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Department

DEMOGRAPHIC PROCESSES AND SPATIAL HETEROGENEITY IN COMMUNITY STRUCTURE AND DYNAMICS OF CORALS ON THE REEF CREST

Thesis submitted by
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in December 1994

for the degree of Doctor of Philosophy in the Department of Marine Biology at
James Cook University of North Queensland

Dedicated to the memory of my father,
David Nelson

for whatever we lose (like a you or a me)
it's always ourselves we find in the sea

ee cummings

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ABSTRACT

This study investigates some of the demographic processes (recruitment, mortality, fragmentation and fission) which cause spatial heterogeneity in coral reefs. Permanent quadrats at four sites (separated by 100s to 1000s of metres) on the reef crest at Lizard Island were photographed approximately every three months for 33 months. The total number of colonies, percent cover and composition of corals showed no substantial changes over 33 months but differed markedly among sites. The total abundance and percent cover of corals varied two- to threefold among sites. Species composition differed among sites, but Acroporids dominated the composition of assemblages at all four sites. Three of the sites had similar species composition, dominated by *Acropora hyacinthus*, but the fourth was characterised by a suite of species that were rare at other sites

Recruitment was an important process influencing differences among sites in total abundance and composition of corals. More than 3000 sexual recruits were detected in 80 m^2 over two years. Rates of recruitment differed by twofold among sites, and species composition also differed. The abundance and composition of recruits were closely correlated with the abundance and composition of established assemblages. Three sites had similar composition of recruits, while the fourth site was distinguished by species that were rare elsewhere.

Post-recruitment mortality also played an important role in determining relative abundances of species at a site. Fewer than 25% of recruits survived over two years (< 25%). Rates of mortality differed by twofold among sites and exaggerated differences among sites established by recruitment. There was no evidence of density-dependent mortality during the two years of the study; survival of recruits was not correlated with density or cover of established colonies, nor with density of recruits. Survival of recruits differed fourfold among species, ranging from 13% for *Montipora* spp. to 52% for *Pocillopora damicornis*. The three most abundant species on the reef crest, *A. hyacinthus*, *A. gemmifera* and *P. verrucosa*, all had high rates of recruit survival (45% over 2 years).

Mortality of colonies already established at the start of the study also differed among sites. Mortality was significantly greater at one site (71%) than at the other three (53 - 56%). Survival of established colonies differed fivefold among species. Robust and/or large species (*A. gemmifera, P. eydouxi, A. monticulosa, A. cuneata* and *A. hyacinthus*) had > 60% survival, while smaller, more delicate species had lower (< 30%) survival (e.g. *Montipora* spp, *A. nobilis*).

Colonisation of bare substratum on the reef crest by fragments is apparently uncommon, but can occur for some species. Over 423 fragments were detected in the quadrats over 33 months, but 90% died or moved out of the quadrats at all sites. Ninety-one percent of fragments were Acroporids. Fragments of *A. hyacinthus* had the highest survival, with 19% of fragments still alive after 12 months. Fragments of *A. nana* and *A. nobilis* had greater rates of mortality, with 5% and 8%, respectively, still alive after 12 months.

Local abundances of some species (e.g. *A. monticulosa*, *A. robusta*) may have been enhanced by fission, but daughter colonies of the majority of common species on the reef crest did not survive. Fission of colonies occurred frequently (7.2 daughter colonies.m^{-2}.yr^{-1}) and in all taxonomic groups. There was a tenfold difference among sites in the number of daughter colonies produced by fission which was related to the species composition of assemblages at each site. Survival of daughter colonies differed by more than 25-fold among species, with daughter colonies of *A. monticulosa*, *A. gemmifera*, *Porites* sp and *A. robusta* all with survival greater than 20% over 2 years.

In summary, differences among sites in numerical abundance and composition were largely determined by recruitment, but differential mortality among sites and species was also important. The study clearly illustrated that coral communities differed greatly in both structure and dynamics among sites on the reef crest. For this reason, a general understanding of the processes important in shaping assemblages of corals is dependent on quantifying both spatial and temporal variation in these processes.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Coral reefs can be viewed as mosaics of patches at different successional stages, with abundance and composition of corals determined by the interplay among disturbance, competition and recovery (Grassle 1973; Connell & Keough 1985; Hughes 1989; Jackson 1991). Disturbance and recovery are spatially variable (e.g. Woodley *et al.* 1981; Connell & Keough 1985), leading to differences in successional trajectories among patches within the mosaic (Warwick *et al.* 1990; Tanner *et al.* in press). Coral reefs thus show similar characteristics to the intertidal mussel beds described by Paine & Levin (1981) who advocated sampling many sites to describe the dynamics of the community as a whole. A similar plea has been made for studies investigating the dynamics of coral at many sites within a reef habitat because "Only with the resulting data will we be able to test more critically the extent to which niche diversification, disturbance and recruitment interact to determine the diversity of coral reef communities." (Jackson 1991, p 481). Although there have been many studies on the structure and dynamics of coral assemblages, studies that sampled multiple places within a zone on one reef are rare (but see Connell 1973, 1976, 1978; Grigg 1983; Rylaarsdam 1983; Connell & Keough 1985; Witman 1992; Bythell *et al.* 1993). However, those few studies have shown considerable patchiness in density, cover and species composition within reef zones, reinforcing Jackson's (1991) point that to understand the dynamics of corals, it is important to take into account the variation among patches at a scale of 100s to 1000s of metres.

Coral communities are naturally dynamic (e.g. Connell 1973, 1978; Glynn 1976; Loya 1976a; Bak & Luckhurst 1980; Harriott 1983; Hughes & Jackson 1985). Much of this variation is due to the effects of disturbance (e.g. Connell 1978; Woodley *et al.* 1981; Hughes 1989; Done 1992; Rogers 1993). However, in the absence of disturbance, assemblages of coral can also be highly dynamic because of demographic flux (e.g. Bak & Luckhurst 1980; Harriott 1983; Hughes & Jackson 1985; Hughes 1988). An understanding of demographic processes which increase or decrease counts of colonies can provide insights into the dynamics of coral assemblages.

The role of recruitment in determining the structure and dynamics of open communities and populations has recently been much discussed (e.g. Sale 1977; Underwood & Denley 1984; Connell 1985; Gaines & Roughgarden 1985; Doherty & Williams 1988). Coral recruitment is spatially and temporally variable at many scales. Recruitment of some species is highly localised because of limited dispersal by planulae, resulting in clumped distributions of adults (e.g. Gerrodette 1981). Clumped distributions can also be caused by gregarious settlement of planulae (e.g. Lewis 1974; Goreau *et al.* 1981), or preferential settlement (or differential survival) of planulae in surface irregularities (Birkeland & Randall 1981; Carleton & Sammarco 1987). At larger spatial scales, rates of recruitment of corals and the composition of recruits vary at different depths (e.g. Birkeland 1977; Birkeland *et al.* 1981; Wallace 1985a,c) and at different sites within a depth range (e.g. Connell 1973; Harriott & Fisk 1987, 1988; Babcock 1988; Sammarco & Andrews 1989).

Recruitment is also variable within and among years. For example, on the Great Barrier Reef, where the majority of corals are broadcast spawners and spawn only once a year (Harrison *et al.* 1984; Willis *et al.* 1985; Babcock *et al.* 1986), recruitment is highly seasonal (Harriott & Fisk 1987, 1988; Wallace 1985c; Babcock 1988; Fisk & Harriott 1990). Long-term studies of recruitment also show that the abundance and composition of recruits is variable among years (e.g. Connell 1973; Wallace 1985c). The overall view emerging from the large number of studies on recruitment of corals is that of widely variable rates and composition of colonisers.

How this variable supply of colonisers relates to patterns of distribution and abundance of adult colonies is poorly known. Studies in the Caribbean have shown that the distributions of recruits and adults are extremely different (Bak & Engel 1979; Rylaarsdam 1983; Rogers *et al.* 1984). These authors suggest that either post-recruitment mortality or temporal variation in mortality determine the distribution and abundance of adults. In contrast, on the Great Barrier Reef, the distribution and composition of recruits appear to be broadly similar to distribution and composition of adults (Connell 1973; Harriott 1985). While the distribution and abundance of recruits does not fully explain the distribution and abundance of adults, the relationship seems to be much closer than observed in the Caribbean. More studies on recruitment and post-recruitment mortality within already established assemblages are urgently needed to assess the role of recruitment in determining community structure of corals.

Whether recruitment is a major influence on community and population dynamics depends on patterns in mortality (Warner & Hughes 1988; Holm 1990; Hughes 1990). Patterns in recruitment will be retained in the structure of adult assemblages if mortality is density-independent or only weakly density-dependent (*ibid.*). Patterns in mortality were positively related to patterns in recruitment at Lizard Island, but there appeared to be little relationship between rates of mortality and total densities of established corals in different transects (Harriott 1985). Harriott's (1985) study is the only study to compare rates of mortality of corals with density. Clarification of the relationship between rates of mortality and density and the relative function of rates and patterns of recruitment and mortality in determining the structure and dynamics of assemblages of coral await further work.

Mortality plays an important role in structuring assemblages of coral, particularly during disturbances (Connell 1978; reviews in Karlson & Hurd 1993; Rogers 1993). Differential mortality of common species can maintain or increase species diversity (Connell 1976, 1978, Connell *et al.* 1984; Hughes 1989). Similarly, differences in abundance and composition of corals among sites may be maintained by differential mortality among sites. Rates of mortality of corals are typically greater in shallow water than on deeper reefs (Bak & Luckhurst 1980; Hughes & Jackson 1985). One of the factors influencing rates of mortality in shallow water is disturbance from waves. However, in a study comparing the dynamics of coral assemblages at a wave-exposed and a sheltered site, Witman (1992) found that wave exposure did not explain differences in mortality between sites which had different histories of disturbance and therefore different species compositions. The role of mortality in structuring assemblages is complex and must be considered together with the history of recruitment and disturbance (Hughes 1989).

The capacity of corals to undergo fragmentation and fission also has important implications for the structure and dynamics of their populations and assemblages (Hughes & Jackson 1980; Highsmith 1982). Because fragments typically only move a few metres from the parent colony (e.g. Smith 1992), and daughter colonies produced by fission can only move by growth, these modes of asexual reproduction result in local proliferation of clones. Species that fragment easily share a suite of characteristics that enable them to colonise quickly and dominate space (e.g. branching *Acropora cervicornis*: Tunnicliffe 1981; Highsmith 1982). Species that undergo fission and survive well can persist and maintain space (e.g. *Montastrea annularis*: Hughes 1988). There have been few studies on asexual propagation by fragmentation and fission on the Great Barrier Reef (but see Bothwell 1981; Heyward & Collins 1985; Wallace 1985b; Babcock 1991; Smith 1992). Consequently, the importance of these modes of propagation in life histories of Great Barrier Reef corals has only begun to be explored.

Life history theory predicts that species with the ability to recruit fast will be more successful in disturbed or unpredictable habitats because they can take advantage of newly opened space (Williams 1975; Maynard Smith 1978). Often the ability to disperse is associated with a greater reliance on sexual reproduction because in unpredictable environments there is an advantage in producing genetically diverse offspring, some of whom may have higher fitness than the parental genotype (Williams 1975; Maynard Smith 1978). Hence, it might be predicted that corals on highly disturbed shallow reefs should have high rates of recruitment and use a predominantly sexual and/or dispersive mode of reproduction (Loya 1976b; Van Moorsel 1983; Szmant 1986).

Clearly, the roles of recruitment, mortality, fragmentation and fission in determining the structure and dynamics of coral communities are complex. A demographic approach to monitoring coral assemblages can help to identify some of the processes important in creating and maintaining patchiness in coral reefs. That coral reefs are patchy strongly suggests the need to sample multiple sites within zones.

1.2 Thesis synopsis

The aim of this study is to quantify community structure and dynamics of corals at multiple sites within a reef zone, and to investigate the roles of wave exposure, recruitment, mortality, fission and fragmentation in maintaining spatial variation of coral communities. To achieve this aim, permanent quadrats were established at four sites (two exposed and two less exposed) on the reef crest at Lizard Island. These quadrats were monitored photographically at approximately three-monthly intervals over 33 months.

Chapter Two quantifies spatial and temporal variation in the abundance, percent cover and composition of assemblages of coral at the four sites on the reef crest at Lizard Island, comparing the two wave exposed with the two more sheltered sites. Community structure (density, percent cover and composition) did not change substantially over 33 months, but differences among sites were marked. There were no detectable differences between wave-exposed and more sheltered locations, but sites within locations varied greatly. The results of Chapter Two suggested that there was a balance between processes of recruitment (both sexual and asexual) and mortality, and that there was some mechanism promoting and maintaining variation among sites.

In Chapter Three, the role of recruitment in promoting differences among sites in abundance and composition of coral assemblages is investigated. Spatial and temporal patterns in recruitment are quantified and the abundance and composition of the assemblage of recruits is compared with the structure of assemblages of corals at the beginning of the study. Patterns of recruitment were closely related to patterns of abundance in the established assemblage.

Although the abundance and composition of recruits were similar to patterns in the established assemblage, the role of recruitment in determining the structure of assemblages can only be determined by comparison with patterns in mortality. Chapter Four quantifies mortality of recruits and original colonies and investigates the role of differential mortality among sites as a determinant of spatial variation in the structure of communities. There was very little variation in mortality of either recruits or established colonies among sites, and what variation there was tended to reinforce patterns established by recruitment.

The processes of fragmentation and fission can also promote spatial variation in abundances of corals by increasing local abundances of some species. The role of asexual reproduction by fragmentation and fission in promoting variation among sites in abundance and composition of assemblages is investigated in Chapter Five. Fragments did not survive on the reef crest, but some common species appeared to benefit from fission as a means of increasing local populations.

In Chapter Six, data on rates of recruitment, mortality, fragmentation and fission calculated in the previous chapters are combined for some common species and their life history strategies in the disturbed habitat of the reef crest are discussed. The rates of recruitment, mortality and asexual population processes are synthesised in a discussion of the role of demographic processes in structuring coral assemblages on the reef crest. The study showed that coral assemblages differed greatly in both structure and dynamics among sites, and that these differences were largely maintained by differences in recruitment.

CHAPTER 2: SPATIAL AND TEMPORAL VARIATION IN ABUNDANCE AND COMPOSITION OF CORAL ASSEMBLAGES

2.1 INTRODUCTION

The abundance and composition of coral assemblages fluctuate greatly over short time-scales (days to hundreds of years; e.g. Loya 1976a; Connell 1978; Woodley *et al.* 1981). Much of the literature on temporal variation in the abundance and composition of assemblages of coral has been dominated by studies on extreme changes after cyclones (e.g. Woodley *et al.* 1981; Done 1992a), infestations of crown-of-thorns starfish (e.g. Pearson 1981; Moran 1986; Colgan 1987), mass bleaching (e.g. Warwick *et al.* 1990; Glynn 1991), overgrowth by algae (e.g. Hughes *et al.* 1987) and pollution (reviewed in Brown & Howard 1985). In contrast, there is very little information on temporal dynamics without major disturbances (but see Bak & Luckhurst 1980; Hughes & Jackson 1985; Porter & Meier 1992; Bythell *et al.* 1993). Bak & Luckhurst (1980) documented little change in cover of coral in Curaçao over five years, while the abundance of five species of foliaceous corals in Jamaica also changed very little over a period of four years (Hughes & Jackson 1985). The apparent stability of the assemblages in these two studies concealed great changes in spatial arrangement and turnover of individuals. Such stability is not always true of undisturbed reefs. In Florida, five of six sites declined in cover of coral over seven years without observable disturbance (Porter & Meier 1992). Similarly, constancy is not necessarily associated with a lack of disturbance. On the Great Barrier Reef, coral cover on 20 to 33% of reefs did not change in five year periods between 1980 and 1990, despite outbreaks of crown-of-thorns starfish and several cyclones (Done 1992a). Rogers *et al.* (1982) documented substantial damage to coral populations in the U.S. Virgin Islands after two consecutive cyclones, but reported no alteration in "overall functioning" of reefs. Thus, a particular community's trajectory is not necessarily predictable in either direction or rate.

This study was designed to investigate the dynamics of coral assemblages at short time-scales (within years) and at multiple sites within a depth zone. Studies on coral dynamics have typically censused populations at yearly intervals or longer (e.g. Connell 1973; Hughes & Jackson 1985; Colgan 1987). However, a study at Lizard Island showed that the abundance of 10 genera did not change among 2 month periods over 20 months, despite fast turnover of individuals (Harriott 1983). Harriott calculated that annual censuses would have the turnover of individuals by 33%, and suggested that such high rates of turnover indicate the potential for great changes in the structure of assemblages of coral.

One of the many factors affecting the abundance and composition of assemblages of sessile marine organisms is disturbance from waves (e.g. Connell 1975; Denny *et al.* 1985). Wave energy may be a major force structuring coral assemblages (Connell 1978; Bradbury & Young 1981; Dollar 1982; Done 1983; Huston 1985), but other causes for the observed patterns (e.g. larval settlement patterns) were not investigated. The effect of wave energy on the structure of assemblages of coral in a single habitat (depth range) has not yet received much attention (but see Connell 1978; Witman 1992). There is some evidence that the differences in abundance and composition of assemblages of coral between exposed and sheltered sites is not a function of average wave climate, but rather a result of differences in timing and magnitude of major disturbances (Connell 1978; Witman 1992; Connell *et al.* in prep). Whether average wave climate is a major force structuring assemblages of coral remains open, however, because these studies have confounded the effects of site and habitat with wave exposure, since each study had only one sampling site at each depth and exposure.

Assemblages of coral, like many other sessile organisms, show great variation within a depth zone among sites, at a scale of 100s of metres (e.g. Grassle 1973; Connell 1973, 1978; Grigg 1983; Connell & Keough 1985; Witman 1992; Bythell *et al.* 1993; Tanner *et al.* in press). Consequently, Jackson (1991) recently called for studies investigating the dynamics of assemblages of coral at multiple sites within a depth zone. This chapter describes the structure of coral assemblages at four sites on the reef crest at Lizard Island, two on the southeastern side of the island, exposed to the full force of waves generated by the southeast trade winds, and two on the northeastern side of the island, only obliquely exposed to waves. Permanent quadrats at each of these sites were photographed every three months for nearly three years to investigate spatial and temporal patterns in the abundance and composition of coral assemblages within a depth zone at sites separated by 100 - 1000 metres.

2.2 METHODS

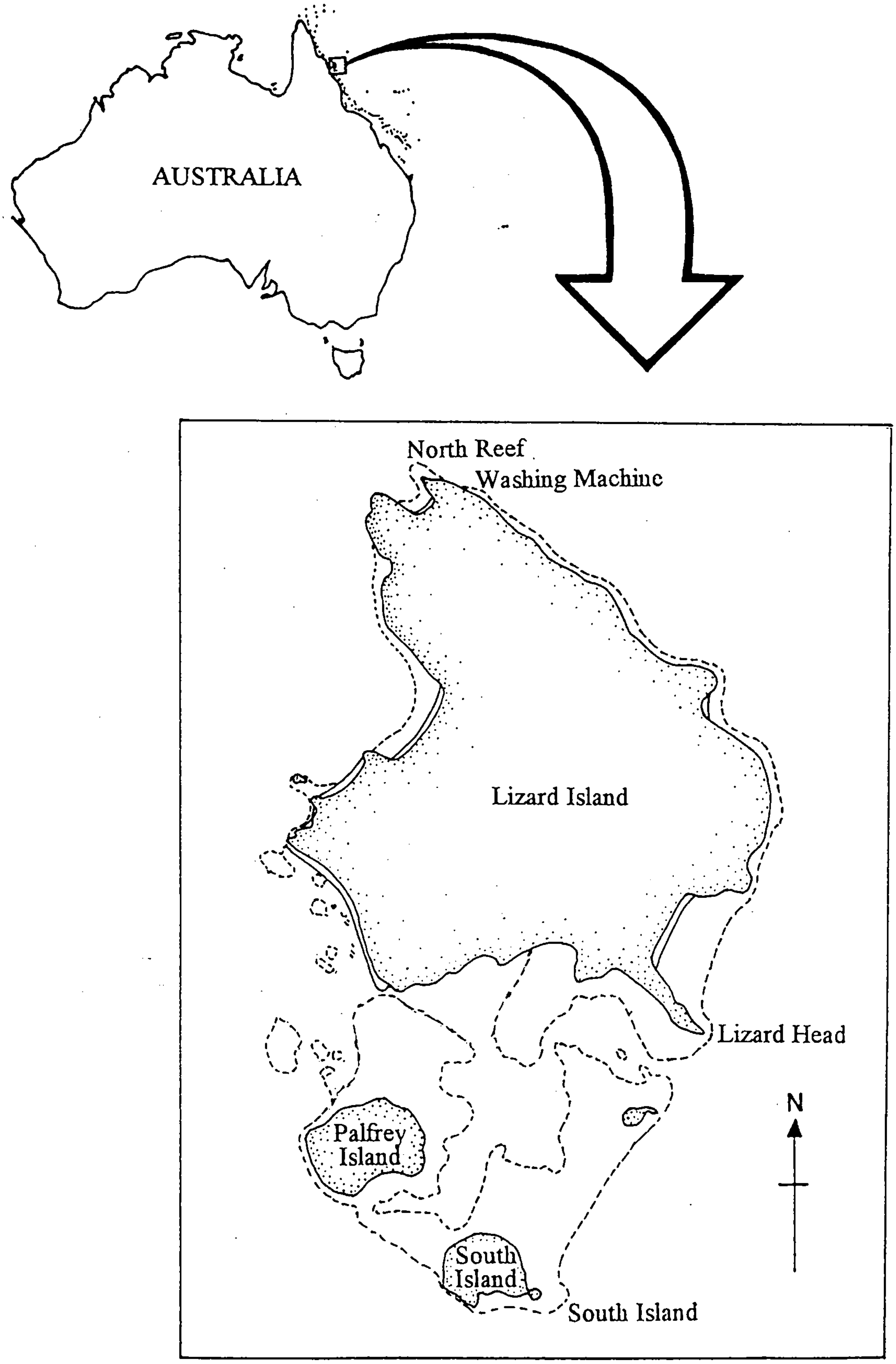
2.2.1 Sampling design and data collection

To monitor the abundance and composition of coral assemblages, five, 2m x 2m permanent quadrats were established on the reef crest at Lizard Island at four sites: North Reef, Washing Machine, Lizard Head and South Island (Fig 2.1). Lizard Head and South Island were on the southeastern side of the island, exposed to the predominant southeast trade winds, and were separated by approximately 2 km. North Reef and Washing Machine were on the less exposed northeastern side of the island, separated by approximately 1 km. Quadrats at each site were 2 to 10m apart and were placed to avoid large colonies of *Acropora hyacinthus*.

Each quadrat was marked with a central star-picket and eight reinforced steel stakes at approximately 1m intervals around the perimeter of the area. The stakes were placed so that a 1m x 1m quadrat frame fitted outside them. The quadrat frame was divided into four 0.25 m^2 subquadrats with string.

Quadrats were monitored photographically every 3 months from May 1990 to February 1993. Because of logistic difficulties, the first census that included all 5 quadrats at all 4 sites was in February 1991. At each census, photographs (64 ASA Kodachrome slide film) were taken of each 0.25 m^2 subquadrat (16 photographs make up one 2m x 2m quadrat) with a Nikonos V underwater camera fitted with a 28mm lens and SB-103 strobe. Photographs were taken from approximately 1m directly above the quadrat.

Figure 2.1 Map of Lizard Island showing study sites.



Each slide was projected at half life size onto a screen and maps of each 1m x 1m quadrat were traced (four slides to a map). These maps were compiled to make up a composite map of the entire 2m x 2m quadrat (overlaps were adjusted). Coral colonies were identified to species where possible and assigned individual numbers. The area of each colony was measured using a Houston Instrument Hipad Plus digitiser with Jandel Scientific Sigmascan 3.92 software. Colonies on the edges of quadrats were numbered, measured and used to estimate total coral cover, but were not used in analysis of population dynamics.

2.2.2 General statistical considerations

Monitoring permanently marked quadrats presents some major difficulties for statistical analysis. In this study, the same quadrats and often the same individuals within quadrats were monitored through time, violating assumptions about independence. Most questions about spatial and temporal variation in the data have been analysed with multivariate repeated measures analysis of variance (MANOVAR). The multivariate form of this technique was used to avoid restrictive assumptions about the correlation structure of the data (Green 1993).

In all analyses, data were used from censuses from December 1990 to February 1993, excluding May 1992 because of missing data at two sites. Although data were available for two sites before December 1990, these data were dropped to maintain a balanced design. There were missing values for Washing Machine Quadrats 3, 4 and 5 in August 1992 because one slide film was blank. These missing values were replaced with averages calculated from May and November 1992.

Before running analyses, data were checked for multivariate normality using multivariate normality plots, and for homoscedasticity using multivariate Levene's test[1] (McArdle, unpublished notes).

2.2.3 Spatial and temporal variation in numbers and cover of corals

To document spatial and temporal patterns in the abundance of colonies, the number of colonies in each quadrat at each time was counted and their individual areas summed to estimate the total area of each quadrat covered by coral. Spatial and temporal variation in the number and cover of corals were analysed using MANOVAR. Location was a fixed factor (Southeast vs Northeast), with two Sites nested within each Location. Sites were considered as random factors, with quadrats as replicates (n = 5) and times (n = 8) as multiple variables.

To investigate spatial and temporal patterns in the structure of assemblages in more detail, colonies were classified into one of 6 "family" groups: Acroporidae, Pocilloporidae, Faviidae, Poritidae, Other Corals and Unidentified Corals. Included in the category Other Corals were Mussids (primarily *Symphyllia* spp.), the Merulinid *Hydnophora microconos*, soft corals (*Sarcophyton* sp, *Sinularia* spp. and *Lobophytum* spp.) and hydrocorals (*Millepora* spp.). MANOVAR was used to test for differences

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[1] SAS Macros for multivariate normality plots and multivariate Levene's test were written by Dr Brian McArdle, Biostatistical Unit, Auckland University, New Zealand.

in the mean number of colonies and cover of each group among sites and times. Data were transformed where appropriate [either ln(x) or ln(x+1), depending on whether there were zeros in the data]. Spatial and temporal patterns were analysed for each family separately, with Location as a fixed factor, Site as a random factor nested within Location, quadrats as replicates and census times as multiple variables.

2.2.4 Spatial and temporal patterns in species composition

To investigate spatial patterns in species composition, the number and cover of colonies of thirteen common species and three species groups were compared among sites. The species were *Acropora cuneata, A. gemmifera, A. hyacinthus, A. millepora, A. monticulosa, A. nana, A. nobilis, A. robusta, A. secale, Montipora* spp., *Goniastrea* spp., *Pocillopora damicornis, P. eydouxi, P. verrucosa, Stylophora pistillata* and *Porites* sp. To test whether species composition was different among sites, multivariate analysis of variance (MANOVA) was done on numbers or area of the sixteen species/species groups per quadrat at four sites at each of three times (February 1991, February 1992, February 1993). A ln(x+1) transform normalised the data.

2.3 RESULTS

2.3.1 Spatial and temporal variation in total numbers and cover of corals

There was a 3-fold range in densities of colonies among sites, which remained ranked in the same order over time, despite significant temporal variation (Fig 2.2).

Figure 2.2 Mean number of corals per quadrat (± S.E.) at four sites over 33 months. Missing points indicate missing data.

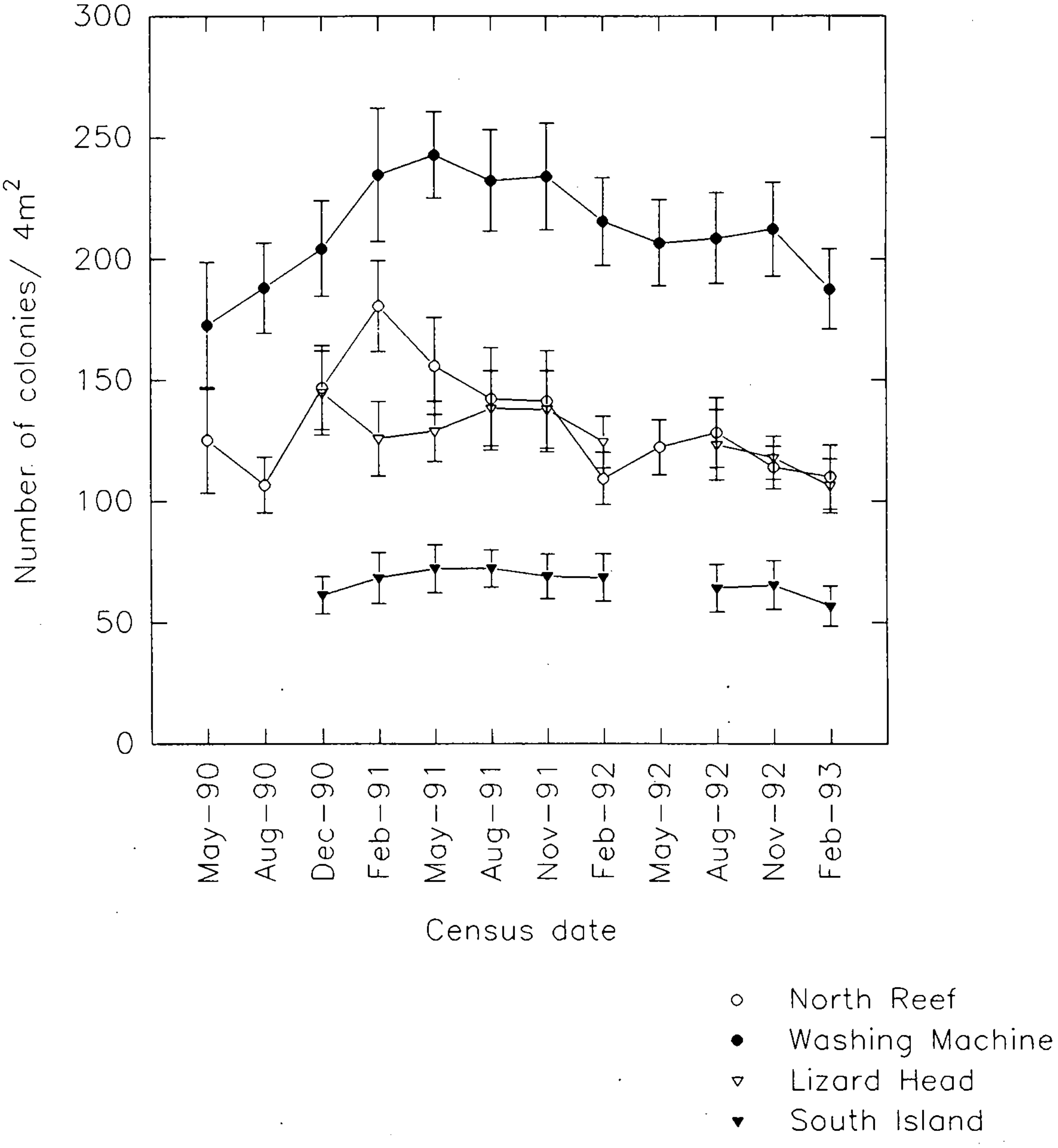


Table 2.1 MANOVAR on total numbers of corals per quadrat (n = 5) at two sites within each of two locations over 26 months from December 1990 to February 1993 (excluding May 1992). Data transformed [ln(x)].

