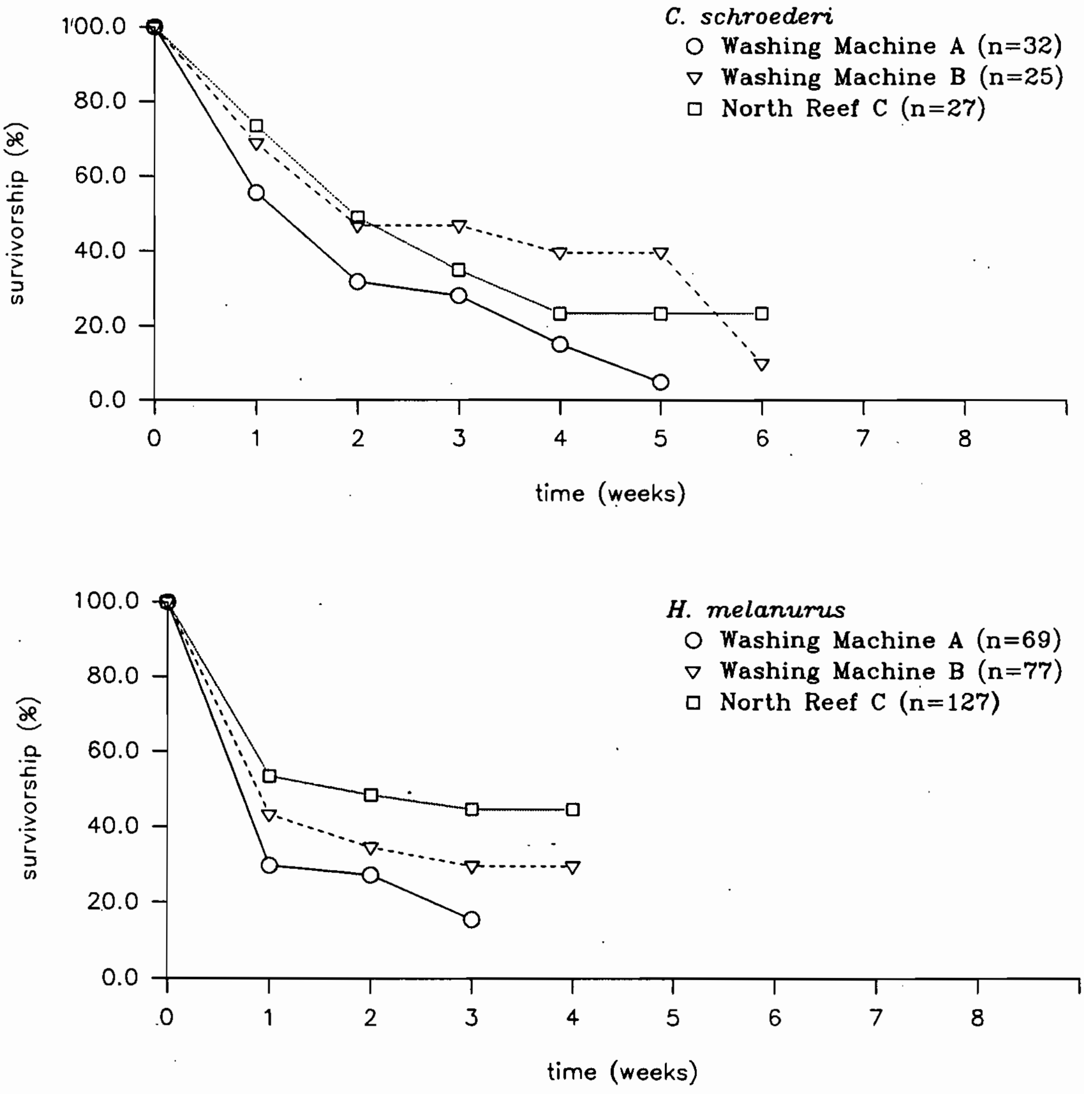


Figure 5.8.
Survivorship of *Coris schroederi* in *Dischistodus prosopotaenia* territories in two consecutive years.

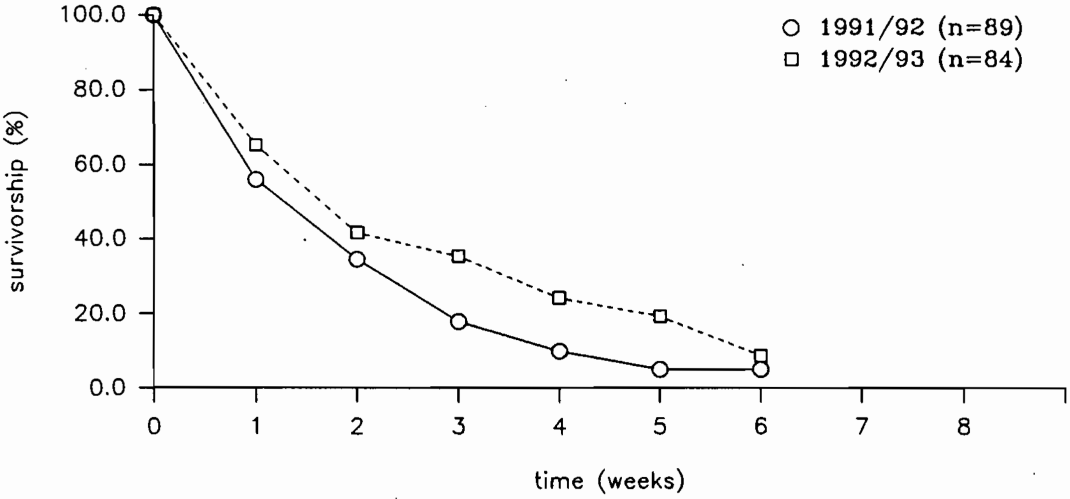
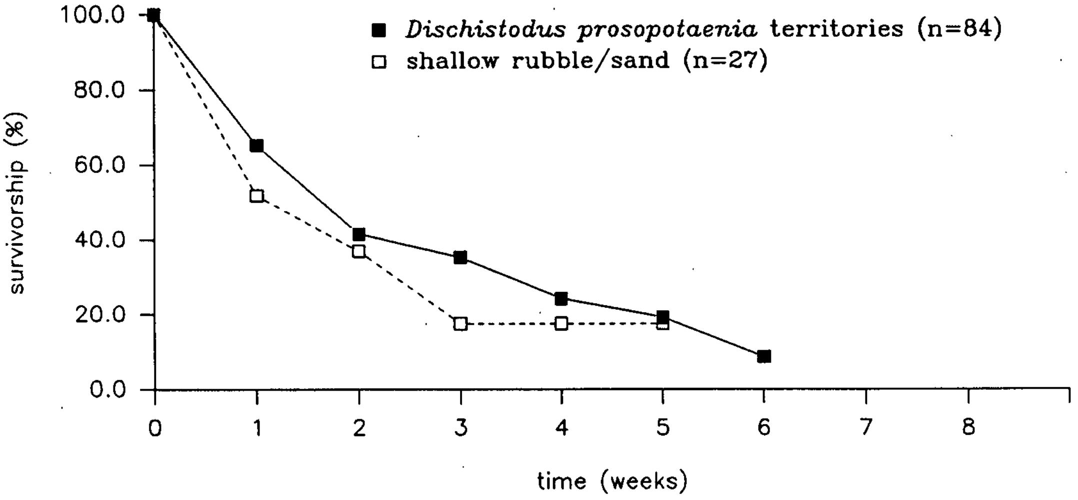


Figure 5.9.
Survivorship of *Coris schroederi* in territories of each of two species of damselfish, and adjacent rubble/sand patches.



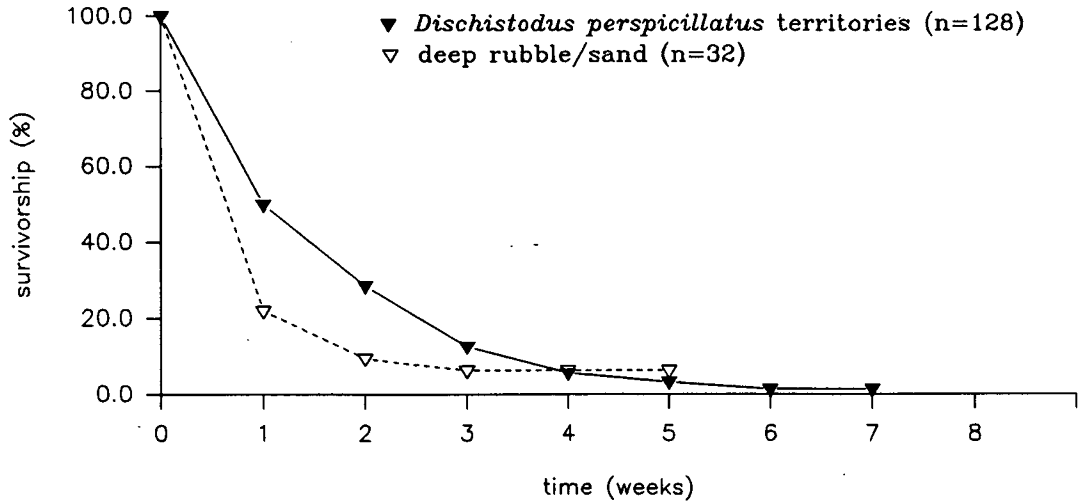


Figure 5.10.
Survivorship of *Halichoeres melanurus* recruits in *Dischistodus prosopotaenia* territories and the adjacent reef matrix, at each of three sites.

