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# Dynamics of outbreak populations of crown-of-thorns starfish (*Acanthaster planci* L.), and their effects on coral reef ecosystems.

Thesis submitted by

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in October, 2001

for the degree of Doctor of Philosophy in Marine Ecology, within the School of Marine Biology and Aquaculture, James Cook University.

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# Abstract

Population outbreaks of crown-of-thorns starfish (*Acanthaster planci* L.) represent one of the most significant, but also least understood processes affecting coral reef communities. Limited understanding of crown-of-thorns outbreaks is due, at least in part, to a critical lack of data on the structure and dynamics of *A. planci* populations. Therefore, this study examined fine-scale (within reef) patterns in the size structure, distribution, and abundance of starfish populations, during an outbreak of *A. planci* in the northern Great Barrier Reef. The outbreak resulted from steady and prolonged increase in starfish densities, over a three year period. Furthermore, starfish populations comprised individuals from at least four different year classes, suggesting that the outbreak was caused by progressive accumulation of starfish from multiple recruitment events. Overall densities of *A. planci* increased to 1.0 starfish per 200m$^2$ (±0.1 SE), in January 1997, and then remained fairly constant until June 1998, after which time starfish densities declined rapidly. During the outbreak, densities of *A. planci* varied greatly among locations (separated by 0.5-8km), and also between reef zones (<5m apart). Densities of *A. planci* were consistently highest at locations in sheltered back reef habitats, but considerable numbers of starfish were also recorded at depth (>7 metres) in some exposed locations. Fine-scale patterns in the distribution and abundance of *A. planci* were partly attributable to spatial variation in wave exposure (whereby starfish avoid turbulent environments), but also resulted from spatial patterns established at settlement.

Outbreak populations of *A. planci* caused substantial coral mortality, and also significantly altered the structure of coral communities. Scleractinian coral cover declined by 32%, from a mean of 32.2% cover (± 1.1SE) in October 1996 down to 21.9% cover (± 1.2SE) in January 1999. The impacts of *A. planci* were however, very patchy. At the most severely affected locations (in sheltered back reef habitats) coral cover declined by 72% between 1996 and 1999, whereas at several other locations (e.g., lagoonal habitats) there was no observable change in scleractinian coral cover. Crown-of-thorns starfish also had varying impacts among different coral species, caused by significant selectivity in their patterns of feeding. In general, starfish had a disproportionate impact on fast growing branching corals (e.g. *Acropora* spp. and pocilloporids), tending to avoid slow growing massive corals (e.g., *Diploastrea* spp., *Porites* spp.).

Crown-of-thorns starfish are well adapted to feed on a wide range of different coral prey, and it is not known why they consistently target a restricted suite of different coral species. Herein, I tested the role of coral symbionts in structuring the feeding preferences of *A. planci*, for common branching coral species (*Acropora* spp. and pocilloporids). To test the role of coral symbionts, this study compared feeding preferences of *A. planci* for six different coral species, with and without their usual complement of coral symbionts. Crown-of-thorns starfish had a clearly defined hierarchy of preference for the six different corals when they contained symbionts (*Acropora gemmifera* > *A. nasuta* = *A. loripes* > *Seriatopora hystrix* > *Pocillopora damicornis* > *Stylophora pistillata*). In contrast, when coral symbionts were removed, starfish readily consumed all six corals and did not exhibit any significant selectivity. For the six coral species tested, it is clear that coral symbionts (and particularly trapeziid crabs) do have a marked influence on the feeding preferences of crown-of-thorns starfish. However, despite the protection provided by coral symbionts, *Acropora* and pocilloporid corals were among the first corals eaten by field populations of *A. planci*. Therefore, other factors (e.g., the size, morphology, chemical defence and/ or nutritional value of corals) may be more important in determining overall feeding preferences of *A. planci* (across a broader range of different coral species).

Clearly, crown-of-thorns starfish have a major impact on coral communities, but impacts of starfish outbreaks may also extend to a wider range of reef associated organisms, such as coral reef fishes. Despite a close association between reef fishes and benthic habitats, there has been little consideration for how disturbances to benthic reef habitats (particularly, extensive reductions in coral cover) affect coral reef fishes. It is likely that impacts will be most pronounced in those fish species which exhibit a direct reliance on scleractinian corals, such as coral feeding butterflyfishes. This study examined long-term changes in the distribution and abundance of butterflyfishes throughout the course of a crown-of-thorns outbreak. Depletion of scleractinian corals resulted in significant reductions in the abundance of seven butterflyfish species (*Chaetodon auriga*, *C. citrinellus*, *C. kleinii*, *C. plebius*, *C. rainfordi*, C. *trifascialis*, and *C. unimaculatus*), whereas there was no change in the abundance of *C. aureofasciatus*, C. *baronessa*, *C. ephippium*, *C. lunulatus*, *C. melannotus* or *C. vagabundus*. *Chaetodon* species affected by coral depletion mostly had a high dependence on live coral for food. However, at least on non-coral feeding butterflyfish, *C. auriga*, was also affected. Among corallivorous butterflyfish, impacts of coral depletion varied in accordance with their degree of feeding specialisation. For example, declines in the abundance of the coral-feeding specialist, *C. trifascialis* were much more pronounced than declines in the abundance of the generalist coral feeding species *C. baronessa*. *Chaetodon baronessa* responded to the depletion of prey resource by expanding both the range of prey it consumed and also its depth distribution, thereby mediating impacts of resource depletion on its population size. This study demonstrates that major disturbances to coral reef habitats can have significant follow-on affects for coral feeding butterflyfishes. However, the specific responses of individual species vary in accordance with their diet, distribution and ecological versatility (specialist versus generalist).

In addition to feeding on scleractinian coral, many reef fish species also rely on scleractinian corals for shelter. Therefore, declines in coral cover may lead to a reduction in habitat availability, and corresponding declines in the local abundance of coral reef fishes. This study explores changes in the abundance and habitat associations of six coral-dwelling damselfish species, during extensive and wide-spread reductions in the availability of suitable host corals, caused by outbreak populations of *A. planci*. Coral-dwelling damselfishes occupied a very limited suite of available habitat categories, showing strong preference for only a limited range of habitat types (mostly specific coral species). Patterns of habitat use by coral-dwelling damselfish were also very consistent among locations and between years, despite significant variation in both the total abundance of corals and the relative abundance of different coral species. Live coral cover declined by 16-59% at locations affected by *A. planci*, causing declines in the abundance of *Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus* and *Pomacentrus moluccensis*, but not *C. atripectoralis* or *P. amboinensis*. Species not affected (*C. atripectoralis* and *P. amboinensis*) often inhabited skeletons of dead corals, whereas all other species were strongly dependent on live coral as shelter. Variation in the abundance of obligate coral-dwelling species (*C. viridis*, *D. aruanus*, *D. reticulatus* and *P.moluccensis*) was strongly associated with variation in the abundance of corals that they most frequently occupied. This study demonstrates that infestations of *A. planci* can significantly effect the distributions and abundances of reef fishes with strong dependence on live corals.

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## Statement on Sources

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

31 October, 2001

Morgan S. Pratchett

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# CHAPTER 1: General Introduction

## 1.1 Effects of disturbance on ecological communities

Disturbance, defined as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985: Page 7) exerts a major influence on the structure and dynamics of ecological communities in a wide range of environments (e.g., Sousa 1984, Pickett and White 1985, Karlson and Hurd 1993). However, the effects of disturbances on ecological communities vary greatly, depending on the type, intensity and areal extent of the disturbance (Petraitis et al. 1989, McCabe and Gotelli 2000), the incidence and recurrence of past disturbances (Hughes 1989, Death 1996), as well as a multitude of other factors which may have structured the community in the time leading up to the disturbance (e.g., Fukami 2001). The classical successional theory of ecological communities viewed disturbances as temporary interruptions in the progression of communities towards a climax equilibrium (Clements 1916, Elton 1927, Odum 1969). Within this context, disturbances were regarded as relatively rare events, causing little permanent or lasting change in the structure of ecological communities (Odum 1969, Sutherland 1974). Contrary to these views, more recent studies have shown that disturbances occur frequently within the life-span of most organisms (see reviews by Sousa 1984, Pickett and White 1985, Petraitis et al. 1989), and not only interrupt the successional process, but can change the trajectory of successional sequences (e.g., Holling 1973, Sousa 1984) and in some cases deflect the community structure towards a different equilibrium state (e.g., Syms and Jones 2000, Fukami 2001). Disturbances mostly occur too frequently for ecological communities to ever reach an equilibrium state (Preston 1962, Tanner et al.

1994). However, disturbances can have large and long-term effects on community structure by altering species composition, modifying outcomes of species interactions, and altering the susceptibility of communities to subsequent disturbances (e.g., Sousa 1979, Hughes 1989, Death 1996).

Disturbances influence the structure of ecological communities either through selective mortality of particular individuals, or by random, localised mass-mortality of a wide range of different individuals (often termed "catastrophic mortality") that clears space for recolonisation (Petraitis et al. 1989). Small-scale or relatively discrete disturbance events (e.g., predation events) usually have a disproportionate impact on certain individuals (Petraitis et al. 1989), and can thereby alter both population and/ or community structure through the selective removal of certain components of the community. Such events may promote diversity among competing species by reducing the abundance of competitively dominant species, and allowing inferior competitors to persist (e.g., Porter 1972, 1974). However, disturbances that differentially affect different individuals may also reduce diversity by disproportionately affecting rare species, thereby increasing the dominance of already abundant species (e.g., Glynn 1974, 1976). Catastrophic disturbances (e.g., volcanic eruptions, severe tropical storms, or intense fires), which generally have broad-scale impacts extending across a wide range of organisms (e.g., Connell et al. 1997), vary in their affect on community structure depending on the frequency and/ or severity of the disturbance (Petraitis et al. 1989). In general, catastrophic disturbances eliminate most (if not all) of the species in an area, thereby increasing future species diversity by preventing dominant species from monopolising all available resources (Petraitis et al. 1989). If however, disturbances are too frequent or too severe, very few species will be capable of occupying the area (mostly fugitive species which can rapidly colonise cleared space). The *Intermediate Disturbance Hypothesis* (Connell 1978) predicts that the maximum number of species will coexist at some intermediate level of catastrophic disturbance, whereby the competitive exclusion of species is prevented, but species extinctions due to the disturbance are also minimised.

The importance of disturbance in structuring ecological communities is particularly apparent on tropical coral reefs, which are subject to a wide variety of natural disturbances (see reviews by Stoddart 1969, Connell and Keough 1985, Karlson and Hurd 1993, Brown 1996). Chronic disturbances, such as tidal exposure, wave action and predation, determine fine-scale (within reef) distributions and abundances of many coral reef organisms (e.g., Done 1982, 1983, Huston 1985, Cox 1986, Acevedo and MorLock 1988). Most notably, these chronic disturbances generate striking patterns of depth zonation in coral reef organisms (*ibid*) which are a very conspicuous feature of coral reef communities world-wide (Goreau 1959, Stoddart 1969). Coral reefs are also subject to many acute and often catastrophic disturbances, resulting from unpredictable events such as severe tropical storms, freshwater plumes, unseasonal temperature extremes, and infestations of coral predators, which generate over-riding patterns in the community structure of coral reef organisms (e.g., Loya 1976, Porter et al. 1982, Kaufman 1983, Hughes 1989, Dawson-Shepherd et al. 1992, Bythell et al. 1993, Connell et al. 1997). These catastrophic disturbances increase persistence of multi-species assemblages by clearing space and preventing competitive exclusion of subordinate species (Porter 1974, Loya 1976, Porter et al. 1982, Rogers 1993), but can also cause differential mortality among populations or species, thereby directly affecting community structure (e.g., Woodley et al. 1981, Moran 1986, Hughes 1989, 1994, Marshall and Baird 2000).

A common feature of disturbances on coral reefs is that their impacts are very patchy. Even large-scale catastrophic disturbances, such as severe tropical storms (cyclones, hurricanes or typhoons), have highly varied impacts across a wide range of spatial and temporal scales, and vary in their affect on different populations or species within the community (e.g., Fenner 1991, Bythell et al. 1993, Hughes 1994, Connell et al. 1995, 1997). At very small spatial scales, several studies (Highsmith et al. 1980, Knowlton et al. 1981, Done 1982) have shown that the impacts of disturbance can vary within or between adjacent coral colonies, with some colonies or parts of them surviving to regenerate and reoccupy cleared space. Connell et al. (1997) showed considerable variation in the effects of cyclones among closely positioned locations (100-1,800 metres apart), whereby some locations experienced a 90% decline in live coral cover, but there was no detectable change in coral cover at nearby locations (see also Bythell et al. 1993). The spatial extent and severity of coral damage also varied between consecutive cyclone events, which was not related in any simple way to the intensity or proximity of the cyclones (Connell et al. 1995, 1997). Most disturbances vary in their effects among depths, with greatest damage generally occurring at shallow sites and a precipitous decline in the extent of damage caused at increasing depths (e.g., Hughes 1994, Connell et al. 1997, Moran and Reaka-Kudla 1991). Patchiness in the effects of disturbances result from the complex interplay of many physical variables (depth, topography, gradient, orientation etc.), as well as from differential susceptibilities among different organisms. For example, when cyclones affect coral communities dominated by delicate branching or tabulate corals, massive reductions in coral cover are likely to occur (e.g., Hughes 1994), whereas cyclones will have relatively little impact on coral communities dominated by massive corals (but see Bythell et al. 1993). The selectivity of most major disturbances is a key issue in their influence on ecological communities, with significant implications for the subsequent rate and nature of recovery. Endean and Cameron (1985) suggested that the severity of a disturbance affecting coral communities should be judged not only by how much coral is killed, but also the type of coral killed. They argued that the removal of very long-lived and slow growing species is likely to have much longer felt effects on community structure, than the removal of short-lived, fast-growing species (Endean and Cameron 1985). Most disturbances to scleractinian coral communities tend to have a disproportionate impact on fast-growing coral species (e.g. freshwater plumes, Jokiel et al. 1993; sedimentation, Acevedo and MorLock 1988; infestations of coral predators, Moran 1986, Turner 1994; coral bleaching, Marshall and Baird 2000), far more so than on slow-growing massive corals. However, some disturbances can cause massive destruction of coral communities (e.g., more than 90% decline in coral cover), with impacts extending across a broad range of taxa (e.g., Pearson and Endean 1969, Chesher 1969, Randall 1973, Colgan 1987, Connell et al. 1997).