Within Quadrats

Source of variation	Pillai's trace	F	num df	den df	*p*
Time	0.95	19.64	8	9	< 0.0001
Location*Time	0.77	3.78	8	9	< 0.03
Site(Location)*Time	1.41	2.98	16	20	< 0.01

Between Quadrats

Source of variation	SS	df	MS	F	*p*
Location	18.08	1	18.08	2.34	> 0.2
Site(Location)	15.48	2	7.74	14.87	< 0.0002
Error	7.80	15	0.52		

Northeastern sites showed a decrease in numbers of colonies of 28% from Febraury 1991 to February 1993, while southeastern sites only decreased in abundance by 16% (Location*Time; Table 2.1). Within locations, sites had different temporal trajectories (Site(Location)*Time; Table 2.1). Corals at North Reef decreased in abundance by 39% from February 1991 to February 1993, while those at Washing Machine declined by only 20% (Fig 2.2). At Lizard Head, numbers remained steady for most of the study, only declining by 15% in the final 6 months. The change of 6% at South Island over two years was biologically insignificant, representing a mean loss of only 4 colonies per quadrat (Fig 2.2).

Cover of coral consistently varied twofold among sites (Fig 2.3). Temporal trajectories varied between sites within locations (Site(Location)*Time; Table 2.2), altering the rank order of cover at Washing Machine and Lizard Head (Fig 2.3). At North Reef, cover increased from 32 ± 4% to 46 ± 6% over 31 months (Fig 2.3). Coral cover also increased slightly at Washing Machine (26 ± 3% to 34 ± 3%) and South Island (18 ± 5% to 22 ± 5%) (Fig 2.3). However, at Lizard Head, coral cover decreased from 33 ± 3% in December 1990 to 27 ± 4% in February 1993, a decline that only occurred in the last 6 months of the study (Fig 2.3).

Table 2.2 MANOVAR on total cover of corals per quadrat (cm^2, n = 5) at two sites within each of two locations over 26 months from December 1990 to February 1993 (excluding May 1992). Data transformed [ln(x)].

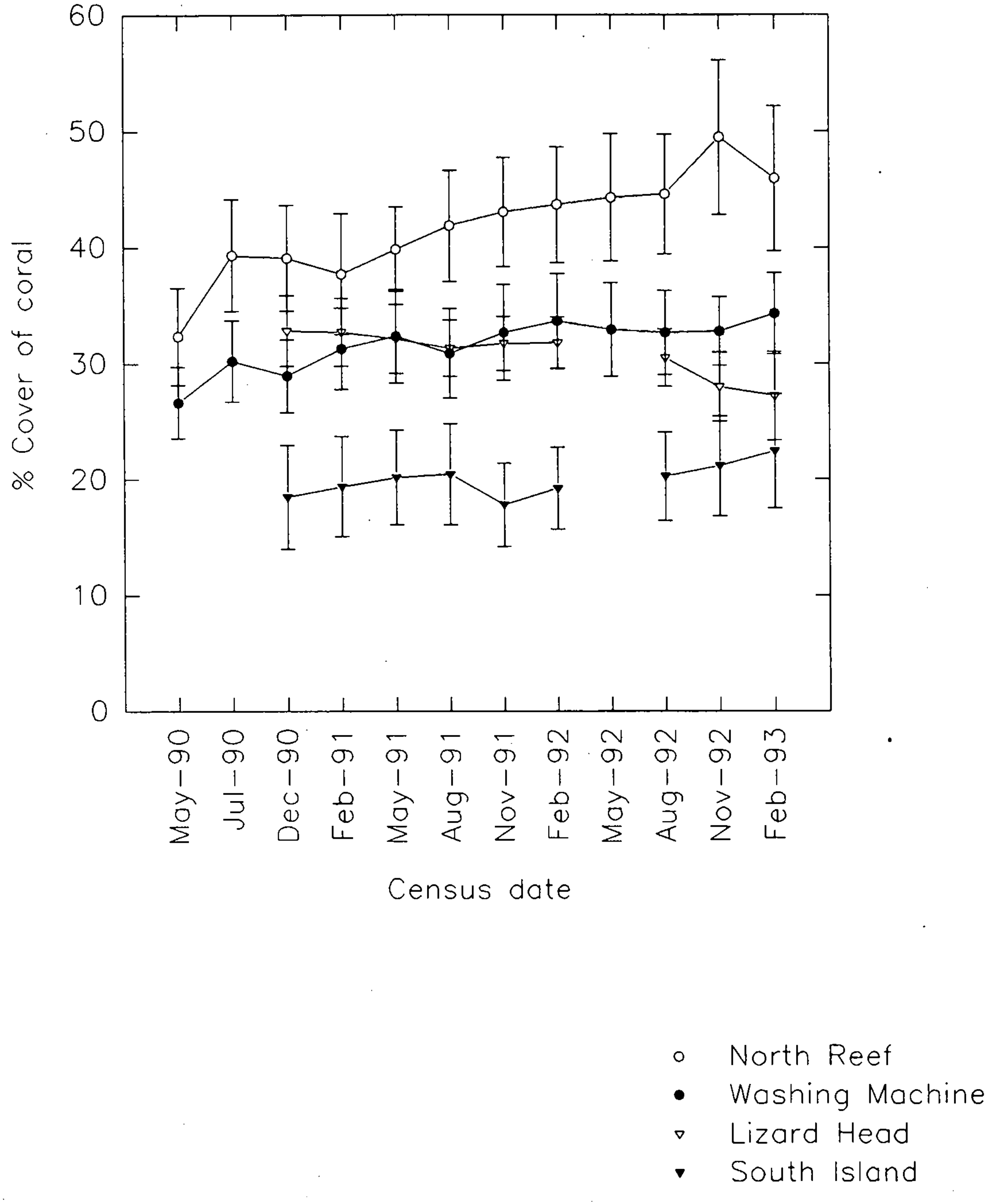
Within Quadrats

Source of variation	Pillai's trace	F	num df	den df	*p*
Time	0.73	2.97	8	9	> 0.06
Location*Time	0.40	0.74	8	9	> 0.65
Site(Location)*Time	1.36	2.66	16	20	< 0.02

Between Quadrats

Source of variation	SS	df	MS	F	*p*
Location	8.34	1	8.34	2.20	> 0.27
Site(Location)	7.56	2	3.78	4.85	< 0.02
Error	12.48	16	0.78		

Figure 2.3 Mean percent cover of corals per quadrat (± S.E.) at four sites over 33 months. Missing points indicate missing data.



2.3.2 Spatial and temporal variation in the abundance and cover of family groups

Spatial patterns in abundance of all family groups remained constant through time, with sites retaining their rank order throughout the study (Fig 2.4). The only groups with statistically significant temporal variation were Acroporids, Poritids and Unidentified Corals (Table 2.3). The total abundance of Acroporids (irrespective of locations or sites) decreased over time by 12% from 87 ± 9.3 (SE) to 75 ± 8.5 colonies per quadrat. At North Reef the density of Poritids decreased from 11.8 ± 2.2 per quadrat in February 1991 to 5.6 ± 1.5 in February 1993, a decline of 53%. At Lizard Head, the density of corals fluctuated between 6.6 ± 2.2 and 7.2 ± 2.4 from December 1990 to February 1992, then decreased to 5.6 ± 1.6 in February 1993 (Fig 2.4). The abundance of Poritids remained constant through time at other sites (3.6 ± 0.5 per quadrat at Washing Machine and 1.8 ± 0.2 at South Island; Fig 2.4). The densities of Unidentified corals were similar at all sites after August 1991 (1 - 2 per quadrat at each census), but there were differences in the timing of fluctuations at southeastern and northeastern sites up to August 1991 (Location*Time; Table 2.3). There was a peak in abundance at northeastern sites in February 1991 (8.9 ± 2.4 colonies per quadrat), but at the southeastern sites, there was a peak in abundance of Unidentified Corals in December 1990 (6.2 ± 1.7 per quadrat).

Spatial patterns in numerical abundance of all families were marked and relatively consistent over time (Fig 2.4). Acroporids were four times more abundant at Washing Machine and twice as abundant at North Reef and Lizard Head than at South Island (Site; Table 2.3; Fig 2.4). Similarly, Pocilloporids were twice as

Figure 2.4 Mean numbers of colonies per quadrat of corals in six taxonomic groups at four sites over 33 months. Missing points indicate missing data. Note differing scales on y axes.

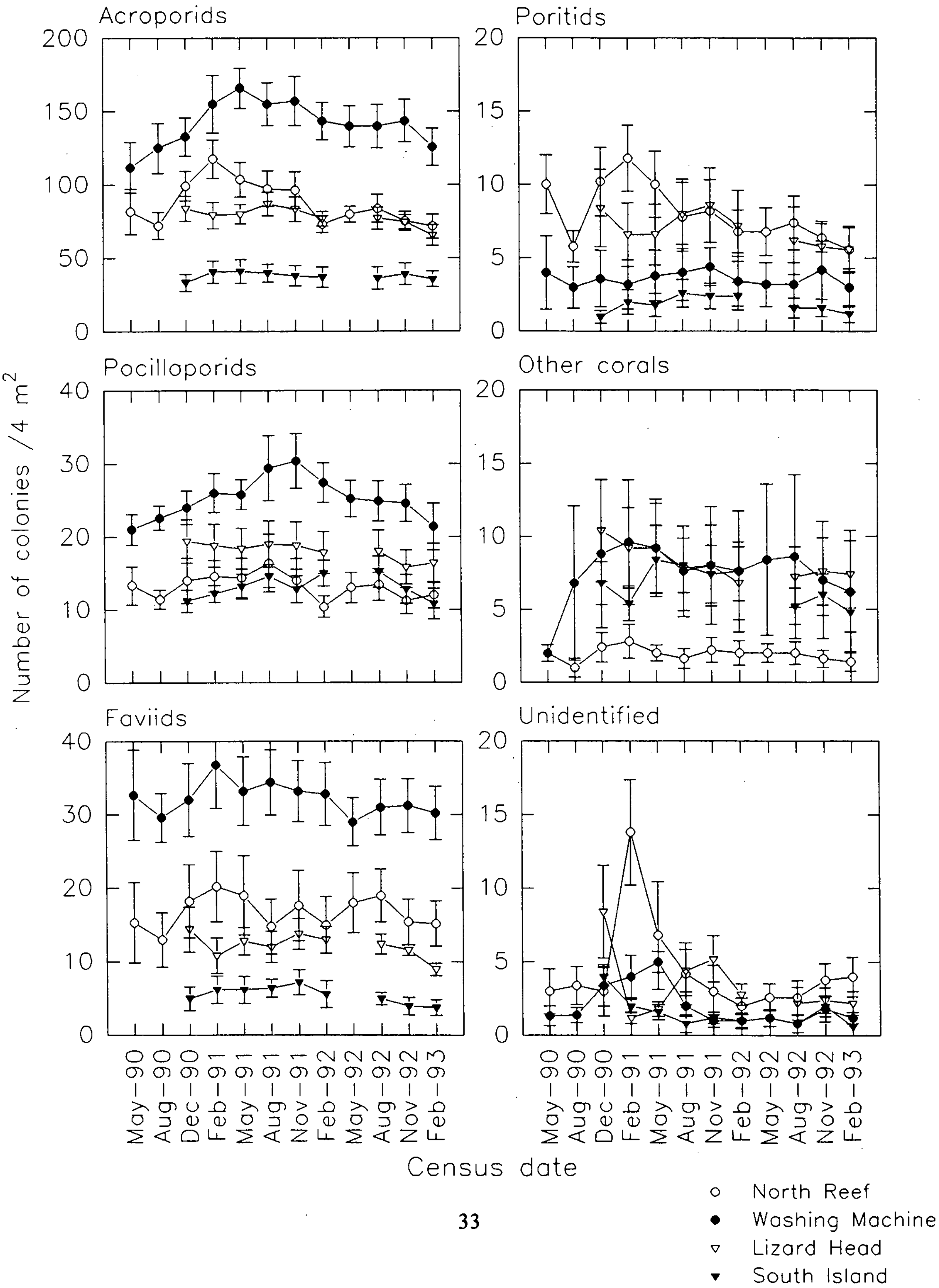


Table 2.3 (facing) MANOVAR on numbers of corals per quadrat at two sites within each of two locations for six taxonomic groups. Data for numbers of Acroporids transformed to ln(x), data for numbers of Unidentified Corals transformed to ln(x+1).

Taxon	Source of variation	Pillai's trace	F	num df	den df	*p*
Acroporid	Time	0.817	5.02	8	9	< 0.02*
	Location*Time	0.551	1.38	8	9	> 0.31
	Site(Location)*Time	1.266	2.16	16	20	> 0.05
Pocilloporid	Time	0.715	2.82	8	9	> 0.07
	Location*Time	0.453	0.93	8	9	> 0.53
	Site(Location)*Time	1.054	1.39	16	20	> 0.24
Faviid	Time	0.558	1.43	8	9	> 0.30
	Location*Time	0.739	3.18	8	9	> 0.05
	Site(Location)*Time	1.092	1.50	16	20	> 0.19
Poritid	Time	0.678	2.37	8	9	> 0.11
	Location*Time	0.668	2.26	8	9	> 0.12
	Site(Location)*Time	1.420	3.06	16	20	< 0.01*
Other coral	Time	0.653	2.12	8	9	> 0.14
	Location*Time	0.663	2.22	8	9	> 0.13
	Site(Location)*Time	1.076	1.45	16	20	> 0.21
Unidentified	Time	0.688	2.48	8	9	> 0.09
	Location*Time	0.892	9.28	8	9	< 0.002*
	Site(Location)*Time	1.230	2.00	16	20	> 0.07

Between quadrats

Taxon	Source of variation	df	MS	F	*p*
Acroporid	Location	1	26.070	2.76	> 0.24
	Site(Location)	2	9.442	15.59	< 0.0002*
	Error	16	0.606		
Pocilloporid	Location	1	762.613	0.37	> 0.61
	Site(Location)	2	2065.474	9.29	< 0.002*
	Error	16	222.378		
Faviid	Location	1	11680.56	3.60	> 0.20
	Site(Location)	2	3244.49	7.91	< 0.004*
	Error	16	409.96		
Poritid	Location	1	104.272	0.19	> 0.70
	Site(Location)	2	537.072	4.51	< 0.03*
	Error	16	119.089		
Other coral	Location	1	252.05	0.57	> 0.53
	Site(Location)	2	441.272	1.46	> 0.26
	Error	16	301.945		
Unidentified	Location	1	1.513	0.33	> 0.63
	Site(Location)	2	4.659	3.71	< 0.05*
	Error	16	1.255		

abundant at Washing Machine and 1.5 times as abundant at North Reef and Lizard Head than at South Island (Fig 2.4). Faviids were also most abundant at Washing Machine, with densities six times greater there than at South Island (Fig 2.4). Faviids at North Reef and Lizard Head were 3- and 2-times more abundant than at South Island. Thus, the three most abundant families were most abundant at Washing Machine and least abundant at South Island. There were no statistically significant differences among sites in the abundance of Poritids nor Other Corals, because of the large variation among quadrats within sites (Table 2.3).

Patterns in cover of families were different from the patterns in numerical abundance (Fig 2.5). There was temporal variation in cover of Acroporids and Unidentified corals but not for any other family (Table 2.4). The cover of Acroporids increased from 35.7 ± 4.9% to 43.6 ± 6.8% at North Reef, but the increase in cover at Washing Machine and South Island was only 4.8% and 4.1%, respectively, and cover decreased from 25.2 ± 2.7% to 19.8 ± 3.3% at Lizard Head (Fig 2.5). The cover of Unidentified corals fluctuated differently on each side of Lizard Island (Location*Time; Table 2.4) but these fluctuations are of little biological interest because the cover of Unidentified Corals was less than 0.1% at all sites (Fig 2.5).

Percent cover of families of corals varied greatly among sites consistently over time (Table 2.4). There was significant variation among sites in the cover of Acroporids, Faviids, Poritids and Unidentified Corals (Site, Table 2.4). Acroporids had the greatest cover of all taxonomic groups at all sites, but varied 3-fold among sites, with

Figure 2.5 Mean percent cover of colonies per quadrat (± S.E.) of corals in six taxonomic groups at four sites over 33 months. Missing points indicate missing data. Note differing scales on y axes.

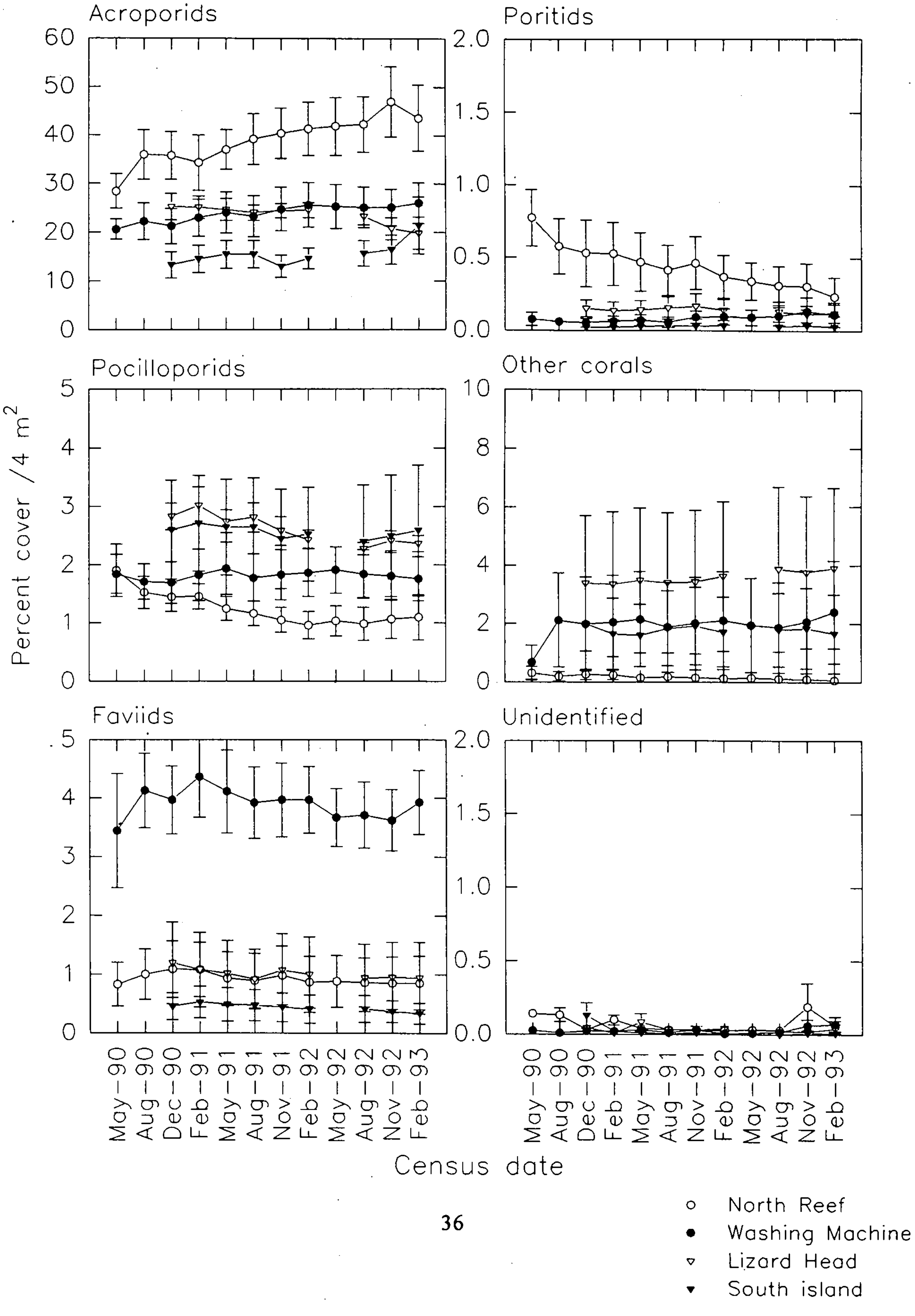


Table 2.4 (facing) MANOVAR on cover of corals per quadrat at two sites within each of two locations for six taxonomic groups. Data for cover of Acroporids and Faviids transformed to ln(x), data for cover of Poritids, Other Corals and Unidentified Corals transformed to ln(x+1).

Taxon	Source of variation	Pillai's trace	F	num df	den df	*p*
Acroporid	Time	0.687	2.47	8	9	> 0.09
	Location*Time	0.455	0.94	8	9	> 0.53
	Site(Location)*Time	1.335	2.01	16	20	< 0.03*
Pocilloporid	Time	0.659	2.17	8	9	> 0.13
	Location*Time	0.578	1.54	8	9	> 0.27
	Site(Location)*Time	0.802	0.84	16	20	> 0.64
Faviid	Time	0.734	3.10	8	9	> 0.05
	Location*Time	0.513	1.18	8	9	> 0.40
	Site(Location)*Time	0.823	0.88	16	20	> 0.60
Poritid	Time	0.619	1.83	8	9	> 0.19
	Location*Time	0.431	0.85	8	9	> 0.58
	Site(Location)*Time	0.809	0.85	16	20	> 0.63
Other coral	Time	0.607	1.74	8	9	> 0.21
	Location*Time	0.526	1.25	8	9	> 0.37
	Site(Location)*Time	1.027	1.32	16	20	> 0.28
Unidentified	Time	0.617	1.81	8	9	> 0.19
	Location*Time	0.765	3.68	8	9	< 0.03*
	Site(Location)*Time	0.877	0.98	16	20	> 0.51

Between Quadrats

Taxon	Source of variation	df	MS	F	*p*
Acroporid	Location	1	11.601	1.91	> 0.44
	Site(Location)	2	6.076	5.9	< 0.01*
	Error	16	1.030		
Pocilloporid	Location	1	8639420.41	11.25	> 0.08
	Site(Location)	2	768195.07	0.41	> 0.67
	Error	16	1868456.08		
Faviid	Location	1	77.518	1.21	> 0.39
	Site(Location)	2	63.867	4.91	< 0.02*
	Error	16	13.020		
Poritid	Location	1	46.302	0.806	> 0.46
	Site(Location)	2	57.467	3.74	< 0.05*
	Error	16	15.35		
Other coral	Location	1	125.54	1.63	> 0.33
	Site(Location)	2	77.18	2.78	> 0.09
	Error	16	27.73		
Unidentified	Location	1	4.201	0.36	> 0.60
	Site(Location)	2	11.628	3.84	< 0.05*
	Error	16	3.027		

greatest cover at North Reef and least cover at South Island (Fig 2.5). Cover of Faviids was 9 times greater at Washing Machine and 2 times greater at North Reef and Lizard Head than at South Island (Fig 2.5). Poritids covered 13 times more space at North Reef, 5 times more space at Lizard Head and 3 times more space at Washing Machine than at South Island (Fig 2.5), on average, but this ratio changed (non-significantly) over time. Although there was a five-fold range in cover of Unidentified Corals (Fig 2.5), they covered less than 0.1% of the space at all sites, so the differences among sites are trivial.

2.3.3 Spatial and temporal variation in species composition

Species composition based on numerical abundance was characteristic at each site over three years (Fig 2.6). Coral assemblages at North Reef and South Island were dominated by *A. hyacinthus*, with 30% and 37%, respectively, of the total number of abundant corals represented by this species (Fig 2.6). In contrast, *A. hyacinthus* represented only 10% of the numbers of 16 species at Washing Machine, and 26% at Lizard Head (Fig 2.6). Washing Machine was distinguished from other sites by a suite of species that occurred there in greater abundances than at other sites (*A. cuneata*, *A. monticulosa*, *A. robusta*, *A. secale* and *A. nana*) (Fig 2.6). The species that separated Lizard Head from other sites were *P. verrucosa* and *A. monticulosa*, while South Island had similar composition to North Reef but all species were half as abundant there than at North Reef (Fig 2.6).

Spatial variation in relative cover of species was also great (Fig 2.7). At North Reef,

Figure 2.6 Mean numbers of colonies per quadrat of 16 species at four sites. Values are means and standard errors of 5 quadrats over 10 time periods.

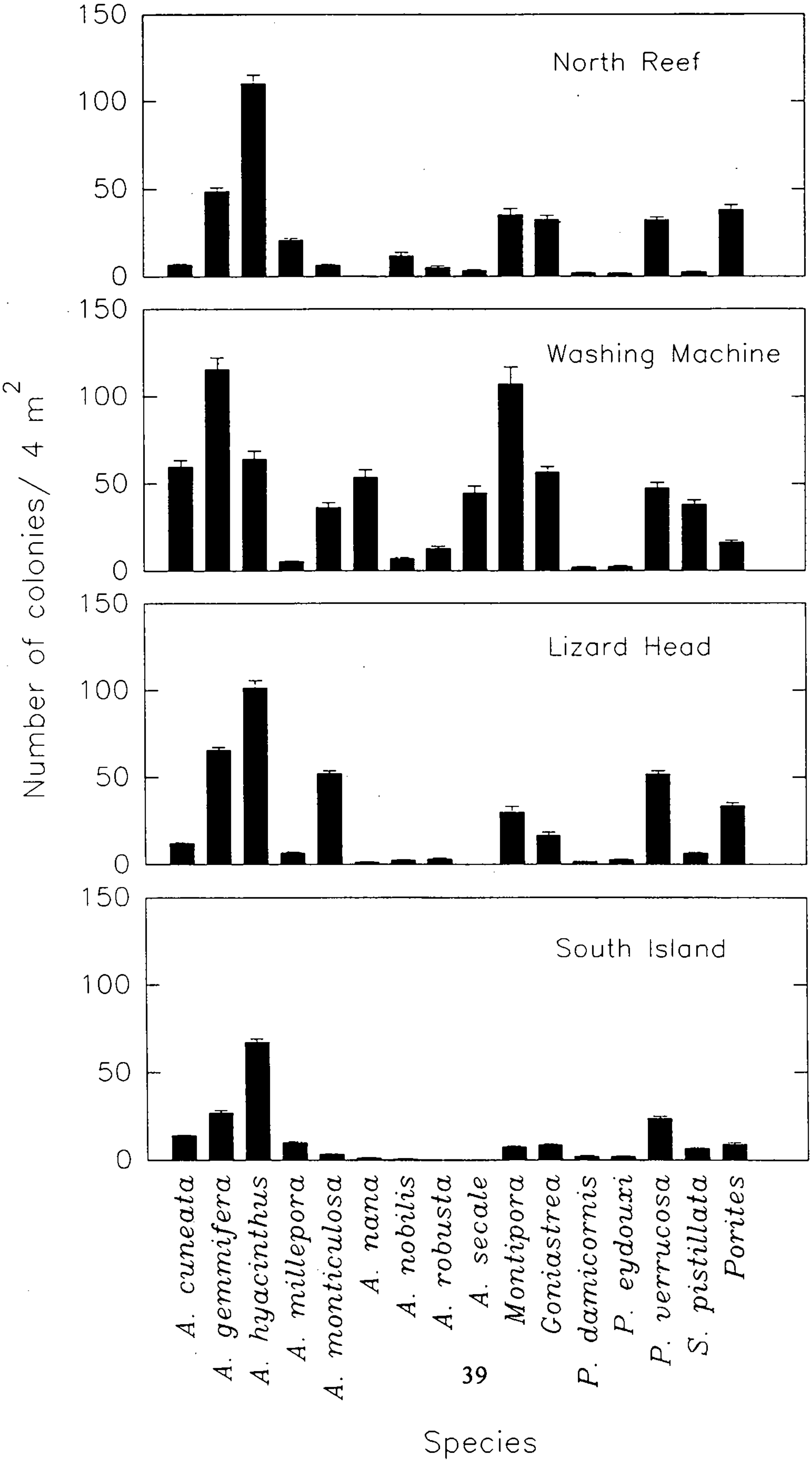
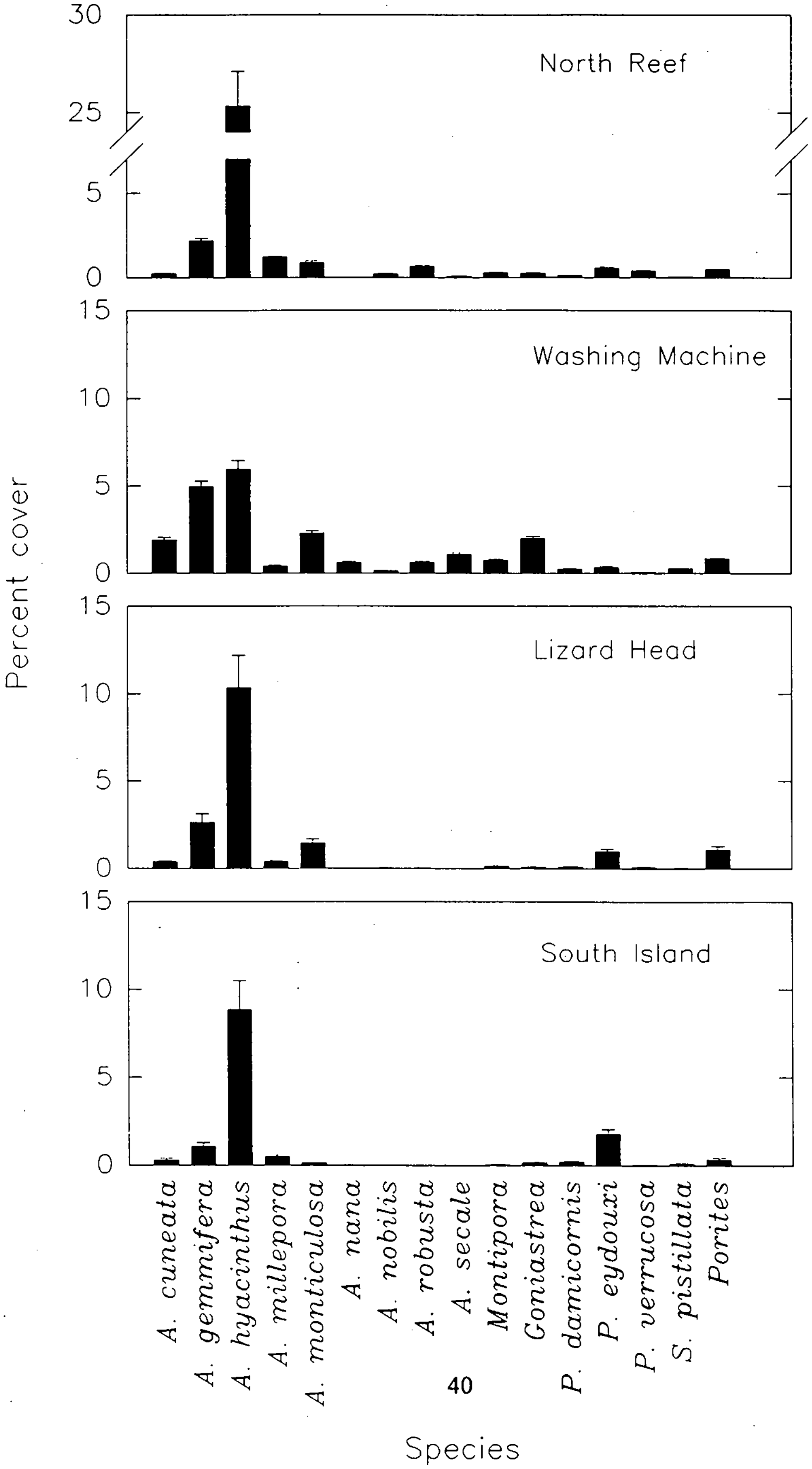


Figure 2.7 Mean percent cover per quadrat of 16 species of coral at four sites. Values are means and standard errors of 5 quadrats over 10 time periods.