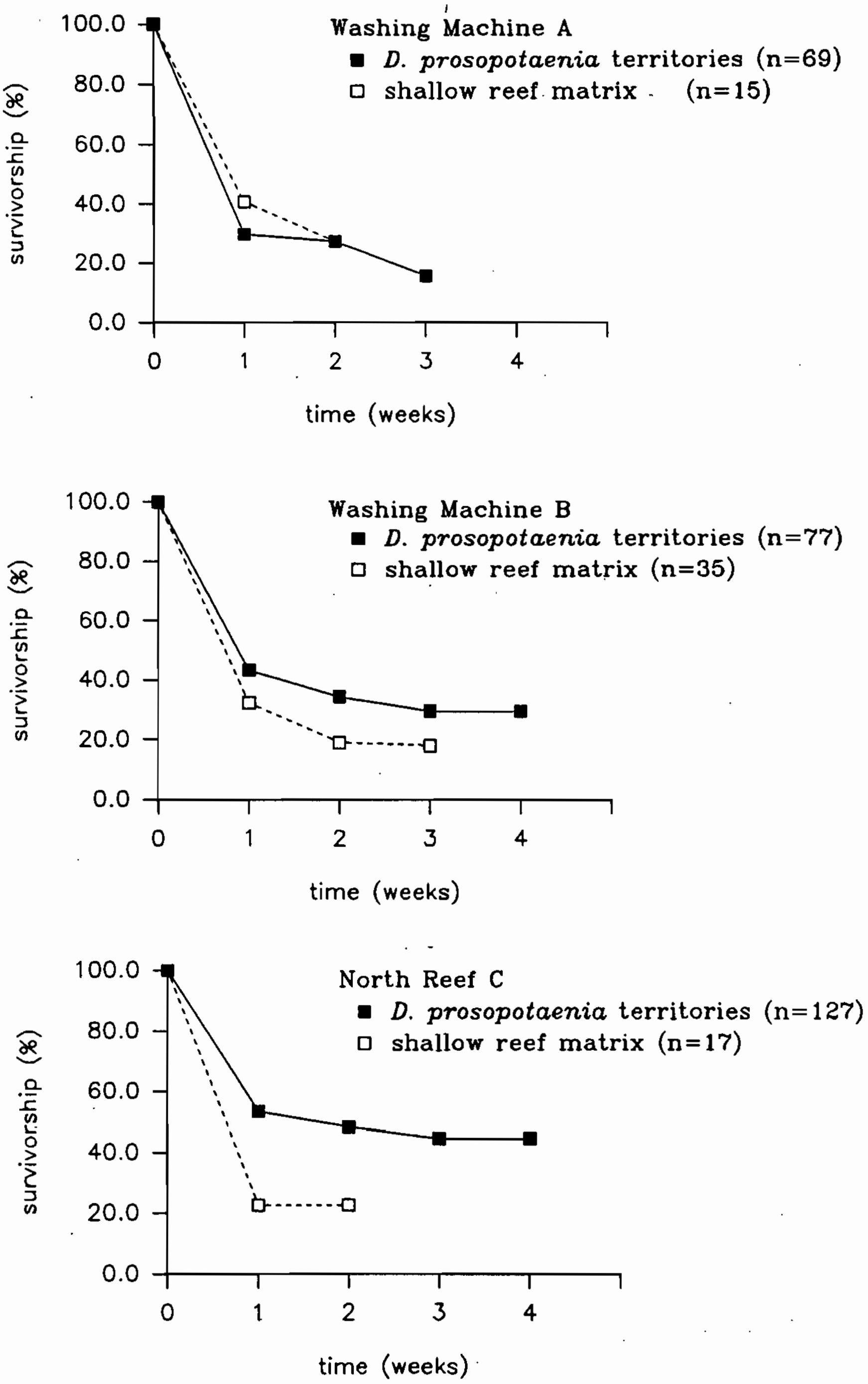
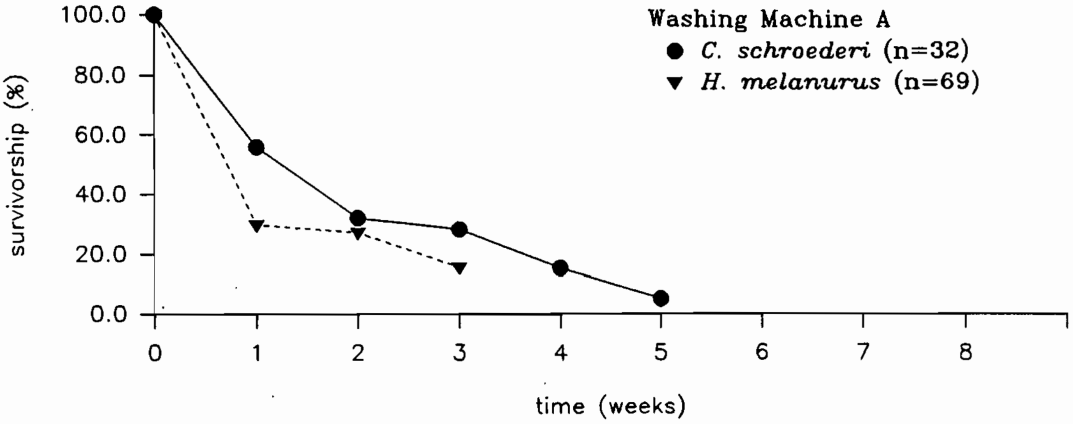
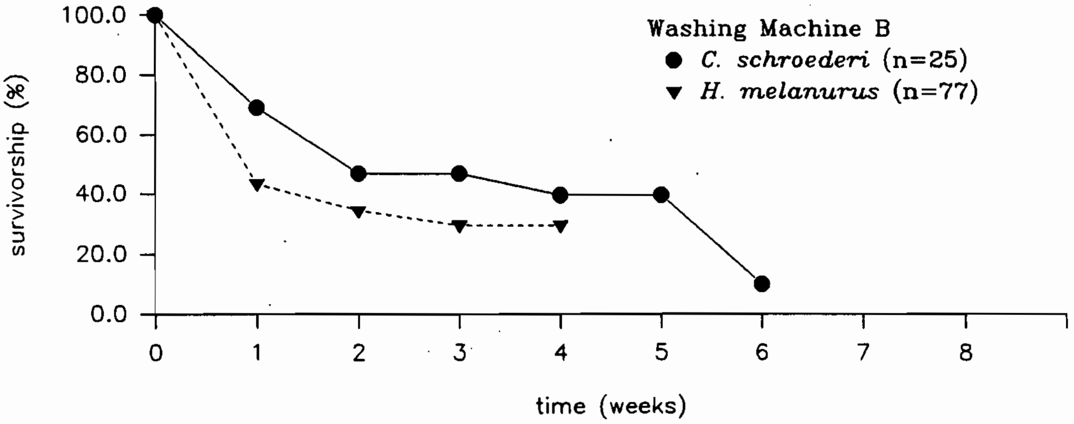


Figure 5.11.
Survivorship of *Coris schroederi* and *Halichoeres melanurus* recruits in *Dischistodus prosopotaenia* territories at each of three sites.





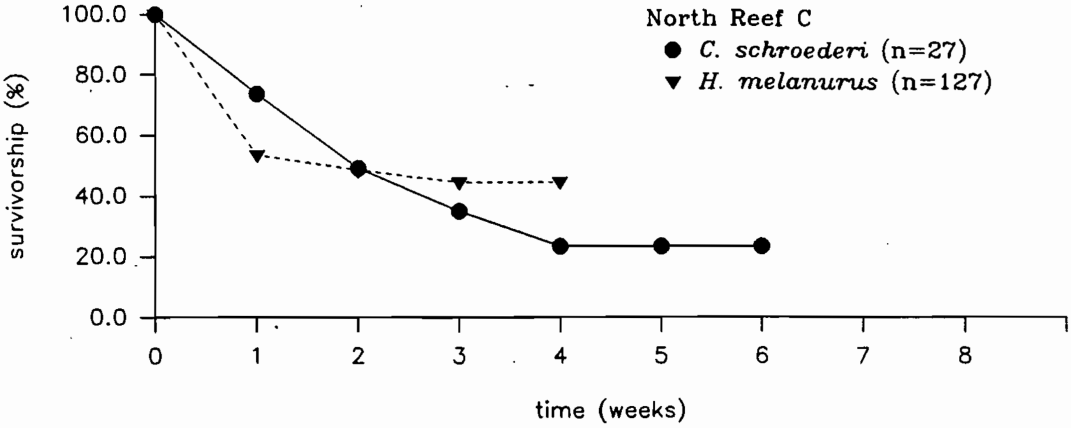
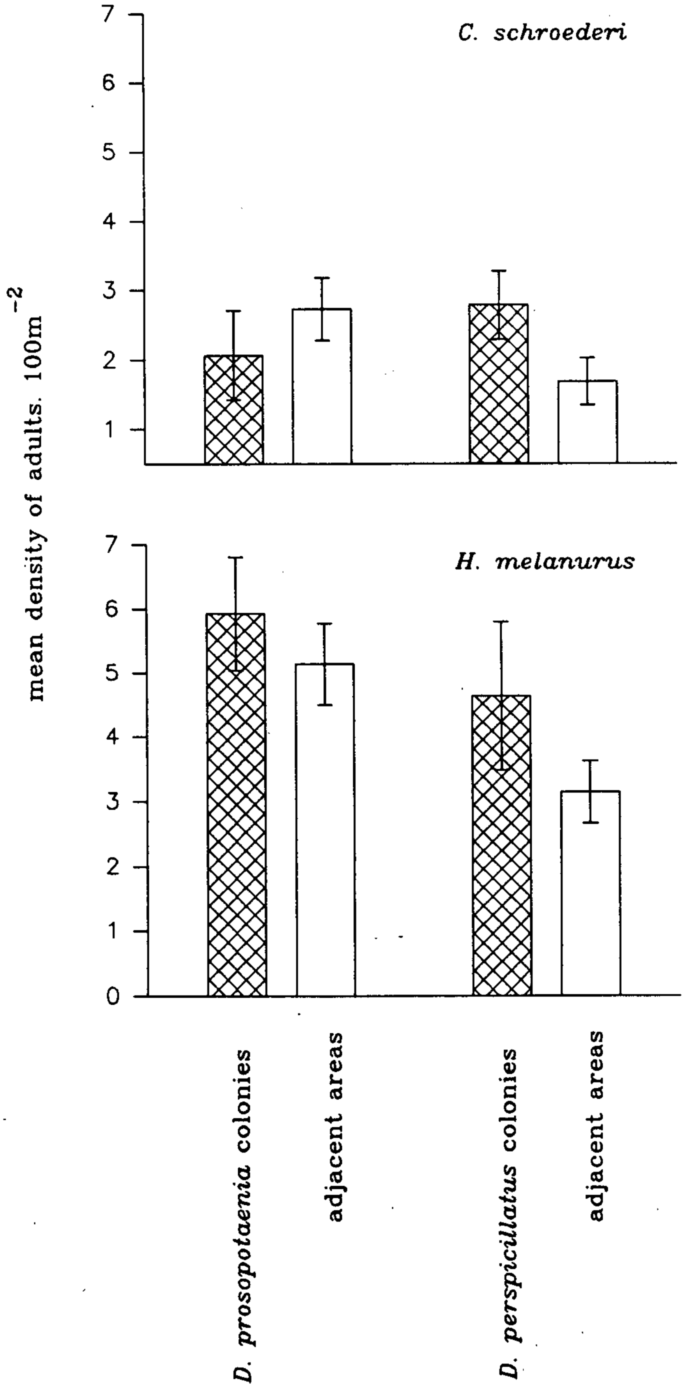


Figure 5.12.
Mean density (+/– se) of *Coris schroederi* and *Halichoeres melanurus* adults in areas with and without colonies of *Dischistodus prosopotaenia* and *Dischistodus perspicillatus*.



substratum at North Reef C ($\chi^2=4.92$, df=1, $p<0.0266$), but not at the other two sites ($\chi^2=0.50$, df=1, $p<0.4191$ at Washing Machine A; $\chi^2=1.02$, df=1, $p<0.3120$ at Washing Machine B).