In reviewing the recovery of coral communities following various different types of disturbance, Pearson (1981) suggested that one of the most significant disturbances on tropical coral reefs are caused by infestations of the coral eating crown-of-thorns starfish, *Acanthaster planci* Linnaeus 1978 (see also Moran et al. 1988). Pearson (1981) argued that infestations of *A. planci* caused damage to scleractinian corals that was more extensive and more wide-spread than caused by any other natural or anthropogenic disturbances. Since 1981, coral bleaching has developed as the major cause of disturbance on tropical coral reefs (McClanahan et al. 2001, Knowlton 2001). However, infestations of *A. planci* continue to occur throughout the Indo-Pacific region, causing extensive and widespread damage (Lourey 2000, Sweatman et al. 2000). *Acanthaster planci* is a natural inhabitant of tropical coral reefs, distributed throughout the Indian and Pacific Oceans from the Red Sea to the west coast of Panama (Potts 1981). Crown-of-thorns starfish are also found in a wide range of latitudes, from 34°N on sub-tropical reefs in the Ryukyu Islands, Japan (Yamaguchi 1986), to 32°S at Lord Howe Island (DeVantier and Deacon 1990). Throughout their geographic range, *A. planci* occur mostly at very low densities (< 1 starfish.ha$^{-1}$) and have very little impact on scleractinian coral communities (e.g., Glynn 1973, Zann et al. 1990). However, populations of *A. planci* occasionally undergo rapid and dramatic increases in abundance, termed "outbreaks", whereby starfish densities may increase to more than 10,000 starfish.ha$^{-1}$ (e.g., Pearson and Endean 1969, Branham et al. 1971). Outbreaks of *A. planci* have been recorded on many reefs throughout the Indian and Pacific oceans, and almost invariably cause massive destruction of scleractinian corals (reviewed by Moran 1986). In extreme cases, outbreak populations of *A. planci* have killed more than 90% of scleractinian corals over expansive areas (e.g., Pearson and Endean 1969, Chesher 1969, Randall 1973, Colgan 1987). At Green Island (northern GBR), for example, outbreak populations of *A. planci* killed approximately 80% of scleractinian corals across the entire reef, from the shallow reef crest (<2 metres depth), down to a depth of 40 metres (Pearson and Endean 1969).

The extensive and wide-spread destruction of coral communities by outbreaks of *A. planci* has generated considerable concern over the long-term outlook for coral reef ecosystems (e.g., Chesher 1969, Vine 1970). As a consequence, there have been numerous studies on the biology and ecology of *A. planci*, as well as many studies exploring the impacts of *A. planci* on tropical coral reefs (see reviews by Potts 1981, Moran 1986, Birkeland and Lucas 1990, and references therein). Despite this plethora of studies (>1200 published studies regarding *A. planci*), many questions still remain about the occurrence of crown-of-thorns outbreaks as well as their impacts on coral reef ecosystems. Most notably, it is still not known what causes crown-of-thorns outbreaks (see reviews by Potts 1981, Moran 1986, Birkeland and Lucas 1990). Perhaps even more importantly, it is not known whether crown-of-thorns outbreaks are caused, or exacerbated by human activities. Many theories have been put forward linking crown-of-thorns outbreaks with anthropogenic effects such as overfishing, pollution, and coastal development (see reviews by Potts 1981, Moran 1986, Birkeland and Lucas 1990). However, the role of anthropogenic factors in the occurrence of outbreaks is not certain, and many scientists advocate minimal human intervention in the progression of starfish outbreaks until this matter is resolved (e.g., Newman 1970, Birkeland and Lucas 1990, Antonelli et al. 1990, Kenchington and Kelleher 1992). Opinion is also divided on the long term impacts of *A. planci* on coral reef ecosystems. While some authors regard crown-of-thorns outbreaks as a major tragedy, causing overall degradation of tropical coral reefs (e.g., Endean and Cameron 1985, Endean et al. 1988, Seymour and Bradbury 1999, Lourey et al. 2000), others view outbreaks as routine disturbances from which coral reef communities will recover (e.g., Newman 1970, Pearson 1981, Done 1985, Moran et al. 1985, Ninio et al. 2000). Whatever their cause and their effects, outbreaks of crown-of-thorns represent a unique ecological phenomenon warranting considerable scientific attention (Seymour and Bradbury 1999).

## 1.2 The *Acanthaster* Phenomenon

Extreme variability in adult abundance is very common among marine organisms, particularly those with planktonic larvae (Thorson 1950, Roughgarden et al. 1988). However, few marine organisms exhibit changes in abundance of the magnitude, or rate, exhibited by the crown-of-thorns starfish. The abundance of *A. planci* can increase by as much as six orders of magnitude within one to two years (reviewed by Birkeland and Lucas 1990). At Tutuila Island, American Samoa, the overall abundance of *A. planci* increased from 1-2 starfish in 1976 to more than 200,000 starfish in late 1977 (Birkeland and Randall 1979, in Birkeland and Lucas 1990). Similarly, at Tanguisson Reef, Guam, densities of *A. planci* increased from less than 0.1 starfish.ha$^{-1}$, to more than 1,000 starfish.ha$^{-1}$ during the course of 1967 (Chesher 1969). Numerous hypotheses have been put forward to explain rapid and dramatic increases in the abundance of crown-of-thorns starfish (reviewed by Moran 1986, Birkeland & Lucas 1990). These hypotheses place importance either on factors affecting recruitment rates of the starfish (i.e. "Natural Causes hypothesis", Vine 1973; "Larval Recruitment hypothesis", Lucas 1973; "Terrestrial-Runoff hypothesis", Birkeland 1982), or changes in the behaviour and/ or survivorship of post-settlement individuals (i.e. "Predator-Removal hypothesis" Endean 1969; "Adult Aggregation hypothesis", Dana *et al.* 1972; "Prey-Threshold hypothesis", Antonelli & Kazarinoff 1984). While several of these hypotheses have been considered biologically improbable (e.g., Potts 1981, Birkeland and Lucas 1990), there is insufficient data at present to either accept or reject any or all of these hypotheses. Many biologists and theoretical ecologists do however, concur that single factor hypotheses put forward to explain the occurrence of crown-of-thorns outbreaks present oversimplified accounts of the *Acanthaster* phenomenon (reviewed by Birkeland & Lucas

1990, Bradbury and Antonelli 1990). Sudden and dramatic increases in the abundance of starfish must be at least partially the result of successful recruitment (Birkeland and Lucas 1990), but both pre- and post-recruitment processes are likely to contribute to the dynamic nature of *A. planci* populations (Bradbury and Antonelli 1990), as has also been shown for many other marine organisms (e.g., Jones 1987, 1991, Hughes 1990).

Unifying theories of population outbreaks were proposed by scientists working in terrestrial environments long before outbreaks of the crown-of-thorns starfish were even recognised (e.g., MacArthur 1955, Elton 1958). Both MacArthur (1955) and Elton (1958) argued that the dynamics of biological populations are inextricably linked to intrinsic properties of their life-history strategies, as well as the physical and biological environment. Within this context, outbreaks are regarded as manifestations of inherent instability within certain systems, attributed to either i) particular life-history characteristics (e.g., high fecundity, short generation times, high mortality during their early life-history, and generalised patterns of prey and habitat use) which predispose an organism to major fluctuations in population size, or ii) major changes in the physical and/ or biological environment that release the outbreaking population from usual regulating factors (Andrewartha and Birch 1984, Berryman 1987). *Acanthaster planci* exhibits all the life history characteristics of a species likely to experience major fluctuations in population size (Stump 1992). Firstly, *A. planci* have extremely high fecundity, with female starfish producing up to 60 million eggs each year (Conand 1985). Moreover, *A. planci* have very short generation times, capable of reproducing within two years of settlement (Lucas 1973). Although there is very little information on the survivorship of *A. planci* during larval stages, it is clear that very few of the millions of fertilised gametes produced during each spawning season actually survive to settle on coral reefs (Moran 1986), and there is also considerable mortality (ca 30% mortality) of juvenile *A. planci* immediately after settlement (Keesing and Halford 1992, Sweatman 1995). *Acanthaster planci* also exhibits considerable behavioural, distributional and dietary plasticity, with the ability to adapt to a variety of situations (Stump 1992, Birkeland 1996a). In summary, *A. planci* has a major propensity to undergo rapid and dramatic fluctuations in population size (Stump 1992, Birkeland 1996a), but this does not explain when and why outbreaks actually occur (Birkland and Lucas 1990). After reviewing various crown-of-thorns outbreaks and revealing similarities in the timing and spatial patterns of outbreaks, Bradbury and Antonelli (1990) suggested that there must be some common underlying process (or processes) that explains the onset of outbreaks (see also Moran 1986).

The most widely accepted (but as yet unproven) theory for the incidence of outbreaks is that crown-of-thorns outbreaks are initiated by temporary increases in larval survival caused by high levels of terrestrial run-off (reviewed by Brodie 1992, Engelhardt and Lassig 1992). The argument follows that increased organic matter within the water column, caused by terrestrial run-off, could increase survivorship of larval starfish by increasing the availability of prey resources (e.g., Pearson and Endean 1969, Lucas 1973, 1975, Pearson 1975, but see Ayukai 1992). Support for this theory comes from research showing that larval survivorship of *A. planci* is enhanced by increased prey availability, lowered salinities and increased temperatures (Lucas 1975, Pearson 1975), all of which may be associated with increased levels of terrestrial run-off. Moreover, there appears to be a reasonable degree of spatial and temporal correlation in the incidence of crown-of-thorns outbreaks and high levels of terrestrial run-off (e.g., Pearson and Endean 1969, Pearson

1975, Birkeland 1982, Brodie 1992, but see Babcock and Munday 1992). Even very slight increases in the survivorship of larval *A. planci* could lead to a marked increase in the size of starfish populations (Birkeland and Lucas 1990). However, Pearson (1981) warns that successful recruitment of *A. planci* to adult populations is also dependant on the availability of prey resources for juveniles (i.e. coralline algae) and sub-adults (i.e. scleractinian coral) . Bradbury et al. (1985) put forward a theoretical model of coupled oscillations between crown-of-thorns populations and coral communities, based on the initial concept by Antonelli and Kazarinoff (1984), suggesting that outbreaks will only occur when and where there is sufficient coral cover to support high densities of adult starfish (e.g., coral cover greater than 40-50%). By their own admission (see Bradbury et al. 1985, Bradbury and Antonelli 1990), this model does not account for the absence of crown-of-thorns outbreaks on many reefs with high coral cover, but it is the simultaneous occurrence of high coral cover; increased survival of larval starfish and probably a number of other factors which would be necessary for outbreaks to occur.

Understanding of the causes of crown-of-thorns outbreaks has been greatly hindered by a lack of data on temporal changes in the population structure and dynamics of *A. planci* (Moran 1986). In particular, there is little data on changes in *A. planci* populations during the period immediately preceding an outbreak. This is because most studies of outbreak populations (e.g., Pearson and Endean 1969, Chesher 1969, Branham et al. 1971, Sakai 1985) are initiated after starfish densities have already increased to outbreak levels. Also, very few studies (aside from those measuring only starfish abundance) have repeatedly surveyed *A. planci* populations at the same location through time (Moran 1986). Several studies have reported changes in the population structure of *A. planci* between censuses conducted 1-2 years apart (e.g., Kenchington and Morton 1976, Zann et al. 1990), however the rate at which changes occur in the structure of outbreak populations necessitates sampling at intervals of months rather than years (e.g., Moran et al. 1985).