A. hyacinthus had 12 times greater cover than *A. gemmifera*, the species with second highest cover (Fig 2.7). This degree of dominance by *A. hyacinthus* was also found at South Island and Lizard Head, where it had 8 and 4 times greater cover than *A. gemmifera* (Fig 2.7). Thus *A. hyacinthus* accounted for 77% of the total cover of 16 abundant species at North Reef, 58% at Lizard Head and 66% at South Island. At Washing Machine, *A. hyacinthus* did not dominate the assemblage, accounting for only 26% of the total cover of abundant species (Fig 2.7). Cover at Washing Machine was more evenly spread among species, with cover of *A. hyacinthus* and *A. gemmifera* similar (5.96 ± 0.47% and 4.96 ± 0.31%, respectively) and three other species accounting for 28% of the total cover of 16 species at that site (*A. monticulosa*, *A. cuneata* and *Goniastrea* spp.).

2.4 DISCUSSION

2.4.1 Changes in abundance and cover of coral

There were no consistent patterns in temporal trends across sites within a reef, nor were patterns of change in density and cover similar. These inconsistencies among sites and measures of community structure suggest that monitoring studies need to investigate multiple sites with a variety of measures to understand the dynamics of assemblages of coral (Nelson 1992; Rogers 1992).

At North Reef, total density declined by 39% (Fig 2.2), but cover increased by 44% (Fig 2.3). These patterns were most strongly influenced by the decline in abundance of Acroporids (Fig 2.4) and their increase in cover (Fig 2.5). Since North Reef is dominated by *A. hyacinthus* (30% of total numbers and 77% of total cover; Figs 2.7, 2.9), it is reasonable to hypothesise that the dynamics of the assemblage is driven primarily by the population dynamics of *A. hyacinthus*. It is interesting that, although the assemblage at South Island is also dominated by *A. hyacinthus* (37% of total abundance and 66% of total cover; Figs 2.7, 2.9), there was no change in total abundance (Fig 2.2), total cover (Fig 2.3) or the abundance and cover of Acroporids (Figs 2.4, 2.5) at this site. *Acropora hyacinthus* is abundant in relative terms at South Island, but its absolute abundance and cover are low, suggesting that its influence on the dynamics of the assemblage may be less at South Island than at North Reef.

There was very little change in the abundance and cover of corals other than Acroporids. In a similar study at Lizard Island, Harriott (1983) found no change in the abundance of any genera over 20 months. Constancy in this study (Figs 2.2, 2.3) may indicate that monitoring did not continue long enough to detect changes in abundance and cover of long-lived organisms. This is unlikely because there were significant changes detected in the abundance and cover of both Acroporids and Poritids (Figs 2.4, 2.5). The absence of any detectable increase in the cover of Faviids may be because they grow slowly (e.g. Stephenson & Stephenson 1933), but there is no reason that a decrease in abundance or cover should be undetected. These results show that over a period of approximately three years, the abundance and cover of coral assemblages at Lizard Island remained fairly constant. Such constancy has been recorded in other studies without major disturbances, but has been found to conceal both changes in spatial arrangement (Bak & Luckhurst 1980) and rapid turnover of populations (Harriott 1983; Hughes & Jackson 1985).

2.4.2 Spatial variation in assemblages of coral

There were no consistent differences in abundance, cover or composition of assemblages between the northeastern and southeastern sites. This suggests that using exposure to waves generated by trade winds as an *a priori* classification of wave exposure at sites is not useful. The actual wave climate at these sites may not be related to their locations on the reef. Bell & Denny (1994) quantified wave exposure at intertidal sites in Canada, and were surprised to find that their *a priori* categorisation of sites did not agree with measured maximal water velocities because of individual characteristics of the sites. Although Lizard Head and South Island were on the southeastern side of the island, and exposed to the full impact of southeasterly swells, they were slightly (< 1 m) deeper than North Reef and Washing Machine. The impact of waves may not have been as great as assumed at the two southeastern sites, since the force of breaking waves is rapidly attenuated with depth (Roberts *et al.* 1975). The site at Washing Machine was not only shallower than the other sites, but was also unusual in that the reef flat was narrower and ended at a vertical granite wall that reflected waves back across the reef causing increased water motion on the reef crest. The unusual topography of this site may mean that its label "sheltered" is a misnomer. Without quantification of water motion *in situ*, it is impossible to address whether average wave energy affects the abundance and composition of assemblages of coral (Bell & Denny 1994).

Variation in abundance, cover and composition of assemblages was substantial, but there were some consistent patterns that are characteristic of reef crests. Acroporids dominated assemblages at all sites (Figs 2.4, 2.5), a characteristic of shallow assemblages on mid-shelf reefs on the Great Barrier Reef (Wallace & Dale 1977; Done 1982, 1983). Assemblages at all sites in this study were dominated by *A. hyacinthus* and *A. gemmifera*, typical of wave-exposed habitats on the reef flat and slope (Done 1982).

Despite these similarities, the four sites differed greatly in total coral density and cover, abundances and cover of family groups and species composition. Each site had a characteristic species assemblage that did not change over time (Figs 2.6, 2.7). Some species were abundant at all sites, but ranged widely in abundance among sites (e.g. *A. hyacinthus*, *A. gemmifera*, *P. verrucosa*, *Montipora*, *Goniastrea*; Figs 2.6, 2.7). Other species were abundant at only one or two sites (e.g. *A. nana*, *A. monticulosa*, *A. secale*, *S. pistillata*, *A. cuneata*; Figs 2.6, 2.7), and sometimes only in one or two quadrats at each site (e.g *A. nana* in Quadrats 1 and 5 at Washing Machine). Differences among sites in abundance and composition of assemblages may arise from spatial variation in rates and patterns of recruitment, fission, fragmentation or mortality at various stages of the life history (post-settlement, early juvenile or adult mortality). These hypotheses are investigated in detail in the following chapters.

CHAPTER 3: SPATIAL AND TEMPORAL PATTERNS IN SEXUAL RECRUITMENT

3.1 INTRODUCTION

The role of recruitment in determining the size and structure of populations and assemblages has evoked much recent interest (e.g. Sale 1977; Underwood & Denley 1984; Connell 1985; Roughgarden *et al.* 1985; Doherty & Williams 1988; Roughgarden 1989; Underwood & Fairweather 1989). This interest in recruitment as a structuring force is not new (Underwood & Fairweather 1989); the importance of recruitment in fisheries has been studied since at least the turn of this century (Fogarty *et al.* 1991). Recruitment plays an important role in structuring some populations and assemblages (Grosberg 1982; Lewin 1986; Roughgarden *et al.* 1985; Gaines & Roughgarden 1985; Menge *et al.* 1993), and failure of recruitment can cause collapse of populations (e.g. McShane *et al.* 1988; Zajac & Whitlach 1989; Hughes 1990).

Variation in the abundance and composition of recruits has important consequences for the structure and dynamics of populations and assemblages of marine organisms. Fluctuations in the abundance and composition of recruits can promote coexistence in competing species (Keough 1984; Warner & Chesson 1985; Sutherland & Ortega 1986), determine the outcome of succession (e.g. Connell & Slatyer 1977; Tilman 1994), the species composition of an assemblage (e.g. Keough 1983; Sale & Douglas 1984) and spatial patterns in adult assemblages (e.g. Grosberg 1982; Menge *et al.* 1993). Spatial variation in the abundance and composition of recruits may lead to variation in the abundance and composition of adults in an assemblage, and therefore affect the dynamics of the assemblage (Underwood & Fairweather 1989).

The abundances of recruits of many organisms vary at many spatial and temporal scales (e.g. Keough 1983; Caffey 1985; Connell 1985; Gaines *et al.* 1985; Butler 1986; Davis 1988; Doherty 1991; Levin 1993). However, recruitment does not necessarily vary from place to place (Gotelli 1988). Recruitment of corals varies among depths (Birkeland 1977; Birkeland *et al.* 1981; Rogers *et al.* 1984; Wallace 1985a,c), within a depth zone (e.g. on the windward and leeward sides of a reef at 3 - 5 m depth: Harriott & Fisk 1987, 1988; Fisk & Harriott 1990; at sites 7 - 10 m deep on the reef slope and lagoon: Babcock 1988) and at different distances from a reef (Baggett & Bright 1985; Sammarco & Andrews 1989). Corals vary in their rates of recruitment to artificial substrata both seasonally and annually (e.g. Harriott & Fisk 1987; Wallace 1985c), with most recruitment on the Great Barrier Reef occurring after a summer spawning period. Recruitment to artificial substrata may not reflect real rates of recruitment to natural reef substratum for all species, if species respond to different settlement cues (Birkeland & Randall 1981; Wallace 1985a; Harriott & Fisk 1987; Morse *et al.* 1988). Recruitment to natural substrata is also variable in space and time (e.g. Pearson 1981; Colgan 1987), but few published studies have investigated patterns of recruitment to natural substrata at more than one site (but see e.g. Connell 1973; Rylaarsdam 1983).

Investigating the relationship between the abundance and composition of recruits and adult assemblages is an important first step in generating hypotheses about processes that structure ecological assemblages. Patterns in recruitment of corals do not reflect patterns in the relative abundance of species in the adult assemblage on most Caribbean reefs, suggesting that post-recruitment mortality may play a role in determining the composition of assemblages (Bak & Engel 1979; Rylaarsdam 1983; Rogers *et al.* 1984). Similarly, the composition and abundance of recruits on settlement panels differed from composition and abundance of adults at two sites in Hawaii (Fitzhardinge 1985). Two studies in the Pacific have also investigated the distribution of juveniles and adults on natural substrata (Harriott 1985; Colgan 1987). Harriott (1985) found that juveniles and adults of seven genera were similarly distributed among depths, but that juveniles of the four most abundant genera were distributed differently from adults. She suggested that either recruitment was variable among years or that post-recruitment mortality affected the relative abundance of some species. Similarly, Colgan (1987) described significant associations between the abundances of species of juveniles and adults along a depth gradient that were maintained by both non random settlement and differential survival of recruits.

The abundance and composition of assemblages of coral at Lizard Island vary greatly among sites (Chapter 2). This spatial variation may in part be a result of patterns in recruitment. To investigate the hypothesis that recruitment may be important in determining spatial variation in the abundance and composition of assemblages, spatial and temporal patterns in recruitment was quantified. The abundance and composition of recruits were compared with the abundance and composition of the established assemblage as a preliminary step to investigate whether patterns in recruitment or post-recruitment mortality are important in controlling the structure of assemblages of coral.

3.2 METHODS

3.2.1 Identification and definition of recruits

In this study, recruitment (*sensu* Keough & Downes 1982) is defined as the detection of previously unrecorded corals in photographs. Sexual recruits start out as encrusting circular or ovoid colonies ranging in size when first detected from < 1 cm^2 to approximately 20 cm^2. These larger recruits were usually discovered underneath colonies when the overtopping colony disappeared or fragmented. The new corals identified in each photograph are of unknown age. A size of 1 cm^2 represents a coral approximately 1 year old for Acroporids (Wallace 1983; Babcock 1985), but this estimate may not hold for slower growing massive corals (Babcock 1985) or very fast-growing Pocilloporids. Therefore, the patterns in recruitment described here are a result of unknown patterns in larval settlement and post-settlement mortality. All new individuals were counted and identified to family or, if possible, to genus or species (or species group). Identification to species or species group was possible for those species that survived and grew fast (e.g. *Acropora hyacinthus*) or were large when detected (e.g. recruits of *Goniastrea* and other Faviids). Thus, patterns in recruitment of species are potentially systematically biased towards overestimation of the abundance of fast-growing species. Identification to family is not as biased because of the lower resolution required to distinguish between Acroporids, Pocilloporids, Faviids, Poritids and Other Corals.

3.2.2 Spatial and temporal patterns in arrival of new colonies

Recruits were counted in five, 4 m^2 quadrats set up at each of the four sites around Lizard Island (see Section 2.2.1). Data used for analysis were censuses for which there were data for all four sites (i.e. February, May, August and November 1991, February, August and November 1992, and February 1993). There were missing values for Quadrat 1 at North Reef in February 1992 and Quadrat 4 at Washing Machine in August 1992. Spatial and temporal patterns in recruitment were analysed using a one-way multivariate repeated measures analysis of variance (MANOVAR) with Sites as a random factor, quadrats as replicates and times as multiple variables. First, patterns in total recruitment were investigated, then patterns for each of six family groups (Acroporids, Pocilloporids, Faviids, Poritids, Other Corals and Unidentified Corals; see Section 2.2.3). Testing for interactions among families was not possible because data were not statistically independent among families. For instance, if there were a change in the abundance of one family, it is likely that there would be a change in the abundance of another family because of the limited space available inside a 4 m^2 quadrat. Data were checked for multivariate normality and homoscedasticity before analysis using multivariate normality plots and multivariate Levene's test (McArdle, unpublished notes). Data on the total number of recruits were transformed to natural logarithms while total numbers of recruits in families were transformed to $\ln(x+1)$ to reduce heterogeneity.

Temporal patterns in the arrival of recruits of particular species were not investigated because few individuals of most species recruited at each time. To test the null hypothesis that there were no differences among sites in species composition of recruits, Chi-squared analysis of heterogeneity was used to compare the total number of new colonies that arrived between February 1991 and February 1993.

3.2.3 Relationship with adult community structure

The relationship between composition of recruits and the established assemblage was investigated in two ways. The relationship between total abundances of recruits over the period February 1991 - February 1993 and established colonies (in February 1991) was investigated using Pearson correlations. Correlations were done to analyse the relationship between total recruitment and total established abundance, and between recruitment into each family (Acroporids, Pocilloporids, Faviids, Poritids, Other corals and Unidentified corals) and that family's initial abundance. The relationship between recruitment and established abundance of individual species was also investigated in this way. Secondly, the relationship between the composition at each site of new colonies recruited over the period February 1991 - February 1993 and colonies already established in February 1991 was analysed with log-linear analysis of the abundances of recruits and established colonies in six families at four sites. To compare the composition of recruits and established colonies at the level of species and species groups, a χ^2 test of homogeneity on frequencies of recruits (February 1991 - February 1993) and colonies already established in February 1991 was done. Expected values were calculated using data for 16 species or species groups (*Acropora cuneata*, *A. gemmifera*, *A. hyacinthus*, *A. millepora*, *A. monticulosa*, *A. nana*, *A. nobilis*, *A. robusta*, *A. secale*, *Montipora* spp., *Goniastrea* spp., *Pocillopora damicornis*, *P. eydouxi*, *P. verrucosa*, *Stylophora pistillata* and *Porites* sp.), then data were pooled across species to ensure that expected frequencies were greater than 5.

3.3 RESULTS

3.3.1 Spatial and temporal variation in sexual recruitment

A total of 3017 larval recruits was detected over the 2-year period from February 1991. The total abundance of recruits differed by twofold among sites (Site; Table

Table 3.1 MANOVAR on total numbers of new colonies detected per quadrat (n = 5) at four sites. Data transformed to ln(x).

Within Quadrats

Source	Pillai's trace	F	num df	den df	*p*
Time	0.821	5.26	7	8	< 0.02
Time*Site	1.972	2.74	21	30	< 0.006

Between Quadrats

Source	MS	F	df	*p*
Site	2.449	3.86	3	< 0.04
Error	0.634		14	

3.1). On average, Washing Machine had the largest number of new colonies per 4 m^2 quadrat per census (17.5 ± 1.3) and South Island fewest (8.9 ± 0.6). North Reef (15.9 ± 1.1) and Lizard Head (11.3 ± 1.0) were intermediate between these two extremes. There was also significant temporal variation in recruitment at all sites (Table 3.1) probably due to the large number of recruits detected in February 1991 at North Reef and Washing Machine (Fig 3.1). There was no obvious seasonal or annual pattern in recruitment (Fig 3.1).

The total number of new colonies detected between February 1991 and February 1993 at each site was significantly correlated with the number of colonies already at the site in February 1991 ($r = 0.94$, $n = 20$, $p < 0.001$, Fig 3.2a). There was no correlation between the numbers of new colonies and percent cover of corals at each site ($r = 0.43$, $n = 20$, $p > 0.05$; Fig 3.2b).

3.3.2 Recruitment of family groups

Spatial and temporal patterns in recruitment differed among families (Table 3.2). Although MANOVAR on log-transformed data showed that there were significant effects of time, site or both on the recruitment of most families, patterns in raw data were not clear (Fig 3.3). Acroporid recruits were 5 - 10 times more abundant than recruits in other families at all sites, averaging 8 recruits per quadrat per census, while recruitment in other families ranged from 0.6 to 1.6 recruits per quadrat per census (pooled across sites). Ranking of recruitment among sites differed for each family. Recruitment of Acroporids was greatest at Washing Machine, averaging

Table 3.2 Results of manovar on the number of recruits detected at four sites over two years. Data untransformed for Acroporids, Pocilloporids, Poritids and Unidentified Corals. Data for Faviids and Other Corals were ln(x+1) transformed.

Within Quadrats

Taxon	Source of variation	Pillai's trace	F	num df	den df	p
Acroporid	Time	0.905	10.82	7	8	< 0.002*
	Site*Time	1.624	1.69	21	30	> 0.09
Pocilloporid	Time	0.559	1.45	7	8	> 0.30
	Site*Time	1.262	1.04	21	30	> 0.45
Faviid	Time	0.752	3.46	7	8	> 0.05
	Site*Time	0.840	0.56	21	30	> 0.91
Poritid	Time	0.383	0.71	7	8	> 0.66
	Site*Time	0.988	0.70	21	30	> 0.79
Other Corals	Time	0.644	2.07	7	8	> 0.16
	Site*Time	1.868	2.36	21	30	< 0.02*
Unidentified	Time	0.854	6.67	7	8	< 0.008*
	Site*Time	1.480	1.39	21	30	> 0.19

Between Quadrats

	Source of variation	df	MS	F	*p*
Acroporid	Site	3	486.177	17.84	< 0.001*
	Error	14	27.248		
Pocilloporid	Site	3	6.039	3.46	< 0.05*
	Error	14	1.746		
Faviid	Site	3	2.218	6.73	< 0.005*
	Error	14	0.330		
Poritid	Site	3	1.737	2.10	> 0.14
	Error	14	0.828		
Other Coral	Site	3	0.087	0.34	> 0.79
	Error	14	0.254		
Unidentified	Site	3	4.975	2.39	> 0.11
	Error	14	2.085		

Figure 3.1 Mean number of sexual recruits per quadrat (± S.E.) at four sites over 30 months.

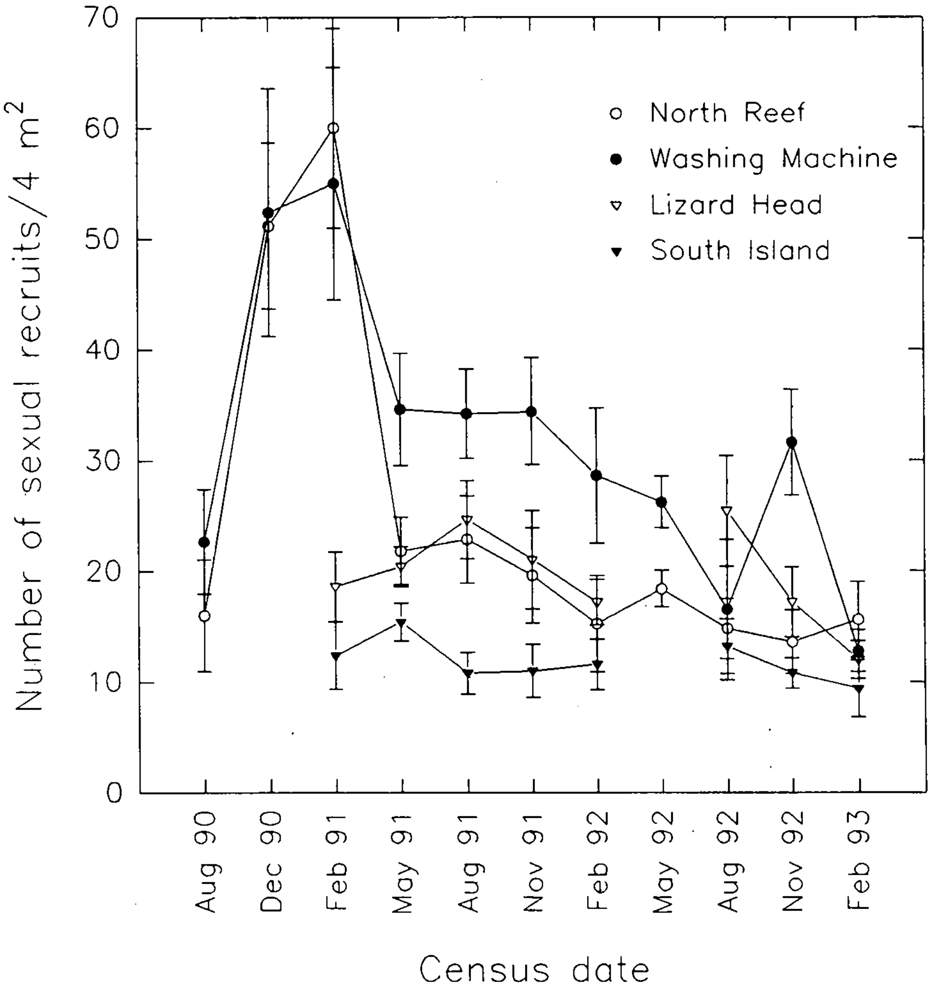
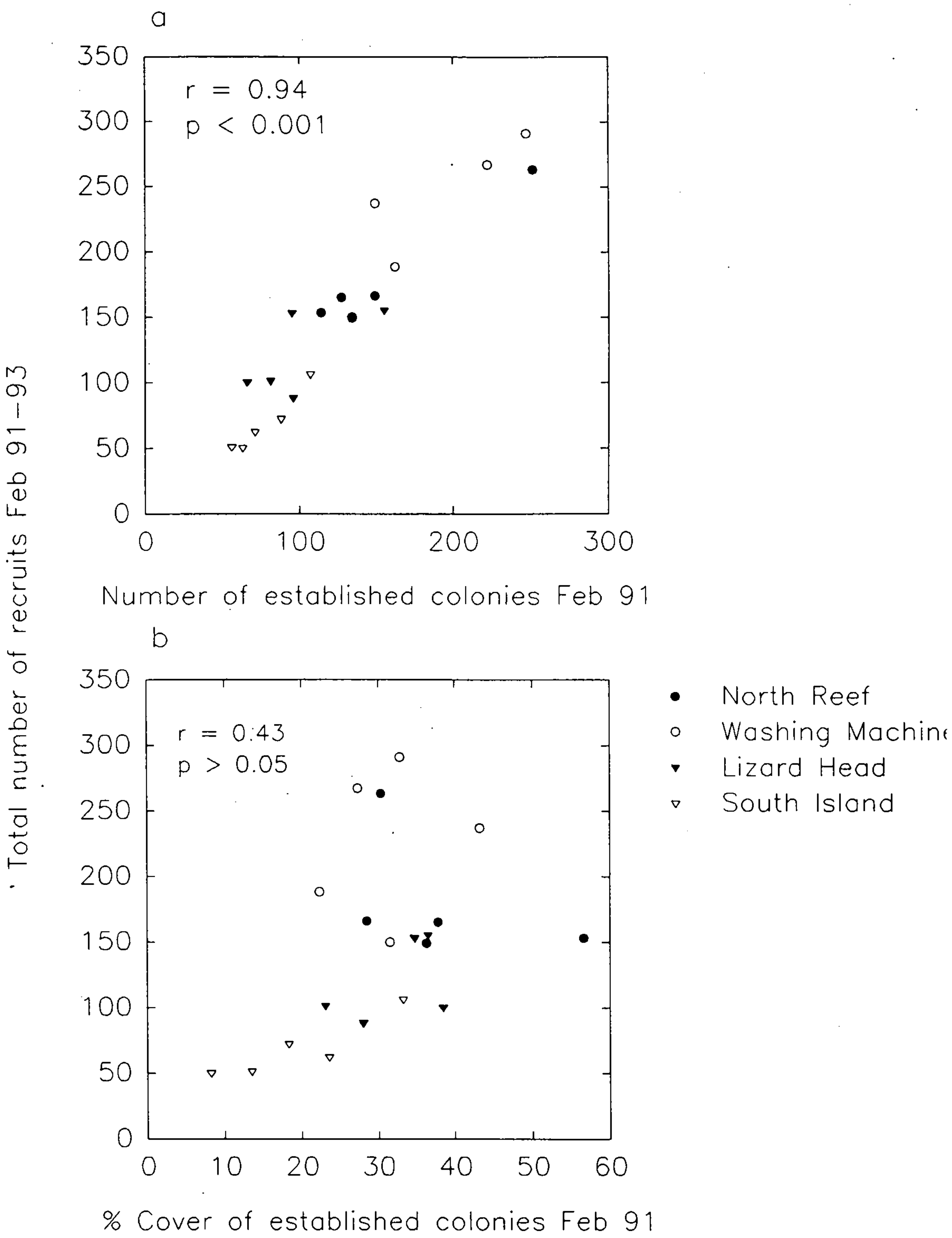


Figure 3.2 Correlations between the total number of recruits detected over 24 months from February 1991 and (a) the number of colonies and (b) the cover of colonies already established in February 1991. Symbols represent different sites with n = 5 quadrats per site.



12.2 ± 1.7 recruits per quadrat per census, and leastat South Island (4.1 ± 0.4 recruits). In contrast, the greatest recruitment of Pocilloporids was at South Island, averaging 2 ± 0.2 recruits per quadrat per census and least at Lizard Head 1.1 ± 0.2. Recruitment of Faviids was smallest at South Island (0.45 ± 0.15 recruits per quadrat per census) and largest at North Reef (1.7 ± 0.2).

Correlations between the abundance of recruits and established colonies in each family were significant and positive for Acroporids, Faviids, Poritids and Other corals but not for Pocilloporids and Unidentified colonies (Table 3.3). This means that sites with greater initial abundances of the former four families also received greater abundances of recruits of these families.

Table 3.3 Correlations between total number of recruits of six taxonomic groups detected in quadrats from February 1991 to February 1993 and the number and cover of corals of the same groups in quadrats in February 1991. Adjusted $\alpha = 0.008$, $n = 20$. * Correlation significant at $\alpha = 0.008$.

Taxon	Number of adults		Cover of adults	
	r	*p*	*r*	*p*
Acroporid	0.80	0.00002*	0.15	0.5
Pocilloporid	0.26	0.2	0.06	0.7
Faviid	0.70	0.001*	0.52	0.02
Poritid	0.59	0.006*	0.41	0.07
Other	0.64	0.002*	0.42	0.06
Unidentified	0.34	0.1	0.23	0.3

Figure 3.3 Mean number of sexual recruits per quadrat (± S.E.) in six taxonomic groups at four sites over 30 months.