No significant difference was found in survivorship of the two species at each of the three study sites (Figure 5.11: $\chi^2=0.65$, df=1, $p<0.4218$ at Washing Machine A; $\chi^2=1.88$, df=1, $p<0.0620$ at Washing Machine B; $\chi^2=0.34$, df=1, $p<0.5609$ at North Reef C).

5.3.2 Comparison between local adult abundances in areas with and without damselfish territories

Abundances of adult *C. schroederi* and *H. melanurus* did not differ significantly between areas with and without damselfish territories (F=1.42, df=11, $p<0.3064$ for *C. schroederi*; and F=2.00, df=11, $p<0.1923$ for *H. melanurus*; Figure 5.12).

5.4 DISCUSSION

Use of damselfish territories by labrid recruits resulted in no negative effects on their early post-settlement diet, growth and survivorship. These results are consistent with two of the proposed scenarios: that patterns of microhabitat use by labrid recruits are either reinforced or unchanged by early post-settlement processes. Similar results have also been described by Jones (1986), who found that a pomacentrid survived and grew better in its "preferred" microhabitat. These results are surprising given the much higher density of recruits inside than outside territories, since density has been shown to have negative effects on labrid growth (Jones 1980, 1984b; Victor 1986a) and survivorship (Hunte von Herbing & Hunte 1991; but see Victor 1986a). Negative effects of higher densities on growth and survivorship have also been reported for pomacentrids in most situations (see review in Jones 1991; Booth 1992), although two species have been shown to grow (Thresher 1983) or survive better with increased density (Thresher 1983; Jones 1988).

The results of this study can be understood in the context of resource availability and behaviour. Diet and growth of labrid recruits may not be negatively affected by higher densities in territories because prey abundances were much higher also. Moreover, the absence of density-dependent effects on growth may be related to trophic and behavioural characteristics of the study species. Most previous studies that have found negative density-dependent effects on growth have been based on either planktivorous or herbivorous pomacentrids, in which aggression among conspecifics results in asymmetric growth of individuals (*sensu* Begon 1984; Doherty 1982; Jones 1987a,b; Booth 1992). In these situations, some individuals grew much faster than others, and limited access to food by subordinate individuals by aggressive behaviour. It was not clear if asymmetric growth occurred among labrid recruits in the high densities within damselfish territories. However, in a similar scenario to that described by Doherty (1982) and Thresher (1983), juvenile labrids did show an increase in variance in mean size of juveniles as they grew, which may have indicated asymmetric growth (see review in Jones 1991). However this was unlikely, since variation in growth was not higher where density was higher. A more likely scenario is that the increase in variance with mean size in this study was an artifact of the otolith aging technique, which may be less reliable as age increases (see Meekan *in press*).

The availability of resources may also account for the absence of negative density-dependent effects on labrid survivorship within territories. For example, shelter from predators may be higher within territories than in other microhabitats. Protection from predators may result from the physical shelter afforded by the dense stands of macroalgae (Shulman 1985; Jones 1984a; Figures 3.6, 3.7), and the exclusion of predators by the aggressive behaviour of the damselfish. At present it is not possible to discern between these two factors, since the macroalgae and the damselfish usually co-occur. However, behavioural observations confirmed that damselfish do not exclude all piscivores from their territories (Figure 3.4, see Appendix III): *D. prosopotaenia* and *D. perspicillatus* chased 9.1% (n=373) and 28.8% (n=215) of piscivores from their territories respectively. One known predator of juvenile fishes, the labrid *Cheilinus diagrammus*, was only chased by resident *D. prosopotaenia* and *D. perspicillatus* on 3.2% (n=63) and 16.7% (n=24) of the occasions that it entered their territories respectively (see also Frontispiece). These data suggest that the higher survivorship of labrids within territories may be primarily due to protection afforded by the macroalgae. Similarly, differences in survivorship of pomacentrids using different microhabitats has been attributed to differences in shelter (Jones 1988). Experimental manipulations of both the damselfish and algae are required to separate the influence of these confounding effects on labrid survival in damselfish territories.

The absence of negative effects of density on post-settlement growth and survival in territories, suggests that patterns of high abundance of labrid recruits in areas with damselfish aggregations should be translated into higher local abundances of adults. However this was not the case, with similar adult densities in adjacent areas with and without damselfish aggregations. These results suggest that patterns of local adult densities are influenced primarily by post-settlement processes which occurred after the first two months of benthic life.

Ontogenetic changes in behaviour may be responsible for the similar abundances of adult labrids around damselfish aggregations and in adjacent areas. I observed that juvenile labrids formed loose aggregations with low apparent levels of aggression. However intra-specific aggression between adults were not infrequent, and appeared to associated with territorial behaviour (*pers. obs.*). For example, adult *C. schroederi* were involved in a mean of 2.9 (se=0.45, n=80) acts of intra-specific aggression per hour (A. Green *unpubl. data*)). I suggest that as these fishes grow, some individuals establish territories that encompass damselfish territories (*pers. obs.*), while others are aggressively excluded and move into adjacent areas. This scenario is similar to that described for a temperate labrid (Jones 1984a), and future studies are required to test this hypothesis by tagging recruits and following their movements throughout their lives.

The fact that different patterns of post-settlement growth and survivorship were detected at different sites and times in this study, demonstrates that these processes are dynamic and their contribution to structuring reef fish populations may vary in space and time. These results highlight the importance of spatial and temporal replication of population studies (see Jones 1991), and the dangers of extrapolating beyond the scope of the study. Large scale manipulations over space and time are now required to test if the use of damselfish aggregations as recruitment sites by labroids, results in higher local densities of labrids in these aggregations and adjacent areas.

H. melanurus showed strong patterns of apparent prey "selectivity" in this study, although the reasons for this apparent selectivity are unclear. For example, *H. melanurus* may be actively selecting copepods on the basis of their size, morphology or nutritional value (see Alheit & Scheibel 1982; Main 1985; Jones *et al.* 1991). Alternatively, *H. melanurus* may be non-selective carnivores which eat small copepods because they are most "available" prey in terms of their appearance or behaviour (see Kislalioglu & Gibson 1976; Berg 1979; Main 1985; Ryer & Orth 1987). In this study, prey size is likely to be important, since juveniles are small and have small mouths (see also Kislalioglu & Gibson 1976; Ryer & Orth 1987). However, larger invertebrates may be eaten as the fishes grow, as size-specific dietary changes are a common feature of carnivores including labrids (Bernstein & Jung 1979; Holbrook & Schmitt 1984; Jones 1984a; Schmitt & Holbrook 1984).

Many labroids feed extensively on harpacticoid copepods as juveniles (Jones 1984a; Bellwood 1988; this study), and prey selectivity by these abundant fishes raises the question of the relative importance of their predation on the population dynamics of copepods (see reviews in Choat 1982; Jones et al. 1991). In this study, it is unlikely that *H. melanurus* was having a major effect on copepod populations, because an instantaneous estimate of the number of copepods in *D. prosopotaenia* territories (mean.territory^{-1}=139,973.0, se=614.98, n=18) and in stomachs of resident fish (mean.territory^{-1}=371.2, se=686, n=18), showed that the number of prey in *H. melanurus* stomachs was <0.3% of the number remaining in the territories. However, in the absence of information on turnover rates of prey and daily intake by predators, this relationship remains unclear (see Jones *et al.* 1991). Nonetheless, I believe that territories provide an excellent opportunity for future manipulative experiments aimed at quantifying the influence of labrid recruits on prey population dynamics.

Chapter 6
GENERAL DISCUSSION

Herbivorous damselfish exclude trophic competitors and disruptive benthic carnivores from their territories (see Section 3.4). This behaviour has direct effects on benthic assemblages by increasing algal biomass (Hixon 1983; Horn 1989; Figures 3.8, 3.9) and in some cases algal species richness (Hixon 1983; Horn 1989; Figures 3.6, 3.9). Consequently damselfish have been described as keystone species which help maintain high algal diversity on coral reefs (Hixon & Brostoff 1982, 1983). However this does not apply in cases where species, such as *D. perspicillatus*, establish monospecific stands of macroalgae (Montgomery 1980a,b; Figures 3.7, 3.9).

The high algal biomass within damselfish territories may have important indirect effects on reef processes and other organisms (see reviews in Hixon 1983; Horn 1989). For instance, damselfish such as *D. perspicillatus* may increase rates of nitrogen fixation on reefs, where they increase the biomass of nitrogen fixing blue-green algae (Lobel 1980; Hixon 1983; Figures 3.7, 3.9). The presence of territories may also affect invertebrate populations (Hixon 1983; Horn 1989). Many microinvertebrates (especially copepods) are herbivores (Zeller 1988; Klumpp & Polunin 1989), and territories provide them with an abundant food resource which can be almost absent from adjacent microhabitats (Figures 3.8). The result is that microinvertebrates occur in territories at much higher densities than in adjacent areas (Lobel 1980; Hixon & Brostoff 1982; Figure 3.10). By establishing these distinct algal stands, territorial damselfish have also been shown to affect the recruitment, growth, and bioerosion of corals (see review in Horn 1989).