## 1.3 Direct effects of crown-of-thorns outbreaks

The crown-of-thorns starfish has gained considerable notoriety, not only because of their tendency to undergo rapid and dramatic increases in populations size, but also because of their potential to cause extensive and widespread depletion of scleractinian corals (e.g., Pearson and Endean 1969, Chesher 1969, Randall 1973, Colgan 1987). The crown-of-thorns starfish is just one of many different coral-reef organisms that feed on scleractinian corals (reviewed by Glynn 1988). Other corallivorous species include a number of different echinoderms (both asteroids and echinoids), several species of polychaetes, a few different gastropods, and a small number of reef fish species (Glynn 1988, Birkeland 1989). However, *A. planci* exert considerable influence on the abundance of scleractinian corals, far more so than any other corallivorous species (Glynn 1988, Birkeland 1996a, Carpenter 1996). Most corallivores are limited in their rate of feeding because scleractinian corals have only a very thin veneer of living tissue over the surface of an indigestible calcareous skeleton (Keesing 1990). As a consequence, corallivores must selectively pick live tissues from the surface of corals (which tends to limit the rate of feeding), or otherwise cope with ingesting large quantities of calcium carbonate (which is energetically costly) (Motta 1988). *Acanthaster planci* (and other asteroid species) overcome this limitation by digesting coral tissues *in situ*, leaving behind the calcareous skeleton. These asteroids feed by everting their stomach through their oral opening and spreading it over the surface of live corals or any other benthic prey (Jangoux 1982). Enzymes are then secreted through the gastric tissues which digest coral tissues within 3-5 hours (Goreau 1964, Brauer et al. 1970). The distinctive feature of *A. planci* compared to other corallivorous asteroids (e.g., *Culcita novaeguineae*) is that they have a much larger stomach for a given body size, enabling them to consume scleractinian corals 2-5 times faster than other corallivorous asteroids (Birkland 1989). Even so, crown-of-thorns starfish feed very slowly, consuming between 150-250cm$^2$ of live coral per day (Chesher 1969, Glynn 1973). At low densities (<10 starfish. ha$^{-1}$), *A. planci* have negligible impact on scleractinian coral cover (e.g., Glynn 1973, Zann et al. 1990). However, the combined feeding activities of very large numbers of crown-of-thorns starfish have affects on coral cover that are immediately obvious. For example, Chesher (1969) reported on an aggregation of *A. planci* that was observed on the fringing reefs around Guam in 1967-1969. This aggregation of starfish formed a front that moved across the reef at the rate of one kilometre per month, killing virtually all scleractinian corals (>90% coral mortality) as it went. High densities of *A. planci* persisted for 30 months and killed virtually all scleractinian corals (from 1-65 metres depth) along 38 kilometres of Guam's coastline (Chesher 1969).

Although outbreaks of *A. planci* can cause extensive and widespread coral depletion (e.g., Pearson and Endean 1969, Chesher 1969, Randall 1973, Colgan 1987), not all outbreaks produce such destruction. At Molokai Island, Hawaii, high densities of *A. planci* (>20,000 starfish.ha$^{-1}$) persisted for more than 18 months (1969-70), but there was no change in live coral cover during this period (Branham et al. 1971). Similarly, in Panama, high density populations of *A. planci* caused only negligible reductions in the live cover of scleractinian corals (Glynn 1974, 1976). Large aggregations of many hundreds to thousands of crown-of-thorns starfish have been reported on reefs throughout the Indian and Pacific oceans, including Panama (Glynn 1974, 1976), Samoa (Birkeland and Randall 1979), Micronesia (Chesher 1969, Colgan 1987), southern Japan (Nishihira and Yamzato 1974, Keesing 1992), the Great Barrier Reef (e.g., Moran et al. 1988, Reichelt et al. 1990,), Cocos-Keeling Islands (Colin 1977) and the Red Sea (Ormond and Campbell 1974). However, incidences of large-scale destruction of scleractinian corals by outbreaks of *A. planci* have occurred primarily within the western Pacific (Moran 1986, Birkeland and Lucas 1990). More specifically, devastating outbreaks of *A. planci* have occurred in only three distinct regions of the western Pacfific; the Great Barrier Reef (Pearson and Endean 1969), Micronesia (Chesher 1969, Colgan 1987), and southern Japan (Nishihira and Yamzato 1974, Keesing 1992). It is not known why outbreaks of *A. planci* vary in their impact among geographical regions, but it may be related to geographical differences in coral composition (Birkeland 1996b). Notably, the effects of outbreaks of *A. planci* appear to be more severe in locations (namely the western Pacific) where coral communities are dominated by acroporid (Family Acroporidae) corals, which are most susceptible to crown-of-thorns effects (Glynn 1974, 1976).

Crown-of-thorns starfish are well adapted to feed on a wide range of different coral species, but often exhibit striking preference for only a very small suite of available prey species (e.g., Brauer et al. 1970, Collins 1975, Ormond et al. 1976, Colgan 1987, Keesing 1990, De'ath and Moran 1998). As a result, outbreaks of *A. planci* can significantly affect the distribution and relative abundances of coral species, as well as the species composition and diversity of coral communities (e.g., Porter 1972, 1974, Glynn 1974, Colgan 1987). Mostly, *A. planci* feeds on relatively abundant coral species (eg. *Acropora* spp. and *Montipora* spp.), increasing the prevalence of less abundant coral species (e.g., Ormond et al. 1976, Colgan 1987, Keesing 1990, De'ath and Moran 1998), which can have the effect of increasing coral diversity (Porter 1972, 1974). In the eastern Pacific, however, Glynn (1974, 1976) found that coral symbionts prevent crown-of-thorns starfish from feeding on the most abundant coral species *Pocillopora damicornis*. Consequently, *A. planci* fed mostly on rarer coral species, further increasing the dominance of *P. damicornis* and reducing coral diversity (see also Branham et al. 1971). Variation in the feeding behaviour of crown-of-thorns starfish (i.e. their feeding rates and selectivity) appears to have a considerable influence on the overall impact of starfish outbreaks, probably more so than actual starfish densities (Moran 1986, Keesing 1990, Birkeland 1996a). However, the factors affecting the feeding behaviour of *A. planci* are only poorly understood.

## 1.4 Indirect effects of crown-of-thorns outbreaks

In addition to causing massive reductions in the abundance of scleractinian corals, outbreaks of *A. planci* also have broad-scale impacts on a wide variety of other coral reef organisms; increasing the abundance of soft-corals (e.g., Endean 1971, Chou and Yamazato 1990), algae (Larkum 1988), urchins (Belk and Belk 1975) and herbivorous fish species (Endean and Stablum 1973, Wass 1987), while causing declines in abundance of corallivorous fish species (e.g., Williams 1986, Munday et al. 1997), and coral-associated invertebrates (Garlovsky and Bergquist 1970). Changes in the abundances of these coral reef organisms result, indirectly, from the massive reductions in the abundance of scleractinian corals. For example, increases in the abundance of urchins (specifically, *Echinometra mathaei* and *Diadema* spp.) following outbreaks of *A. planci* have been related to increased food availability, as algae invade the space left empty by the extensive depletion of scleractinian corals (e.g., Belk and Belk 1975, Larkum 1988). Given the severity of starfish outbreaks, it is not surprising that many coral reef organisms are indirectly affected. However, very few studies (Williams 1986, Hart et al. 1996, Fabricius 1997) have dealt specifically with secondary impacts resulting from outbreaks of *A. planci*. Most reports of secondary impacts come from anecdotal observations or largely qualitative studies lacking in rigorous quantitative data (Moran 1986).

Of the few studies that have considered secondary impacts of crown-of-thorns outbreaks, most have measured changes in the abundance of coral reef fishes (e.g., Williams 1986, Hart et al. 1996). Distributions and abundances of many reef fish are closely related to the distribution and abundance of scleractinian corals (e.g., Bell & Gazlin 1984, Bouchan-Navaro et al. 1985, Kuwamurra et al 1994, Jennings et al 1996, Munday et al 1997, Holbrook et al. 2000) and so extensive coral depletion caused by outbreaks of *A. planci* would be expected to have devastating impacts on coral reef fish communities. Contrary to expectations, very few fish species have been shown to decline in abundance during outbreaks of *A. planci* (Williams 1986). Aside from herbivorous fish species, which are suggested to increase in abundance after crown-of-thorns outbreaks (Endean and Stablum 1973, Wass 1987, but see Williams 1986, Hart et al. 1996), the only other coral reef fishes shown to be significantly affected are coral-feeding butterflyfish (Bouchan-Navaro et al. 1985, Williams 1986), and coral-dwelling gobies (Munday et al. 1997). Williams (1986) explored temporal variation in the densities of 69 reef fish species from five different families (Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, and Scaridae) on reefs affected by *A. planci*, but only three species of butterflyfish showed changes in abundance that could be ostensibly related to impacts from *A. planci*. Williams (1986) argued that outbreaks of *A. planci* are likely to have broad-scale impacts across a range of coral reef fish species, but that most studies have lacked experimental power necessary to link changes in fish abundances with outbreaks of *A. planci* (see also Sano et al. 1987). Also, the effects of starfish outbreaks on coral reef fishes may be sublethal (e.g., causing changes in their distribution, diet, patterns of habitat-use, size, growth, longevity or recruitment), while previous studies (e.g., Bouchan-Navaro et al. 1985, Williams 1986, ) have considered only more devastating impacts causing changes in fish abundance.

## 1.5 Thesis outline

The overall objective of this thesis was to examine the structure and dynamics of outbreak populations of crown-of-thorns starfish, and investigate the effects of these outbreaks on coral reef ecosystems. Current understanding of the cause(s) of crown-of-thorns outbreaks is limited, in part, by a lack of information on the population structure and temporal dynamics of starfish aggregations (Moran 1986, Zann et al. 1990). To redress this requirement, I examined fine-scale changes in the distribution, abundance and size structure of starfish populations, throughout the entire course of an outbreak (i.e. before, during and after the outbreak). Having obtained significant information on the progression of an outbreak, this data was then used to relate spatial variation in the size and abundance of starfish with their varied impacts on coral reef communities. Aside from measuring impacts on benthic assemblages of scleractinian coral and other sessile invertebrates, this study also sought to investigate impacts of crown-of-thorns outbreaks on coral reef fish assemblages.

This thesis comprises four data chapters (chapters 2-5), each representing a complete and entirely independent study into the causes and/ or effects of outbreaks of *A. planci*. The first of these studies (Chapter Two) examines the structure and dynamics of *A. planci* populations. The study was conducted within the confines of a single reef (<5 kilometres across), thereby limiting the spatial scope of sampling, to facilitate frequent and detailed monitoring of starfish populations, and their corresponding impacts. Considerable data already exists on large-scale patterns (i.e. among reefs, and between geographical regions) in the distribution and abundance of *A. planci*. For example, extensive regional surveys of *A. planci*, using coarse sampling techniques (e.g. manta-tow surveys), have been conducted in the Red Sea (Ormond and Campbell 1974), Micronesia (Chesher 1969, Dana et al. 1972), and along the length of the Great Barrier Reef (e.g., Moran et al. 1988, Sweatman et al. 1998, 2000). However, comparatively little data exists on the fine scale patterns (e.g., within reef, between depths) in the abundance of *A. planci* (see Dana et al. 1972, Moran et al. 1985, Sakai 1985). In this study, local populations of *A. planci* were surveyed at each of ten different locations, at regular intervals (every 3-6 months) throughout an entire outbreak. Variation in the size and abundance of crown-of-thorns starfish was then related to spatial variation in the extent of coral depletion observed among the different locations.

In addition to causing extensive and widespread coral destruction, crown-of-thorns starfish can also alter the community structure and diversity of coral assemblages by feeding differentially on different coral species (e.g., Glynn 1974, 1976, Ormond et al. 1976, Colgan 1987). Chapter Three examines the feeding selectivity of *A. planci*, testing feeding preferences for six different coral species (*Acropora gemmifera*, *A. nasuta*, *A. loripes*, *Seriatopora hystrix*, *Pocillopora damicornis*, and *Stylophora pistillata*). Feeding experiments were conducted under controlled conditions of prey availability (in aquaria), to avoid the confounding influence of differences in the size, abundance and/ or accessibility of different corals, and thereby explicitly showing the order of feeding preferences. Many previous studies have shown that *A. planci* are very selective in their choice of prey, but relatively few have employed methodologies necessary to determine which coral prey are most preferred (see De'ath and Moran 1998). Even fewer studies have considered factors affecting the feeding preferences of *A. planci* (Moran 1986). This study tested the influence of coral symbionts on feeding preferences of starfish, considered to be influential in limiting consumption of pocilloporid corals in the eastern Pacific (Glynn 1974, 1976). The influence of coral symbionts was tested by examining feeding preferences of *A. planci* for the six coral species (*Acropora gemmifera*, *A. nasuta*, *A. loripes*, *Seriatopora hystrix*, *Pocillopora damicornis*, and *Stylophora pistillata*) with their symbionts removed, and comparing feeding preferences of starfish for the same corals which contained symbionts.

Chapter Four considers the impacts of *A. planci* on coral reef fishes, looking specifically at impacts on *Chaetodon* butterflyfishes (family Chaetodontidae). Scleractinian corals represent the primary food source for most *Chaetodon* butterflyfish (Birkeland and Neudecker 1981), and so it follows that extensive coral depletion, such as that caused by outbreaks of *A. planci*, would impact significantly on the abundance of these coral reef fishes. However, not all corallivorous butterflyfish species appear to be affected by outbreaks of *A. planci* (e.g., Sano et al. 1984, 1987, Bouchan-Navaro et al. 1985, Williams 1986). For example, Williams (1986) found that only 50% (3/6) of different coral feeding butterflyfish declined in abundance during outbreaks of *A. planci* on reefs in the central GBR. Variation in the species-specific responses of butterflyfish may be related to differences in their ecological versatility (*sensu* MacNally 1995), whereby more versatile species could mediate impacts of coral depletion by moving to areas relatively unaffected by *A. planci*, and/ or by utilising alternate prey resources. Chapter Four represents a long-term study (conducted over five years) to monitor impacts of *A. planci* on *Chaetodon* butterflyfish. The response of different butterflyfish to disturbances caused by crown-of-thorns outbreaks was monitored not only in terms of changes in abundance, but also through changes in their local distributions (e.g., among reef zones), and utilisation of different prey resources.