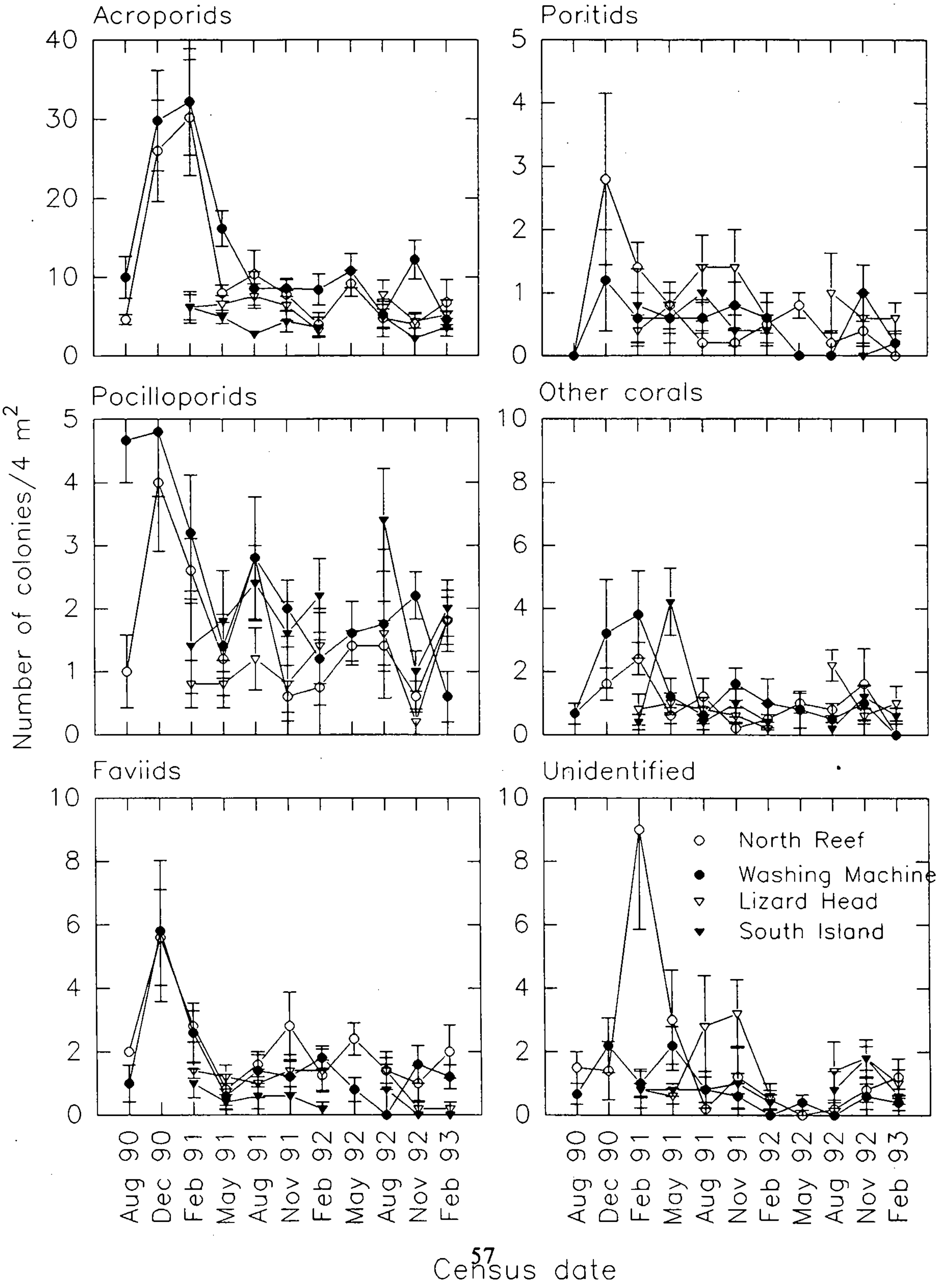
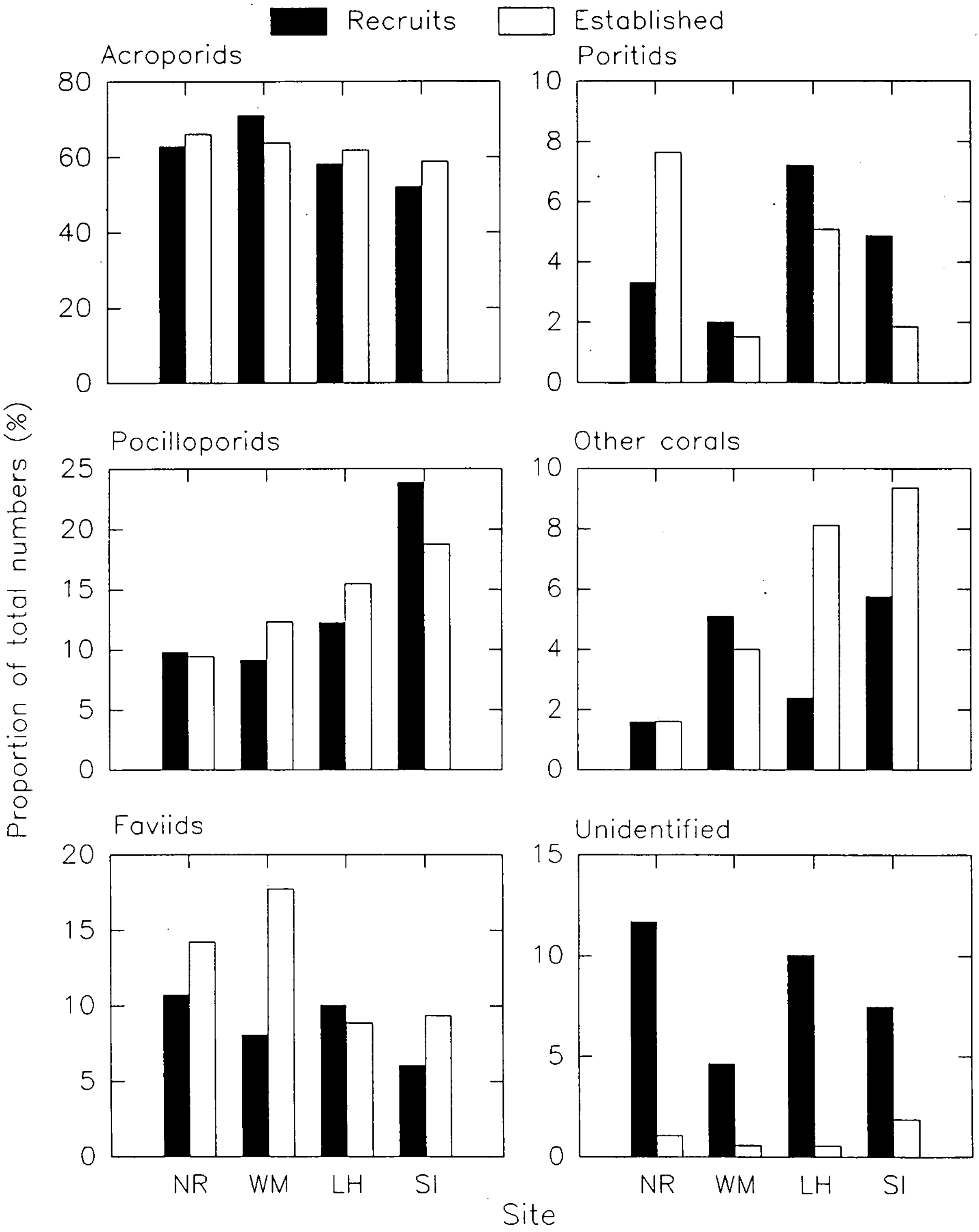


Table 3.4 Results of three-way loglinear analysis comparing the distribution among six families of larval recruits with established colonies at four sites.

Source of variation	df	χ^2	p
Site	3	61.81	0.0001
Family	5	3476.08	0.0001
Site*Family	15	143.95	0.0001
Recruit/Established (R/E)	1	24.75	0.0001
Site*R/E	3	3.78	0.29
Family*R/E	5	92.54	0.0001
Site*Family*R/E	15	58.89	0.0001

The composition of recruits and established colonies differed in different ways at each site (Site*Family*R/E; Table 3.4). All sites had a smaller proportion of unidentified, established colonies than unidentified recruits, because established colonies were larger on average than recruits, and hence easier to identify. Other deviations in the distributions of recruits and established colonies differed among sites (Fig 3.4). Differences in the proportions of Acroporid and Pocilloporid recruits and established colonies were small (only 1 - 5%). Faviids made up twice the proportion of the established assemblage as the assemblage of recruits at Washing Machine, but the ratio of established:recruit abundance was smaller at the other sites (1.3, 0.9 and 1.6 at North Reef, Lizard Head and South Island respectively; Fig 3.4). The proportion of Poritids in assemblages of recruits and established colonies varied from 2 to 8% and the ratio of established colonies to recruits varied from 0.7 to 2.3, with the largest deviation at North Reef (Fig 3.4). While there were 2.3 times as

Figure 3.4 Spatial variation in the family composition of assemblages of recruits and established colonies at four sites.



NR ■ n = 633
□ n = 563

WM ■ n = 843
□ n = 852

LH ■ n = 458
□ n = 530

SI ■ n = 348
□ n = 267

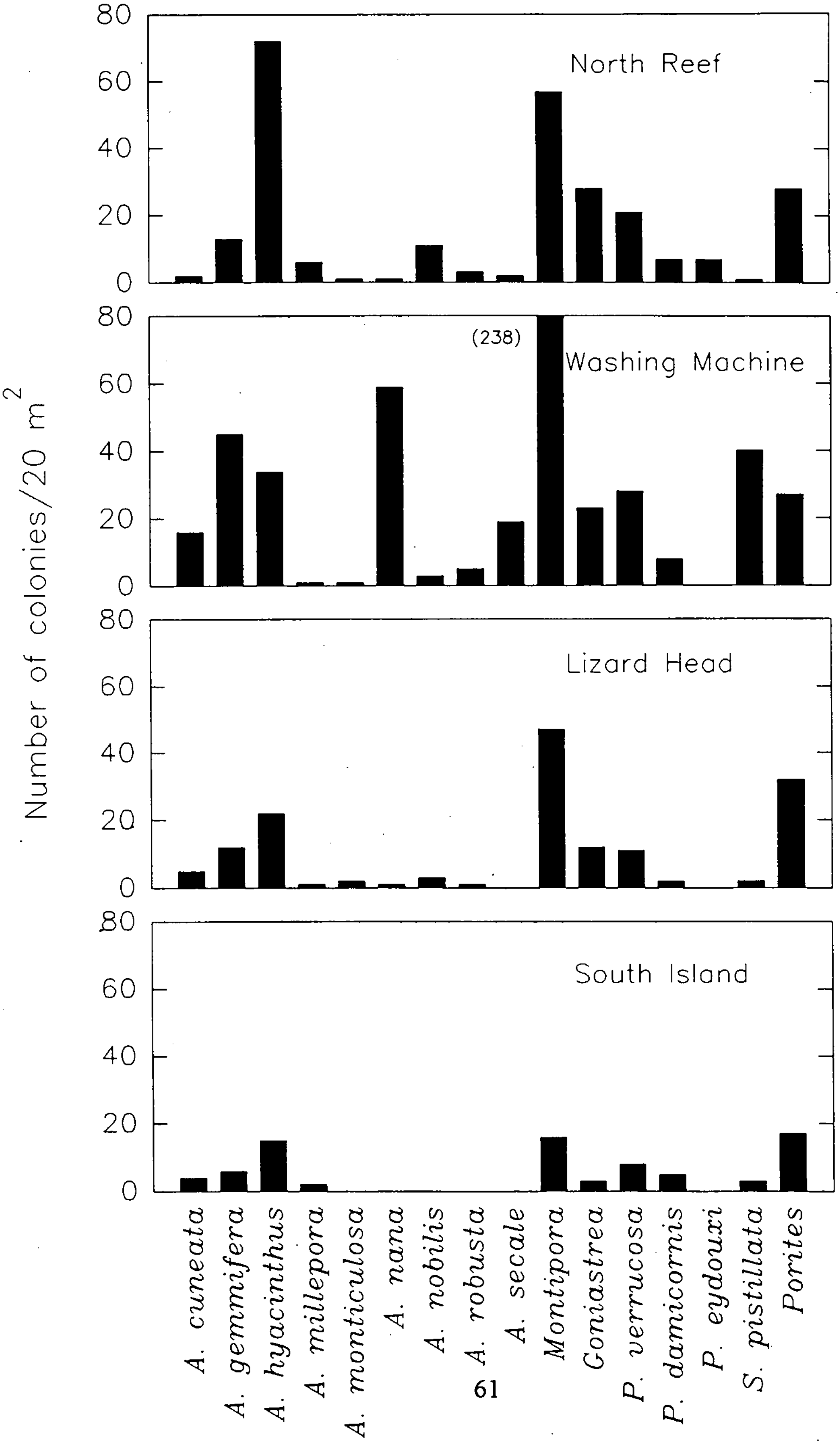
many Poritids in the established assemblage than in the assemblage of recruits, this represented the difference between 8% and 4% of the total numbers of established colonies and recruits. Similarly, although there were 3.4 times as many established colonies as recruits of Other Corals at Lizard Head, Other Corals only made up 2% of recruits and 8% of established colonies (Fig 3.4). Thus, although there were statistically significant differences in the composition of recruit and established assemblages, the largest deviations occurred in rarer families and the absolute differences were small.

3.3.3 Spatial and temporal patterns in recruitment of species

The species composition of recruits varied among sites ($\chi^2 = 284.48$, 45 df, $p < 0.0001$; Fig 3.5). *Acropora hyacinthus*, *Montipora* spp. and *Porites* sp made up 55 to 66% of the recruitment of 16 species at all four sites, but the relative abundance of recruits of these species varied among sites (Fig 3.5). Recruitment at North Reef, Lizard Head and South Island was qualitatively similar because of the dominance by *A. hyacinthus*, *Montipora* spp. and *Porites* sp (Fig 3.5). At Washing Machine, however, there were abundant recruits of a suite of species that were much rarer at the other three sites, namely *A. cuneata*, *A. nana*, *A. secale* and *S. pistillata* (Fig 3.5).

The link between the abundance of established colonies and recruits was evident even at the level of species. Analysis of the relationship between recruits and established colonies by species showed that the number of recruits was highly correlated with the number of adults for five out of seven species that occurred at all four sites, the

Figure 3.5 Species composition of recruits at four sites. Data are the total numbers of recruits of 16 species detected in 5 quadrats at each site over 24 months from February 1991.



exceptions being *A. hyacinthus* and *P. verrucosa* (Table 3.5). Both species had fewer recruits at Lizard Head and South Island than expected based on their abundance in the established assemblage. There were significant correlations between the number of recruits and the cover of established colonies for *A. cuneata* and *Montipora* spp. (Table 3.5).

Table 3.5 Correlations between number of recruits of six species or species groups and numbers and cover of established colonies at four sites. Adjusted $\alpha = 0.008$, $n = 20$. * Correlations significant at $\alpha = 0.008$.

Species	Number of adults		Cover of adults	
	r	*p*	*r*	*p*
A. cuneata	0.70	0.001*	0.83	0.00001*
A. gemmifera	0.83	0.00001*	0.45	0.04
A. hyacinthus	0.41	0.07	0.10	0.6
Montipora spp.	0.84	0.00001*	0.74	0.0002*
Goniastrea spp.	0.82	0.00001*	0.39	0.09
P. verrucosa	0.36	0.1	0.05	0.8
Porites spp.	0.59	0.006*	0.35	0.1

The species composition of recruits differed from the species composition of the established assemblage at all four sites (Fig 3.6; Table 3.6). Some species and species groups were more abundant in the assemblage of recruits than in the established assemblage at all sites. *Montipora* spp. were 2 - 5 times more abundant as recruits than as adults (Fig 3.6). In contrast, *A. monticulosa*, *A. gemmifera*, *A.*

Figure 3.6 Comparison between the species composition of recruits and established colonies of 16 species at four sites. Numbers of recruits are the total detected in 5 quadrats at each site over 24 months from February 1991. composition of the established assemblage is the total number in 5 quadrats at each site in February 1991.

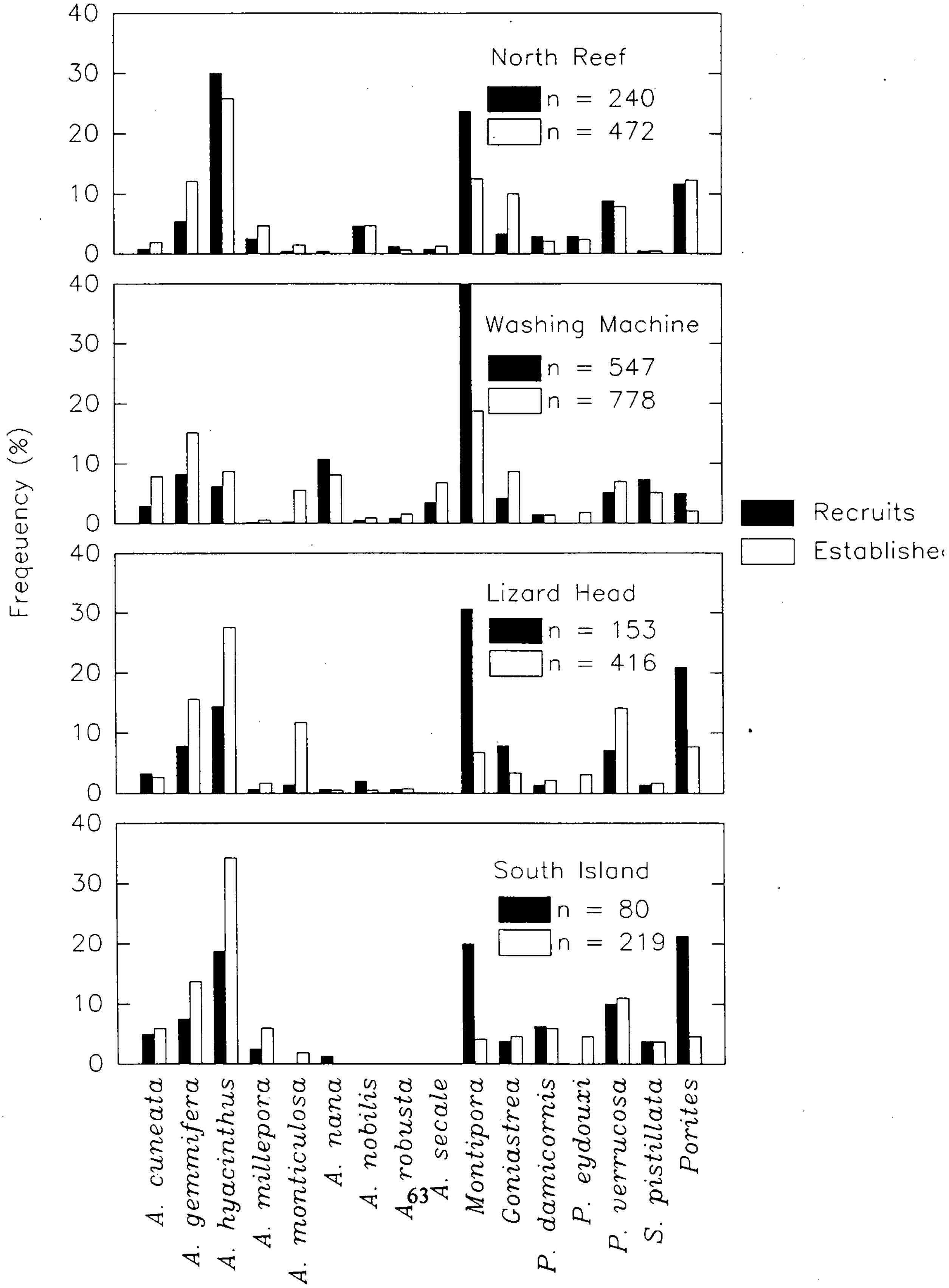


Table 3.6 Results of χ^2 analysis of heterogeneity comparing the species composition of recruits and established colonies at each of four sites.

Site	N	χ^2	df	p
North Reef	647	67.89	10	0.0001
Washing Machine	1120	215.07	14	0.0001
Lizard Head	518	104.98	9	0.0001
South Island	259	65.51	7	0.0001

millepora and *A. secale* made up a smaller proportion of the assemblage of recruits than the established assemblage at all sites (Fig 3.6). Most species had varying ratios of recruits:established colonies among sites. For instance, *A. hyacinthus* was 2 times more abundant as established colonies than as recruits at Lizard Head and South Island, but 1.2 times more abundant as recruits than as established colonies at North Reef (Fig 3.6). Similarly, *Porites* sp accounted for 2 to 5 times greater proportions of the assemblage of recruits than established colonies at Washing Machine, Lizard Head and South Island, but recruits and established colonies made up equal proportions of the total assemblages at North Reef (Fig 3.6). On average, the six most abundant species in the established assemblage (*A. hyacinthus, A. gemmifera, Montipora* spp., *P. verrucosa, Porites* sp and *Goniastrea* spp.) were also the six most abundant species in the assemblage of recruits, despite different composition among sites.

3.4 DISCUSSION

The abundance and composition of recruits varied greatly among sites. Factors which cause spatial variation in recruitment have been intensely studied in many systems (e.g. Connell 1985; Butman 1987; Roughgarden *et al.* 1988). They fall into three broad categories: factors causing variation in larval supply, in larval settlement and in post-settlement mortality. Relative abundance of total recruits among sites (Fig 3.1) may be influenced by the distribution and relative abundance of pre-settlement larvae in the water column, as has been described for reef fish at Lizard Island (Milicich *et al.* 1992) and temperate intertidal barnacles (e.g. Grosberg 1982; Gaines *et al.* 1985). Larval supply is directly related to physical transport processes for many organisms (e.g. Gaines & Roughgarden 1985; Shanks & Wright 1987; Roughgarden *et al.* 1988; Kingsford *et al.* 1991; Milicich 1994; Milicich & Doherty 1994). Hydrodynamic modelling indicates that spatial variation in larval recruitment is consistent with patterns of circulation around reefs, at least for some species (Black & Moran 1991; Black 1993). Thus, supply of larvae from offshore may contribute to differences among sites in abundance of recruits found in this study (Fig 3.1).

Another possible explanation for spatial variation in the abundance of recruits (Fig 3.1) is that sites are self-seeded. In this way, the number of recruits to a site would be correlated with the reproductive output of that site. Modelling of larval dispersion around reefs has shown that self-seeding is a possibility on the scale of whole reefs, based on flushing times and patterns of circulation within and between reefs (Black *et al.* 1991), but there is little evidence that sites within reefs may be self-seeding.

Some authors have suggested that patterns in abundance of recruits could be explained by self-seeding (Baggett & Bright 1985; Andrews *et al.* 1988; Sammarco & Andrews 1989), but the evidence for such conclusions is only correlative, based on patterns of settlement to artificial substrata at various distances from reefs. Alternatives to self-seeding were not ruled out and the question remains controversial (Harriott & Fisk 1988; Fisk & Harriott 1990). Slicks of coral larvae have been observed miles away from reefs (Babcock & Heyward 1986; Willis & Oliver 1988; Wolanski *et al.* 1989), indicating that propagules can travel long distances. In addition, Fisk & Harriott (1990) showed that recruits were abundant on a reef with a depauperate adult assemblage, suggesting that larvae must have dispersed from another reef. However, the fact that a depauperate reef was colonised rapidly does not negate the possibility that recruitment may also be associated with local retention under some circumstances. If reefs are self-seeding, the strength of local recruitment will vary among reefs depending on their shape, and also among years depending on the strength of the coastal current (Wolanski *et al.* 1989; Black *et al.* 1991).

The close relationship between the abundance and composition of recruit and established assemblages (Figs 3.4, 3.6) may also be explained by local larval retention. It is particularly interesting that the suite of species that characterise the established assemblage at Washing Machine (Chapter 2) also distinguish the assemblage of recruits (Fig 3.5). Such similarities might be expected if recruitment is related to reproductive output due to larval retention.

Local recruitment does occur in some brooding species that release larvae ready to settle (e.g. solitary corals: Gerrodette 1981; Fadlallah 1983; ascidians: Olson 1985; Davis 1987; Carlon & Olson 1993). Some authors have speculated that local recruitment occurs in brooding corals, based on correlations between the abundance of recruits and adults (e.g. Fisk & Harriott 1990; Jackson 1991) and the clonal structure of populations (e.g Stoddart 1984). The limited distribution of *Acropora cuneata* and *Stylophora pistillata* in this study (Fig 3.5) may be due to limited larval dispersal, since both are brooding species (Richmond & Hunter 1990). Nevertheless, *Pocillopora verrucosa* is also a brooder (Harrison & Wallace 1990; Richmond & Hunter 1990), and there was no correlation between the abundances of its recruits and adults (Table 3.5). The correlation between abundance of recruits and adults shown in Jackson (1991) for *Agaricia agaricites* and *Porites astreoides* in the Caribbean clearly does not apply to all brooding species.

Spatial patterns in recruitment may also be affected by larval choice at settlement (Keough 1988). Black & Moran (1991) point out that the availability of suitable substrata for settlement may decouple the relationship between currents and larval recruitment. Fisk & Harriott (1990) found that a simple hydrodynamic model did not adequately explain spatial variation in recruitment of corals at Green Island. They suggested that larval supply did not limit the abundance of recruits, but rather space free from sediment and competing algae did. Many marine invertebrate larvae, including coral planulae, show decided preferences for particular types of substratum and microhabitats (e.g. Keough & Downes 1982; Raimondi 1990; reviews in Butman 1987; Pawlick 1992). There have been few studies on the settlement preferences of coral larvae (reviewed in Harrison & Wallace 1990), but they appear to settle preferentially in surface irregularities (or survive better there) (Birkeland 1981; Carleton & Sammarco 1987). The four sites investigated in this study certainly differ in their surface complexity (pers. obs.) with the most complex surface at Washing Machine and the least rugose surface at South Island, corresponding to rates of recruitment. If different species have different preferences for microhabitats, then the differences in surface characteristics among sites may also lead to spatial variation in the species composition of recruits (Fig 3.5). Clearly, there is a need for further studies on factors that influence settlement of coral larvae.

The similarity in the taxonomic composition of recruits and established colonies (Figs 3.4, 3.6) may arise from the life-history characteristics of families and species adapted to life in the wave-swept reef crest of reefs where cyclones frequently occur. In such disturbed environments, species that recruit quickly and grow fast before the next disturbance are expected to do well (Williams 1975; Loya 1976a,b). The most abundant corals on the reef crest at Lizard Island are also the most abundant recruits. The similarities in the composition of recruits and established colonies may be a result of the types of species that survive well there (Loya 1976a,b). In disturbed habitats, such as shallow reefs, it is advantageous for corals to be able to exploit new space created by disturbance. Thus, species that have abundant recruits should be disproportionately represented in the adult assemblage, as was found in this study.

Although there were close relationships between the numbers of recruits and established colonies, correlations between numbers of recruits and cover of established colonies were few (Fig 3.2; Tables 3.3, 3.5). This is because numerical abundance and cover were not necessarily related (Chapter 2). It was only in groups with little variation in size among sites, or where size structure (i.e. cover) was correlated with density that there were significant correlations between the abundance of recruits and both abundance and cover of established colonies (*A. cuneata* and *Montipora* spp.; Table 3.5). These data suggest that recruitment will rarely be predictable from estimates of percent cover, but estimates of numerical abundance are likely to be good predictors of relative rates of recruitment among sites.

CHAPTER 4: SPATIAL PATTERNS IN MORTALITY OF RECRUITS AND ESTABLISHED COLONIES

4.1 INTRODUCTION

Mortality of corals is important in determining the abundance and composition of coral assemblages, especially after major disturbances that differentially affect some species over others (e.g. Loya 1976a; Connell 1978; Hughes 1989; Rogers 1992; Witman 1992; Bythell *et al.* 1993; Karlson & Hurd 1993). Without major disturbances rates of mortality can also be high, with some species having naturally high rates of turnover (e.g. Harriott 1983; Hughes & Jackson 1985; Hughes & Connell 1987). The role of mortality in determining the distribution and abundance of corals under undisturbed conditions depends on the rate of recruitment (e.g. Hughes 1990) and on whether mortality is density-dependent (e.g. Warner & Hughes 1988; Holm 1990).

There has been considerable interest in the relative roles of recruitment versus post-recruitment processes in controlling the dynamics of many communities (e.g. fish: reviews in Doherty & Williams 1988; Doherty 1991; Jones 1991; barnacles: Connell 1985; Gaines & Roughgarden 1985; soft-sediment invertebrates: reviewed in Butman 1987; plants: Wilson 1992; Tilman 1994). Studies comparing patterns of recruitment and post-recruitment mortality with patterns of abundance and composition in adult assemblages of corals conclude that post-recruitment mortality is important in determining adult abundances (Bak & Engel 1979; Rylaarsdam 1983; Harriott 1983).

Spatial variation in the abundance and composition of assemblages (Chapter 2) may be related to patterns in survival of recruits and established colonies. Survivorship of corals was 26% lower at a shallow site than at a deep site in Jamaica (Hughes & Jackson 1985). Similarly, in a study at Lizard Island, Harriott (1983) showed that rates of mortality of ten genera varied among transects at different depths. In contrast, survival of juveniles in Curaçao did not vary among depths despite zonation of adults (Bak & Engel 1979). Bak & Engel (1979) suggested that temporal variation in rates of mortality, particularly in shallow sites, may be responsible for the lack of variation in mortality over six months. Some studies have shown that rates of mortality also vary within a depth zone. Connell (1973) found that mortality of recruits varied twofold between $1m^2$ quadrats at two locations at Heron Island. Mortality of *Acropora hyacinthus* differed among patch reefs in the lagoon of Enewetak atoll (Stimpson 1985). In a study in the U.S. Virgin Islands, Bythell *et al.* (1993) found that mortality from both cyclones and "routine chronic mortality" varied among sites on the north and south sides of St. Croix. Differences in rates of mortality among sites within a depth zone may be due to differences in the causes of mortality as was found for differences in rates of mortality among depths (Bak & Luckhurst 1980). However, Witman (1992) found that differences in mortality from Hurricane Hugo between sites on exposed and sheltered reefs were not consistent with *a priori* classifications based on wave exposure, but were explained by the time since the previous storm and morphological composition of assemblages. Sites with different histories of disturbance and recovery are likely to show differences in susceptibility to damage by storms (Hughes 1989), and therefore rates of mortality are likely to vary among them.

Mortality of corals varies widely among taxonomic groups and species (e.g. Bak & Engel 1979; Rylaarsdam 1983; Hughes & Jackson 1985; Hughes & Connell 1987; Witman 1992; Bythell *et al.* 1993). This variation may be due in part to differences in size-distributions of species because mortality is strongly dependent on colony size (e.g. Connell 1973; Hughes & Jackson 1980; Babcock 1991). Comparisons of size-specific rates of mortality, however, indicate that there are differences in mortality among species unrelated to differences in size-distributions (Hughes & Jackson 1985; Hughes & Connell 1987; Babcock 1991). Rates of mortality are associated with other life history traits of species (Jackson 1979), with fast-growing, "mobile" species having greater rates of mortality than slower-growing, "stationary" species (Jackson & Hughes 1985; Hughes & Jackson 1985).

In this chapter, spatial variation in rates of mortality of recruits and previously established colonies is investigated to determine whether patterns in abundance and composition of assemblages of coral are affected by differential mortality among sites and species. Rates of mortality of recruits and established colonies are compared among species and related to morphology, size and growth rate to see how generalisations from life history theory (e.g. Jackson 1979; Jackson & Hughes 1985) relate to patterns of mortality among Great Barrier Reef corals.