In some cases, territorial damselfish have been reported to benefit other species of herbivorous fish, which share their food resource (Horn 1989). In two cases, the damselfish were unable to exclude the other species from their territories because of their size-based dominance (Robertson 1984) or because they took refuge in holes (Roberts 1987). In another case, herbivorous damselfish shared the territories of larger, herbivorous surgeonfish in a mutalistic relationship (Robertson & Polunin 1981).

This study is the first to demonstrate that carnivorous fish benefit from the territorial behaviour of herbivorous damselfish (see Sections 3.4, 5.4), although Klumpp & Polunin (1989) noticed that some adult labrids fed on invertebrates within damselfish territories. In this study, both labrids and scarids were shown to use damselfish territories heavily as recruits (Tables 3.6, 3.7; Figures 3.11, 3.12, 3.13). Scarid recruits used them for the first few weeks of benthic life, before they were excluded from the territories by the damselfish (see Section 3.4). This coincided with the size at which scarids undergo an ontogenetic shift from carnivory to herbivory, and become trophic competitors to the damselfish (see Section 3.4). In contrast, some labrids continued to use these territories throughout their lives (see Section 3.4), with adult *C. schroederi* spending more than half of their time within damselfish territories (Figure 3.15).

Labrids which used damselfish territories as recruits did not show negative effects of their increased density in these "preferred" microhabitats (see Section 5.4). Indeed, the early post-settlement diet, growth and survivorship of recruits was improved in some situations in territories (see Section 5.4). These results can be understood in the context of resource availability (see Section 5.4). The carnivorous labrids did not suffer growth deficits in territories, because the density of prey (copepods) was much higher than it was in other microhabitats (Figure 3.10). Similarly, mortality may not be increased in territories, because shelter from predators was higher due to the cover afforded by the macroalgae (see Section 5.4). However, the aggressive behaviour of the damselfish may not provide protection for recruits, because not all potential predators were excluded from the territories (see Section 3.4).

These observations pose the question of whether the relationship between territorial damselfish and labrids which use their territories, is a case of commensalism or mutualism. Labrids clearly benefit from this situation (see Sections 3.4, 5.4), but do the damselfish? The presence of the labrids within the territories may be beneficial to the damselfish in at least two ways. First, labrids are carnivores and feed on benthic invertebrates within territories (Figure 5.1). Many of these invertebrates are herbivores and are present in very high densities amongst the macroalgae (Figure 3.10). Hence, they may be important trophic competitors to the damselfish (Klumpp & Polunin 1989). By feeding on them, labrids may minimise the impact of invertebrates on the algae. However, whether this impact is significant remains to be established, although it seems unlikely given high prey abundances (see Section 5.4), with possibly high turnover rates (see Jones *et al.* 1991). The damselfish may also benefit from this relationship by the importation of nutrients to the territories by the labrids. The faeces of the carnivorous labrids would contribute nutrients to the territories, which may fertilise the algae (Klumpp *et al.* 1987) or supplement the diet of the damselfish (Robertson 1982).

Alternatively, damselfish may not benefit from the presence of labrids, and the relationship may be simply commensal. Labrids may not be excluded from territories because they are not a threat to the resources that the damselfish are defending (see Section 3.4), or it may not be energetically rewarding to exclude them (Robertson & Polunin 1981). In order to examine the basis of this relationship in more detail, manipulative experiments of the algae, invertebrates and fishes would be required. Damselfish territories provide an excellent opportunity for such manipulative experiments (Green *in press*).

This study provided insights into the processes that are responsible for ontogenetic shifts in microhabitat use by some species (see Section 5.4). During the first two months of benthic life, the spatial patterns of microhabitat use by recruits were not modified by differential growth and mortality in territories and adjacent microhabitats (see Section 5.4). This suggests that recruitment patterns were modified by subsequent post-settlement processes, such as movement by older juveniles or adults (see Section 5.4). These movements may be induced by an increase in intra-specific interactions as the fishes grow (see Section 5.4). Many adult labrids established territories that encompassed damselfish territories (*pers. obs.*), which may have caused other individuals (juveniles or adults) to move out onto adjacent areas where there were no damselfish territories (see Section 5.4). However this hypothesis needs to be tested by a tagging program. Moreover, the possible benefits to adults which use territories over those that do not, also remains to be examined. Overall, these results suggest that damselfish aggregations act as important focal sites for the recruitment of labrid fishes (Figure 3.14, Section 5.4), which may result in higher local abundances of these labrids in areas with, and adjacent to, damselfish aggregations (see Section 5.4). However large scale manipulations of damselfish territories will be required to test this hypothesis, because the damselfish and labrids co-occur in most situations (*pers. obs.*).

The Value of a Generalised Model for Reef Fish Ecology based on Pomacentrid Fishes

To date the majority of studies on the early life history of reef fishes have focused on pomacentrids, and it has been suggested that they can be used as models for studying reef fish ecology in general (Doherty 1983a, 1991). The results of this study and others, highlight the differences between pomacentrids and labroid fishes (see Section 1.1), and question the validity of this assumption.

Pomacentrids and labroids have different life history characteristics, which influence their recruitment patterns (see Section 4.1). For example, pomacentrids show strong lunar cyclic patterns of reproduction and relatively invariant planktonic durations, which result in distinctive recruitment pulses of high magnitude and short duration, which are associated with lunar phase (see Section 4.1). In Chapter 4, I suggested that patterns of labroid recruitment may be inherently different to those of pomacentrids (see Sections 4.1, 4.4). Many labroids recruit in low to moderate rates over long periods, which do not appear to show strong patterns of lunar entrainment (Figures 4.1, 4.2, 4.3, see Section 4.1, 4.4). This may be because many species do not spawn over restricted, lunar cyclic breeding cycles, but do so on a daily basis over many months (see Sections 1.1, 4.1, 4.4). Moreover, many species have quite variable planktonic larval durations, which may uncouple temporal patterns of larval production and supply (see Section 4.1).

These two families also have different characteristics which influence their early post-settlement ecology. For example, pomacentrids undergo metamorphosis prior to settling onto the reef, and recruits are large and both morphologically and ecologically similar to adults (Section 1.1). As a result, most settle into adult habitats and do not show strong ontogenetic shifts in their post-settlement diet and habitat use (Allen 1991; Williams 1991). In contrast, labroid recruits undergo metamorphosis after settling onto the reef and recruits are small and very different to adults both morphologically and ecologically (Bellwood 1986, 1988; A. Green *unpubl. data*; see Sections 1.1, 5.4). For example, preliminary evidence suggests that scarids settle as carnivores and shift to herbivory after the first few weeks of benthic life (Bellwood 1986, 1988). Other morphological changes, such as development of locomotory and sensory capabilities, may also take place after settlement (McCormick 1993; McCormick & Shand *in press*). The result is that the early post-settlement phase may be crucial for labroids, since they may be especially vulnerable to predation at this time. This may explain why labroids undergo ontogenetic shifts in habitat use, using microhabitats which offer shelter during this crucial period after settlement (Victor 1983a, 1986a; Jones 1984a; Figures 5.7 - 5.11, see Section 3.4, 5.4). Shelter may become less important as labrids grow and reach a size refuge from many predators (Shulman *et al.* 1983), and older individuals may move out into other habitats as their need for shelter decreases (Jones 1984a; Victor 1986a see Section 5.4). As such, studies of the recruitment and early post-settlement ecology of pomacentrids, may not identify the processes that are important to labroids at this important time. Moreover, the difference in trophic status and associated behaviour between pomacentrids and labrids (see Section 1.1), may result in different responses of the two families in similar situations (see Section 5.4). Further intensive studies are clearly required to examine the influence of life history characteristics on recruitment and early post-settlement ecology of reef fish. Given the wide variety in life history patterns exhibited by reef fish families (see Leis & Rennis 1983; Leis 1991; Victor 1991; McCormick 1992), such comparisons should be extended to include a wider variety of taxonomic groups.

In this study, the territories of two species of damselfish at Lizard Island allowed me to examine the early life history of a selection of labroid fishes, which have been difficult to study in the past. There are many species of herbivorous damselfish (Allen 1991), and representatives occur in most shallow reefal habitats, both tropical and temperate (Horn 1989; Allen 1991). They are frequently abundant and their territories may cover high proportions of the substrate (Sammarco & Williams 1982; Klumpp *et al.* 1987; Table 3.3). As such there is potential for damselfish territories to provide opportunities for studying the early life history of many labroid species in many locations, in order to build a broader understanding of the ecology of this group. Similar situations may also be available for studying other families, which have not been identified to date. If this is true, then it may not be necessary to rely on reef fish "models" to understand the ecology of reef fish in general.

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Appendix I

PILOT STUDY OF VISUAL CENSUS TECHNIQUES FOR COUNTING ADULT LABRIDS

I.1 INTRODUCTION

Many types of visual census techniques have been proposed for describing the distribution and abundance of reef fishes (Brock 1954; Jones & Thompson 1978; De Martini & Roberts 1982; Kimmel 1985; Thresher & Gunn 1986), and methods used vary with the aims of the project (Bellwood & Alcala 1988). Strip transects were used in this study, because they have been demonstrated to provide good quantitative estimates of the distribution and abundance of many other families of reef fish (Choat & Bellwood 1985; Fowler 1987; Lincoln Smith 1988, 1989; McCormick 1989).