The impact of crown-of-thorns outbreaks on coral reef fishes is likely to be most pronounced for fish species which rely heavily on scleractinian corals, either for food (e.g., butterflyfish, Williams 1986; pufferfish, Guzman and Robertson 1989) or shelter (e.g., coral-dwelling damselfish, Sano et al. 1984; coral gobies, Munday et al. 1997). Having already explored the impacts on coral feeding butterflyfishes (Chapter Four), Chapter Five examines the impact of *A. planci* on a suite of six coral-dwelling damselfishes (*Chromis atripectoralis*, *C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis* and *P. moluccensis*). These coral-dwelling damselfish tend to live within the immediate vicinity of a single branching coral colony, in which they seek shelter at the approach of danger (Sale 1971, Robertson & Lassig 1980). The abundance of coral-dwelling damselfish has been related to the availability of coral habitats (Holbrook et al 2000), and consequently we might expect reductions in the abundance of these fishes following coral depletion caused by outbreaks of *A. planci* (see also Sano et al. 1984, 1987). Even if there are no direct effects on damselfish abundance, the reduction in habitat availability may influence patterns of habitat use of coral-dwelling damselfish, which may further influence growth, survival and/ or reproductive success. Chapter five examined spatial and temporal patterns of habitat use by each of the six coral-dwelling damselfish, and then determined whether their abundance and/ or patterns of habitat use changed in response to the coral depletion, caused by localised infestations of crown-of-thorns starfish.

In order to tie together the results from each of the four separate studies (Chapters 2-5), I have included a general discussion (Chapter Six) that provides a general overview of all major findings, and further considers both the significance and implications of this research. This discussion focuses on explaining spatial variation in the impacts of crown-of-thorns starfish, that is very apparent across a wide range of different spatial scales (Moran 1986, Birkeland and Lucas 1990). Most notably, impacts of outbreaks of *A. planci* vary between geographic regions, with major impacts limited to the western Pacific (Moran 1986). However, during outbreaks of *A. planci* there are also marked differences in the extent of coral depletion observed among closely positioned reef zones (e.g., Endean and Stablum 1973). Explaining these fine-scale patterns of starfish impacts, brings together data collected on the distribution, abundance and size structure of starfish populations, the cover and composition of scleractinian corals, and also the specific feeding preferences of *A. planci*. The general discussion also highlights key areas of future research that will further enhance understanding of outbreaks of *A. planci* and their effects on coral reef ecosystems.

Finally, I have attached eight publications (all published or accepted for publication) as appendices at the end of this thesis. These publications represent additional research in which I was involved during the course of my PhD and cover a diversity of topics, including patterns of coral recruitment, links between adult fecundity and recruitment in corals, the comparative palatability of coral eggs, and the ecological significance of fish predation on coral gametes. Many of these publications (6/8) are not directly related to the study of *A. planci*, but have been included to provide a complete picture of all scientific research conducted during my candidature as a doctoral student.

# CHAPTER 2: Fine scale variation in the population dynamics and effects of *Acanthaster planci.*

## 2.1 ABSTRACT

Population outbreaks of crown-of-thorns starfish (*Acanthaster planci* L.) represent one of the most significant, but also least understood processes affecting coral reef communities. Limited understanding of crown-of-thorns outbreaks is due, at least in part, to a critical lack of data on the structure and dynamics of *A. planci* populations. This study examined fine-scale patterns in the size, distribution, and abundance of crown-of-thorns starfish, during an outbreak of *A. planci* at Lizard Island, on the northern Great Barrier Reef. The outbreak resulted from steady and prolonged increase in starfish densities, over a period of three years. Starfish populations comprised individuals from at least four different year classes, suggesting that the outbreak was caused by progressive accumulation of starfish from multiple recruitment events. Overall densities of *A. planci* increased to 1.0 starfish per 200m$^2$ (±0.1 SE), in January 1997, and then remained fairly constant until June 1998, after which starfish densities declined rapidly. During the outbreak, densities of *A. planci* varied greatly among locations, and also between depths. Starfish densities were highest at locations in sheltered back reef habitats, but considerable numbers of starfish were also observed at some exposed locations. At severely affected locations (where starfish densities significantly exceeded 0.8 starfish per 200m$^2$) scleractinian coral cover was reduced by 45-72%. There were, however, several locations which were largely unaffected by outbreaks of *A. planci*. This study demonstrates considerable fine-scale variation in the distribution, size and abundance of crown-of-thorns starfish, which results in considerable patchiness in the effects of *A. planci* on coral reef communities.

## 2.2. INTRODUCTION

Population outbreaks of coral eating crown-of-thorns starfish, *Acanthaster planci* Linnaeus 1758, represent one of the most significant disturbances on tropical coral reefs (Pearson 1981, Moran et al. 1988). Mostly, crown-of-thorns occur at very low densities (typically < 1 starfish.ha$^{-1}$) and cause little decline in the abundance of reef corals (e.g., Glynn 1973, Zann et al. 1990). However, when *A. planci* occur at very high densities, during outbreaks, the resulting destruction of coral communities can be extensive (reviewed by Moran 1986, Birkeland and Lucas 1990). In 1962, at Green Island on the northern Great Barrier Reef, outbreak populations of *A. planci* killed 80% of scleractinian corals across the entire reef, from the shallow reef crest (<2 metres depth) down to a depth of 40 metres (Pearson and Endean 1969). Outbreaks of *A. planci* have also caused similar levels of coral destruction (killing up to 90% of scleractinian corals) in Guam (Chesher 1969, Randall 1973), southern Japan (Yamaguchi 1986), and elsewhere on the Great Barrier Reef (e.g., Done 1985). In reviewing the recovery of coral communities from various forms of disturbance, Pearson (1981) suggested that coral destruction caused by outbreaks of *A. planci* was more extensive and more widespread than caused by any other natural or anthropogenic disturbance (see also Moran et al. 1988). Moreover, outbreaks of *A. planci* can also alter the species composition and structure of coral communities, causing marked changes in the relative abundance of different corals (e.g., Pearson 1975, Glynn 1976, Done and DeVantier 1990), altering the spatial distributions (particularly depth zonation) of coral species (e.g., Moran et al. 1985), and reducing coral diversity (e.g., Glynn 1976, Randall 1973, Colgan 1987).

Despite their significance, outbreaks of *A. planci* are one of the least understood processes affecting coral reef communities. There has been considerable research into the biology and ecology of crown-of-thorns starfish (see reviews by Potts 1981, Moran 1986, Birkeland and Lucas 1990, and references therein). However, despite this plethora of studies (>1200 published studies), the ultimate cause(s) of outbreaks of *A. planci* are still not known (Engelhardt et al. 1999). Crown-of-thorns starfish are predisposed to major population fluctuations, due to inherent properties of their life history (e.g., immense fecundity, short generation times) (Moore 1978, Stump 1992). However, the incidence of crown-of-thorns outbreaks is not random (Bradbury and Antonelli 1990), suggesting that there must be some common underlying process (or processes) that explain the onset of outbreaks (see also Moran 1986). A variety of factors have been proposed to initiate outbreaks of *A. planci*, including high levels of terrestrial run-off (Birkeland 1982), and temporary increases in sea surface temperatures (Lucas 1973), which could both lead to increases in the survival of larval *A. planci* (reviewed by Brodie 1992). Alternatively, some authors have suggested that outbreaks may result from the increased survival of post-settlement individuals, caused by either a reduction in predation pressure (e.g., Endean 1969), or increased availability of coral prey (e.g., Antonelli & Kazarinoff 1984, Bradbury et al. 1985). An evaluation of such hypotheses has been greatly hindered by limited demographic information on *A. planci* populations. However, it is most likely that outbreaks of *A. planci* result from a combination of several different factors (Birkeland and Lucas 1990, Bradbury and Antonelli 1990, Zann et al. 1990, Keesing and Halford 1992), and the ultimate cause(s) of crown-of-thorns outbreaks may vary among locations (Zann et al. 1990, Stump 1996).

Essentially, there are two ways in which outbreaks of *A. planci* may arise; either from a single mass recruitment event, or the progressive accumulation of starfish from multiple cohorts (Johnson 1992). Pronounced fluctuations in the year to year recruitment of *A. planci* (e.g. Yokochi and Ogura 1988, Zann et al. 1987, 1990), and also the uniform size (and age) of starfish comprising most outbreak populations (e.g., Dana et al. 1972, Glynn 1973, Sakai 1985, Zann et al. 1987, Stump 1992), support the idea that outbreaks result from a single mass recruitment event (Johnson 1992). Moreover, outbreaks of *A. planci* generally do result from sudden and dramatic increases in the abundance of starfish over only a few months (e.g. Chesher 1969, Branham et al. 1971, Moran et al. 1985), which must be at least partially the result of a massive influx of new recruits (Birkeland and Lucas 1990). There is, however, increasing evidence that outbreaks of *A. planci* can also result from a very steady and prolonged build-up in starfish densities over many years (e.g., Zann et al. 1987, 1990, Stump 1996). In some instances, outbreak populations have been shown to comprise fairly equal numbers of starfish from several different cohorts (e.g., Stump 1994, 1996, Engelhardt et al. 1999), representing the progressive accumulation of starfish from several successive recruitment events. Factors which cause massive increases in the recruitment of *A. planci* (e.g., increased survivorship of starfish larvae, Lucas 1973, Birkeland 1982), leading to a rapid and dramatic increases in starfish densities, are likely to be fundamentally different from those which cause slow, progressive increases in starfish densities (Johnson 1992). The demographics (particularly, the age or size structure) of outbreak populations is therefore critical in identifying the potential cause(s) of crown-of-thorns outbreaks.

Many authors (e.g., Moran et al. 1985, Moran 1986, Zann et al. 1990, Stump 1996, Engelhardt et al. 1999) have highlighted the critical lack of information on the structure and dynamics of outbreak populations of crown-of-thorns starfish. However, most field surveys of *A. planci* continue to focus on describing broad-scale patterns in the extent of starfish activities (e.g., Sweatman et al. 1998, 2000). Extensive regional scale surveys of *A. planci* have been conducted in the Red Sea (Ormond and Campbell

1974), Micronesia (Chesher 1969, Dana et al. 1972), and along the length of the Great Barrier Reef (e.g., Moran et al. 1988, Sweatman et al. 1998, 2000). These broad-scale surveys provide important information on the spatial and temporal extent of starfish outbreaks, which is essential for management (Birkeland and Lucas 1990). However, they do not provide accurate estimates of starfish densities (Moran 1986, Birkeland and Lucas 1990, Moran and De'ath 1992), and rarely consider the structure or dynamics of starfish populations (e.g., Dana et al. 1972). Surprisingly few studies have examined starfish populations throughout the course of an outbreak and, consequently, there is little information on growth, longevity, mortality, movement or feeding by *A. planci* (Moran 1986, Stump 1994). This information is, however, important not only in identifying the potential cause(s) of crown-of-thorns outbreaks, but also in predicting the effects of crown-of-thorns outbreaks on coral reef communities.

Outbreaks of *A. planci* are a highly variable phenomenon, varying not only in their size and extent, but also in their effects on coral communities (Moran 1986). Major outbreaks of *A. planci* are clearly capable of causing very extensive and widespread coral depletion (e.g., Pearson and Endean 1969, Chesher 1969, Randall 1973, Colgan 1987), but not all outbreaks produce such destruction. For example, at Molokai Island, Hawaii, high densities of *A. planci* (>20,000 starfish.ha$^{-1}$) persisted for more than 18 months (1969-70), but caused little change in the abundance of scleractinian coral (Branham et al. 1971). In general, incidences of large-scale destruction of scleractinian corals by outbreaks of *A. planci* are restricted to the western Pacific (Moran 1986, Birkeland and Lucas 1990). However, the effects of crown-of-thorns outbreaks also vary across very small spatial scales (e.g., within reefs), among locations (Moran et al. 1985) and between reef zones (e.g., Endean and Stablum 1973, Colgan 1982, Moran et al. 1985). During outbreaks, crown-of-thorns starfish are not distributed evenly across the surface of reefs, but tend to form large aggregations which then proceed to move across the reef *en masse* (e.g. Pearson and Endean 1969, Endean and Stablum 1973, Saikai 1985, Moran et al. 1985). Spatial variation in the effects of *A. planci* are partly the result of fine-scale patterns in the distribution of *A.* planci (Moran 1986). However, any attempt to account for spatial variation in the effects of *A. planci* will require complete knowledge of both past and present patterns of their distribution and abundance (Moran et al. 1985).