4.2 METHODS

4.2.1 Mortality of recruits

Survival curves for recruits at each site were generated by calculating the rate of depletion of cohorts of recruits detected at each census, then summing over all cohorts. Thus, the sample size for each survivorship curve was the total number of recruits counted during the study. Survival curves were compared using a non-parametric log-rank test (Savage 1956, cited in Kalbfleisch & Prentice 1980). If survivorship curves were significantly different, pairwise multiple comparisons determined which pairs of curves differed. Type I error rate was adjusted for multiple comparisons using the Dunn-Sidák adjustment (Day & Quinn 1989).

Analysis of differences among sites in survivorship of species was done on the six most abundant species that recruited at all four sites (*Acropora gemmifera*, *A. hyacinthus*, *Goniastrea* spp., *Montipora* spp., *Pocillopora verrucosa* and *Porites* spp., but *Goniastrea* spp. at South Island had only 3 recruits). Comparisons of survivorship among species were done on data pooled across sites to increase sample sizes.

4.2.2 Mortality of established colonies

Loglinear modelling was used to analyse spatial variation in the mortality rates of colonies that were already established in February 1991. Data analysed were counts of individuals initially present in February 1991 that were dead or alive in February 1993. Analysis was done at three taxonomic levels - all colonies combined, colonies classified by family (Acroporids, Pocilloporids, Faviids, Poritids, Other corals and Unidentified corals), and corals classified by species. In this last case, only species with sample sizes large enough to ensure expected frequencies > 5 were used. These species were *A. hyacinthus*, *A. gemmifera*, *P. verrucosa*, *Montipora* spp., *Goniastrea* spp. and *Porites* sp. The first three of these species occurred in reasonable numbers at all four sites, while the latter three only occurred at North Reef, Washing Machine and Lizard Head in large enough numbers to analyse (see Chapter 2).

4.3 RESULTS

4.3.1 Mortality of larval recruits

Survival of new colonies differed twofold among sites ($\chi^2 = 18.90$, 3 df, $p < 0.0003$). Survival was greatest at Washing Machine (23% of recruits survived for at least 24 months), where the abundance of recruits was also greatest (see Fig 3.1). Survival was lowest at South Island (12%; Fig 4.1). There were no detectable differences in survival of sexual recruits at other pairs of sites (Fig 4.1; Table 4.1).

There was no evidence of density dependence in survival of recruits (Fig 4.2). There was no relationship between the density or cover of established colonies and survival of recruits in quadrats ($r = 0.22$, -0.11, respectively, $n = 20$, $p > 0.3$ for both), nor between the total number of recruits to a quadrat and their survival ($r = 0.14$, $n = 20$, $p > 0.5$).

Figure 4.1 Survival of larval recruits at four sites on the reef crest at Lizard Island. Sample sizes are the total number of recruits that were detected over 2 years.

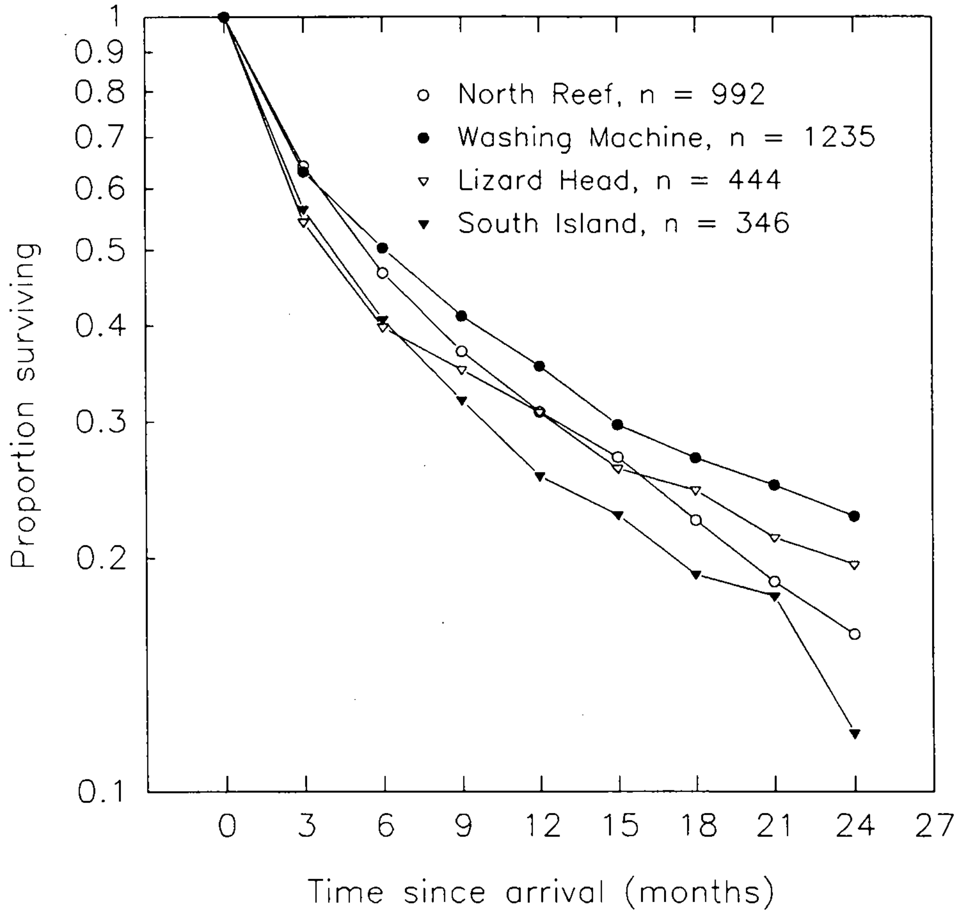


Figure 4.2 Correlations between A. Density of established colonies and survival of recruits. B. Cover of established colonies and survival of recruits. C. Density and survival of recruits. n = 20 in each case

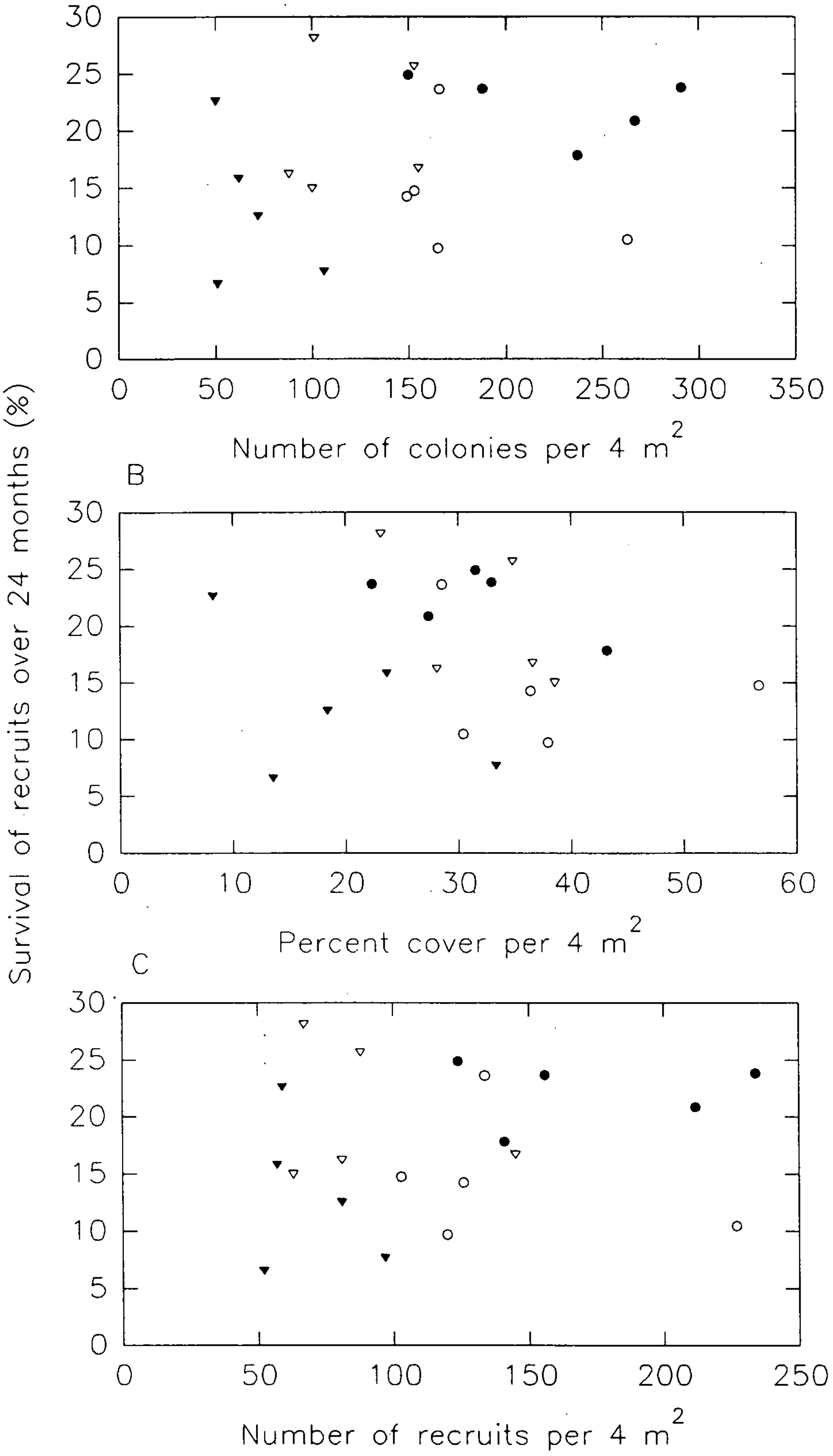


Table 4.1 Pairwise multiple comparisons among sites of survival of recruits. Adjusted error rate = 0.008. NR = North Reef, WM = Washing Machine, LH = Lizard Head, SI = South Island. * Comparison significant at $\alpha = 0.008$

Comparison	X^2	df	p
NR - WM	9.89	1	0.002*
NR - LH	0.15	1	0.6
NR - SI	3.05	1	0.08
WM - LH	4.80	1	0.02
WM - SI	12.01	1	0.0005*
LH - SI	1.24	1	0.2

Table 4.2 Results of log-rank tests for six taxonomic groups at four sites. Adjusted $\alpha = 0.008$.

Taxon	χ^2	df	p
Acroporids	6.93	3	0.07
Pocilloporids	13.32	3	0.004*
Faviids	2.41	3	0.4
Poritids	1.71	3	0.6
Other corals	2.51	3	0.4
Unidentified corals	15.99	3	0.001*

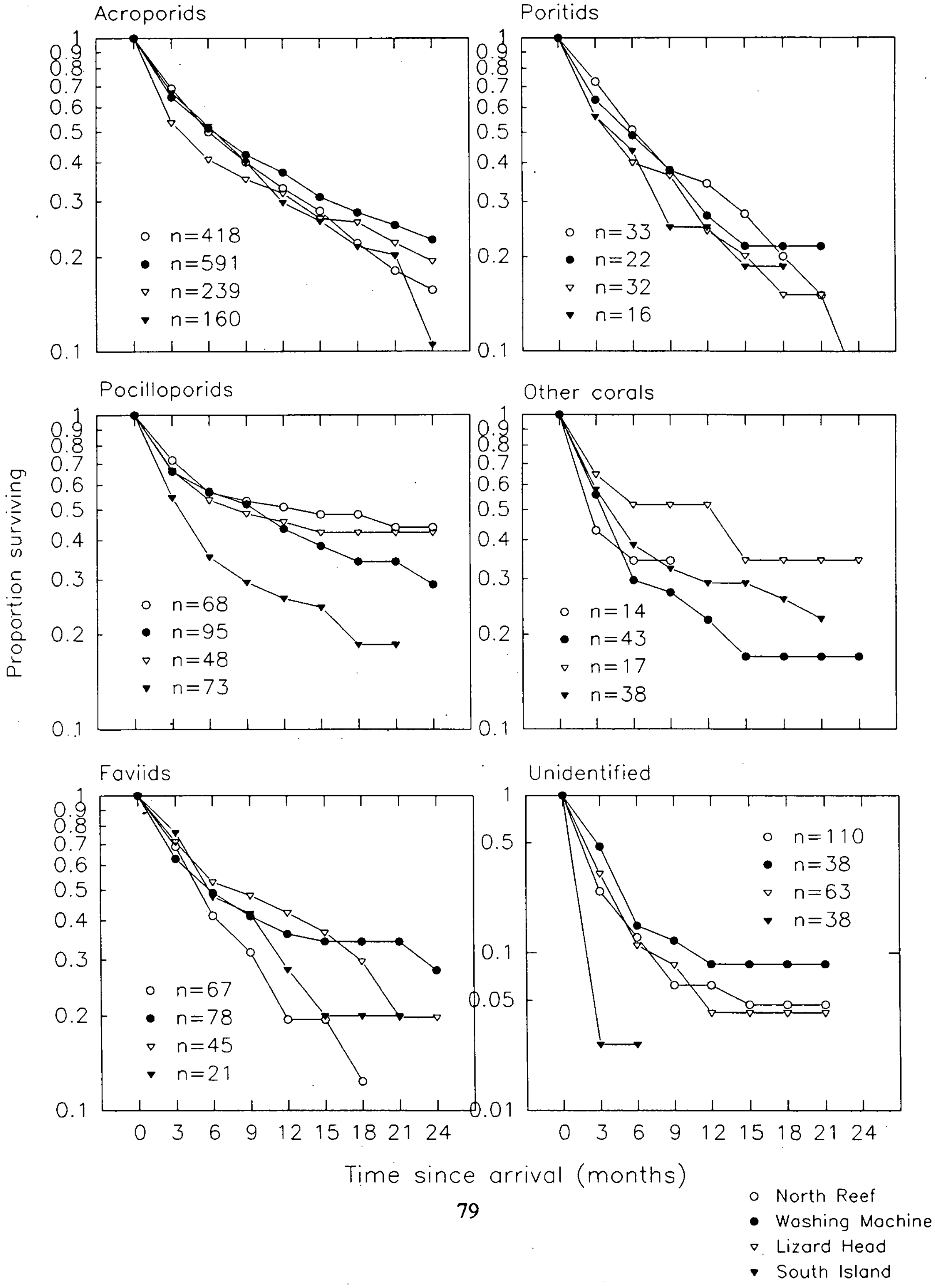
There were significant differences in survivorship of larval recruits among sites for only two of the six family groups, Pocilloporids and Unidentified Corals (Table 4.2). Pairwise multiple comparisons among sites for these two taxa showed that in both cases, recruits at South Island had half the rate of survivorship than at the other three sites (Figure 4.3). Pocilloporids at North Reef, Washing Machine and Lizard Head had survivorship of 38% (averaged across sites) over 24 months, while at South Island, only 19% of recruits survived for 24 months. No Unidentified Corals survived for more than three months at South Island, while 4 - 8% survived for at least 24 months at other sites. Multiple comparisons among the remaining four families that did not show significant spatial variation detected no differences in survivorship among families (varying 3% among taxa). Over all sites and taxa, Pocilloporids at North Reef, Washing Machine and Lizard Head had highest survival (38% over 24 months), Other Corals, Faviids, Poritids, Pocilloporids at South Island and Acroporids formed a group with survival ranging from 21% for Other Corals to 17% for Acroporids, and Unidentified Corals had lowest survivorship of 4 - 8% at North Reef, Washing Machine and Lizard Head, and 0% at South Island (Fig 4.3).

Table 4.3 Results of log-rank tests on survival of six species or species groups at four sites. Adjusted $\alpha = 0.008$

Species	χ^2	df	p
Acropora gemmifera	4.15	3	0.2
A. hyacinthus	3.01	3	0.4
Goniastrea spp.	1.02	3	0.7
Montipora spp.	18.35	3	0.0004*
Pocillopora verrucosa	2.65	3	0.4
Porites spp.	0.56	3	0.9

At the level of species, survivorship of recruits that were detected at all four sites

Figure 4.3 Survival of larval recruits of six taxonomic groups at four sites on the reef crest at Lizard Island. Sammple sizes are the total number of recruits that were detected over 2 years. Note different scale on y axis for Unidentified corals.



varied among species and among sites. Survivorship was the same among sites for all species except *Montipora* spp. (Table 4.3) whose recruits had lower survivorship at Lizard Head (6% over 18 months) than elsewhere, where survival ranged from 17% over 18 months at North Reef to 24% over 18 months at South Island (Figure 4.4).

Survival of recruits varied fourfold among the sixteen most abundant species on the reef crest (Table 4.4). Recruits fall into three broad groups based on their estimated survival over 24 months. Species with the highest survival were *Pocillopora damicornis*, *Acropora monticulosa*, *P. verrucosa*, *A. hyacinthus*, *A. gemmifera*, *A. nana* and *A. robusta*, all with survival rates greater than 40%. Species with intermediate survivorship (20 - 40%) were *A. cuneata*, *A. millepora*, *P. eydouxi*, *A. secale* and *Goniastrea* spp. Recruits of *Stylophora pistillata*, *Porites* sp, *A. nobilis* and *Montipora* spp. survived poorly (12 - 20%).

4.3.2 Mortality of established colonies

Mortality of established corals differed among sites (Table 4.5). Seventy-one percent of established colonies at North Reef died over the two years between February 1991 and February 1993, while 56% died at South Island and 53% at Washing Machine and Lizard Head. It is interesting that sites near each other did not have similar rates of mortality and corals at the most sheltered site, North Reef, suffered the highest rates of mortality.

Figure 4.4 Survival of larval recruits of four species and two species groups at four sites on the reef crest at Lizard Island. Sample sizes are the total number of recruits that were detected over 2 years. Note different scale on y axis for *Montipora*.

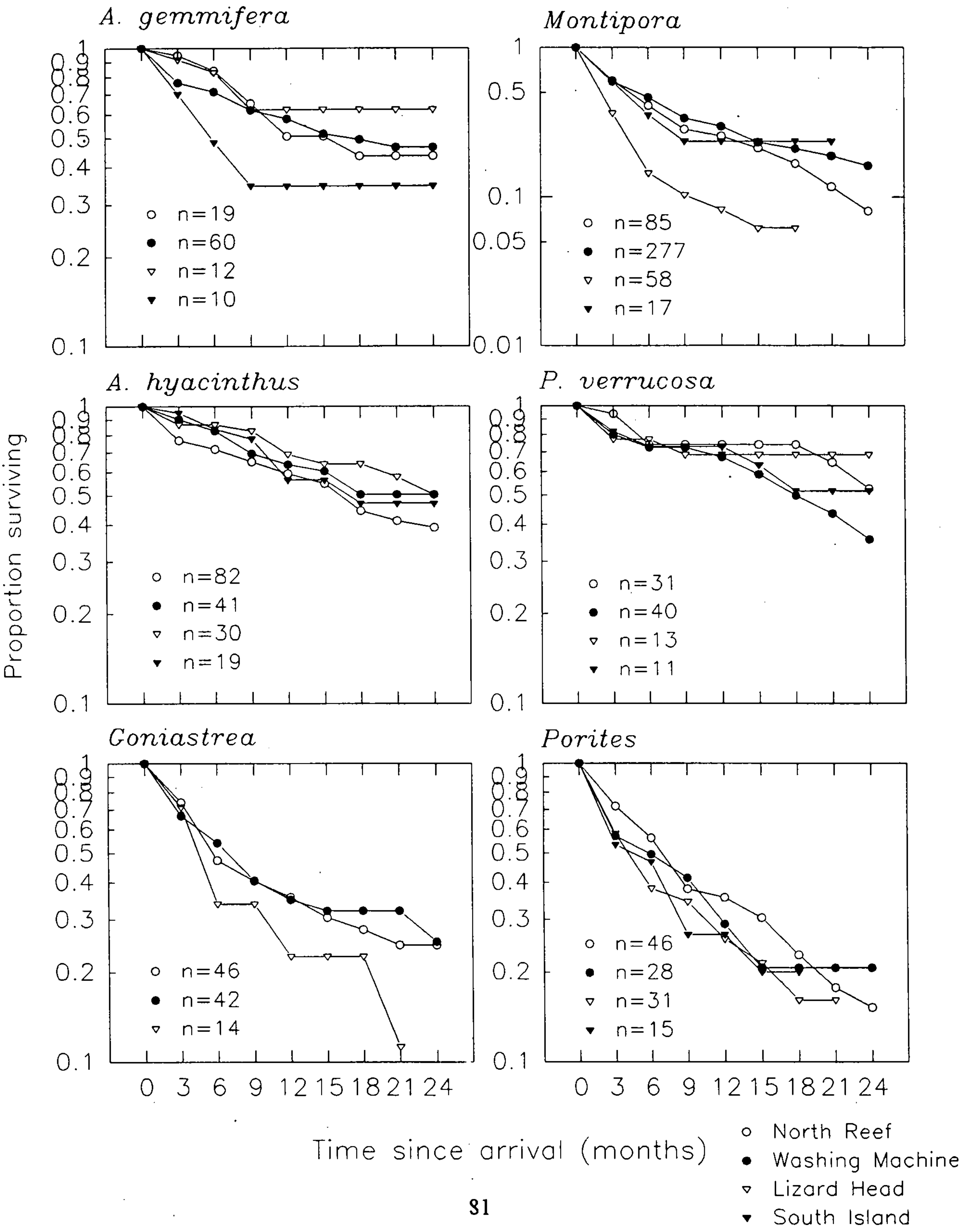


Table 4.4 Estimated survivorship over 24 months of sixteen species of sexual recruits at Lizard Island. Data pooled across four sites. Sample sizes are the total number of sexual recruits detected per species.

Species	Sample size	Estimated survival (%)
Pocillopora damicornis	28	51.9
Acropora monticulosa	14	48.1
P. verrucosa	95	45.2
A. hyacinthus	172	44.6
A. gemmifera	101	44.5
A. nana	68	40.7
A. robusta	10	40.0
A. cuneata	41	33.5
A. millepora	19	29.6
P. eydouxi	22	29.2
A. secale	30	27.1
Goniastrea spp	105	23.2
Stylophora pistillata	55	15.9
Porites sp	120	15.6
A. nobilis	27	14.6
Montipora spp	437	13.0

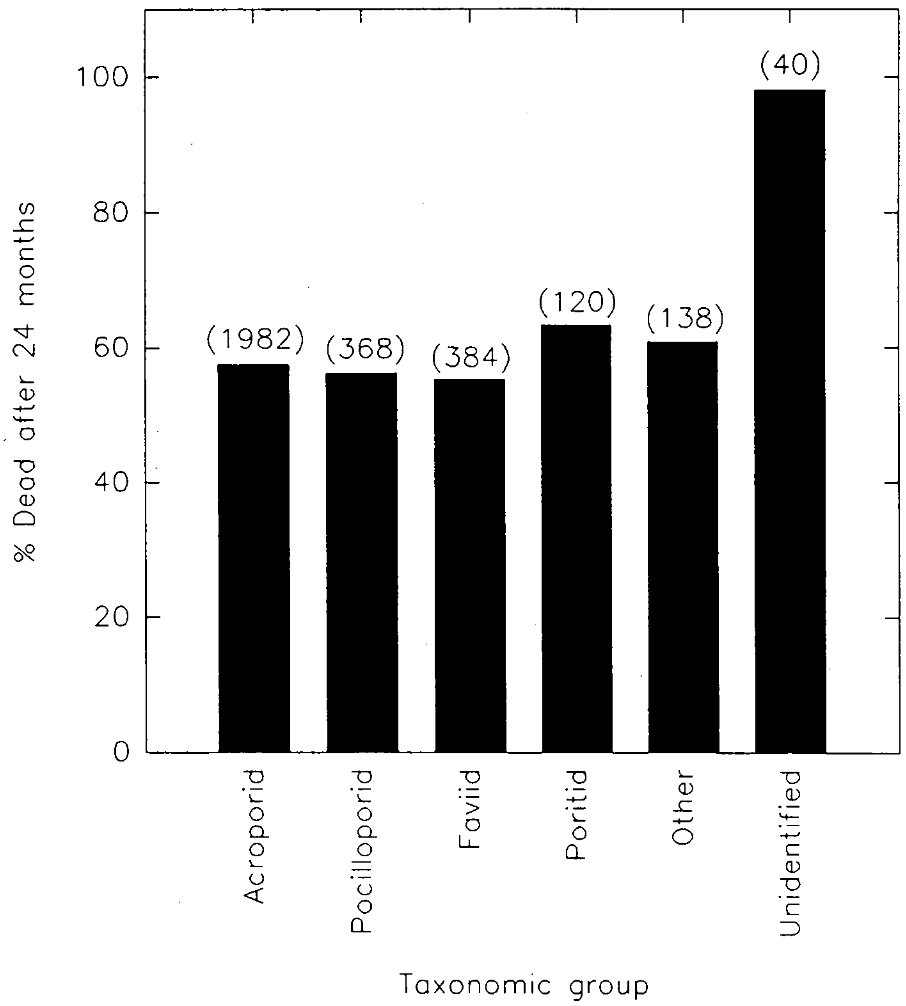
Table 4.5 Tests of significance (partial likelihood χ^2) for a two-way loglinear analysis on the proportion of original colonies dead after two years (D/A) at four sites (total n = 3142).

Source	df	χ^2	p
Site	3	441.74	0.0001
D/A	1	99.79	0.0001
Site*D/A	3	91.46	0.0001

Corals in different family groupings died at different rates, but these rates did not differ among sites (Table 4.6a). Unidentified corals suffered the highest rates of mortality, with 98% of individuals dying between February 1991 and February 1993. Reanalysis of mortality rates among families excluding Unidentified Corals showed that rates of mortality did not vary among families (Table 4.6b). Rates of mortality of corals in the other five family groups differed by only 8% among families, Faviids having the lowest rate (55%) and Poritids the greatest (63%) (Fig 4.5).

There were no detectable differences among sites in mortality of established colonies for the six most abundant species (Table 4.7). Therefore, sites were pooled to test for differences in the amount of mortality among sixteen species. Survival of established colonies varied almost fivefold among species. The species which survived best (60 - >70% survival over 24 months) were *A. gemmifera, Pocillopora eydouxi, A. monticulosa* and *A. cuneata*, all robust species, and *A. hyacinthus*, a fragile plating species. *Acropora nobilis* survived poorly (15%), as did *Montipora* spp. (26%). All other species had survival rates ranging from 38% for *A. secale* to

Figure 4.5 Mortality of six taxonomic groups of corals already established in February 1991 expressed as a percentage of original numbers. Sample sizes are above bars.



59% for *A. robusta* (Table 4.8).

Table 4.6 Tests of significance (partial likelihood χ^2) for three-way loglinear analysis of the proportion of original colonies dead after 2 years (Fate) in six taxonomic groups (Acroporids, Pocilloporids, Faviids, Poritids, Other Corals and Unidentified Corals) at four sites. Total n = 3099. A) Analysis performed on all six groups. B) Analysis excluding Unidentified Corals

A

Source	df	χ^2	p
Site	3	76.09	0.0001
Taxon	5	2128.75	0.0001
Site*Taxon	15	151.39	0.0001
Fate	1	37.02	0.0001
Site*Fate	3	62.43	0.0001
Taxon*Fate	5	17.26	0.004
Likelihood ratio	12	11.24	0.5

B

Source	df	χ^2	p
Site	3	84.77	0.0001
Taxon	4	2091.46	0.0001
Site*Taxon	12	116.01	0.0001
Fate	1	53.73	0.0001
Site*Fate	3	62.66	0.0001
Likelihood ratio	16	14.37	0.57

Table 4.7 Tests of significance (partial likelihood χ^2) for three-way loglinear analysis comparing the proportion of original colonies dead (D/A) among six species or species groups (*Acropora gemmifera*, *A. hyacinthus*, *Pocillopora verrucosa*, *Montipora* spp *Goniastrea* spp and *Porites* sp) and four sites. Total n = 830. Data from South Island were not included for *Montipora* spp, *Goniastrea* spp and *Porites* sp because of small sample sizes.

Source	df	χ^2	*p*
Species	5	42.47	0.0001
Site	3	16.53	0.0009
Species*Site	12	91.47	0.0001
D/A	1	0.52	0.46
Species*D/A	5	71.20	0.0001
Site*D/A	3	12.27	0.0065
Likelihood ratio	12	14.60	0.26

Table 4.8 Survival of established colonies of sixteen species over 24 months. Data pooled across four sites. Sample sizes are the total number of colonies per species present in February 1991.

Species	Sample size	Proportion surviving (%)
Acropora gemmifera	173	71.1
Pocillopora eydouxi	47	70.2
A. monticulosa	102	68.6
A. cuneata	94	63.8
A. hyacinthus	203	63.1
A. robusta	27	59.3
A. millepora	46	54.4
Goniastrea spp	109	50.5
Porites sp	91	45.1
P. damicornis	41	43.9
P. verrucosa	133	42.1
A. nana	63	41.3
Stylophora pistillata	48	39.6
A. secale	56	37.5
Montipora spp	148	26.4
A. nobilis	27	14.8

4.4 DISCUSSION

4.4.1 Spatial variation in survival

Survival of larval recruits varied among sites, but the size of the difference in survivorship among sites is not great enough to account for all the variation in abundance of corals among sites. For example, assuming constant rates of mortality at Washing Machine (23%) and South Island (12%) and constant annual recruitment of 50 sexual recruits at each site, after 10 years, the difference in abundance of survivors at the two sites would be 2-fold (30 colonies at Washing Machine compared with 14 at South Island), whereas observed abundance differed by 3-fold. However, post-recruitment mortality clearly does play a role in determining the relative abundance of corals among sites.

Species composition of recruits differed among sites but survivorship of most family groups and species did not (Tables 4.6, 4.7). At the level of families, Pocilloporids had lowest survival at South Island (Fig 4.2), but this variation in survival was not reflected in the abundance of Pocilloporids at South Island compared with other sites, since Pocilloporids were least abundant at South Island and North Reef (Chapter 2). Unidentified corals had exceptionally low survivorship at all sites because they were small (< 25 cm^2 area). The proportion of Unidentified corals at each census was very low (Chapter 2) and they accounted for less than 1% of coral cover (Chapter 2), so a difference of 6% in mortality of Unidentified corals is biologically irrelevant. *Montipora* spp. was the only species group that showed any differences in survivorship among sites, but again there was no relationship between the patterns in survival and patterns in abundance over time (Chapter 2). Recruits of *Montipora* spp. survived equally well at North Reef, Washing Machine and South Island (Fig 4.3), but average densities of this species group varied 15-fold among these sites (Chapter 2). Clearly, previously established patterns of abundance for most species

(Chapter 2) were not consistent with rates of mortality measured during this study, indicating that spatial patterns are either unrelated to patterns in mortality or that recruitment and/or mortality rates are temporally variable (see below).