However, since previous studies have demonstrated that the precision of these techniques are dependent on the methods used and the nature of the study species (Sale & Sharp 1983; Fowler 1987; Bellwood & Alcala 1988; Lincoln Smith 1988, 1989), a pilot study was done to determine the methods that were appropriate for censusing adult labrids at Lizard Island. Transect dimensions and observer swimming speed were tested, because each have been described as important sources of bias in past studies (Sale & Sharp 1983; Fowler 1987; Lincoln Smith 1988, 1989). In addition, the number of replicate transects and sites necessary to achieve an acceptable level of precision was determined (see Underwood 1981; Andrew & Mapstone 1987). The chosen technique was then tested in several habitat zones and sites to determine if an acceptable level of precision was maintained by the technique in a range of situations (see Andrew & Mapstone 1987). The accuracy of underwater size estimation was also measured (see Bell *et al.* 1985).

I.2 METHODS

transect dimensions

Sixteen combinations of transect dimensions (10, 20, 30 and 50m lengths and 1, 2, 3 and 5m widths) were tested on the Crest at North Reef in August 1990. Five replicate transects of each size were done by counting and estimating the total length of each labrid along the transects, while simultaneously measuring the length (using a 50m tape), and width (using my known body proportions) of the transect. Transects were located within a 300mx10m area of Crest. The starting position of each transect and the order in which the transects were censused were randomly determined. No individuals <25mm total length (TL) were included in the counts, and speed of censusing was standardised at 60 seconds/10m^2. All counts were done between the hours of 0800 and 1700 hrs to ensure spawning times were excluded.

The precision of estimated labrid density (#.10m^{-2}) was calculated for each transect size using the formulae: precision=standard error/mean (Andrew & Mapstone 1987). A two way analysis of variance was done to determine if the length or width of the transect had a significant effect on the recorded density of labrids, using transformed data ($\sqrt{[x+{}^1/_2]}$) to homogenise variances.

observer swimming speed

The influence of observer swimming speed on precision of counts was also measured based on five 50mx3m transects which were done at each of three speeds: 30, 60 and 90 seconds/10m^2.

number of replicate transects and sites

Five replicate transects were done on the Crest at three sites (see Section 2.2) using the chosen transect dimensions and observer swimming speed (50mx3m transects; speed=60 seconds/10m^2: see Section I.4). A cost-benefit analysis was done on these results to determine the most appropriate division of time and effort between replicating transects and sites (see Underwood 1981) .

testing the techniques in a range of habitats and sites

The chosen technique (five 50x3m transects per habitat per site; speed=60 secs/10m^2: see Section I.4) was tested in 6 habitat zones at three sites (see Section 2.2), to determine if the desired level of precision (see above) of the technique was maintained in a variety of situations.

The number of replicate transects required to maintain an acceptable level of precision (0.2: see Andrew & Mapstone 1987) in each zone at each site was calculated empirically using the formulae: number of replicates=[standard deviation/(precision x mean)]^2 (see Andrew & Mapstone 1987).

accuracy of estimating fish sizes

The accuracy in visually estimating total length underwater was measured by estimating the size of individuals, capturing them in a small barrier net and then measuring their actual size.

I.3 RESULTS

transect dimensions

All 16 transect sizes showed an acceptable level of precision ($\leq$0.2: Table I.1), with the greatest precision (0.07) attained by four transect sizes: 10mx3m, 20mx3m, 50mx3m and 50mx1m. Transect width had a significant effect on the density of labrids counted but transect length did not (Table I.2).

Table I.1: Precision (se/mean) attained in censusing labrids for 16 transect sizes on the Crest at North Reef.

transect width	transect length			
	10m	20m	30m	50m
1m	0.20	0.20	0.15	0.07
2m	0.14	0.15	0.11	0.15
3m	0.08	0.07	0.11	0.07
5m	0.15	0.12	0.09	0.10

Table I.2: Results of the two way analysis of variance on the influence of transect length and width on the density of labrids recorded on the Crest at North Reef.

source	df	MS	F	p
length	3	0.12	1.47	0.2309
width	3	1.39	16.34	<0.0001
length*width	9	0.10	1.19	0.3159
error	64	0.09		
total	79			

observer swimming speed

Precision was higher at a speed of 60 seconds/10m^2 (precision=0.05), than it was for speeds of 30 seconds/10m^{-2} and 90 seconds/10m^2 (precision of 0.11 and 0.12 respectively).

number of replicate transects and sites

The cost benefit analysis determined that the most appropriate allocation of time was three replicates transects ($n_{replicates}$=2.88) at one site only (n_{sites}=0.30). However, since a significant difference was detected in the density of labrids on the Crest at the three sites (One Way ANOVA: df=14; F=5.25; p<0.0230), it was decided to use at least 5 replicates at each of two sites for future studies.

testing the techniques in a range of habitats and sites

A precision of <0.2 was maintained for these methods in five of the six habitat zones at each site (Table I.3). However precision was lower on the Inner Reef Flat at two sites.

Table I.3: Precision (se/mean) of labrid density attained for 50mx3m transects in six habitat zones at each of three sites at Lizard Island.

site	Inner Reef Flat	Outer Reef Flat	Crest	Reef Slope	Reef Base	Sand Flat
North Reef	0.26	0.09	0.06	0.17	0.10	0.1014
Washing Machine	0.24	0.08	0.14	0.18	0.11	0.0663
North Reef C	0.07	0.07	0.14	0.16	0.11	0.1318

Four replicate transects were adequate to attain the desired level of precision in 5 of the 6 habitat zones (Table 1.4). However 8-9 replicates were necessary to attain this level of precision on the Inner Reef Flat at two sites.

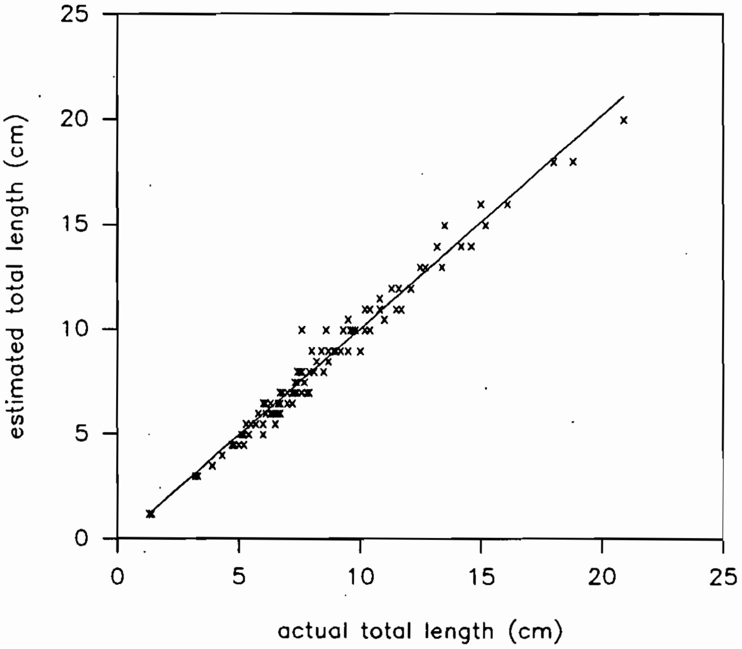
Table I.4: Number of replicates required to attain a precision of 0.2 for labrid density in each habitat zone at each site.

	Inner Reef Flat	Outer Reef Flat	Crest	Reef Slope	Reef Base	Sand Flat
North Reef	8.5	1.1	0.4	3.7	1.2	1.1
Washing Machine	7.3	0.7	2.3	3.9	1.6	0.5
North Reef C	0.6	0.1	2.5	3.0	1.5	2.2

accuracy of estimating fish sizes

There was a significant correlation ($r^2=0.9879$, $n=112$, $p<0.0001$: see Figure I.1) between estimated and actual total length of individuals of 10 species: *Cheilinus chlorourus* (n=4), *Cheilinus diagrammus* (n=2), *Coris schroederi* (n=41), *Cirrhilabrus punctatus* (n=9), *Halichoeres melanurus* (n=27), *Halichoeres trimaculatus* (n=3), *Hologymnosus annulatus* (n=1), *Stethojulis bandanensis* (n=1), *Thalassoma jansenii* (n=3), *Thalassoma lunare* (n=21). Size estimation was closer to actual size for smaller individuals (<10cm TL), and

Figure I.1.
Comparison between estimated and actual total length of labrids (r^2 =0.9879, n=112, $p<-.0001$)



became slightly less reliable as the size of the fish increased. However, when averaged over all individuals, the mean error was the technique was small when expressed as a percentage of the total length of the individuals (mean percent error of TL=3.6%, se=0.60, n=112).

I.4 DISCUSSION

Transect dimensions (especially width) were found to influence the precision of the technique, which supports the conclusions of Sale & Sharp (1983). Four transect sizes were found to show similar high levels of precision: 10mx3m, 20mx3m, 50mx3m and 50mx1m. Of these sizes, 50x3m transects were selected for two reasons. First, a width of 3m was chosen because it showed consistently higher levels of precision than did a width of 1m. Second, a length of 50m was chosen because larger study units are more likely to cover all microhabitats and include rare species (Kimmel 1985; *pers. obs.*), as well as being larger in size than the home range or spatial distribution patterns of most species (see Eckert 1985b; Andrew & Mapstone 1987).

An observer swimming speed of 60 seconds/10m^2 was chosen because this speed produced the most precise estimates of labrid density. This was probably because it was fast enough to avoid counting highly mobile individuals more than once along the transect (Lincoln Smith 1988), and slow enough to minimise the disturbance to the study species (Brock 1982; Fowler 1987).

Five replicate transects were selected for future studies, because they were found to attain an acceptable level of precision in 5 of the 6 habitat zones tested. More replicates (n=9) were required on the Inner Reef Flat at two sites to attain the desired precision. This was because of the patchy aggregations of abundant species such as *Halichoeres* species, and the highly mobile schools of *Stethojulis bandanensis*. Similarly, variation in precision among sites in other habitat zones (eg. Crest), was caused by patchy aggregations of abundant species such as *Thalassoma hardwicke*. However nine replicate 50m transects were not selected because of time and space constraints (study sites were <300m long). As such it must be accepted that surveys of the Inner Reef Flat using the selected survey techniques may not yield precise estimates of labrid densities and should be interpreted with caution. A minimum of two study sites were also selected for future studies, because of differences in abundance between sites.

This study confirmed that reliable estimates of fish sizes could be obtained by estimating their sizes underwater. As such, fish size will continue to be estimated in future surveys, although regular validation of the technique will be required (Bell *et al.* 1985; *pers. obs.*).