This study surveyed outbreak populations of *A. planci*, recording the distribution, abundance and sizes of starfish at Lizard Island, on the northern Great Barrier Reef. The study was conducted within the confines of a single reef (<5 kilometres across), thereby limiting the spatial extent of sampling, to facilitate frequent and detailed monitoring of starfish populations, and their corresponding effects. Repeated intensive surveys of populations of *A. planci* have only rarely been conducted (Moran et al. 1985, Fisk 1992), but are essential to determine the recent history of starfish activity at any given location (Moran 1986). A number of studies have reported changes in the distribution and abundance of *A. planci* between censuses conducted 1-2 years apart (e.g., Kenchington and Morton 1976, Zann et al. 1990), however the rate at which changes can occur in their fine-scale patterns of distribution and abundance, particularly during outbreaks, necessitates sampling at intervals of months rather than years (e.g., Moran et al. 1985). In this study, local populations of *A. planci* were surveyed every few months throughout an entire outbreak. Changes in the abundance and structure of coral communities were also documented over the same time frame, to detail the specific effects of crown-of-thorns outbreaks on coral communities.

## 2.3 METHODS

### Study Site

This study was conducted at Lizard Island (14°40'S, 145°27'E), situated 30 kilometres off the mainland coast in the far northern section of the Great Barrier Reef

(GBR), Australia. Lizard Island is a high continental island surrounded by very extensive fringing reef. On the southern side of the island the reef extends southward, connecting Lizard Island with three much smaller islets (South Island, Palfrey Island, Bird Islet) and almost entirely enclosing a large shallow lagoon. Sampling for this study was carried out at two replicate locations on each of northern, eastern, southern and western sides of the island, and also within the lagoon (Figure 2.1). The ten sampling locations (North Reef, Washing Machine, Coconut Beach, Lizard Head, South Island, South Bay, Casuarina, Corner Beach, East Palfrey and Middle Lagoon) were chosen to account for spatial variation in the abundance of crown-of-thorns starfish that might occur due to differences in wave exposure and/ or habitat-type. The ten locations vary in their exposure to wind and wave action, which is predominantly from the south-east, such that each of the locations may be categorised as i) directly exposed (Coconut Beach, Lizard Head, South Island, South Bay), ii) partially (or obliquely) exposed (North Reef, Washing Machine), or iii) sheltered (Casuarina, Corner Beach, East Palfrey and Middle Lagoon). The reef habitat also varies among locations, mostly in accordance with variation in exposure. The reef habitat at each of the exposed and partially exposed locations is comprised of contiguous reef matrix which forms an extensive fringing reef around most of the outer perimeter of the island group. However, on the more sheltered western side (at Casuarina and Corner Beach) of the island the reef is comprised of large patch reefs (up to 500 metres in diameter), separated by 100-200 metres by shallow regions (<10metres) of fine sand. Lagoon habitats (East Palfrey and Middle Lagoon) are comprised of large areas of mostly contiguous reef matrix, with a reef top at 7-15 metres above the sandy lagoon floor.

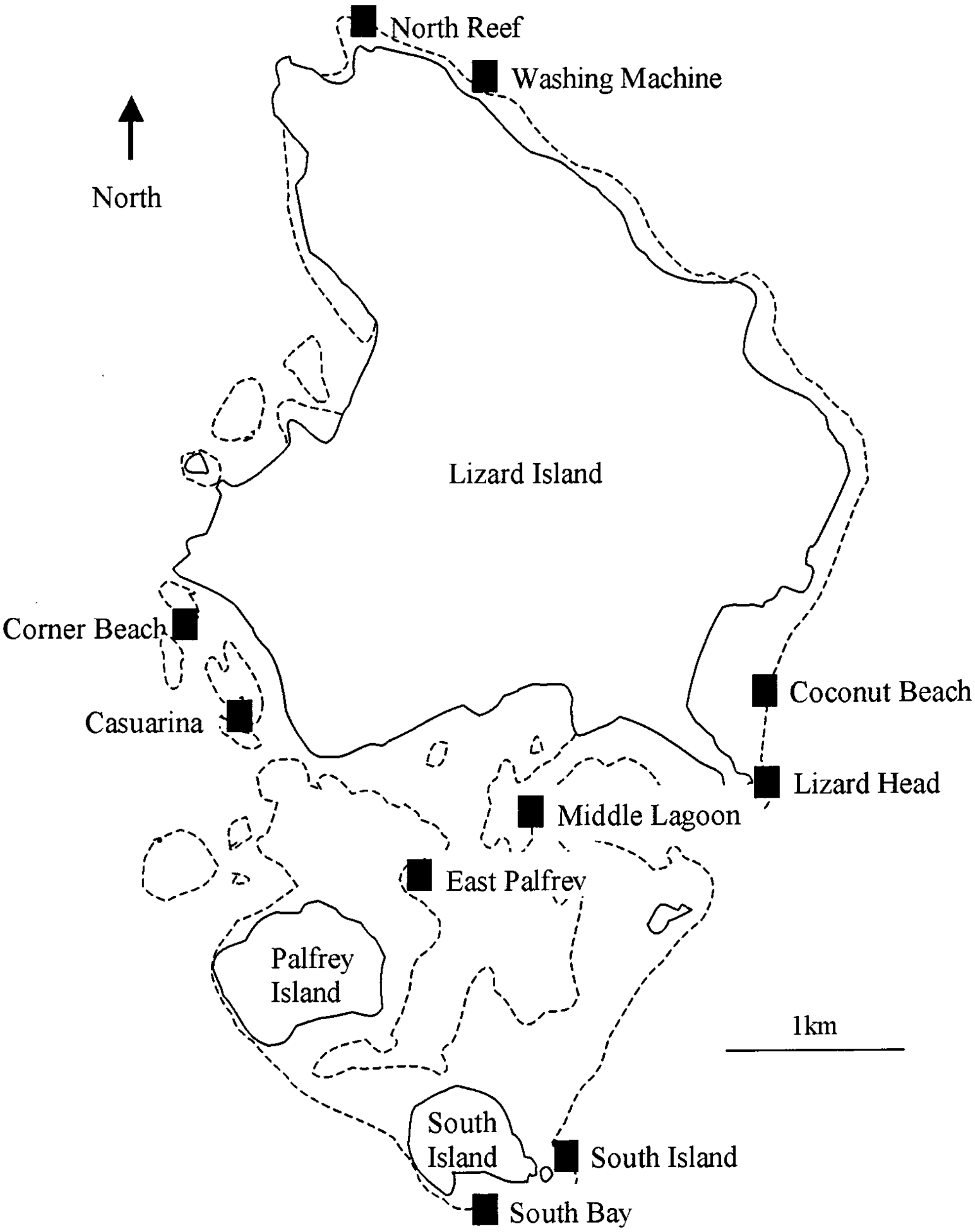

**Figure 2.1.** Map of Lizard Island showing the ten sampling locations (black boxes) used to assess dynamics of *A. planci* populations as well as corresponding changes in benthic reef assemblages. Solid lines delineate land and dashed lines delineate approximate outline of reef.

## Population dynamics of *A. planci*

In order to document temporal and spatial variation in the size and abundance of *A. planci*, sampling was conducted at each of the ten locations at regular intervals throughout a 28 month period from October 1996 until January 1999. All sampling was conducted during daylight hours (0900hrs – 1600hrs). Sampling was conducted every 3-6 months, with a total of nine separate surveys conducted over the period of the study: October 1996, December 1996, February 1997, June 1997, November 1997, February 1998, June 1998, November 1998, and January 1999. To quantify the abundance of crown-of-thorns I used replicate 50 x 4 metre ($200m^2$) belt transects. To explore depth variation in the distribution of *A. planci*, ten replicate transects were run at each of two depths (3 and 7 metres) at each of the ten locations. Specific depths were selected to represent the distinct reef zones: reef crest (3 metres) and reef slope (7 metres). Transects were laid parallel to the reef crest and run from a haphazardly selected starting point at each depth. The area of each transect was then searched at least twice to maximise the detection of cryptic individuals. A total of 1,800 transects, with a total sample area of $3.6 \times 10^5$ square metres, were censused throughout the course of the study.

Whilst assessing the abundance of crown-of-thorns starfish I also recorded the size of every starfish on each transect. When easily accessible, the size of starfish was measured *in situ*, but often the starfish had to be removed from within the reef complex before being measured. Starfish were carefully removed from among coral branches, or within crevices using large metal tongs, and then laid flat on the reef matrix before being measured. For each individual starfish, I recorded both the whole body diameter (from the tips of opposite arms) and also the diameter of the oral disc. Previously, some authors (e.g. Yamaguchi 1974) have advocated the use of oral disc diameters to assess the size of *A. planci*, because the length of their arms may vary with the physiological condition of individual starfish. In this study however, the whole body diameter and oral disc diameter of *A. planci* were very highly correlated ($r^2 = 0.94$, n = 1,312). Therefore, all size data are presented as whole body diameters to enable comparisons with Kenchington (1977), Lucas (1984), and Stump (1996). To examine the size structure of *A. planci*, data was arranged into 5cm size classes (10-15cm, 15–20cm, 20-25cm etc.). This selection of size classes facilitated direct comparisons between size and age, based on previously published growth curves, where juvenile starfish (<2 years) are generally <15cm, sub-adult starfish (2-3 years) are 15-25cm, and sexually mature adult starfish (>3 years) are >25cm (Stump 1996).

### Effects on benthic assemblages

To assess the impact of *A. planci* on benthic assemblages of sessile reef invertebrates, I measured changes in the individual abundance of each of 46 different taxa (listed in Table 2.1) every 3-6 months, throughout the course of the study. Sampling was conducted on eight separate occasions (October 1996, December 1996, February 1997, June 1997, November 1997, February 1998, November 1998, and January 1999), coinciding with censuses of *A. planci* populations (Note: benthic assemblages were not surveyed in June 1998 due to bad weather). The abundance of sessile invertebrates was censused using replicate 10 metre line intercept transects. During each survey, ten replicate transects were run at each of two different depths (3 and 7 metres) at each of the ten locations. Transects were laid roughly parallel to the reef crest and following the contours of the reef substrate. Every sessile organism underlying the transect tape was then identified to one of 46 different taxonomic groupings (Table 2.1), and the intercept length was measured to the nearest centimetre.

Temporal variation in the abundance of sessile invertebrates was analysed using analysis of variance (ANOVA). I tested firstly whether there was any significant temporal decline in the overall abundance of scleractinian corals, during outbreaks of

*A.planci*. Declines in scleractinian coral cover were also compared between depths and among locations to test whether the extent of coral decline varied in accordance with spatial variation in abundances of *A. planci*. Previous studies have suggested that the extent of coral depletion caused by *A. planci* varies with their size and abundance, initial coral cover, and also the proportion of *Acropora* (their most preferred prey) within the coral assemblage (reviewed by Moran 1986). In order to test these hypotheses, best subsets multiple regression was used, relating proportional declines in scleractinian coral cover at each depth, at every location (n = 20) to differences in i) the cumulative number of starfish recorded throughout the study period, ii) the average whole body diameter of *A. planci* at each combination of depth and location, iii) the mean cover of scleractinian coral recorded in October 1996, and iv) the proportion of *Acropora* within coral assemblages at each depth at each location, recorded in October 1996.

In addition to causing extensive and wide-spread coral depletion, outbreaks of *A. planci* can also alter the community structure of local coral assemblages by causing differential mortality among coral species (e.g., Colgan 1987). To test for changes in the community structure of assemblages of sessile invertebrates I used multivariate analysis of variance (MANOVA), following McArdle (2001). Significant variation in the structure of benthic assemblages was then displayed using canonical discriminant analysis (CDA), but instead of using traditional bi-plots, I plotted variation in the first canonical variate along a time series (see also Syms and Jones 2000), thereby explicitly showing temporal variation in the structure of benthic assemblages at each depth and each location. Having shown there was significant variation in community structure, I then examined temporal variation in the individual abundance of different coral taxa, thereby assessing individual susceptibilities of different benthic taxa to disturbances caused by infestations of *A. planci*.