Survival of established colonies also differed among sites (Table 4.7). Corals at North Reef suffered the highest mortality among sites and was the only site that showed a decline in numerical abundance of coral through time (Chapter 2). Thirty-nine percent of the corals that died at North Reef between February 1991 and February 1993 were unidentified small corals. In contrast, 22%, 13% and 24% of corals that died over 2 years at Washing Machine, Lizard Head and South Island, respectively, were unidentified in February 1991. Therefore, greater mortality of established corals at North Reef than other sites was because of the greater proportion of small corals at North Reef in February 1991.

In contrast to the differences among sites in total mortality, there was no detectable spatial variation in survivorship of established colonies among family-level taxa or among species (Tables 4.9, 4.10). This implies that composition of assemblages is not affected by differential mortality of adults among sites. The lack of variation in mortality rates among sites in this study, however, does not necessarily mean that sites will not vary in their rates of mortality at other times. Destructive cyclones are expected to occur on average every 10 to 20 years at Lizard Island (Massel & Done 1993), and may cause increased and patchy mortality of corals (e.g. Woodley *et al.* 1981; Van Woesik *et al.* 1991). The effects of cyclones on particular sites vary according to the history of disturbance at a site, the species composition and size-structure of assemblages and the location of reefs (i.e. near other reefs that provide some protection from waves, or out in the open where wave fetch is greater)(Connell 1973; Woodley *et al.* 1981; Hughes 1989; Witman 1992). It might be predicted that the next cyclone at Lizard Island will cause differential mortality among sites because of the different species composition (Chapter 2) and size structure (unpub. data) of corals at different sites and because of differences in the orientation of sites to wind and waves.

Failure to detect differences in mortality among sites at higher taxonomic levels may also be related to reduced sample sizes. Once sample size decreases below 160, the difference in mortality among sites required to detect a statistical difference is over twofold. Sample sizes for all species and for Poritids and Other Corals were smaller than 160. Lack of power may be responsible for the statistical insignificance of twofold differences in survival of Faviids and Other Corals among sites (Fig 4.3), and twofold differences in rates of survival among sites of *A. gemmifera* and *Goniastrea* (Fig 4.4).

4.4.2 Differences in survival among species

Recruits of most species had lower survivorship than established colonies (Tables 4.4, 4.8). Mortality of corals is strongly size-dependent, small colonies dying completely more often than larger colonies (e.g. Connell 1973; Hughes & Connell 1987; Bythell *et al.* 1993). Recruits were smaller than established colonies for most species in this study, which is reflected in higher rates of mortality of recruits (Table 4.4) than established colonies (Table 4.8). However, there were several species that had similar survivorship as both recruits and established colonies (*P. damicornis*, *P. verrucosa*, *A. nana* and *A. nobilis*). These are species with fast growth and size distributions skewed to small sizes on the reef crest (unpub data). Differences in size between established colonies and recruits would therefore rapidly disappear as the colonies grew. Therefore, it is not surprising that recruits and established colonies had similar rates of survival in these species.

Survival of larval recruits differed fourfold among species (Table 4.4). Variation among species in early survival cannot be explained in terms of initial size, since all recruits detected were initially the same size in this study. Fast growth rate may facilitate an escape in size from high mortality, so it would be expected that species with fast growth rates should survive better as recruits. Fragile species with fast growth rates tended to have high survival of recruits in this study (e.g. *P. damicornis, P. verrucosa, A. hyacinthus, A.nana*), but solid, slow-growing species like *A. monticulosa* also survived well as recruits (Table 4.4). Recruits of species with slow growth (e.g. *Goniastrea* spp., *Porites* sp) generally did not survive well. Thus, there was a general correlation between morphology, growth rate and survival, as predicted by life history theory (e.g. Jackson 1979).

Recruits of brooding corals are expected to have high initial survival (e.g. Bak & Engel 1979; Van Moorsel 1983; Szmant 1986), but the results from this study show that the advantage of producing large planulae with high survival does not extend to later stages. Brooding species had both high (e.g. *A. cuneata*, *P. damicornis*, *P. verrucosa*) and low (e.g. *Stylophora pistillata*) survival of recruits (Table 4.4). Mode of reproduction does not appear to affect the survival of recruits after several years.

Mortality of established corals was lower and more variable than mortality of recruits (Table 4.8). Differences among species are most likely to be related to differences in size distributions of species, since small colonies have higher mortality than larger colonies (e.g. Connell 1973; Babcock 1991) and species differ in their size distributions (Hughes & Jackson 1985; Hall 1992; Soong 1993). In this study, large species (e.g. *P. eydouxi*, *A. monticulosa*, *A. hyacinthus*) had higher survivorship than smaller species (e.g. *P. damicornis*, *A. nana*, *S. pistillata*) (Table 4.8).

Patterns in survival of established colonies among species are also correlated with morphology (Hughes & Jackson 1985; Jackson & Hughes 1985). The five species with the highest survival were mostly robust (*A. gemmifera*, *P. eydouxi*, *A. monticulosa*, *A. cuneata* and *A. robusta*). In contrast, species with low survival of established colonies tended to be delicate (e.g. *P. verrucosa*, *A. nana*, *S. pistillata* and *Montipora* spp.). There were, however, exceptions to these generalisations; *A. secale* and *A. millepora* have similar morphologies, but had widely different ability to survive. Similarly, *A. hyacinthus* has a fragile plating morphology, yet survived comparatively well (63% over 2 years) on the reef crest. The size distributions of these species varied greatly, however. Size-specific mortality rates are needed to assess how important morphology is as an influence on species-specific rates of mortality.

In conclusion, differences among sites in mortality of recruits (Fig 4.1) tended to enhance the differences among sites in rates of recruitment (Chapter 3). Mortality of recruits was not density dependent. These results suggest that both recruitment and mortality play a role in determining the abundances of corals at different sites.

CHAPTER 5: ASEXUAL PROCESSES ON THE REEF CREST: FRAGMENTATION AND FISSION

5.1 INTRODUCTION

Clonal organisms such as coral may increase population size and colonise bare substratum by a variety of asexual means, including fragmentation and fission (e.g. Hughes & Jackson 1980; Highsmith 1982; Hughes *et al.* 1992). Fragments disperse short distances (e.g. Ayre & Willis 1988; Smith 1992) while daughter colonies produced by fission remain in the same place as the original parent colony. In contrast to most sexual reproduction by dispersive larvae, these forms of asexual reproduction lead to local increases in population size. Therefore, both means of asexual reproduction may lead to aggregated distributions (e.g. Lewis 1971; Potts *et al.* 1985). At Lizard Island, some species were abundant at only one or two sites and sometimes only in one or two quadrats (Chapter 2). The local abundance of these species may be attributable to asexual reproduction by fission and fragmentation.

Fragmentation is an important means of clonal propagation for many species (e.g. gorgonians: Lasker 1990; sponges: Wulff 1991; branching corals: Tunnicliffe 1981; Bothwell 1981; Highsmith 1982). Species of coral that fragment share some common characteristics. In particular, most are relatively delicate and break easily in storms (e.g. Highsmith *et al.* 1980; Tunnicliffe 1981; Highsmith 1982; Knowlton *et al.* 1981; Wallace 1985b; Hughes 1985; Heyward & Collins 1985). Many are loosely branching species which can form dense thickets of interwoven branches (Bothwell 1981; Tunnicliffe 1981; Wallace 1985b), but some massive (e.g. Potts *et al.* 1985; Devantier & Endean 1989) and corymbose species (Bothwell 1981) also fragment. The species which successfully reproduce by fragmentation tend to have fast growth rates and produce large fragments (e.g. Highsmith 1982; Wallace 1985b; Smith 1992).

Clonal propagation by fragmentation occurs for some species of coral on the Great Barrier Reef. Bothwell (1981) used histocompatibility tests (later proven to be unreliable indicators of clonal identity: Resing & Ayre 1985; Ayre & Willis 1988) to identify three species of branching Acroporids which used fragmentation as a means of dispersal and colonisation on the reef crest at Heron Island. Wallace (1985b) found that four branching Acroporids on a wave exposed reef front recruited asexually by fragmentation. Fragments of two of these species did not re-cement to the substratum, and were only found in sandy channels, while the other two species rapidly re-cemented after fragmentation. This differential ability to re-attach implies that some species will be more successful as fragments in wave exposed habitats than others. Observations of fragmentation and clumped distributions suggest that fragmentation may be a means of increasing local abundance in some populations of *Porites* spp. in deep water (Potts *et al.* 1985; Devantier & Endean 1989). Fragmentation occurs often on the reef crest at Lizard Island (up to 8 fragments.m^{-2}.yr^{-1}; Smith 1992) but the success of fragmentation as a means of colonising space depends on the size of fragments, habitat and species (Smith 1992). On the reef flat at Magnetic Island, *Montipora digitata* is the most abundant species and colonises new space by fragmentation (Heyward & Collins 1985). Thus, work to date on the Great Barrier Reef suggests that some species, particularly branching Acroporids may propagate by fragmentation in some habitats, especially habitats of high wave energy, but survival of fragments in such habitats will be dependent on their size and ability to reattach.

Daughter colonies are formed by fission as a consequence of partial mortality and are by definition smaller than the original colony. Fission is an important process maintaining populations of some corals in the Caribbean (Hughes & Jackson 1980, 1985). For example, *Montastrea annularis* appears to rely almost exclusively on fission to maintain population size; over a 10 year period, no larval recruits were found, but the population increased in abundance by 40% as a result of fission (Hughes 1988). Similar detailed and long-term studies on populations of corals on the Great Barrier Reef have not yet been published. In a study on the population dynamics of 3 massive species, Babcock (1991) showed that fission accounted for 17% of the total increase in the number of colonies over 2 years. There are no other data on fission of corals on the Great Barrier Reef, despite the importance of this mode of asexual reproduction in the life histories of clonal organisms (Hughes *et al.* 1992).

Both fragmentation and fission involve a cost to the parent colony since reproductive output and survival are lower in small corals (Highsmith 1982; Hughes & Jackson 1985; Kojis & Quinn 1985; Szmant-Froelich 1985; Hughes & Connell 1987; Babcock 1991; Hughes *et al.* 1992). In addition, colonies that have already been injured are likely to be injured again (Hughes & Jackson 1985; Babcock 1991). This cost can only be allayed if the fragments and daughters survive to grow and reproduce. Therefore, to assess whether fragmentation and fission are successful means of colonising space, it is necessary to quantify survival of asexually produced daughter colonies. Survival of daughter colonies is size-dependent (Hughes & Jackson 1985; Hughes & Connell 1987), and varies among species in the Caribbean (Hughes 1988) and on the Great Barrier Reef (Smith 1992).

This chapter documents patterns in asexual recruitment by fragments and daughters at four sites on the reef crest at Lizard Island. Differential rates of fission and colonisation by fragments may account for some of the spatial variation in abundance and composition of assemblages. Patterns of asexual recruitment are compared with patterns in the abundance and composition of assemblages to identify sites, families or species which are more susceptible to asexual propagation. Finally, patterns in the survival of fragments and daughter colonies are compared among sites and taxonomic groups to investigate the importance of asexual propagation as a means of colonising space on the reef crest.

5.2 METHODS

5.2.1 Detection and identification of asexual recruits

As in Chapter 3, recruitment is defined as the detection in photographs of previously unrecorded colonies. Asexual recruits were conspicuously different from sexual recruits. Sexual recruits had an encrusting morphology and lacked branches. In contrast, fragments lacked an encrusting base (at least initially) and had well-defined branching structure. Daughter colonies produced by fission were recognisable because they remained near the original colony, sharing skeleton separated by areas of dead tissue. When a whole colony split, it was classified into a parent (the larger portion of the colony) and daughter colonies. Both fragments and the products of fission are daughter colonies in the sense that they are genetically identical to the colony that produced them (Highsmith 1982). To distinguish between the two types of daughter colonies, daughter colonies produced by fission are henceforth refered to simply as "daughter colonies", and "fragments" refers to initially unattached parts of colonies detected in quadrats. All fragments and daughters produced by fission were counted and identified to family or, if possible, to genus or species.

5.2.2 Spatial and temporal variation in asexual recruitment

Asexual recruits were counted in photographs of five, 4 m^2 quadrats set up at four sites around Lizard Island (see Figure 2.1). Multivariate repeated measures analysis of variance (MANOVAR) was used to document spatial and temporal variation in total recruitment of asexual propagules (fragments and daughters). Data used for analysis were from censuses in February, May, August and November 1991, February, August and November 1992 and February 1993. Data from May 1992 were not used because bad weather prevented access to Lizard Head and South Island.

At higher taxonomic levels (family groups or species), there were too few fragments and daughter colonies per quadrat to investigate spatial and temporal variation using MANOVAR, so data were pooled across times. Spatial variation in recruitment of fragments and daughter colonies were tested using χ^2 analysis of homogeneity. "Families" were Acroporids, Pocilloporids, Faviids, Poritids, Other Corals and Unidentified Corals. The species and species groups investigated were *Acropora cuneata*, *A. gemmifera*, *A. hyacinthus*, *A. millepora*, *A. monticulosa*, *A. nana*, *A. nobilis*, *A. robusta*, *A. secale*, *Montipora* spp., *Goniastrea* spp., *Pocillopora damicornis*, *P. eydouxi*, *P. verrucosa*, *Stylophora pistillata* and *Porites* sp.

5.2.3 Survival of asexual recruits

Because fragments and daughters were detected in every census, variation in survival of asexual recruits among sites and taxonomic groups was analysed by comparing survivorship curves with a log-rank test (see Section 4.2.1). Survivorship curves were generated by calculating the rate of depletion of cohorts of asexual recruits, then summing across cohorts. Where there were no detectable differences in the survival of fragments and daughter colonies among sites, comparisons were made among families and species with data pooled across sites to increase sample sizes. Survivorship curves of fragments reflect both mortality and emigration. They can be used as indicators of whether fragments colonise space on the reef crest, but do not indicate whether fragmentation is a successful life history strategy for some species because the fragments which disappear may attach and grow elsewhere.

5.3 RESULTS

5.3.1 Recruitment of fragments

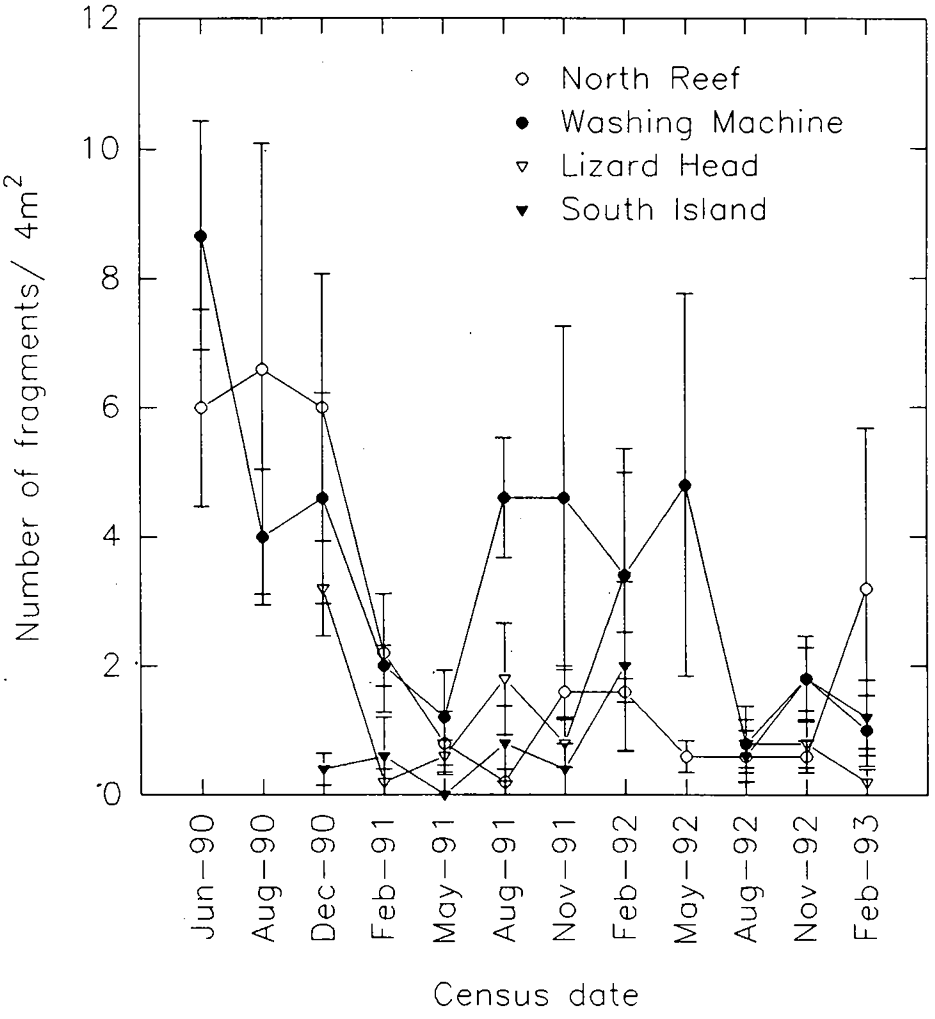
A total of 423 fragments was detected in the quadrats over 33 months (1.4 $m^{-2}.yr^{-1}$). Temporal patterns in recruitment by fragments were different at each site (Site*Time, Table 5.1; Fig 5.1). New fragments fluctuated eightfold at Washing Machine and sixfold at Lizard Head, but this fluctuation in abundance of fragments did not occur at other sites (Fig 5.1). There was a weak correlation between the number of fragments detected in quadrats and the density of coral at each site ($r = 0.58$, $n = 20$, $p < 0.007$), indicating that fragments were more abundant at sites with greater density of coral. There was no relationship between the number of fragments detected in quadrats and percent cover of corals within the quadrat ($r = 0.19$, $n = 20$, $p > 0.40$).

Table 5.1 MANOVAR on total numbers of new fragments detected per quadrat at four sites. Data transformed to ln(x + 1).

Within Quadrats Source of variation	Pillai's trace	F	df	*p*
Time	0.830	5.50	8,9	< 0.01
Time*Site	1.962	2.60	24,33	< 0.006

Between Quadrats Source of variation	df	MS	F	*p*
Site	3	2.785	4.38	< 0.02
Error	16	0.636		

Figure 5.1 Mean number of new fragments (± S.E.) detected in five quadrats at four sites on the reef crest at Lizard Island. Missing values indicate missing data.



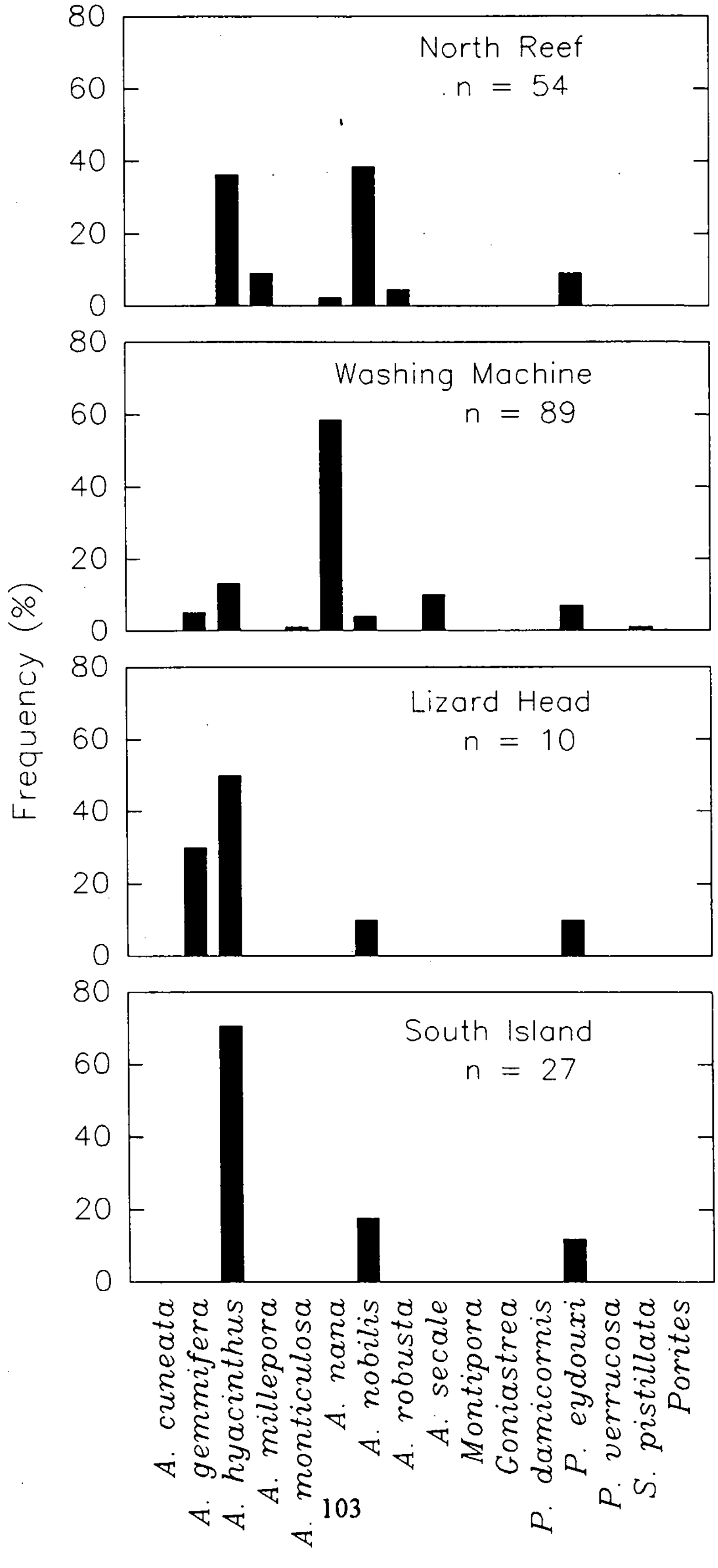
Ninety-one percent of all fragments detected were Acroporids, but the proportion of Acroporid fragments varied among sites (from 79% at North Reef to 98% at Washing Machine; $\chi^2 = 55.11$, 6 df, $p < 0.0001$). Pocilloporids made up 3% of all fragments detected, while fragments of other taxonomic groups were detected at North Reef, Washing Machine and Lizard Head and made up 17, 0.5 and 0.8% of the total number of fragments detected at each site, respectively.

The most abundant fragments of individual species were of *Acropora hyacinthus*, *A. nana* and *A. nobilis* (Fig 5.2). *Acropora hyacinthus* fragments were detected at all sites, but fragments of *A. nana* and *A. nobilis* were only abundant at Washing Machine and North Reef, respectively (Fig 5.2). Average sizes of fragments differed among species. Fragments of *Acropora hyacinthus* were the largest, averaging 63.1 ± 20.2 cm^2. Fragments of *A. nobilis* were smaller (12.6 ± 3.5 cm^2) and *A. nana* fragments were the smallest (4.9 ± 0.6 cm^2). All fragments except for plate *A. hyacinthus* had branching morphologies, ranging from the fragile forms of *A. nana* and *A. nobilis*, to more robust branching forms such as *A. robusta* and *P. eydouxi*. Digitate and corymbose morphologies also fragmented but were not abundant (< 10 fragments over 2 years; Fig 5.2).

5.3.2 Survivorship of fragments

Survivorship of fragments on the reef crest was very poor. Of 394 fragments detected between December 1990 and November 1992, 344 disappeared within three months. Survival of fragments varied among sites ($\chi^2 = 12.75$, 3 df, $p < 0.006$), with

Figure 5.2 Species composition of fragments detected in quadrats at four sites of 2 years from February 1991



the greatest proportion of fragments surviving at South Island (10% of 39 fragments survived for more than 9 months). At the other three sites, fewer than 6% of fragments were still alive after 12 months (Fig 5.3).

Survival of fragments varied among the three species that were abundant as fragments ($\chi^2 = 17.73$, 2 df, $p < 0.0001$; Fig 5.4). Fragments of *A. hyacinthus* survived best, with 19 % still alive after 12 months (Fig 5.4). Fragments of *A. nana* survived poorly, fewer than 5% (3 fragments) surviving after 3 months, and none lasting for more than 12 months (Fig 5.4). Survival of fragments of *A. nobilis* was intermediate between these two extremes, with 8% (4 fragments) still alive after 12 months (Fig 5.4).

5.3.3 Fission

Fission occurred often; 1153 daughter colonies were generated by fission over 2 years (7.2 $m^{-2}.yr^{-1}$). There was significant variation in the number of new daughter colonies at different times, but there was no consistency in temporal patterns among sites (Table 5.2; Fig 5.5). Production of daughter colonies was relatively constant at North Reef and South Island, but more variable at Washing Machine and Lizard Head (Fig 5.6). The abundance of daughter colonies differed 2- to 10-fold among sites at different times, generally four to five times more abundant at Washing Machine and Lizard Head and three times more abundant at North Reef than at South Island (Fig 5.5).

Figure 5.3 Survival of fragments detected in quadrats at four sites. Sample sizes are the total number of all fragments detected at four sites over 33 months.

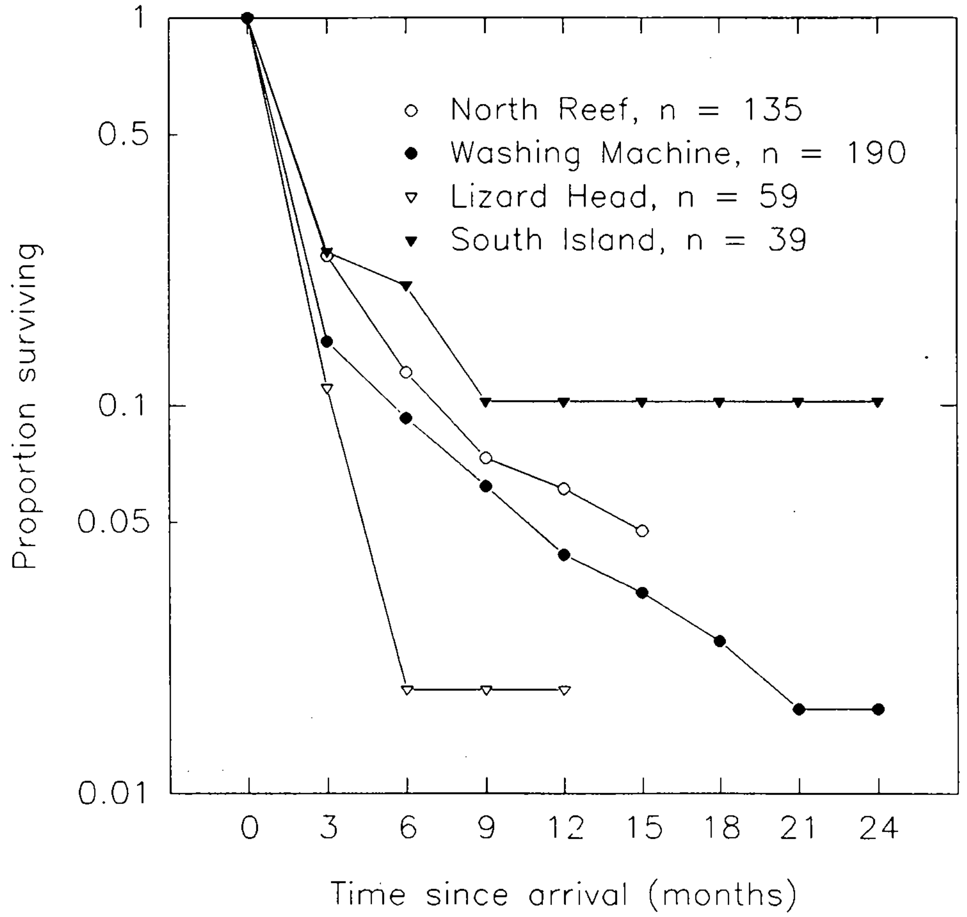


Figure 5.4 Survival of fragments of 3 species on the reef crest. Sample sizes are the total number of all fragments of *A. hyacinthus*, *A. nana* and *A. nobilis* detected over 33 months at all four sites.

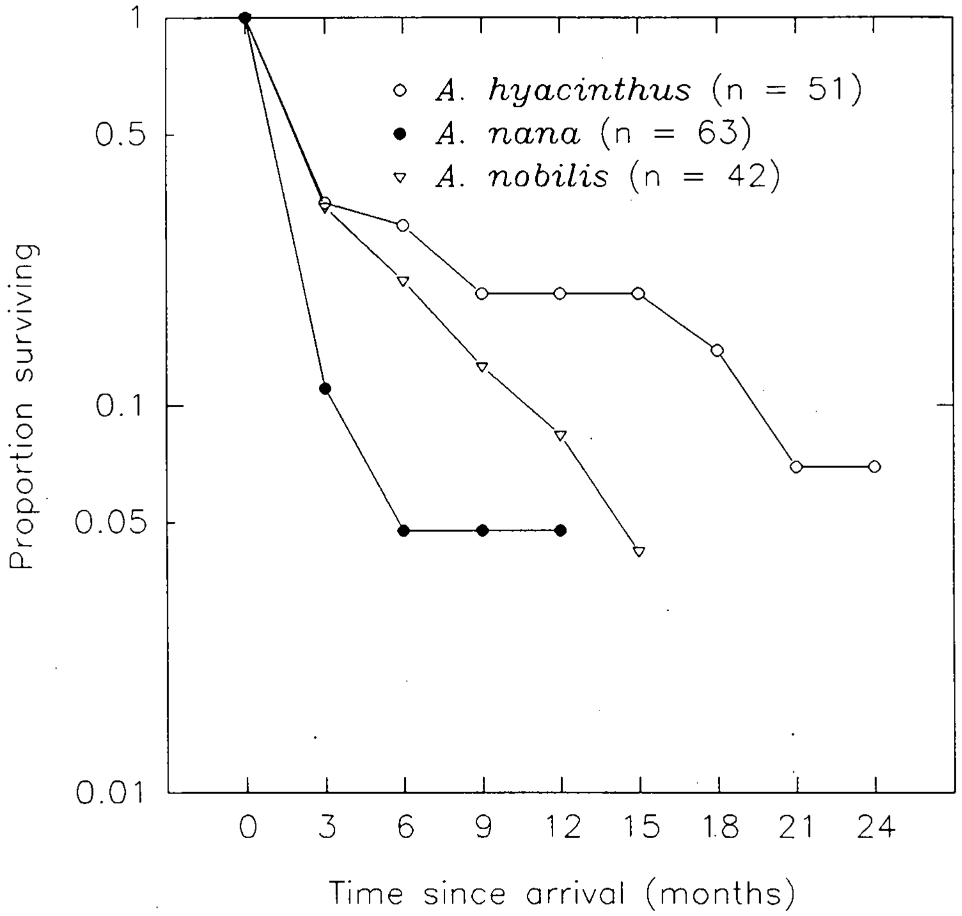


Table 5.2 MANOVAR on total numbers of new daughter colonies detected per quadrat at four sites. Data were untransformed.