In summary, five replicate 50mx3m transects (speed=60 seconds/10m^2) per habitat at each of two sites, were selected to survey the patterns of distribution and abundance of labrid fishes at Lizard Island (see Section 2.1).

Appendix II

CHECKLIST OF LABRID FISHES FROM LIZARD ISLAND

Sixty-four labrid species recorded at Lizard Island over three consecutive years (1990 - 1992), showing minimum size of individuals of each species which were recorded as adults. Where minimum size = $^1/_3$ of maximum recorded adult size (based on Randall *et al.* 1990). All species names were consistent with those used by Randall *et al.* (1990).

species	**minimum size (cm)**
Anampses caeruleopunctatus Ruppell, 1829	14.0
Anampses geographicus Valenciennes, 1840	8.0
Anampses meleagrides Valenciennes, 1840	7.0
Anampses neoguinaicus Bleeker, 1878	5.5
Bodianus axillaris (Bennett, 1831)	6.5
Bodianus diana (Lacepede, 1801)	8.5
Bodianus mesothorax (Bloch & Schneider, 1801)	6.5
Cheilinus chlorourus (Bloch, 1791)	12.0
Cheilinus diagrammus (Lacepede, 1801)	12.0
Cheilinus fasciatus (Bloch, 1791)	12.0
Cheilinus trilobatus Lacepede, 1801	13.5
Cheilinus undulatus Ruppell, 1835	76.5
Cheilio inermis (Forsskal, 1775)	16.5
Choerodon anchorago (Bloch, 1791)	12.5
Choerodon fasciata (Gunther, 1867)	10.0
Choerodon graphicus (De Vis, 1885)	15.5
Choerodon jordani (Synder, 1908)	5.5
Choerodon schoenleinii (Valenciennes, 1839)	30.0
Cirrhilabrus punctatus Randall & Kuiter, 1989	4.5
Coris aygula Lacepede, 1801	33.5
Coris dorsomacula Fowler, 1908	6.5
Coris gaimard (Quoy & Gaimard, 1824)	13.5

Coris schroederi (Bleeker, 1858)	5.5
Epibulus insidiator (Pallas, 1770)	11.5
Gomphosus varius Lacepede, 1801	6.0
Halichoeres biocellatus Schultz, 1960	4.0
Halichoeres chloropterus (Bloch, 1791)	6.5
Halichoeres hortulanus (Lacepede, 1801)	9.0
Halichoeres margaritaceus (Valenciennes, 1839)	4.0*
Halichoeres marginatus Ruppell, 1835	5.5
Halichoeres melanurus (Bleeker, 1851)	3.5
Halichoeres miniatus (Valenciennes, 1839)	3.5*
Halichoeres nebulosus (Valenciennes, 1839)	4.0*
Halichoeres prosopeion (Bleeker, 1853)	4.5
Halichoeres trimaculatus (Quoy & Gaimard, 1834)	6.5
Hemigymnus fasciatus (Bloch, 1792)	16.5
Hemigymnus melapterus (Bloch, 1791)	20.0
Hologymnosus annulatus (Lacepede, 1801)	13.5
Hologymnosus doliatus (Lacepede, 1801)	12.5
Labrichthys unilineatus (Guichenot, 1847)	6.0
Labroides bicolor Fowler & Bean, 1928	4.5
Labroides dimidiatus (Valenciennes, 1839)	4.0
Labroides pectoralis Randall & Springer, 1975	2.5
Labropsis australis Randall, 1981	3.5
Labropsis xanthonota Randall, 1981	4.5
Leptojulis cyanopleura (Bleeker, 1853)	4.5
Macropharyngodon choati Randall, 1978	3.5
Macropharyngodon meleagris (Valenciennes, 1839)	4.0
Macropharyngodon negrosensis Herre, 1932	4.0
Novaculichthys taeniourus (Lacepede, 1801)	10.0
Pseudocheilinus hexataenia (Bleeker, 1857)	2.5
Pseudodax moluccanus (Valenciennes, 1839)	8.5
Stethojulis bandanensis (Bleeker, 1851)	4.0
Stethojulis interrupta (Bleeker, 1851)	4.5

Stethojulis strigiventer (Bennett, 1832)	5.0
Stethojulis trilineata (Bloch & Schneider, 1801)	5.0
Thalassoma amblycephalum (Bleeker, 1856)	5.5
Thalassoma hardwicke (Bennett, 1828)	6.0
Thalassoma jansenii (Bleeker, 1856)	6.5
Thalassoma lunare (Linnaeus, 1758)	8.5
Thalassoma lutescens (Lay & Bennett, 1839)	8.0
Thalassoma quinquivittatum (Lay & Bennett, 1839)	5.5
Thalassoma trilobatum (Lacepede, 1801)	10.0
Xyrichtys pavo Valenciennes, 1840	11.5

*Minimum adult size of 4.0 cm was used for the species complex called *Halichoeres* spp. (*H. margaritaceus, H. miniatus* and *H. nebulosus*).

Appendix III

TROPHIC DESIGNATION OF INTRUDERS IN DAMSELFISH TERRITORIES

Number of intruders of each of 26 families (138 species) that entered territories of *Dischistodus prosopotaenia* and *D. perspicillatus* during the damselfish behavioural study. Trophic categories were assigned to each species based on Randall *et al.* 1990, where: H=herbivore; C=carnivore; O=omnivore; P=planktivore and CL=cleaner. Where: *=carnivores which eat small fishes.

taxonomic group	**trophic category**	**# of intruders**	
		***Disc. pros.* terr.**	***Disc. pers.* terr.**
CLASS OSTEICHTHYES			
Family Acanthuridae			
unidentified	H	-	3
Acanthurus nigricauda	H	3	-
Acanthurus nigrofuscus	H	-	12
Acanthurus triostegus	H	-	1
Ctenochaetus binotatus	H	1	14
Ctenochaetus striatus	H	-	5
Naso annulatus	P	1	-
Naso brevirostris	P	1	-
Zebrasoma scopas	H	2	2
Family Apogonidae			
unidentified	-	1	-
Apogon nigrofasciatus	P	1	1
Family Balistidae			
unidentified	C	-	1
Sufflamen chrysopterus	C	28	31

Family Blenniidae			
Meiacanthus atrodorsalis	H	15	1
Meiacanthus lineatus	H	2	-
Meiacanthus grammistes	H	7	-
Plagiotremus laudandus	C	1	-
Family Caesionidae			
Caesio caerulaurea	P	35	7
Caesio cuning	P	-	23
Pterocaesio marri	P	2	13
Pterocaesio trilineata	P	-	1
Pterocaesio spp.	P	1	5
Family Carangidae			
unidentified	C*	-	4
Carangoides ferdau	C*	-	1
Caranx melampygus	C*	-	1
Family Chaetodontidae			
unidentified	-	4	-
Chaetodon aureofasciatus	O	8	2
Chaetodon auriga	O	6	10
Chaetodon baronessa	O	13	6
Chaetodon ephippium	O	2	2
Chaetodon kleinii	C	3	2
Chaetodon melannotus	C	15	3
Chaetodon plebeius	C	17	1
Chaetodon rainfordi	O	1	2
Chaetodon trifasciatus	C	21	10
Chaetodon unimaculatus	O	-	1
Chaetodon vagabundus	O	18	49

Chelmon rostratus	C	7	1
Heniochus acuminatus	C	-	1
Family Gobiidae			
unidentified	C	30	113
Amblyeleotris spp.	C	1	-
Amblygobius decussatus	C	-	1
Amblygobius rainfordi	C	-	1
Signigobius biocellatus	C	-	1
Valenciennea strigata	C	2	1
Family Haemulidae			
Diagramma pictum	C	3	3
Plectorhinchus goldmanni	C	1	-
Family Holocentridae			
Sargocentron spiniferum	C	2	-
Family Labridae			
unidentified	C	4	-
Anampses caeruleopunctatus	C	1	-
Bodianus mesothorax	C	3	9
Cheilinus chlorourus	C	10	3
Cheilinus diagrammus	C*	63	24
Cheilinus fasciatus	C	6	4
Cheilinus trilobatus	C*	-	1
Choerodon fasciatus	C	35	77
Choerodon jordani	C	-	1
Choerodon schoenleinii	C	1	9
Coris gaimard	C	19	9
Coris schroederi	C	300	211
Epibulus insidiator	C*	23	22

Gomphosus varius	C*	13	3
Halichoeres chloropterus	C	19	5
Halichoeres hortulanus	C	-	5
Halichoeres melanurus	C	11	11
Halichoeres prosopeion	C	-	2
Halichoeres trimaculatus	C	2	-
Hemigymnus melapterus	C	4	15
Hologymnosus doliatus	C	-	2
Labrichthys unilineatus	C	-	5
Labroides dimidiatus	CL	13	36
Labropsis australis	C	-	1
Macropharyngodon negrosensis	C	-	1
Thalassoma lunare	C*	206	81
Family Lethrinidae			
unidentified	C	-	3
Gymnocranius euanus	C	-	6
Lethrinus atkinsoni	C	9	2
Monotaxis grandoculis	C	8	18
Family Lutjanidae			
unidentified	C*	-	1
Lutjanus carponotatus	C*	-	4
Lutjanus fulviflamma	C*	-	5
Lutjanus gibbus	C*	-	2
Lutjanus kasmira	C*	-	1
Lutjanus quinquelineatus	C*	-	1
Family Mullidae			
unidentified	C	-	8
Parupeneus ciliatus	C	-	3
Parupeneus barberinoides	C	3	3