**Table 2.1.** Taxonomic groupings of sessile invertebrates used to assess effects of *A. planci* on benthic reef assemblages. Taxa were grouped according to genus, and or broad morphological differences. *Acropora* species were grouped in to morphological types, following Veron (1986).

| | Family | Genus/ Grouping |
|---|---|---|
| SCLERACTINIAN CORALS | Pocilloporidae | *Pocillopora* |
| | | *Seriatopora* |
| | | *Stylophora* |
| | Acroporidae | *Montipora* |
| | | *Astreopora* |
| | | *Isopora* |
| | | *Acropora humilis* Group |
| | | *Acropora robusta* Group |
| | | *Acropora formosa* Group |
| | | *Acropora aspera* Group |
| | | *Acropora selago* Group |
| | | *Acropora hyacinthus* Group |
| | | *Acropora latistella* Group |
| | | *Acropora nasuta* Group |
| | | *Acropora loripes* Group |
| | | *Acropora florida* Group |
| | Poritidae | Branching *Porites* |
| | | Massive *Porites* |
| | | *Goniopora* |
| | Agariciidae | *Pavona* |
| | | *Leptoseris* |
| | | *Coleoseris* |
| | | *Pachyseris* |
| | Fungiidae | Fungiidae |
| | Oculinidae | *Galaxea* |
| | | *Archelia* |
| | Pectiniidae | *Mycedium* |
| | | *Oxypora* |
| | | *Pectinia* |
| | Mussidae | *Lobophyllia* |
| | | *Symphyllia* |
| | Merulinidae | *Merulina* |
| | Faviidae | *Favia* |
| | | *Favites* |
| | | *Goniastrea* |
| | | *Platygyra* |
| | | *Leptoria* |
| | | *Diploastrea* |
| | | *Cyphastrea* |
| | | *Echinopora* |
| | Dendrophyllidae | *Turbinaria* |
| ALCYONARIANS | Alcyoniidae | *Lobophytum* |
| | | *Sarcophyton* |
| | | *Sinularia* |
| | Helioporidae | *Heliopora* |
| HYDROZOAN CORALS | Milleporidae | *Millepora* |

## 2.4 RESULTS

### Abundance of *A. planci*

Increases in the abundance of crown-of-thorns starfish at Lizard Island were first noted in October 1994 during routine monitoring by the Australian Institute of Marine Sciences (Sweatman et al. 1998). Densities of *A. planci* recorded at this time ($\bar{x} = 0.25$ starfish per $200m^2$) were several orders of magnitude higher than had been recorded at any time since 1986 (Sweatman et al. 1998). Subsequent surveys conducted by Sweatman et al. (1998) from 1995 until 1998, and this study (from October 1996 onwards), showed that densities of *A. planci* continued to increase from October 1994 until December 1996 (Figure 2.2). In December 1996, the average density of *A. planci* across all locations (North Reef, Washing Machine, Coconut Beach, Lizard Head, South Island, South Bay, Casuarina, Corner Beach, East Palfrey and Middle Lagoon) reached 1.05 (± 0.10SE) starfish per $200m^2$, significantly exceeding the threshold density of 0.8 starfish per $200m^2$ (or 40 starfish $ha^{-1}$) that is considered to be the maximum sustainable density of *A. planci* on reefs in the GBR (Moran and De'ath 1992). Overall densities of *A. planci* varied very little during the period from December 1996 until June 1998, remaining at or above the critical threshold density of 0.8 starfish per $200m^2$ (Figure 2.2). However, after June 1998 starfish densities declined by 92% in just seven months, from 0.92 (± 0.10SE) starfish per $200m^2$ in June 1999, down to 0.06 (± 0.02SE) starfish per $200m^2$ in January 1999 (Figure 2.2). Starfish densities then remained very low (<1 starfish per $200m^2$), indicating that the rapid decline in starfish densities represented the end of localised infestations of *A. planci*. The total duration of this infestation, from the initial observations of elevated starfish densities in October 1994 to the eventual collapse of starfish populations in January 1999, was 52 months (4.3 years).

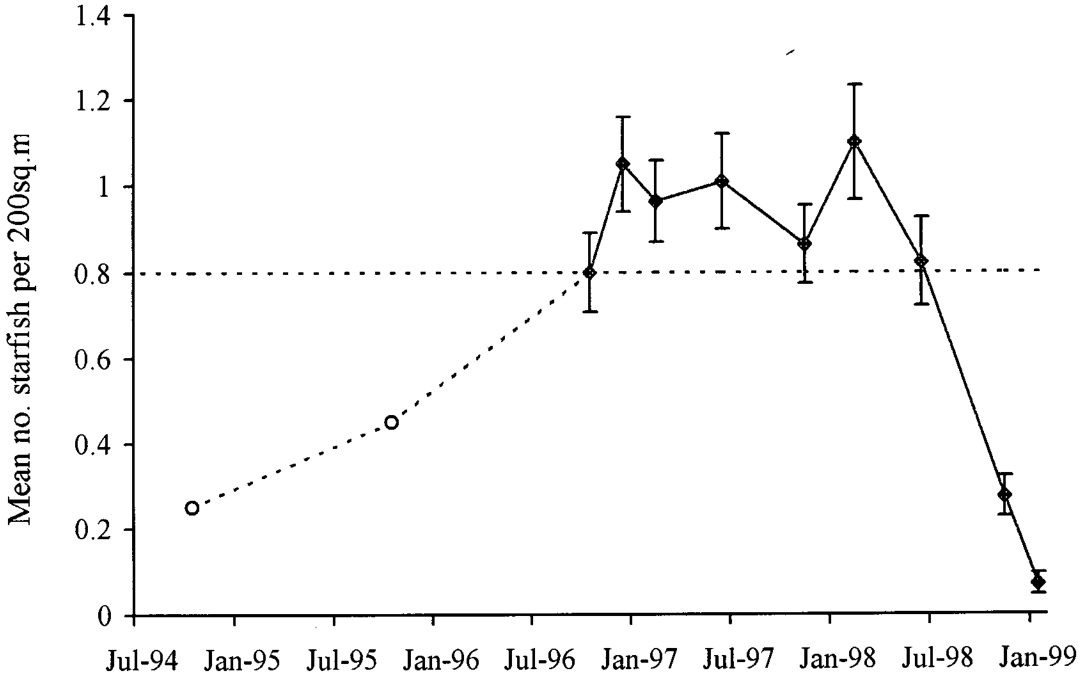

**Figure 2.2.** Temporal variation in the mean abundance (+/- SE) of crown-of-thorns starfish at Lizard Island from October 1994 to January 1999. Initial estimates of starfish densities (o) were derived from Sweatman *et. al.* (1998). Subsequent data was pooled across ten locations and two depths (n = 200 transects for each survey). Starfish densities significantly exceeded the upper threshold density (shown by the dotted line) considered indicative of an outbreak.

During the infestation of *A. planci*, densities of starfish varied greatly both spatially and temporally (Figure 2.3, Table 2.2). Among broadly defined regions (north, east, south, west and lagoon), *A. planci* were always most abundant on the western side of the island (Casuarina and Corner Beach), and least abundant (and often absent) in the lagoon (East Palfrey and Middle Lagoon). Densities of *A. planci* also differed between closely positioned locations within each region (Figure 2.3). Most notably, the overall abundance of *A. planci* recorded at North Reef ($\bar{x}$ = 0.78 ± 0.08SE starfish per $200m^2$) was four times higher than at Washing Machine ($\bar{x}$ = 0.19 ± 0.04SE starfish per $200m^2$), though these two locations were separated by less than one kilometre. In all, there were five locations (North Reef, Lizard Head, South Island, Casuarina and Corner Beach) where starfish densities at times exceeded 1.0 starfish per $200m^2$. These locations were considered to be "severely affected locations", as opposed to other locations (Washing Machine, Coconut Beach, South Bay, East Palfrey and Middle Lagoon) where starfish densities were consistently less than 1.0 starfish per $200m^2$, which were regarded as "relatively unaffected locations" (Figure 2.3).

Densities of *A. planci* also varied significantly between depths (3 and 7 metres) at each location (Figure 2.3). At exposed locations (North Reef, Washing Machine, Coconut Beach, Lizard Head, South Island and South Bay) starfish were always much more abundant on the reef slope (7 metres) than on the reef crest (3 metres) (Figure 2.3). Overall densities found on the reef slope at exposed locations ($\bar{x}$ = 0.76 starfish per $200m^2$), were nearly three times higher than found on the reef crest ($\bar{x}$ = 0.27 starfish per $200m^2$). In contrast, at both Casuarina and Corner Beach, *A. planci* were generally more abundant at 3 metres than at 7 metres (Figure 2.3

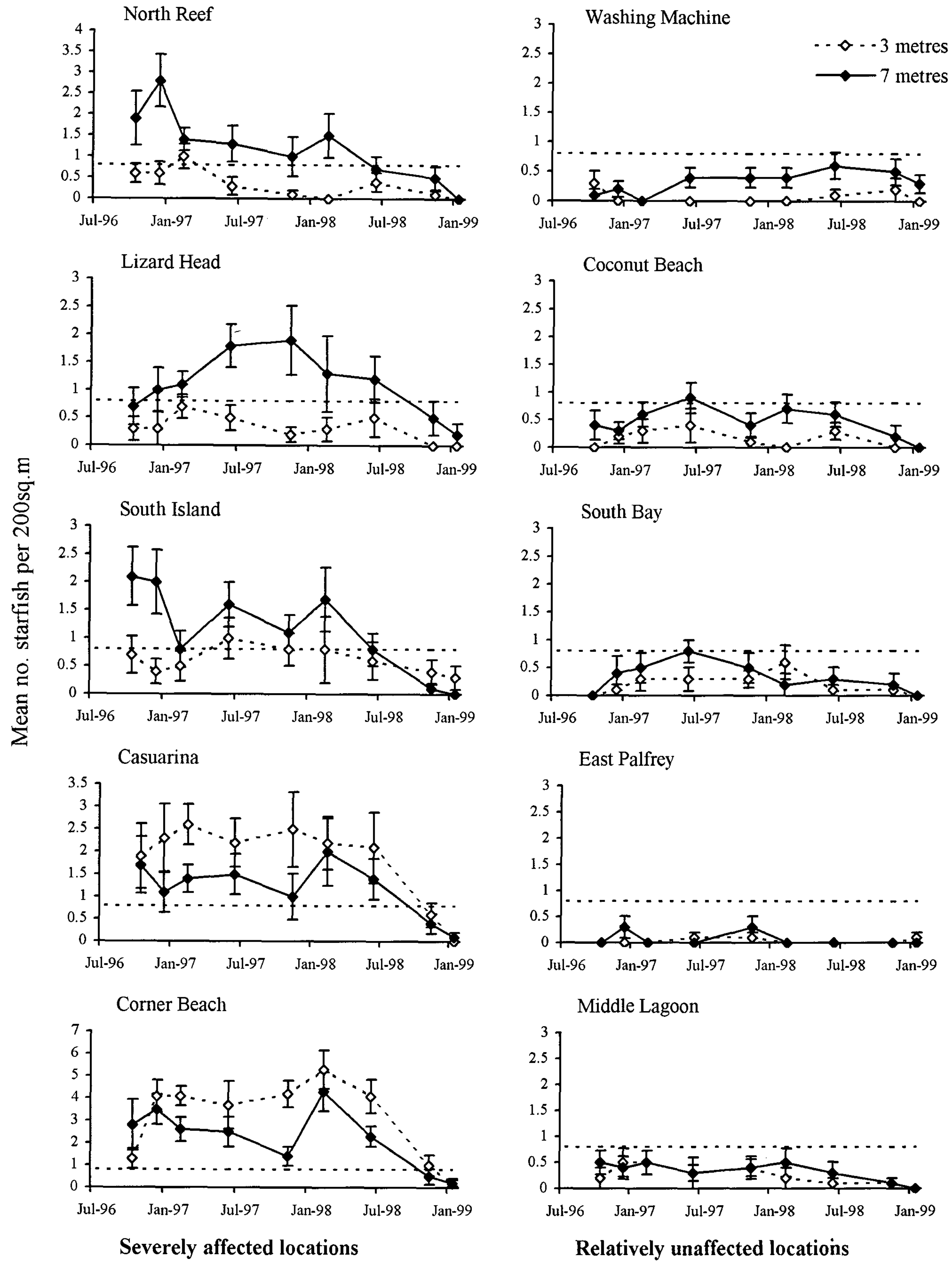

**Figure 2.3.** Temporal variation in the mean abundance (+/-SE) of crown-of-thorns starfish at each depth, at each of ten locations around Lizard Island (n = 10 transects). Locations where starfish densities (minus 1 standard error) exceeded the threshold density of 0.8 starfish per 200sq.m (shown as dotted line) were considered to be severely affected, whereas other locations were regarded to be relatively unaffected.

**Table 2.2.** Three-way ANOVA to explore variation in the abundance of *A. planci*. Data was square root transformed, '*' denotes significant effects (*p<0.05, **p<0.01, ***p<0.001).

| Source | df | MS | F |
|---|---|---|---|
| Survey | 8 | 2.24 | 20.52*** |
| Location | 9 | 8.06 | 73.86*** |
| Depth | 1 | 4.51 | 41.27*** |
| Survey × Location | 72 | 0.43 | 3.94*** |
| Survey × Depth | 8 | 0.21 | 1.90 |
| Location × Depth | 9 | 0.48 | 4.39*** |
| Survey × Location × Depth | 72 | 0.28 | 2.62*** |
| Error | 1620 | 0.11 | |

### Size of *A. planci*

Populations of *A. planci* comprised individuals ranging in size from 11-62cm (whole body diameter), thereby representing at least four (and probably more than six) different age classes; 10-15cm (1-2 years), 15-25cm (2-3 years), 25-40cm (3-4 years), >40cm (>4 years) (see Stump 1996). In October 1996, the population structure was dominated by two distinct cohorts with modal sizes of 20-25cm and 30-35cm, probably representing successive year classes (2+ and 3+ years) which would have recruited in 1994-95 and 1993-94, respectively (Figure 2.4). Very small starfish (10-15cm), indicative of recruitment in the previous year, were also reported in December 1996, February 1998 and January 1999 (Figure 2.4), suggesting that there was additional recruitment of *A. planci* in 1995-96, 1996-7 and 1997-98. Starfish populations tended however, to be dominated by adults (>30cm), while numbers of juveniles (<15cm) and sub-adults (<25cm) declined throughout the study period (Figure 2.4), indicating that there was a reduction in recruitment of *A. planci* from 1996 to 1999.