Within Quadrats				
Source of variation	Pillai's trace	F	df	*p*
Time	0.923	17.15	7,10	< 0.0001
Time*Site	1.700	2.24	21,36	< 0.02

Between Quadrats				
Source of variation	df	MS	F	*p*
Site	3	474.092	15.33	< 0.0001
Error	16	30.928		

The total number of daughter colonies produced by fission at a site was not directly related to the number of colonies available for fission. For example, the numbers of daughter colonies at Lizard Head was approximately equal to the number at Washing Machine (Fig 5.5), despite a twofold difference in the total number of colonies at those sites (Chapter 2). The per-capita rate of fission (proportion of established colonies that underwent fission) varied from 15% and 16% over 2 years at South Island and North Reef, respectively, to 21% at Washing Machine and 25% at Lizard Head over 2 years.

The family composition of daughter colonies varied among sites ($\chi^2 = 100.12$, 15 df, $p < 0.0001$; Fig 5.6). Acroporids were the most abundant daughter colonies at all sites (59 - 73% of all daughter colonies), but there were proportionally more at

Figure 5.5 Mean number of daughter colonies (± S.E.) detected in five quadrats at four sites on the reef crest at Lizard Island. Missing values indicate missing data.

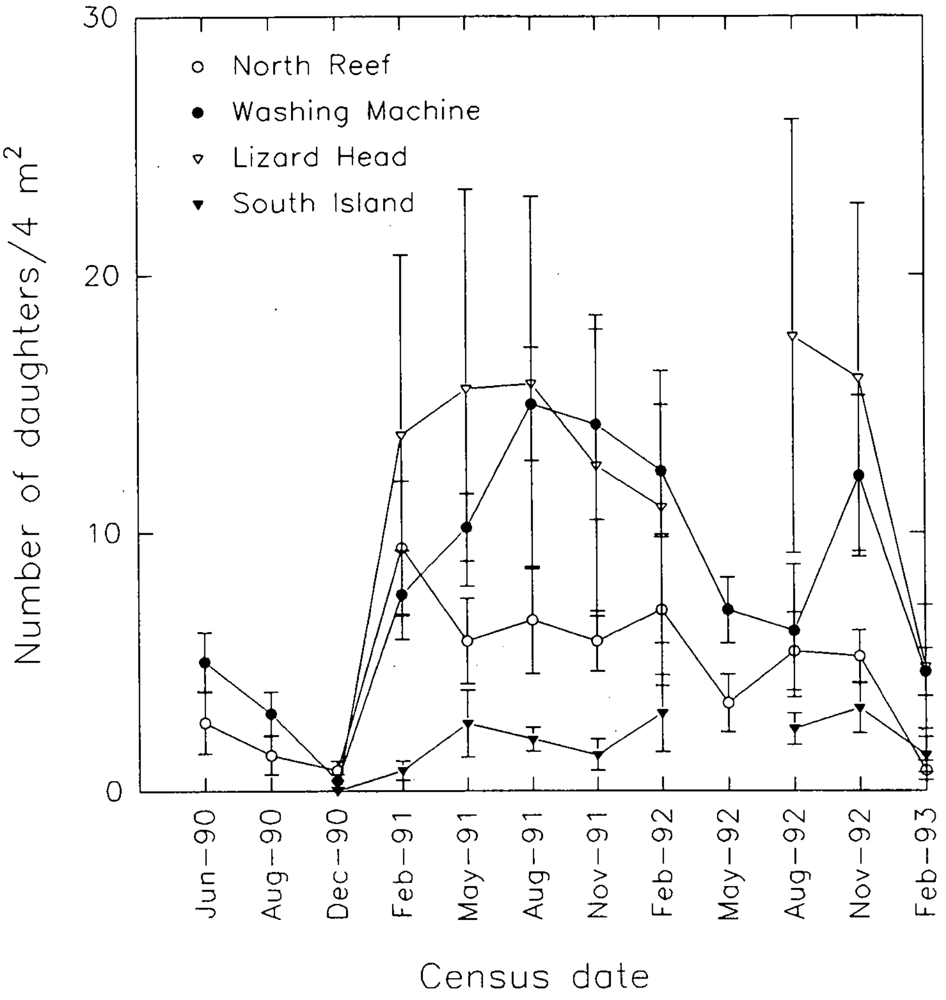
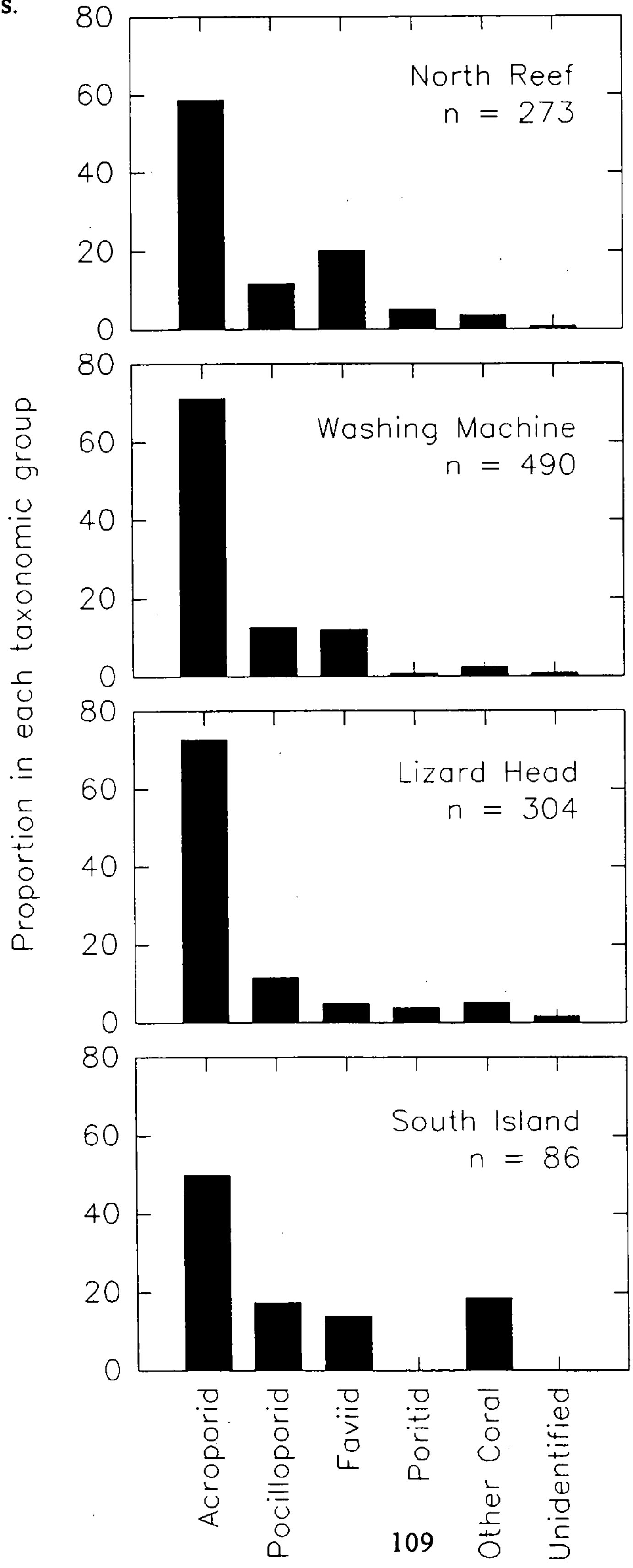


Figure 5.6 Taxonomic composition of daughter colonies detected over 24 months at four sites.



Washing Machine and Lizard Head than elsewhere (Fig 5.6). Pocilloporids made up approximately 12% of the total number of daughter colonies at all sites except South Island, where 17% were Pocilloporids. The abundance of Faviid daughter colonies varied four-fold among sites, with proportionally fewest at Lizard Head. There were relatively few (less than 5%) daughter colonies of Poritids or Unidentified corals at all four sites.

Differences among sites in composition of daughter colonies could be due to spatial variation in (1) composition of established assemblages, (2) the proportion of initial colonies that split or (3) the number of daughter colonies produced by parent colonies. Two analyses were done to investigate these possibilities. First, a loglinear analysis comparing the distribution among families of colonies already established

Table 5.3 Tests of significance (partial likelihood ratio χ^2) for a three-way loglinear analysis comparing the distribution among families of colonies that split (parent colonies) with family composition of the assemblage already established in February 1991 at four sites. Total n = 3644

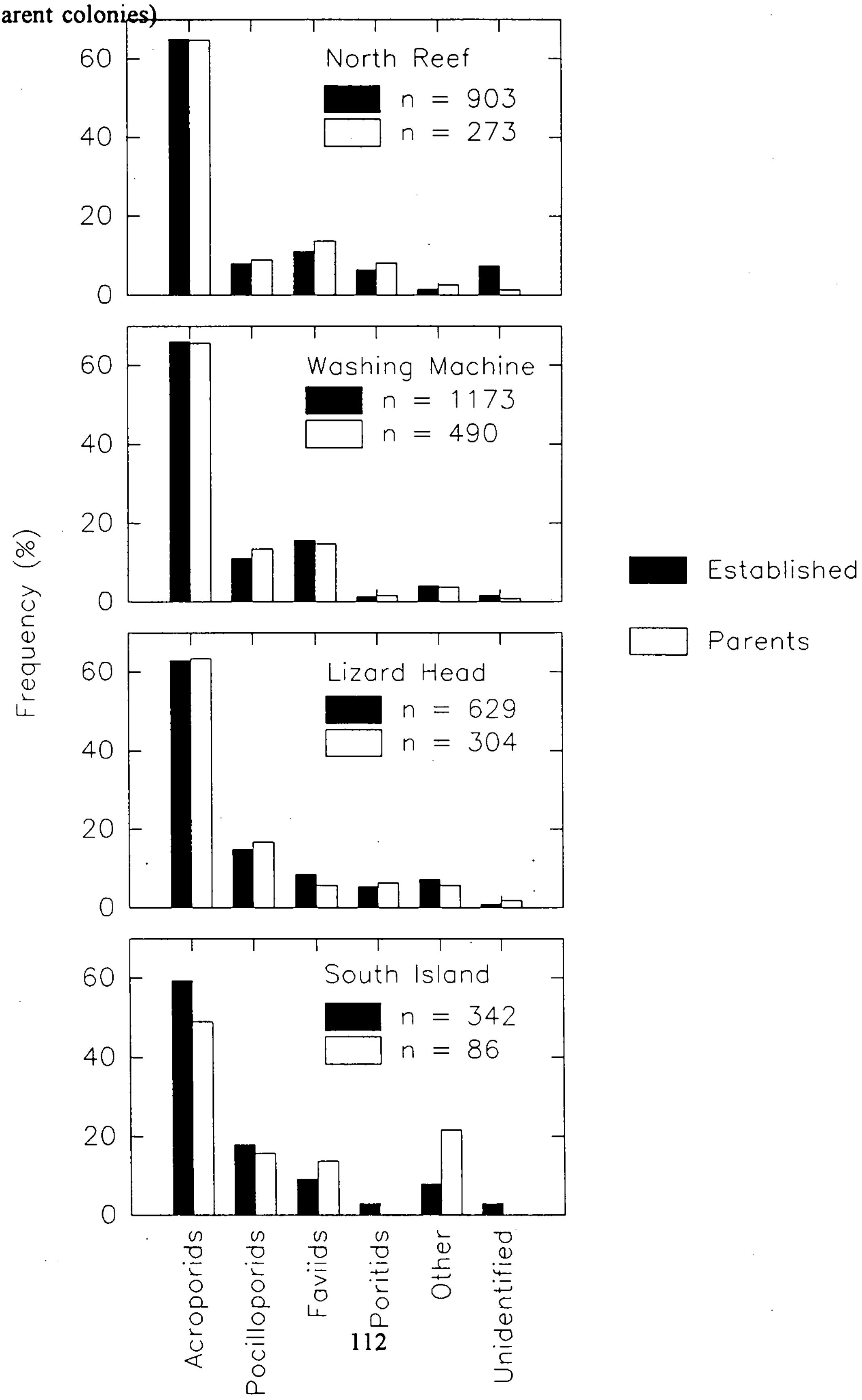
Source of variation	df	χ^2	p
Site	3	74.28	< 0.0001
Family	5	2808.29	< 0.0001
Site*Family	15	199.44	< 0.0001
Parent/Established (P/E)	1	1007.62	< 0.0001
Site*P/E	3	14.58	< 0.002
Likelihood ratio	18	26.64	> 0.08

Table 5.4 Tests of significance (partial likelihood ratio χ^2) for three-way loglinear analysis comparing the distribution among families of parent colonies and daughter colonies at four sites. Total n = 1750

Source of variation	df	χ^2	p
Site	3	3.47	> 0.32
Family	5	847.6	< 0.0001
Site*Family	13	113.12	< 0.0001
Parent/Daughter (P/D)	1	170.41	< 0.0001
Likelihood ratio	21	14.85	> 0.83

in February 1991 and colonies that underwent fission (i.e. parent colonies) showed that the composition of established assemblages was different at each site (Site*Family; Table 5.3; see also Chapter 2), but that there were no significant differences in the taxonomic composition of established colonies and parent colonies (Table 5.3; Fig 5.7). The proportion of colonies splitting differed among sites (Site*P/E; Table 5.3), but the proportion of colonies that split did not differ among families. The proportion of colonies that underwent at least one fission event ranged from 0.15 at South Island to 0.25 at Lizard Head. Second, comparison of the taxonomic distribution of daughter colonies and parent colonies showed that the proportions of parent colonies and daughter colonies did not differ among sites, nor were there any differences in their distributions among families (Table 5.4). This means that no families showed differential propensity to split into daughter colonies. Therefore, differences among sites in composition of daughter colonies were because of differences in the composition of assemblages among sites and also differential

Figure 5.7 Composition by family of the established assemblage in February 1991 and colonies that underwent fission at least once in the 24 months after February 1991 (parent colonies)



rates of fission at different sites.

The species composition of daughter colonies also varied among sites ($\chi^2 = 324.64$, 45 df. $p < 0.0001$; Fig 5.8). At North Reef 46% of all daughter colonies were *Goniastrea* spp., *Montipora* spp. and *A. hyacinthus*. In contrast, the three most abundant species of daughter colonies at Washing Machine were *A. cuneata*, *A. gemmifera* and *Montipora* spp., jointly accounting for 43% of the total number at that site. Daughter colonies of *A. gemmifera*, *A. monticulosa* and *A. hyacinthus* accounted for 54% of the total at Lizard Head. At South Island, the most abundant species of daughter colonies (56% of the total) were *A. hyacinthus*, *A. gemmifera* and *P. verrucosa* (Fig 5.8).

Differences in the species composition of daughter colonies among sites was due in part to differences in species composition among sites. There were no detectable differences in the species composition of parent colonies and the established assemblage at each site (Table 5.5). However, when sites were pooled to increase sample size, there were significant differences in the relative abundances of species between the established assemblage and parent colonies ($\chi^2 = 41.89$, 15 df, $p < 0.0002$). This is because the per capita rate of fission (total number of parent colonies/number of colonies in the assemblage) varied among species (Fig 5.9). Branching *A. robusta* underwent fission most often (52% of all colonies underwent fission; Table 5.6; Fig 5.9). Branching *P. eydouxi* also underwent fission more than other species (40% of colonies underwent fission at least once; Fig 5.9; Table 5.6),

Figure 5.8 Species composition of daughter colonies produced by fission at four sites over 24 months (pooled over quadrats).

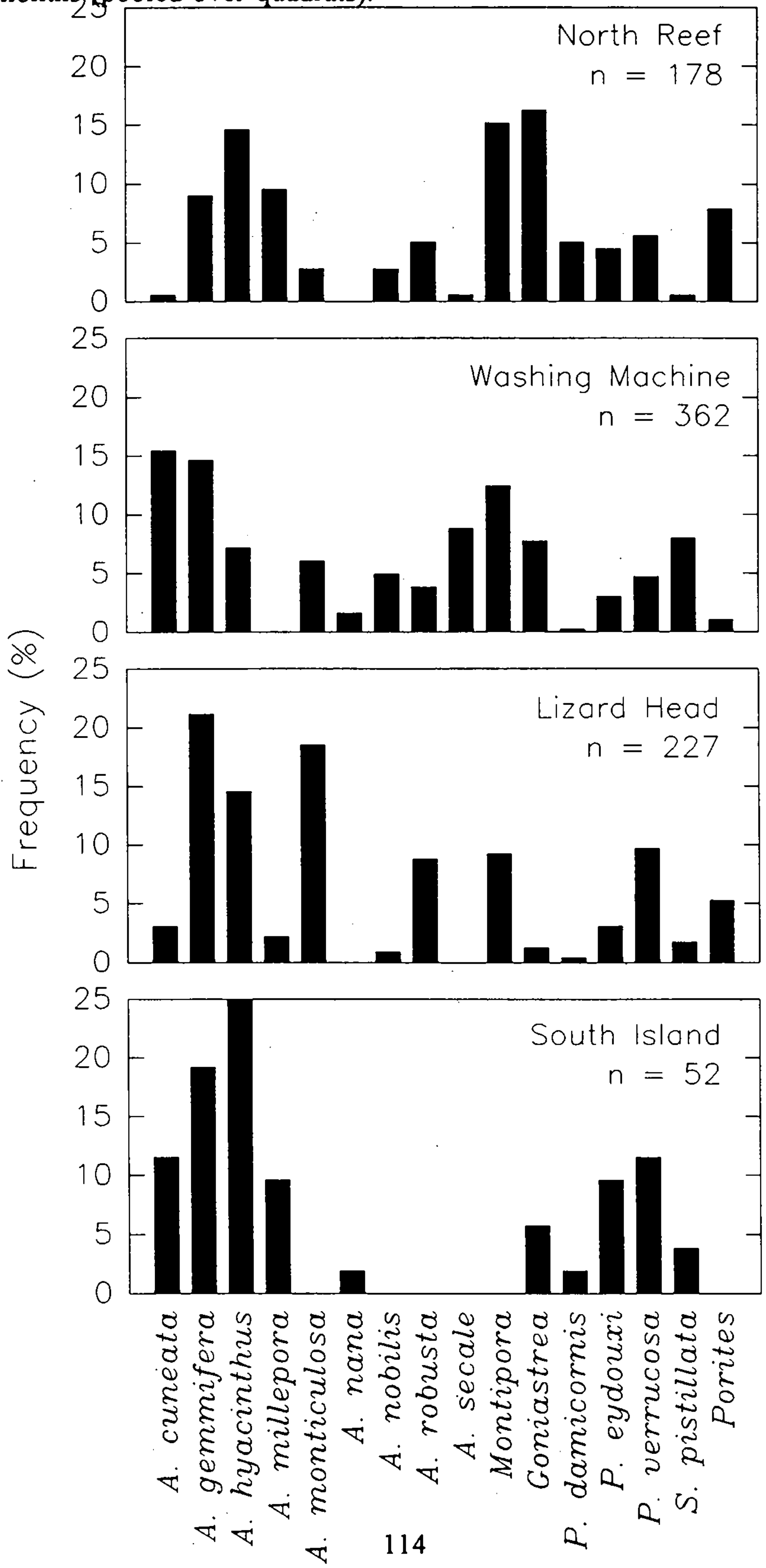


Figure 5.9 Per capita rate of fission (number of parent colonies / number of colonies in the established assemblage in February 1991) of sixteen species

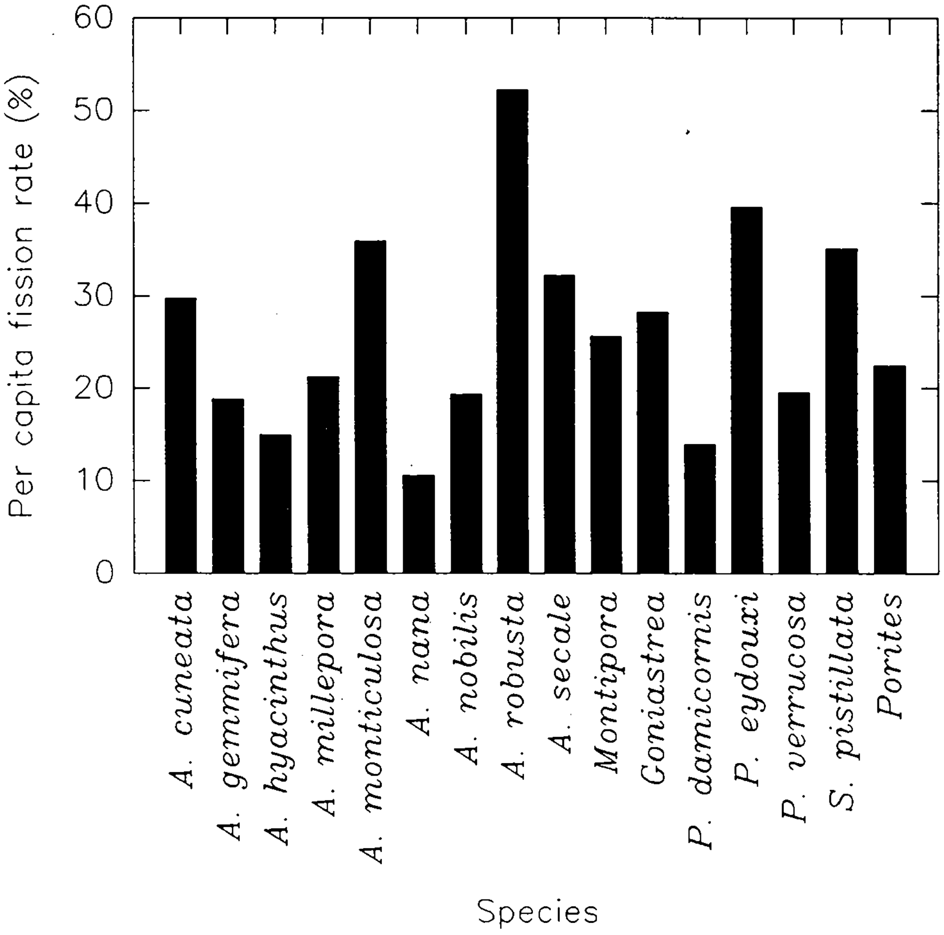


Table 5.5 Results of χ^2 analysis of heterogeneity comparing the species composition of parent colonies and the assemblage already established in February 1991 at each site.

Site	χ^2	df	p	comments
North Reef	10.92	14	> 0.6	4 cells with expected values < 1
Washing Machine	21.28	15	> 0.1	1 cell with expected values < 1
Lizard Head	25.08	14	< 0.04	4 cells with expected values < 1
South Island	14.81	12	> 0.2	8 cells with expected values < 1

but branching *A. nobilis* did not split often (only 19% of colonies underwent fission; Fig 5.9; Table 5.6). Other species with a range of morphologies underwent fission (Fig 5.9); the greatest rates of fission were for robust digitate *A. monticulosa* (36% of colonies), bushy *S. pistillata* (35% of colonies), corymbose *A. secale* (32% of colonies) and submassive *A. cuneata* (30%).

To test whether the differences in species composition of daughter colonies among sites were due to differences among species in the number of daughters produced, the species composition of parent and daughter colonies were compared. There were no detectable differences in the species composition of parent colonies and daughter colonies among sites (Table 5.7), but χ^2 statistics were biased because of small sample size. With sites pooled to increase sample sizes, there were still no detectable differences in the species distributions of parent colonies and daughter colonies ($\chi^2 = 20.69$, 15 df, $p > 0.14$). This was because the majority of species produced only

Table 5.6 Numbers of colonies at each site in February 1991 (Est) and the numbers of parents (P) and daughters (D) counted over 2 years for sixteen species at four sites.

	North Reef			Washing Machine			Lizard Head			South Island		
	Est	P	D	Est	P	D	Est	P	D	Est	P	D
A. cuneata	9	1	1	61	22	56	11	1	7	13	4	6
A. gemmifera	57	14	16	118	19	53	65	15	48	30	3	10
A. hyacinthus	122	18	26	68	10	26	115	20	33	75	9	13
A. millepora	22	4	17	5	0	0	7	2	5	13	4	5
A. monticulosa	7	3	5	43	13	22	49	21	42	4	0	0
A. nana	0	0	0	63	6	6	2	0	0	1	1	1
A. nobilis	22	3	5	7	2	18	2	1	2	0	0	0
A. robusta	3	2	9	12	4	14	8	6	20	0	0	0
A. secale	6	1	1	53	18	32	0	0	0	0	0	0
Montipora	59	18	27	146	33	45	28	11	21	9	0	0
Goniastrea	47	15	29	67	20	28	14	2	3	10	2	3
P. damicornis	10	3	9	11	1	1	9	1	1	13	1	1
P. eydouxi	11	3	8	14	5	11	13	7	7	10	4	5
P. verrucosa	37	6	10	54	11	17	59	15	22	24	2	6
S. pistillata	2	1	1	40	15	29	7	3	4	8	1	2
Porites	58	12	14	16	4	4	32	10	12	10	0	0

Table 5.7 Results of χ^2 analysis of heterogeneity comparing the species composition of parent and daughter colonies at each site.

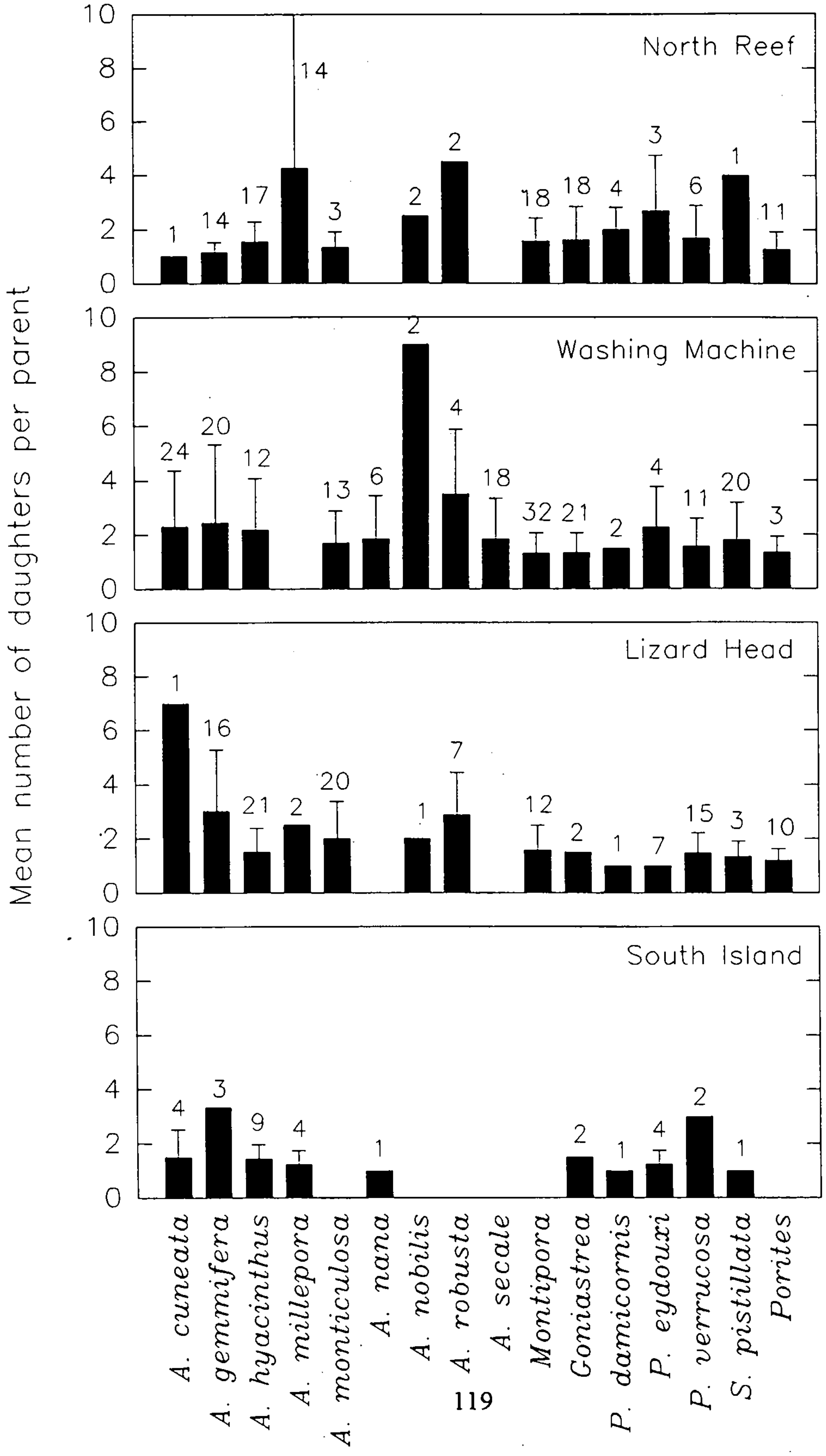
Site	χ^2	df	p	comments
North Reef	8.97	14	> 0.8	5 cells with expected values < 1
Washing Machine	16.76	14	> 0.2	3 cell with expected values < 1
Lizard Head	10.56	13	> 0.6	5 cells with expected values < 1
South Island	2.5	9	> 0.9	11 cells with expected values < 1

one or two daughter colonies per parent (Fig 5.10). Of 445 parent colonies of 16 species, 62% produced only 1 daughter, 19% produced 2 daughter colonies, 8% produced 3 and 10% produced more than 3 daughter colonies over 33 months. Forty-two percent of these last 45 parent colonies produced 4 daughter colonies each, while 15% produced 5 and 13% produced 6 or 7. There was, however, great variation in the number of daughter colonies produced by individual colonies of some species (Table 5.6). For example, one colony of *A. nobilis* produced 17 daughter colonies over 32 months, while a colony of *A. millepora* split into 13 daughter colonies over the same period (Table 5.6). Six colonies of *A. gemmifera* split into 7 or more daughter colonies. These colonies and the colony of *A. millepora* which split into 13 daughter colonies suffered from a disease which spread across the base of the colony, leaving isolated living branch tips which ultimately died.