Parupeneus barberinus	C	2	39
Parupeneus multifasciatus	C	26	40
Family Nemipteridae			
Scolopsis bilineatus	C	47	93
Scolopsis margaritifer	C	11	57
Scolopsis monogramma	C	2	14
Family Pinguipedidae			
unidentified	C*	3	7
Parapercis cylindrica	C*	1	-
Parapercis hexophtalma	C*	17	17
Family Pomacanthidae			
unidentified	-	2	-
Centropyge bicolor	H	5	12
Pomacanthus sexstriatus	C	2	3
Family Pomacentridae			
unidentified	-	7	16
Amblyglyphidodon curacao	O	5	5
Amblyglyphidodon leucogaster	O	-	2
Acanthochromis polyacanthus	O	9	23
Chromis ternatensis	O	1	-
Chromis viridis	O	-	1
Chrysiptera rex	O	-	3
Chrysiptera rollandi	O	2	1
Dascyllus aruanus	O	7	1
Dascyllus reticulatus	O	4	2
Dischistodus perspicillatus	H	-	103
Dischistodus prosopotaenia	H	70	-
Dischistodus pseudochrysopoecilus	H	8	-

Neoglyphidodon nigoris	O	1	-
Pomacentrus amboinensis	O	89	80
Pomacentrus brachialis	O	7	17
Pomacentrus chrysurus	H	2	1
Pomacentrus coelestis	O	2	-
Pomacentrus grammorhynchus	H	17	-
Pomacentrus moluccensis	O	30	11
Pomacentrus nagasakiensis	O	-	15
<u>Family Pseudochromidae</u>			
unidentified	C*	1	-
Pseudochromis fuscus	C*	21	3
<u>Family Scaridae</u>			
unidentified	H	8	21
Cetoscarus bicolor	H	1	-
Hipposcarus longiceps	H	-	1
Scarus altipinnus	H	-	2
Scarus bleekeri	H	1	1
Scarus flavipectoralis	H	22	29
Scarus ghobban	H	-	1
Scarus microrhinos	O	7	3
Scarus niger	H	-	6
Scarus psittacus	H	1	3
Scarus rivulatus	H	-	10
Scarus schlegeli	H	14	5
Scarus sordidus	H	3	4
Scarus spinus	H	-	16
<u>Family Scombridae</u>			
unidentified	C*	-	2

Family Serranidae			
unidentified	C*	6	4
Cephalopholis argus	C*	5	1
Cephalopholis boenak	C*	6	7
Cephalopholis cyanostigma	C*	5	6
Cephalopholis miniata	C*	1	-
Cromileptes altivelis	C*	1	4
Diploprion bifasciatum	C*	3	2
Epinephelus maculatus	C*	-	3
Epinephelus merra	C*	2	-
Plectropomus maculatus	C*	2	1
Family Siganidae			
Siganus corallinus	H	2	24
Siganus doliatus	H	8	-
Siganus puellus	O	5	2
Siganus vulpinnus	H	-	4
Family Synodontidae			
Synodus englemani	C*	1	6
Family Tetraodontidae			
Arothron nigropunctatus	O	5	-
Canthigaster valentini	O	-	2
Family Zanclidae			
Zanclus cornutus	O	-	4
CLASS CHONDRICHTHYES			
Family Carcharinidae			
Carcharhinus albimarginatus	C	-	1
Carcharhinus melanopterus	C	1	-

Family Dasyatidae			
unidentified	C	-	2
TOTAL:		**1519**	**1673**

Appendix IV

PUBLICATION FROM THIS THESIS

One paper is currently in press from this study, which is included in this section:

Green, A. L. *in press* Damselfish territories: Focal sites for studies of the early life history of labroid fishes. *Proc. Int. Coral Reef Symp., 7th*: 601-605.

Damselfish Territories: Focal Sites for Studies of the Early Life History of Labroid Fishes

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Abstract. Territorial pomacentrids modify benthic assemblages in shallow reef areas by facilitating the growth of high density stands of macroscopic algae within the territories. A detailed study of habitat use by 59 species of labrids at Lizard Island demonstrated that *Coris schroederi* and *Halichoeres melanurus* were the most abundant species in the habitats where the territories are located. Newly settled juveniles of these species were significantly more abundant in the territories than on the adjacent substratum. The newly settled juveniles of five scarid species were also more abundant in the territories. As discrete, readily quantified patches of microhabitat, the territories provide excellent focal sites for the study of recruitment and early post-settlement biology of labroid fishes.

Introduction

Many studies have demonstrated the importance of recruitment and early post-settlement processes in structuring reef fish populations (Doherty & Williams 1988.) To date, the majority of these studies have concentrated on species of a single family, the Pomacentridae (Doherty & Williams 1988). Recruits of these species are easy to locate and monitor over time, because they are relatively large and conspicuous (Brothers et al 1983). Moreover, many species recruit in high densities onto patch reefs, which are ideal as replicated units of habitat for ecological studies. By comparison, relatively little is known about the early life history of species in which the recruits are very small and cryptic, such as most labrids and scarids (Brothers et al. 1983). While some species of labrids and scarids do recruit onto patch reefs, they are usually only present in low densities and are difficult to locate. In order to study these species in more detail, it would be necessary to identify a unit of habitat where these individuals are present in high densities, and where they can be easily located and monitored over time.

In 1989, Bellwood & Choat reported that newly settled scarids appeared to be concentrated within the algal gardens of damselfish territories at Lizard Island on the northern Great Barrier Reef. The purposes of this paper are to confirm that: 1) labroid fishes settle and persist in damselfish territories in higher densities than they do on the adjacent substratum; and 2) the territories provide appropriate units of habitat for studies of recruitment and post-settlement biology of these species.

Two abundant species of damselfish *Dischistodus perspicillatus* and *Dischistodus prosopotaenia*, which establish large well defined algal gardens, were selected for this study. Both species occur in a range of exposures and depths at Lizard Island, and in some locations their territories cover >50% of the area of the bottom of the reef slope and the adjacent sand flat (J. H. Choat *pers comm*).

Materials and Methods

Three sites were selected for study on the north-eastern side of Lizard Island, Great Barrier Reef (14° 38'S, 145° 24'E) (see Figure 1). Each site contained large numbers of both *Dischistodus* species, which were at the bottom of the slope and on adjacent bommies (*D. prosopotaenia*) or on the sand flat (*D. perspicillatus*).

Ten territories of each *Dischistodus* species were selected at each site. In order to describe the two types of territories, I measured the area, algal species composition and the heights of the various algae within each territory. Ten controls were established on the adjacent substratum for each type of territory. I used the term control to indicate that the substratum was identical to that where the territories were located, but differed from the territories only in that the substratum was devoid of macro-algae. In each case, controls encompassed space equivalent to the mean territory size (see Table 1).

I counted labrid and scarid recruits within all territories and controls at weekly intervals from 17 November 1991 to 15 January 1992 (n=7). An intensive search of the algae was required to census the territories properly, so the duration of each count was dependent on the size of the territory, but averaged 5–10 mins. Scarid species that were difficult to distinguish in the field when newly-settled (Bellwood & Choat 1989) were pooled as *Scarus* spp. This group included *S. sordidus, S. schlegeli, S. spinus, S. psittacus* and *S. rubroviolaceus.* All other labrid and scarid recruits could be identified to species by sight in the field.

The influence of substratum type and site on density of each of the three most abundant groups (*Coris schroederi, Halichoeres melanurus* and *Scarus* spp.) was tested using a two way fixed factor analysis of variance for each labroid group, with the factors being substratum type (two types of territories and their respective controls) and sites (1 to 3). For these analyses, the data was used from the final count only (January 14–15 1992), because *H. melanurus* was only abundant at that time. The data were transformed by $\sqrt{x+1}$ to satisfy the assumptions of the analysis. Where appropriate, the means were compared using a Student-Newman-Keuls test. All differences were considered to be significant at the $p<0.05$ level.

Results

There were striking differences in the location, size and algal composition of the territories of the two

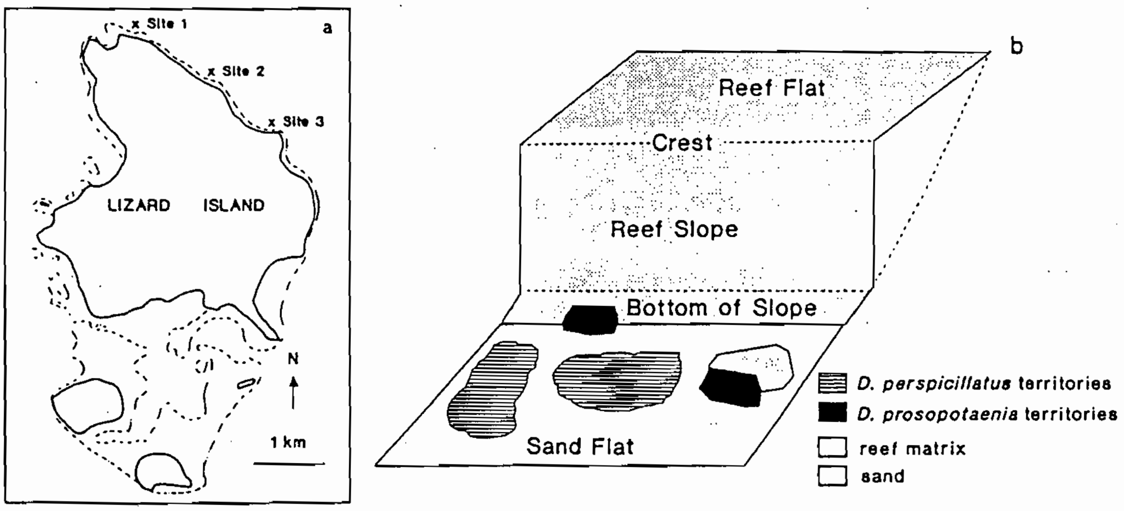

Fig. 1. a. Location of the three study sites on the northeastern side of Lizard Island; and b. Schematic illustration showing the position of *Dischistodus perspicillatus* and *Dischistodus prosopotaenia* territories in relation to the reef profile at the study sites.