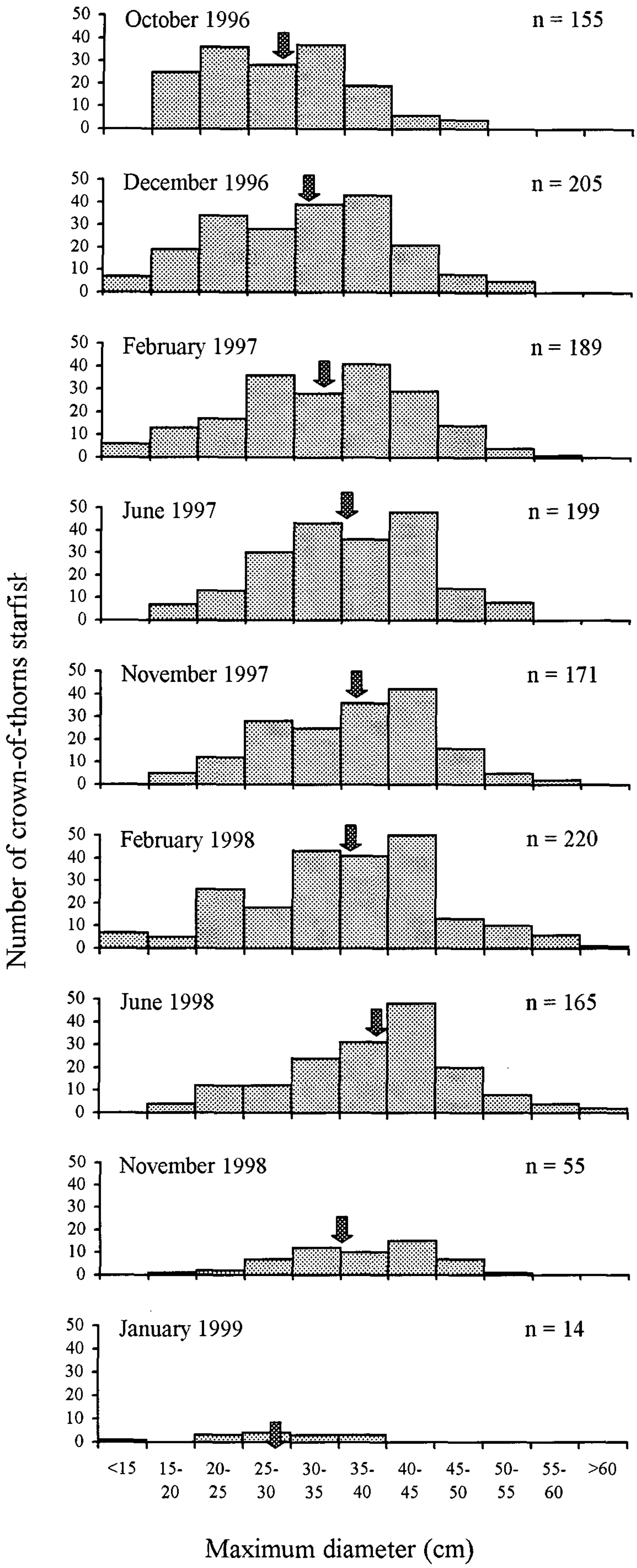

**Figure 2.4.** Temporal variation in the size structure of starfish populations at Lizard Island. Data pooled across all locations and depths. Arrows indicate mean size of all starfish recorded during each survey.

The mean size of starfish varied significantly among surveys (Table 2.3), increasing steadily during the period from October 1996 ($\bar{x}$ = 28.6cm ± 0.7SE) to June 1998 ($\bar{x}$ = 38.6cm ± 0.7SE), but then declined dramatically from June 1998 to January 1999, in direct accordance with declines in starfish abundance. Initial increases in the mean size of starfish corresponded with modal progression in the sizes of early year classes (1993-1995). The modal size of starfish within these cohorts increased through time, until they reached the 40-45cm size class (Figure 2.4). Very few starfish appeared to grow to sizes greater than 45cm. However, the maximum recorded size of starfish increased from 48cm in October 1996, to 62cm in June 1998.

The mean size of *A. planci* also varied locally, among locations, though sizes of *A. planci* did not differ between depths (Table 2.3). Local variation in the sizes of *A. planci* was primarily attributable to differences between severely affected locations versus relatively unaffected locations (Figure 2.5). Overall, the mean size of starfish at relatively unaffected locations ($\bar{x}$ = 38.5cm ± 0.4SE) was 4cm larger than at severely affected locations ($\bar{x}$ = 34.5mm ± 0.5SE). At relatively unaffected locations (Washing Machine, Coconut Beach, South Bay, East Palfrey and Middle Lagoon), starfish populations were dominated by larger size classes (35-50cm), whereas at severely affected locations (North Reef, Lizard Head, South Island, Casuarina and Corner Beach) there was a much higher representation of smaller size classes, resulting in a much more even distribution of different size classes (Figure 2.5). Interestingly, the smallest size class of starfish (10-15cm), representing first year recruits, were found at only three different locations (North Reef, Corner Beach and Casuarina). These three locations were positioned in the northern and western regions of the island, and may represent principal sites for recruitment by *A. planci*.

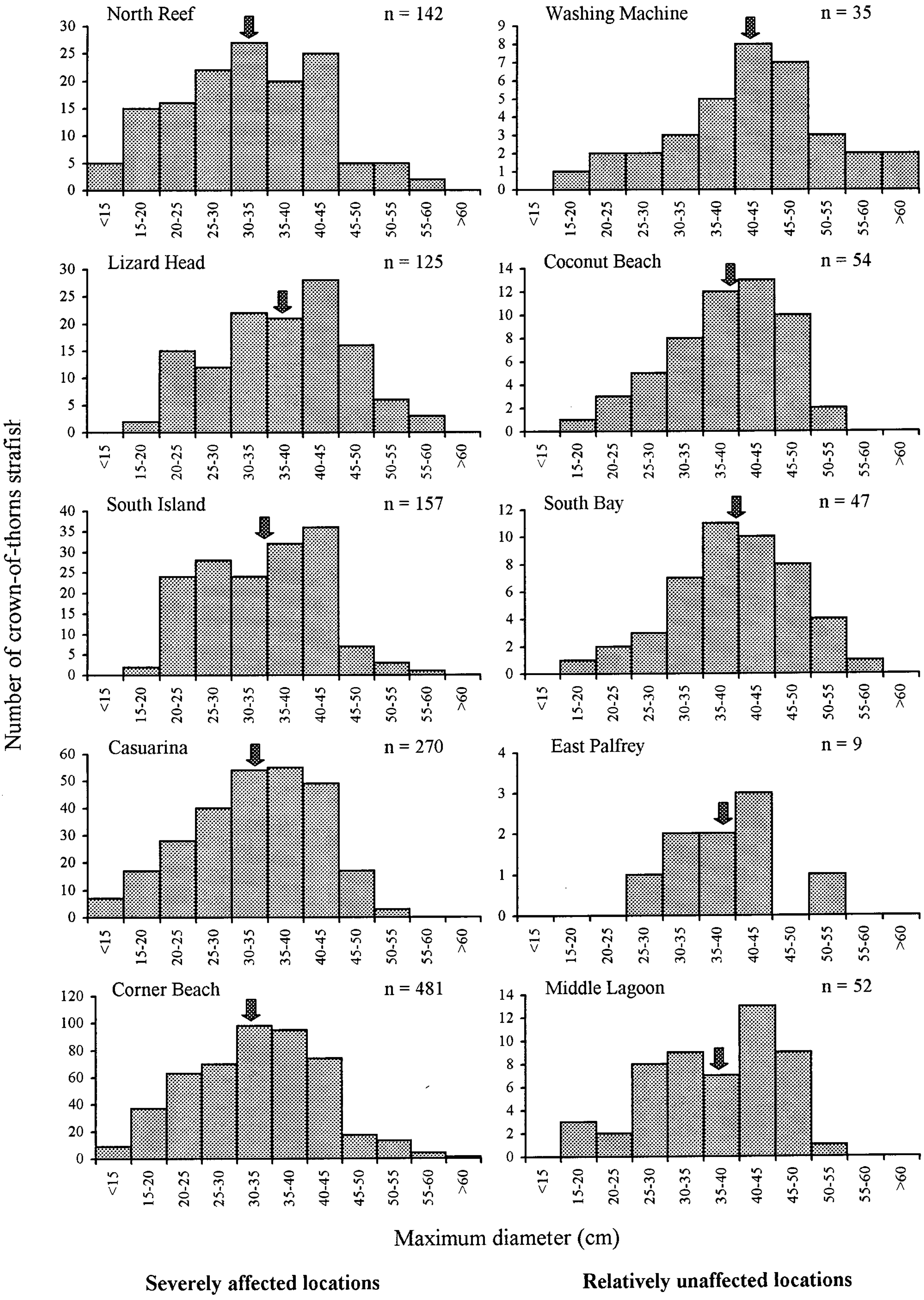

**Figure 2.5.** Spatial variation in the size structure of *A. planci* populations at Lizard Island. Data pooled across nine separate surveys and two depths for each location. Arrows indicate the mean size of starfish for each location.

**Table 2.3** Three-way ANOVA to explore variation in the body size (total body diameter) of *A. planci*. Data was $\text{Log}_{10}$ transformed, '*' denotes significant effects (*p<0.05, **p<0.01, ***p<0.001).

| Source | df | MS | F |
|---|---|---|---|
| Survey | 8 | 0.120 | 8.95*** |
| Location | 9 | 0.050 | 3.69*** |
| Depth | 1 | 0.001 | 0.08 |
| Survey × Location | 59 | 0.017 | 1.30 |
| Survey × Depth | 7 | 0.025 | 1.87 |
| Location × Depth | 9 | 0.009 | 0.73 |
| Survey × Location × Depth | 40 | 0.017 | 1.24 |
| Error | 1097 | 0.013 | |

### Coral mortality

Overall cover of scleractinian corals declined by 32% during the course of the study (data pooled across all locations), from a mean of 32.2% cover (± 1.1SE) in October 1996 down to 21.9% cover (± 1.2SE) in January 1999. During this period, distinctive feeding scars caused by *A. planci* feeding on scleractinian corals, were observed at all locations. However, the extent of coral depletion varied significantly among locations, and also between depths (Table 2.4). Declines in coral cover were most pronounced at the five locations (North Reef, Lizard Head, South Island, Casuarina and Corner Beach) where starfish densities exceeded 0.8 starfish per $200\text{m}^2$ (severely affected locations). At these locations, coral cover declined by 45-72% from October 1996 to January 1999 (Figure 2.6). Moreover, declines in coral cover were apparent on both the reef crest (3 metres), and reef slope (7 metres) (Figure 2.6). The greatest decline in scleractinian coral cover was seen at Corner Beach, where coral cover declined by >72% from 34.8% cover (± 3.3SE) in October 1996, down to just 7.9% cover (± 1.6SE) in January 1999. In contrast to severely affected locations,

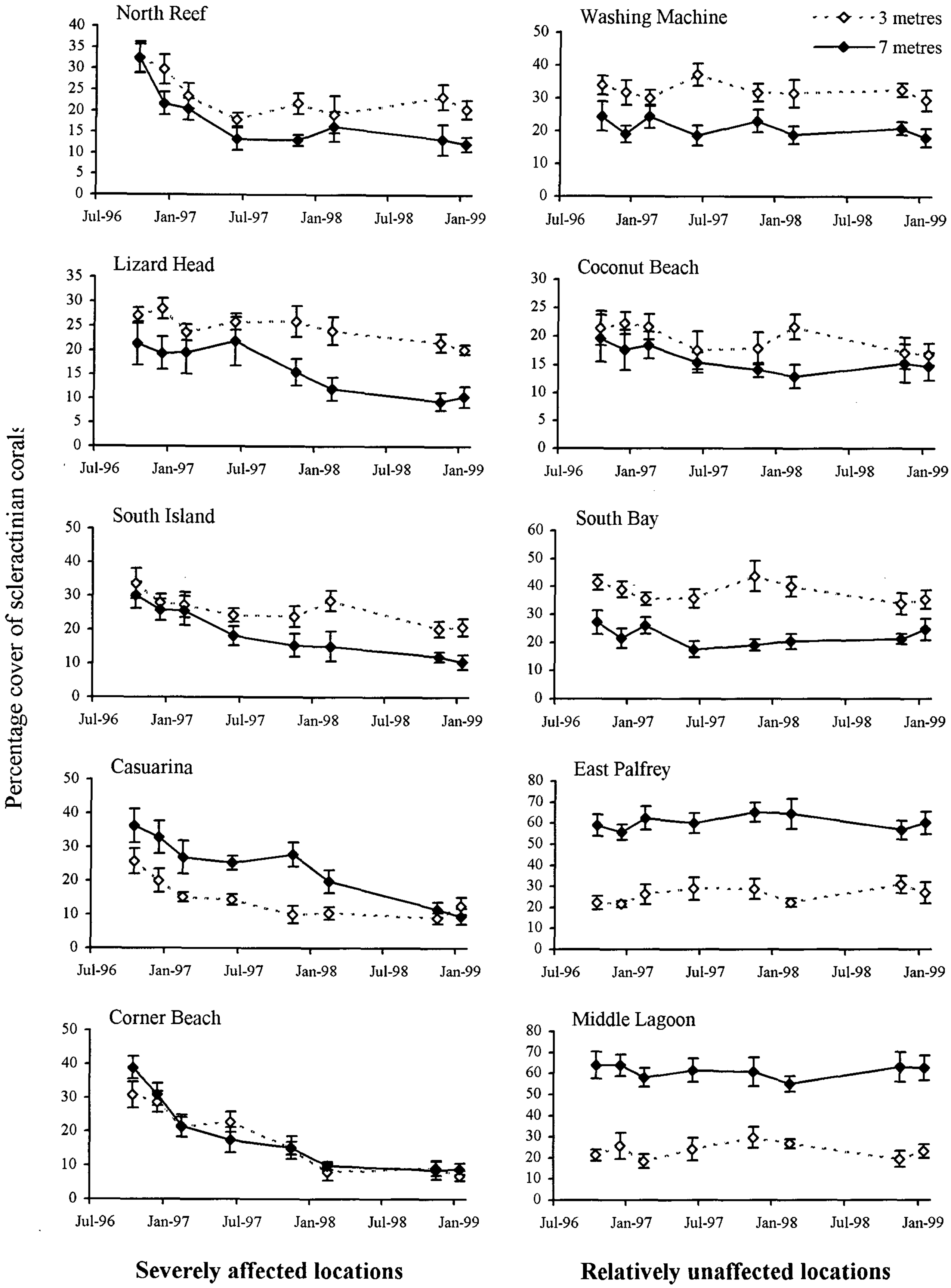

**Figure 2.6.** Temporal variation in mean cover (+/- SE) of scleractinian corals at each depth, at each of ten locations around Lizard Island (n = 10 transects). Severely affected locations are those where starfish densities significantly exceeded 1.0 starfish per 200sq.m, whereas at relatively unaffected locations starfish densities were consistently less than 1.0 starfish per 200sq.m.