5.3.3 Survivorship of daughter colonies

Daughter colonies had low survivorship (< 20% over 2 years, pooled across all

Figure 5.10 Mean number of daughter colonies produced by fission per parent (± S.D.) of sixteen species on the reef crest at four sites. Sample sizes are above bars.



taxonomic groups; Fig 5.10). Rates of mortality of daughter colonies were similar among sites ($\chi^2 = 7.35$, 3 df, $p > 0.06$; Fig 5.11). Survival after 18 months ranged from 8% at South Island to 13% at Lizard Head.

In contrast to survival of daughter colonies pooled across all taxa, survival of daughter colonies differed among sites in the family Acroporidae ($\chi^2 = 12.57$, 3 df, $p < 0.006$; Fig 5.12). Acroporid daughter colonies survived better at Washing Machine and Lizard Head (13% of daughter colonies survived for 24 months) than at North Reef, where only 3% survived for 24 months (Fig 5.12). Survival of daughter colonies of both Pocilloporids and Faviids, however, did not vary among sites ($\chi^2 = 0.52$, 0.37 respectively, 3 df, $p > 0.9$ in both cases; Fig 5.12). Other families did not have large enough sample sizes to test for differences among sites.

At the level of species groups significant variation among sites also occurred in survival of daughter colonies of *Goniastrea* and *Porites* (Table 5.8), although these differences are probably due to small sample sizes. With all sites pooled to increase sample sizes, daughter colonies of different species survived with differing success (Table 5.9). *Acropora monticulosa* had the greatest rate of survival of all sixteen species (27% of 62 daughter colonies survived for at least 18 months). Of the six most abundant species on the reef crest, daughter colonies of *A. gemmifera* and *Porites* sp survived well (22% and 20% over 24 months, respectively; Table 5.9). Daughter colonies of the other four abundant species (*A. hyacinthus*, *Montipora* spp., *Goniastrea* spp. and *Pocillopora verrucosa*) all had rates of survival ≤ 10% over 24

Figure 5.11 Survival of daughter colonies at four sites. Sample sizes are the total number of daughter colonies detected at each site over 33 months.

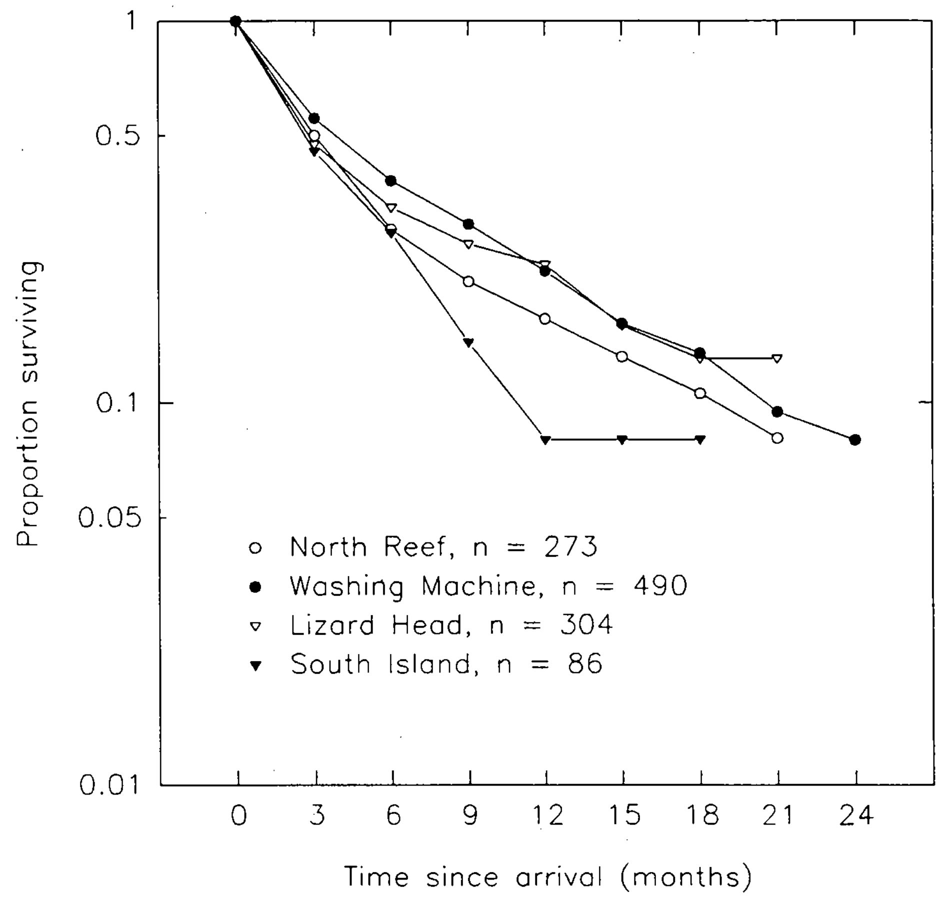


Figure 5.12 Survival of daughter colonies of three families at four sites. Sample sizes are the total number of daughter colonies of each family detected in quadrats over 33 months.

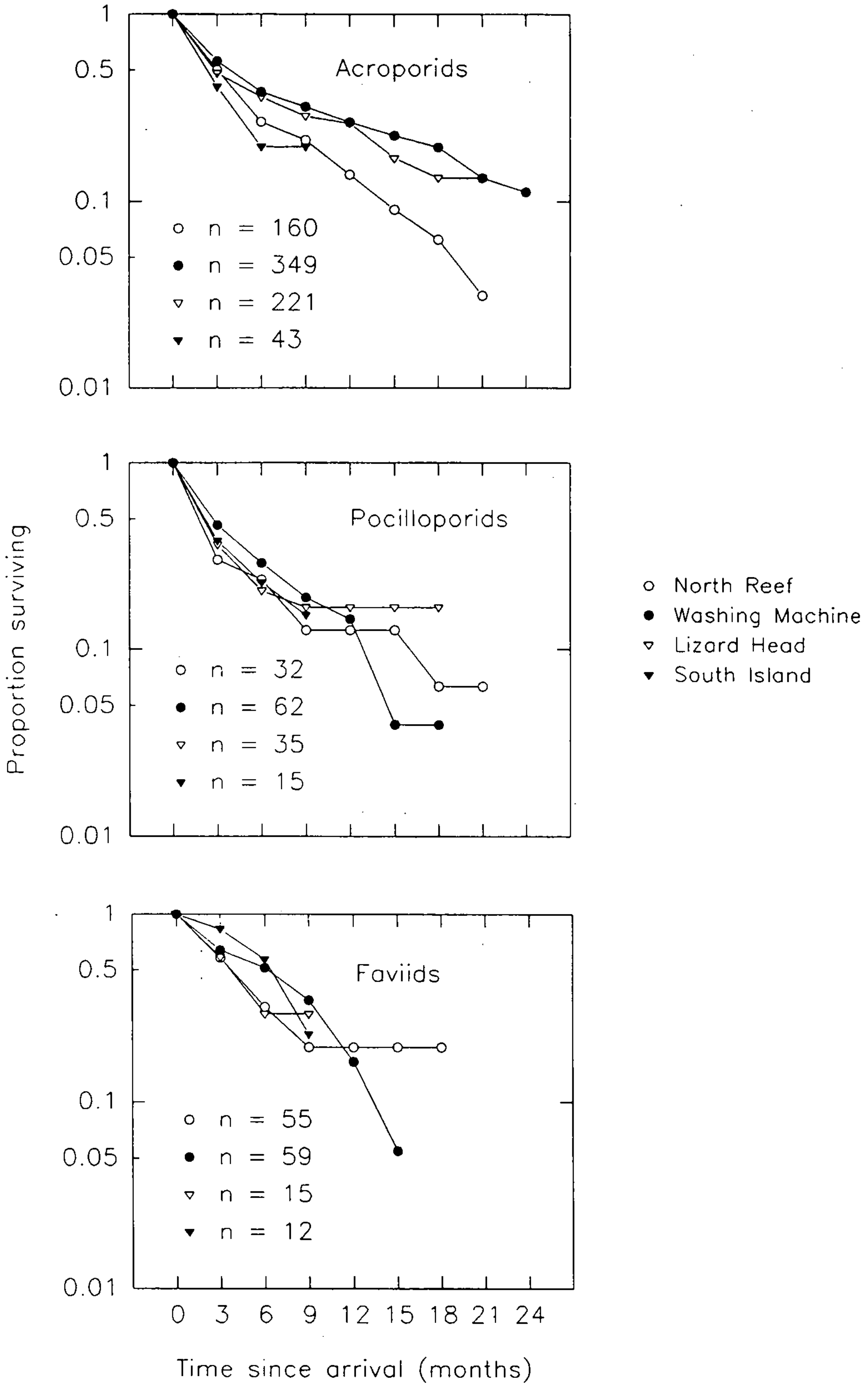


Table 5.8 Results of log-rank tests for differences among sites in survival of daughter colonies of six common species or species groups. Adjusted $\alpha = 0.008$.

Species	χ^2	df	p
Acropora gemmifera	2.57	3	0.46
A. hyacinthus	4.42	3	0.22
Goniastrea spp.	12.29	3	0.006
Montipora spp.*	6.02	2	0.05
Pocillopora verrucosa	4.78	3	0.19
Porites spp.*	13.05	2	0.002

* South Island not included in analysis

months (Table 5.9).

5.4 DISCUSSION

5.4.1 Fragmentation as a means of colonising space on the reef crest

More than 400 fragments were detected in quadrats over 33 months, at a rate of 1.4 fragments.$m^{-2}.yr^{-1}$. This rate is lower than rates of production of fragments on the reef crest at North Reef (8 fragments.$m^{-2}.yr^{-1}$; Smith 1992), perhaps because fragments are washed away from the crest. The rate of recruitment measured here is greater than on reef buttresses on a midshelf reef, where 52 fragments recruited to an area of 75 m^2 over 2 years (0.35 fragments.$m^{-2}.yr^{-1}$), but Wallace (1985b) sampled at a lower frequency than this study (every 4 months). In permanent quadrats in the

Table 5.9 Survival of daughter colonies of 14 species on the reef crest at Lizard Island. a: Percent of daughter colonies alive after the time in column 2. b: The time over which survival is calculated. c: Total number of daughter colonies produced over 24 months, pooled across sites. d: Survival rate extrapolated over 24 months, assuming mortality is constant

Species	measured survival (%)[a]	time period (months)[b]	sample size[c]	extrapolated survival over 24 months[d]
A. monticulosa	26.7	24	62	26.7
A. gemmifera	21.9	24	124	21.9
Porites	23.6	21	30	19.2
A. robusta	27.5	18	20	17.9
A. cuneata	16.0	24	56	16.0
A. nobilis	18.7	18	25	10.7
A. hyacinthus	10.1	24	97	10.1
A. secale	11.5	18	29	5.6
P. eydouxi	4.2	24	31	4.2
P. verrucosa	8.2	18	55	3.6
S. pistillata	8.0	18	29	3.5
Montipora	7.2	18	92	3.0
A. millepora	23.7	9	17	2.2
Goniastrea	4.3	12	62	0.18

Caribbean, up to 27 fragments.m^{-2}.yr^{-1} were detected, largely as a result of a cyclone which generated fragments (Hughes 1985). These differences in the rate of recruitment by fragments probably reflect differences in the species composition of assemblages and disturbance regimes in different places and depths.

Species composition of fragments differed among sites (Fig 5.2). Branching, tabulate and corymbose morphologies dominated the composition of fragments, similar to other studies on GBR reefs (Bothwell 1981; Wallace 1985b; Smith 1992). The species with most abundant fragments (*A. hyacinthus*, *A. nana* and *A. nobilis*) had fragile morphologies, but more robust species (e.g. *A. gemmifera*, *P. eydouxi* and *A. secale*) also fragmented. In deeper water (> 10m), Wallace (1985b) found that only branching Acroporids fragmented, but Smith (1992) found fragments of plate, staghorn and corymbose morphologies on the reef crest at Lizard Island, suggesting that most branching species will undergo fragmentation in shallow water.

In this study, survival of fragments was poor. Over 2 years, 87% of all fragments disappeared or died within 3 months (Fig 5.3). The low survival of fragments may have been because they were washed away before they had a chance to reattach. It has been suggested that re-cementing to the substratum is an important determinant of survival of fragments (Bak & Criens 1981; Wallace 1985b). Smith (1992) found that 32% of artificially generated fragments had moved away from the reef crest after 25 weeks. He also found that only 4% of artificially generated fragments had reattached after 4 months. His data indicate that the opportunity for reattachment on the reef crest is limited. The low survival of fragments in this study does not imply that fragments necessarily died; they may survive elsewhere (e.g. the reef flat; Smith 1992).. Many fragments generated on the reef crest do not remain there (Smith 1992). Heyward & Collins (1985) found that fragments generated on the seaward edge of the reef flat at Magnetic Island were washed landwards across the reef flat.

Therefore, the reef crest may be an important source of fragments that colonise other habitats (e.g. the reef flat; Heyward & Collins 1985; Smith 1992).

Survivorship of fragments varied among species (Fig 5.4). Several factors may contribute to this variation among species, including size of fragments, morphology and ability to regenerate (e.g. Bak & Criens 1981; Highsmith 1982; Smith 1992). *Acropora hyacinthus* had the highest survival of the three species analysed in this study and also had the largest fragments. In contrast, *A. nana* had the smallest fragments and lowest survival. The ranking of the three species in this study is different from the ranking found by Smith (1992), who showed that *A. nobilis* had higher survival than *A. hyacinthus* when fragments were of similar sizes. The difference in the results of the two studies are most likely due to the differences in the average sizes of fragments, since the survival of fragments is often size-dependent (Highsmith 1982; Karlson 1986, Smith 1992).

These results suggest that successful colonisation of space on the reef crest by fragments is rare but may occur for some species. Although there is a constant supply of fragments (Fig 5.1), few attach and grow in this habitat (Fig 5.3). The reef crest is highly disturbed by water motion and corals are often broken but are washed into more benign habitats before attaching (Smith 1992).

5.4.2 Spatial variation in fission as an influence on spatial variation in community composition

Fission occurred frequently, and in all taxonomic groups. The rate of production of daughter colonies varied among sites (Fig 5.5; Table 5.2). Large colonies undergo fission more than smaller colonies (Hughes & Jackson 1985; Babcock 1991), so differences among sites in rates of fission may be related to differences in the size structures of the assemblages at each site. However, the average size of corals was smallest at Washing Machine and largest at North Reef (unpubl. data), so the higher rate of fission occurred at the site with the greater proportion of small corals. Alternatively, differences among sites in rates of fission could be related to variation in the composition of assemblages among sites. Per capita rates of fission differed among species (Fig 5.8) and species varied in abundance among sites (Chapter 2). Therefore, sites with greater abundances of species with high per capita rates of fission might be expected to have higher rates of fission. The species which were more susceptible to fission were differentially abundant at the sites with more abundant daughter colonies (Table 5.6). *Acropora robusta*, *A. monticulosa*, *Pocillopora eydouxi*, *A. cuneata* and *Stylophora pistillata* were all most abundant in the established assemblage at Washing Machine (Table 5.6) and were most susceptible to fission (Fig 5.8). Similarly, *A. monticulosa* was abundant at Lizard Head (Table 5.6) where rates of fission were also high (Fig 5.5). Differences among sites in survival of daughter colonies of Acroporids was also probably due to spatial variation in the composition of assemblages; the Acroporid species which had high survivorship of daughter colonies (*A. monticulosa* and *A. robusta*; Table 5.9) were more abundant at Washing Machine and Lizard Head where Acroporid survivorship was greater (Table 5.6).

Fission in some species may account for differences in their abundance among sites (Chapter 2). For example, *Acropora monticulosa* had few larval recruits at all sites (Chapter 3) but was abundant as daughter colonies at Lizard Head and Washing Machine (Fig 5.7). Other species with few larval recruits (Chapter 3), many daughter colonies (Fig 5.7) and differential abundance among sites (Chapter 2) were *Pocillopora eydouxi* and *A. robusta.* These three species all had high per capita rates of fission (Fig 5.8) and relatively high survival of daughter colonies (Table 5.9). Differences in their abundances among sites are likely to be enhanced by asexual reproduction by fission.

Asexual reproduction by fission may be of benefit to some species on the reef crest (e.g. *Acropora monticulosa*) if daughter colonies collectively have a higher chance of survival than a single parent colony. However, the cost of producing physiologically separate copies of the parental genotype may be great because each copy is smaller than the parent, resulting in a reduction in individual (i.e. ramet) survivorship (Hughes & Connell 1987; Babcock 1991) and fecundity (Kojis & Quinn 1985; Szmant-Froelich 1985). The species in this study which had high per capita rates of fission (Fig 5.8) and high survival of daughter colonies (Table 5.9) were those with robust morphologies likely to be resistant to wave energy (*A. monticulosa* and *A. robusta*). These species may invest more in persistence in the face of disturbance than in mobility (Jackson & Hughes 1985). Fission may be merely an inevitable consequence of a persistent life history strategy in a disturbed habitat because the longer a coral lives, the more likely it is to be damaged. Babcock (1991) concluded that fission in three massive species on the reef flat was not adaptive, because damaged colonies were more likely to suffer more damage, fission reduced genet fecundity and increased the mortality of ramets. If colonies can grow fast to escape the costs of a reduction in size, then those costs may be allayed. Persistent species, however, have slow growth rates (Hughes & Jackson 1985; Smant 1986). Futher detailed study is required to find out whether fission is adaptive or merely a consequence of a persistent life history strategy.

In conclusion, asexual processes do not appear to influence the numerical abundance of the majority of species on the reef crest. Fragmentation occurs frequently as a result of disturbance by waves, but most fragments do not attach and grow in the reef crest habitat. Fission, on the other hand, does appear to benefit some species on the reef crest. The relative roles of asexual and sexual processes in the population dynamics of corals in the disturbed habitat of the reef crest are discussed in the following chapter.

CHAPTER 6: GENERAL DISCUSSION

6.1 Life histories of common corals on the reef crest

Life history theory predicts that species with high rates of recruitment, dispersal and/or sexual reproduction should predominate in unpredictable habitats (Williams 1975; Maynard Smith 1978). The reef crest on Lizard Island is such a habitat, since it is shallow and likely to be disturbed by cyclones every 10 - 20 years, on average (Massel & Done 1993). On the reef crest, there was an overall correlation between rank abundance and rank larval recruitment (Spearman rank correlation; $r = 0.76$, $n = 16$, $p < 0.0006$; Table 6.1); the most abundant species were, in general, the species with greatest recruitment (Table 6.1). This predominance by species with high rates of recruitment has been observed in other shallow, highly disturbed reefs (e.g. Grigg & Maragos 1974; Loya 1976a; Done 1983; Van Moorsel 1983; Richmond & Hunter 1990).

However, corals may display two other strategies for living in disturbed environments: persistence and fragmentation (Highsmith 1982; Szmant 1986). Persistent species withstand disturbance by having robust or massive forms and invest in maintenance rather than reproduction. For example, *Montastrea annularis* in the Caribbean has a thick skeleton resistant to waves and slow growth (e.g. Hughes & Jackson 1985) but very fast regeneration (e.g. Bak *et al.* 1977; Meesters & Bak 1993) and may not reproduce sexually at all (Hughes 1988). It is interesting that even the species with a largely persistent life-history strategy in this study (e.g. *A. monticulosa*, *A. robusta*, *A. cuneata*) also recruited by larval propagules (Table 6.1),

Table 6.1 Summary of abundance, recruitment and mortality of sixteen common species on the reef crest, expressed as ranks (1 = highest, "-" = sample sizes too small to measure survival).

Species	Initial abundance (Fig 2.6)	Recruitment		Survival		
		Larval (Fig 3.5)	Fission (Fig 5.8)	Original colonies (Table 4.8)	Larval recruits (Table 4.4)	Recruits by fission (Table 5.9)
A. hyacinthus	1	2	2	5	4	9
A. gemmifera	2	5	1	1	5	5
Montipora	3	1	3	15	16	12
P. verrucosa	4	6	7	11	3	10
Goniastrea	5	4	6	8	12	13
A. monticulosa	6	15	5	3	2	2
A. cuneata	7	9	4	4	8	7
Porites	8	3	12	9	14	4
A. nana	9	7	16	12	6	-
A. secale	10	10	10	14	11	8
S. pistillata	11	8	9	13	13	11
P. eydouxi	12	13	11	2	10	14
A. millepora	13	14	13	7	9	3
P. damicornis	14	11	15	10	1	-
A. nobilis	15	12	14	16	15	6
A. robusta	16	16	8	6	7	1

unlike *Montastrea annularis*. This may be because of the different disturbanceregimes in shallow reefs on the Great Barrier Reef and deeper reefs in the Caribbean. On shallow disturbed reefs, persistent corals must make considerable investment in dispersal and genetic recombination because of the unpredictable nature of the environment.

Fragmenting corals take advantage of disturbance to propagate asexually (e.g. *Acropora cervicornis*: Tunnicliffe 1981). In this study, the branching coral, *A. nobilis* had low abundances, low larval recruitment, low per capita rates of fission, and high mortality of original colonies, recruits and daughter colonies (Table 6.1). Although the species produced many fragments (Fig 5.3), they did not remain on the reef crest (Fig 5.5). *Acropora nobilis* was found on the reef crest only at North Reef, the most sheltered site in this study (Fig 2.6). Together, these traits suggest that *A. nobilis* does not do well in relatively shallow, highly disturbed habitats.

6.2 Turnover on the reef crest

Turnover of whole colonies on the reef crest was very high (Table 6.2). In total, 60% of the original colonies counted in February 1991 had died by February 1993. Over 2000 larval recruits were detected in 80 m^2 during 2 years, but only 27% of them were still alive at the end of monitoring (Table 6.2). Daughter colonies produced by fission were half as abundant as larval recruits and had lower survival (16% of the total number of daughters generated by fission were alive in February 1993). Over 400 fragments washed into the quadrats in 2 years, 9% of which were

Table 6.2 Turnover of whole colonies at four sites on the reef crest from February 1991 to February 1993. NR = North Reef, WM = Washing Machine, LH = Lizard Head, SI = South Island

	NR	WM	LH	SI	Total
Number of colonies, February 1991	947	1192	633	370	3142
Survivors Feb 93	200	455	273	142	1070
Larval recruits	775	914	493	385	2567
Recruits alive Feb 93	243	342	180	114	879
Fragments	135	190	59	37	421
Fragments alive Feb 93	19	9	2	9	39
Daughters	247	447	304	84	1082
Daughters alive Feb 93	87	132	77	20	316
Number of colonies, February 1993	549	938	532	285	2304

alive in February 1993. These proportions of recruits still alive at the end of the study are inflated because they include recruits detected in the last census (over 13% of the total numbers of colonies in that census). Such high rates of turnover could potentially result in great fluctuations in the density of corals (but not in cover, since most of the dynamic was due to the recruitment and mortality of small corals; see also Harriott 1983). That numbers are essentially constant (Fig 2.2) is extraordinary in the face of such flux. In the absence of disturbance during this study, the constancy observed in density and species composition must have been maintained by the balance between recruitment and mortality.

6.3 Spatial variation in the structure of coral assemblages: the role of demographic processes

Total abundance of corals differed threefold among sites (Fig 2.2), recruitment and mortality of recruits differed 2.5 (Fig 3.1) and twofold, respectively (Fig 4.1). To investigate the relative influence of recruitment and mortality on the total abundance of corals at each site, simple simulations varying rates of recruitment and mortality among sites were done. With numbers of recruits set at 100 per site every 2 years, and mortality of ranging between 12% over 2 years at South Island and 23% at Washing Machine (Fig 4.1), the abundance of survivors at equilibrium varied twofold among sites. However, total abundance (including the most recent recruits) varied only 15% among sites because the number of recruits outweighed the number of survivors. With numbers of recruits set at 400, 500, 260 and 200 at the four sites (approximately equal to total recruitment during this study), and mortality set at 30% at all sites, the total abundance of corals after population growth had reached an asymptote differed by a factor of 2.5. The combination of the above differences in recruitment and survival produced differences in total abundance among sites by a factor of 2.8.. These simulations show that the total abundance of corals is more sensitive to the measured differences in recruitment among sites than in mortality. Even when measured recruitment and observed rates of mortality of recruits are combined, the calculated differences in total abundances of corals among sites were less than the observed differences. This result implies that temporal fluctuations in recruitment and mortality are important in generating the observed differences in total abundance of corals among sites (see below).

Assessing the relative roles of recruitment and mortality in determining differences among sites is difficult because the number of recruits arriving is much greater than the number of recruits surviving from previous recruitment episodes due to high rates of recruitment and mortality (Tables 6.1, 6.2). Because of the large proportion of the assemblage that is made up of new recruits (40%, see Section 6.1 above), patterns in recruitment will be reflected in adult assemblages regardless of whether mortality also structures assemblages (Hughes 1990). There was no evidence of strong density-dependence in mortality of recruits during this study (Fig 4.2), suggesting that during this study recruitment did play an important role in regulating the abundance of corals.

If recruitment is important in structuring assemblages, then some important questions about what causes variation in recruitment need to be addressed. Causes of variability in recruitment have recently been the subject of intense interest (e.g. Grosberg 1982; Keough & Downes 1982; Eckman 1983; Gaines & Roughgarden 1985, 1987; Butman 1987; Keough 1988; Raimondi 1990; Black & Moran 1991; Pawlick 1992). Recent work on populations of coral reef fish (e.g. Milicich & Doherty 1994; Milicich 1994) and intertidal barnacles (e.g. Bertness *et al.* 1992; Rodriguez *et al.* 1993) has indicated that larval supply is an important determinant of recruitment, and that supply is mediated by hydrodynamics and oceanographic features. The availability of appropriate sites for settlement and post-settlement mortality may also be important in determining the magnitude and spatial pattern of recruitment (e.g. Butman 1987; Keough 1988; Bourget *et al.* 1994).

Perhaps the most important question for both theoretical and practical reasons is, "Where do the recruits come from?" Current literature provides conflicting opinions. On one hand, there is evidence from modelling of currents and tidal flushing rates that suggests that local retention of larvae may result in self-seeding of reefs (Black *et al.* 1991). On the other hand, slicks of coral larvae have been detected up to 26km from natal reefs within weeks (Willis & Oliver 1988). Probably both larval retention and dispersal occur (Wolanski *et al.* 1989; Black 1993), in which case it becomes important to know where and when local retention of larvae happens. If some degree of self-seeding occurs, then populations may be closed to a certain extent, and this has implications for the ability of reefs to recover after disturbance and for understanding mechanisms involved in the regulation of populations.

Differences among sites in the composition of assemblages (Fig 2.6) were largely influenced by differences in the composition of larval recruits (Fig 3.6). Although post-recruitment mortality differed among species (Table 4.4), there was little evidence of significant differences among sites in mortality of recruits (Table 4.3) during the study. Differences in composition of recruits and the established assemblage may be because recruitment and post-recruitment mortality are variable (Bak & Engel 1979; Harriott 1985). The abundance and composition of recruits varies greatly over time (Connell 1973; Wallace 1985a,c; Fisk & Harriott 1990). Temporal variation in recrutiment may be reflected in the composition of assemblages on the reef crest at Lizard Island, since mortality was density-independent at least during the period of this study (Fig 4.2).

This study was done during a period in which there were no major disturbances at Lizard Island. Under these conditions, patterns in recruitment closely paralleled patterns in abundance and composition of assemblages, while mortality appeared to play little part in determining differences in density among sites. Whether the balance between recruitment and mortality observed in this study (Fig 2.2) is representative of reefs is yet to be determined. Severe disturbances from many causes have obvious and sometimes long-lasting effects on corals (Hughes 1989; Done 1992b). Some authors have suggested that rare disturbance events structure assemblages (Roughgarden et al. 1985; Cody 1989; Done 1992a). The effects of disturbance are dependent on the species composition and size structure of assemblages at a particular site which, in turn is dependent on the previous history of recruitment and disturbance (Hughes 1989; Witman 1992). Long-term studies can help answer questions about what structures assemblages of corals (e.g. Done 1992a), but they also need to be done at several places because of the site-specific nature of succession (e.g. Tanner *et al.*, in press) and response to disturbance (Hughes 1989; Witman 1992).

6.4 Implications for management

Annual surveys of corals miss much of the turnover identified in this study. Had censuses been annual, up to 68% of larval recruitment (range 40 - 68% across sites) would have been missed. In a similar study at a lagoonal patch reef at Lizard Island, Harriott (1983) found that 33% of turnover of corals monitored every 2 months for 20 months would have been missed by annual surveys. This has implications for designing monitoring studies. Whether censuses are annual or more frequent will depend greatly on the nature of the question investigated. If long-term trends in community structure and dynamics are of interest, then annual censuses are probably adequately frequent, given that there is little change in abundance, cover or composition of assemblages over a year under undisturbed conditions (Harriott 1983; Figs 2.2, 2.3, 2.6, 2.7). However, if early life histories of corals are of interest, then monitoring more frequently is necessary since small corals have high mortality and recruit in large numbers (Table 6.1).

Research on the factors determining rates of recruitment is necessary for management, since the scale of management ought to be determined by the scale at which variation occurs. For instance, if larval supply is of primary importance in determining patterns of recruitment, then management strategies need to embrace many reefs. If patterns in recruitment are primarily determined by available space and larval preferences for particular habitats, then the scale at which reefs need to be managed is much smaller. Future work on the role of recruitment in assemblages of coral needs to identify the causes of patterns in settlement and recruitment.

6.5 Conclusion

This study has clearly illustrated that coral communities differ greatly in both structure and dynamics at sites within the reef crest, a spatial scale of 100s - 1000s of metres. It has shown that studies at one site cannot be used to generalise about patterns and processes in assemblages of coral. This is particularly important because the history of disturbance and recruitment at the level of sites can influence future responses to disturbance (Hughes 1989; Witman 1992). The reliability and representativeness of single observations (in space or time) is limited because of the patchy nature of communities (e.g. Paine & Levin 1981; Underwood *et al.* 1983). Assemblages of corals can be described and understood as landscapes made up of a mosaic of patches at different successional stages (Grassle 1973; Connell & Keough 1985; Jackson 1991). For this reason, a general understanding of the processes important in shaping assemblages of corals is dependent on quantifying both spatial and temporal variation in these processes.

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