Table 1. Characteristics of *Dischistodus perspicillatus* and *Dischistodus prosopotaenia* territories on the northeastern side of Lizard Island, Great Barrier Reef

	D. prosopotaenia (n=30)	*D. perspicillatus* (n=30)
Habitat Type	Bottom of Slope	Sand Flat
Depth Range	6–10m	9–12m
Substratum Type	Reef/Sand Interface	Sand
Mean Area of Territories	$2.42m^2 \pm 0.15$	$6.01m^2 \pm 0.63$
Area of Controls	$2.25m^2$	$6.25m^2$
Algal Assemblages	Multispecific: green, red and brown algae.	Monospecific: blue green algae.
Height of Algae in Territories	Variable (0–12cm)	Uniform (approx. 8cm)

species of damselfish (see Table 1). The *D. prosopotaenia* territories were located in shallow water (6–9m) on the reef/sand interface at the bottom of the slope. They consisted of multispecific assemblages of green (*Halimeda* spp., *Caulerpa urvilleana* and *Udotea* spp.), red (*Gelidiopsis intricata*) and brown (*Padina tenuis*) algae. The heights of these algae varied reaching, a maximum of 12cm. In contrast, *D. perspicillatus* territories consisted of monospecific stands of filamentous blue green algae (*Lyngbya* sp.) of uniform height (approximately 10 cm). These territories were invariably located over a uniform sand substratum in deeper water (9–12m), and were approximately three times the area of those of *D. prosopotaenia.*

A total of 13 species of newly settled labroid fishes (9 labrids, 4 scarids) were found within the territories and controls throughout the summer (see Table 2). Most of the species were rare ($n<20$) and when they were present they were within the territories only. Three abundant taxa, the labrids *Coris schroederi* and *Halichoeres melanurus*, and a complex of closely related scarid species (*Scarus* spp.) were found both in the territories and controls.

Multiple comparisons showed that *Coris schroederi* was significantly more abundant inside each type of damselfish territory relative to the adjacent controls at each site (see Fig 2a). The analysis of variance for this species detected a significant interaction between the two main effects, substratum type and site (see Table 3). This interaction was probably due to the greater density of this species within *D. perspicillatus* territories than *D. prosopotaenia* territories at site 1, in contrast to sites 2 and 3 where the opposite occurred. Despite the interaction, the influence of substratum type on the density of this species remained clear. No significant difference was demonstrated in the density of *C. schroederi* in the two types of territories.

Halichoeres melanurus showed a more consistent pattern of abundance. This species occurred almost exclusively in *D. prosopotaenia* territories, with low numbers recorded from the adjacent controls (see Figure 2b). A few individuals occurred in *D. perspicillatus* territories at site 3 only, but none were seen in the adjacent control plots. There was a significant interaction between substratum type and site (see Table 3), which was probably due to the lower abundance within *D. prosopotaenia* territories at site 2 relative to the other sites, as well as the presence of some individuals in *D. perspicillatus* territories at one site only.

In contrast, the group of scarids were not recorded from any of the control plots, but occurred in moderate densities in all territories at all sites (see Figure 2c). No significant difference between the density of this group in the two types of territories was detected. However, the numbers within territories at each site were highly variable, which made comparisons difficult to interpret. No significant site effect or interaction was detected (see Table 3).

Table 2. Abundance of labrid and scarid groups in damselfish territories ($n=30$ per species) and controls ($n=30$ per species). Where n = total number of individuals recorded over 7 weeks: x = mean density ($.10m^{-2}) per week; and se = standard error of mean

	Dischistodus prosopotaenia						*Dischistodus perspicillatus*					
	Territories			Controls			Territories			Controls		
Labridae	n	x	se	n	x	se	n	x	se	n	x	se
Cheilinus chlorourus	2	0.05	(0.03)	—	—	—	—	—	—	—	—	—
C. diagrammus	6	0.10	(0.05)	—	—	—	3	0.03	(0.02)	—	—	—
Coris schroederi	172	3.80	(0.40)	7	0.15	(0.89)	302	2.78	(0.22)	8	0.06	(0.02)
Halichoeres melanurus	318	6.31	(0.86)	26	0.54	(0.16)	32	0.36	(0.16)	—	—	—
H. trimaculatus	—	—	—	—	—	—	4	0.05	(0.02)	—	—	—
Hemigymnus melapterus	1	0.02	(0.02)	—	—	—	—	—	—	—	—	—
Stethojulis bandanensis	12	0.21	(0.06)	—	—	—	3	0.04	(0.02)	—	—	—
S. strigiventer	2	0.03	(0.02)	—	—	—	2	0.03	(0.02)	—	—	—
Thalassoma lunare	3	0.07	(0.04)	—	—	—	—	—	—	—	—	—
Scaridae												
Cetoscarus bicolor	1	0.02	(0.02)	—	—	—	—	—	—	—	—	—
Scarus frenatus	6	0.10	(0.05)	—	—	—	—	—	—	—	—	—
S. niger	7	0.14	(0.04)	—	—	—	8	0.10	(0.04)	—	—	—
Scarus spp.	415	8.18	(0.50)	1	0.02	(0.02)	481	5.13	(0.44)	—	—	—

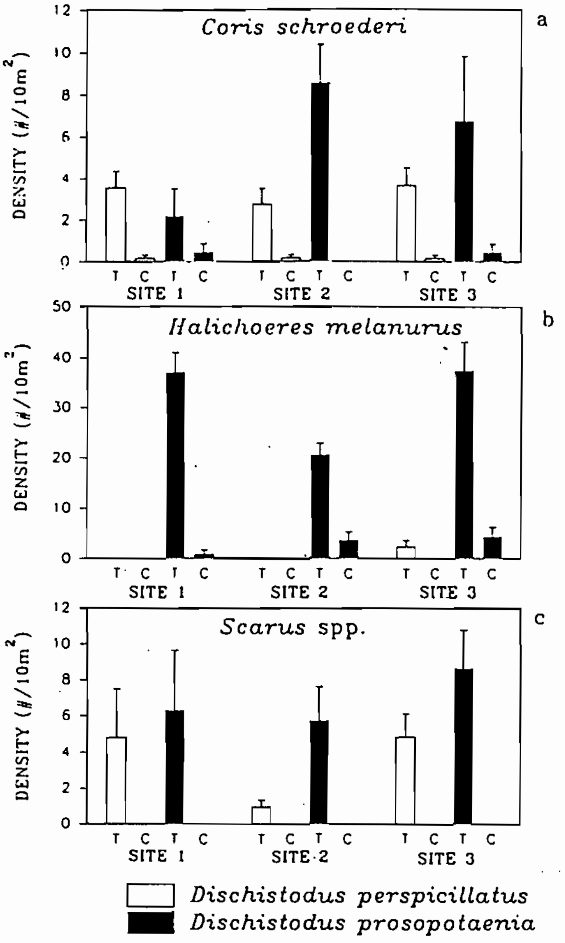

Fig. 2. The mean densities (± standard error) of (a) *Coris schroederi*, (b) *Halichoeres melanurus* and (c) *Scarus* spp. in damselfish territories (T) and controls (C), at three sites, Lizard Island. (Note the different y-axis scale).

Discussion

During the study period, the recruits of three abundant labroid groups (*Coris schroederi*, *Halichoeres melanurus* and *Scarus* spp.) were observed to be concentrated within the territories of one or both damselfish species. These recruits are usually difficult to detect in other habitats, because of their size, cryptic colouration and behaviour. However, they are relatively easy to detect within the territories by a slow speed, systematic search of the algae. Therefore, the territories represent units of habitat where these species are present in high densities, and where they can be reliably detected.

The territories have a number of characteristics in common with patch reefs, which make them ideal to use as replicated units of habitat for ecological studies. They are discrete, and separated by patches of bare substratum. They are also abundant both within sites and among sites, so it is possible to have access to replicate study populations using territories at a number of spatial scales. The territories can also be experimentally manipulated by removal of algae or the resident damselfish, in order to study the interaction between labroid recruits and their habitat. Finally the territories occur in such a wide range of habitats (exposures and depths) that they can be used for a range of ecological studies.

The potential benefits to the labroid recruits living within the territories can be considered in the context of microhabitat. First, several studies have reported that mortality rates of labrids and scarids can be extremely high during the first few days after metamorphosis (Doherty & Sale 1985, Victor 1986, Eckert 1987). The high cover of algae may afford protection from potential predators during this vulnerable life history stage. It is also possible that the aggressive behaviour of the damselfish towards other fish species could be protecting the labroids from predators. However, this appears to be unlikely because preliminary observations indicate that the damselfish do not exclude potential predators of the recruits from the territories, such as lizardfishes and adult labrids (A. Green *pers obs*). Second, scarid recruits feed on micro-invertebrates during the first few weeks of benthic life (Bellwood 1988), and the territories contain a rich and abundant source of micro-invertebrates that are only present in very small numbers on the adjacent substratum (A. Green *unpub data*). Both the fine scale structure of the algal stands and the invertebrate faunas that they contain can be readily quantified.

This study demonstrates that damselfish territories act as recruitment sites and early life history refuges for some labroid species, and that the territories are suitable as replicated units of habitat for studying the patterns of recruitment and early life history of these fishes. The next step is to review recruitment patterns of these species in a range of habitats and microhabitats, to clarify the importance of pomacentrid territories as recruitment sites to these species in the more general sense.

Many of the species of labrids and scarids occurring in the study area are rare as recruits. In some cases the only reliable source of newly settled individuals of some species are damselfish territories. The list of the species that use these microhabitats could probably be expanded by further monitoring, given the rarity of the majority of taxa. Thus the territories provide not only discrete study populations of abundant species, they are also valuable source of rare individuals of both labrids and

Table 3. Results of analysis of variance testing for the effect of substratum type and site on the density of *Coris schroederi*, *Halichoeres melanurus* and *Scarus* spp.

	Coris schroederi			
Factor	df	MS	F	P
Substratum	3	11.48	22.56	<0.001
Site	2	0.79	1.55	0.2144
Substratum*Site	6	1.47	2.89	0.0119
Error	108	0.51		
Total	119			

	Halichoeres melanurus			
Factor	df	MS	F	P
Substratum	3	140.88	212.20	<0.001
Site	2	3.93	5.91	0.0038
Substratum*Site	6	2.08	3.14	0.0072
Error	108	0.66		
Total	119			

	Scarus spp.			
Factor	df	MS	F	P
Substratum	3	15.28	20.83	<0.001
Site	2	1.41	1.92	0.1494
Substratum*Site	6	0.73	0.99	0.4352
Error	108	0.73		
Total	119			

scarids for studies of their early post-settlement biology.

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