there was very little change in scleractinian coral cover at any of the relatively unaffected locations; Washing Machine, Coconut Beach, South Bay, East Palfrey and Middle Lagoon (Figure 2.6). There were slight, though probably not significant declines in scleractinian coral cover at Coconut Beach and South Bay, particularly at 7 metres. However, scleractinian coral cover was remarkably constant at Washing Machine, East Palfrey and Middle Lagoon (Figure 2.6).

**Table 2.4** Three-way ANOVA to explore variation in live cover of scleractinian corals (all corals species combined). Data was $\mathrm{Log}_{10}$ transformed, '*' denotes significant effects (*p<0.05, **p<0.01, ***p<0.001).

| Source | df | MS | F |
|---|---|---|---|
| Survey | 7 | 1844 | 15.03*** |
| Location | 9 | 15075 | 122.81*** |
| Depth | 1 | 4165 | 33.93*** |
| Survey × Location | 63 | 353 | 2.88*** |
| Survey × Depth | 7 | 237 | 1.94 |
| Location × Depth | 9 | 13427 | 109.38*** |
| Survey × Location × Depth | 63 | 312 | 2.78*** |
| Error | 1097 | 112 | |

Variation in the extent of coral decline recorded at different depths and at different locations, was directly related to variation in the overall abundance of *A. planci* (Figure 2.7). Best subsets multiple regression revealed that variation in the overall abundance of *A. planci* was the only one of four variables (starfish abundance, starfish size, initial coral cover and coral composition) that accounted for a significant proportion (68.0%) of variation observed in coral decline among depths and among locations ($R^2 = 56.9$, df = 4, p<0.01). Coral composition (expressed as the proportion of *Acropora* corals in the community) explained an additional 24% of variation in coral decline among depths and among locations, but neither the mean size of starfish or initial coral cover significantly improved model explanation.

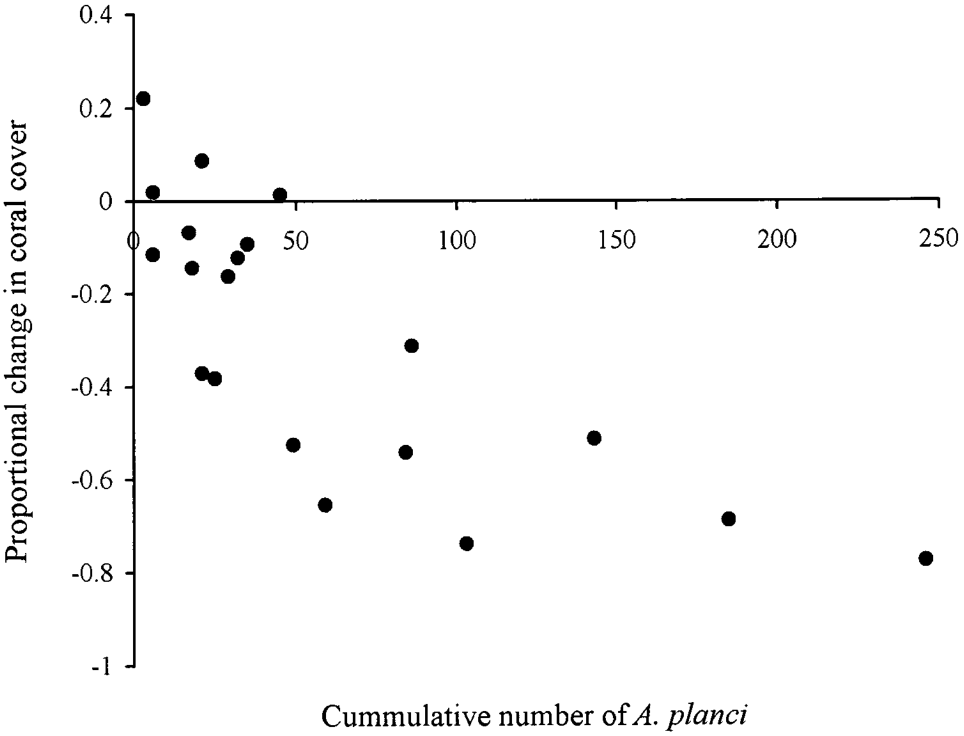

**Figure 2.7.** Relationship between densities of crown-of-thorn starfish and changes in scleractinian coral cover. The cummulative number of starfish recorded at each of two different depths, at each of ten locations around Lizard Island (n =20) is plotted against the proportional change in scleractinian coral cover that occurred, at each site, during the 30 month period from October 1996 to January 1999.

## Community composition of benthic assemblages

In addition to changes in scleractinian coral cover, there were also significant changes in the community structure of benthic assemblages (Table 2.5). Temporal changes in benthic assemblages (as evident by changes in the position of group centroids along first canonical variate) were most pronounced at severely affected locations (North Reef, Lizard Head, South Island, Casuarina, and Corner Beach) (Figure 2.8). By contrast, there was very little change in benthic assemblages at each of the five relatively unaffected locations. Temporal changes in the structure of benthic assemblages at severely affected locations appeared to be due primarily to changes in the abundance of *Acropora hyacinthus*, Branching *Porites*, *Montipora* spp., *Acropora formosa*, *Sarcophyton*, and Massive *Porites* (Table 2.6). However, variation between locations was much greater than observed within locations (Table 2.5, Figure 2.8), and as a consequence, it was difficult to assess which taxa were responsible for changes in benthic assemblages among surveys, versus differences between depths and among locations (Table 2.6).

**Table 2.5** Three-way MANOVA to explore variation in the community structure of benthic assemblages. Data was $\log_{10}$ transformed, '*' denotes significant effects (*$p<0.05$, **$p<0.01$, ***$p<0.001$).

| Source | Pillai's Trace | df | F |
|---|---|---|---|
| Survey | 0.40 | 294 | 2.02*** |
| Location | 2.68 | 378 | 14.21*** |
| Depth | 0.80 | 42 | 137.87*** |
| Survey × Location | 2.33 | 2646 | 1.34*** |
| Survey × Depth | 0.28 | 294 | 1.39*** |
| Location × Depth | 2.28 | 378 | 11.35*** |
| Survey × Location × Depth | 2.10 | 2646 | 1.20*** |

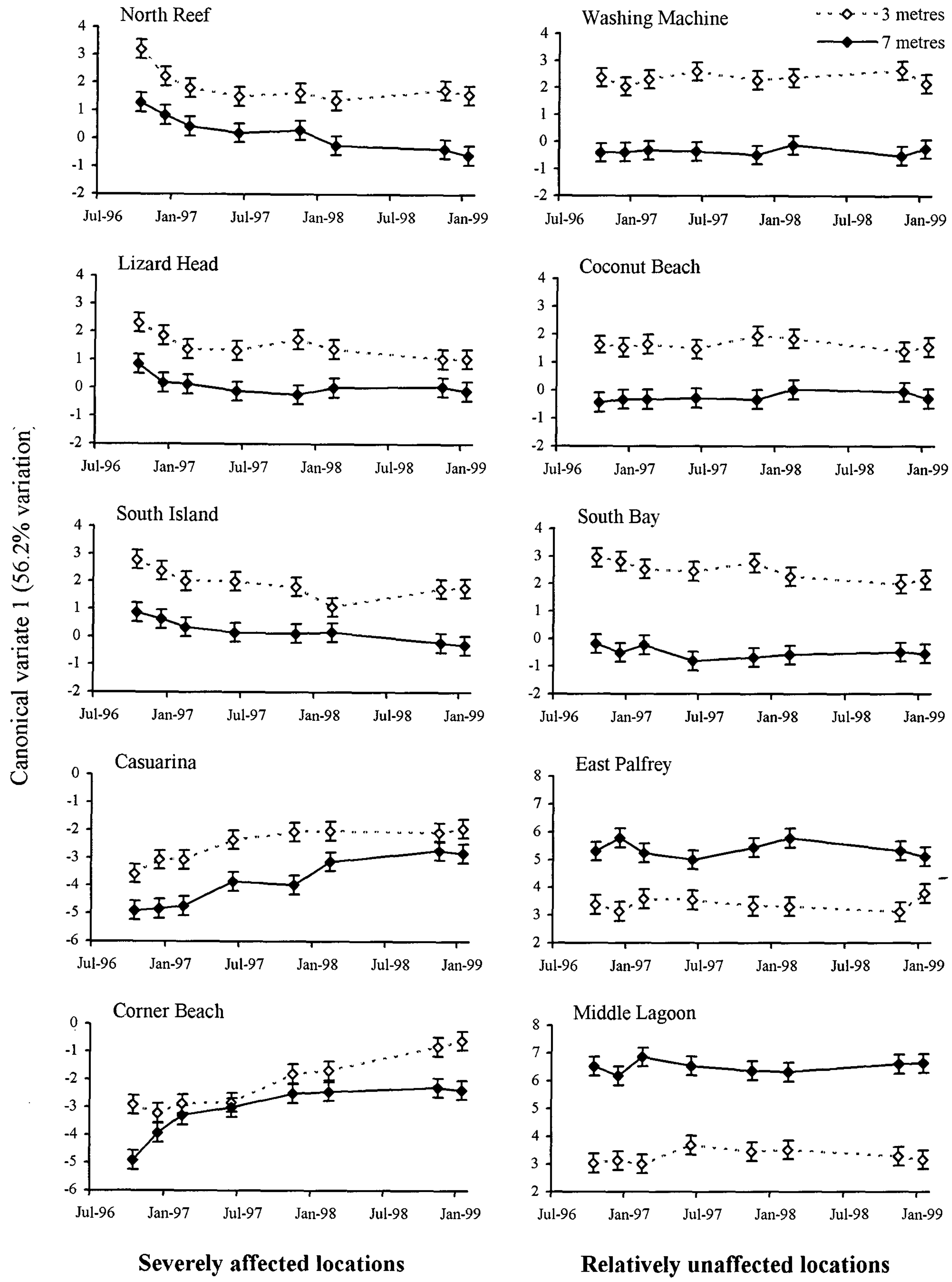

**Figure 2.8.** Temporal variation in structure of benthic assemblages at each depth, at each of ten locations around Lizard Island (n = 10 transects). Severely affected locations are those where starfish densities significantly exceeded 1.0 starfish per 200sq.m, whereas at relatively unaffected locations starfish densities were consistently less than 1.0 starfish per 200sq.m.

**Table 2.6.** Structure coefficients for taxonomic groups of sessile invertebrates used in CDA of benthic assemblages. Correlation coefficients are shown for each 10 taxonomic groups, indicating their importance in distinguishing benthic assemblages from among different surveys, among locations and between depths (NB. Taxa correlated with the first cannonical variate did not necessarily vary in abundance among surveys. Rather, their abundance may vary spatially, among locations and/ or between depths). Only taxonomic groups where coefficients >0.12 are shown.

| Taxa | Correlation with first canonical variate |
|---|---|
| Branching *Porites* | 0.41 |
| *Acropora hyacinthus* Group | 0.32 |
| *Montipora* | 0.19 |
| *Acropora nasuta* Group | 0.17 |
| *Acropora robusta* Group | -0.17 |
| *Acropora formosa* Group | -0.26 |
| *Sarcophyton* | -0.30 |
| Massive *Porites* | -0.37 |

To further explore changes in the community composition of benthic assemblages, I examined temporal variation in the individual abundance of each of 42 different taxonomic groups which were sufficiently abundant for individual analyses (Table 2.7). Sixteen of these taxa exhibited significant changes in abundance at severely affected locations, while varying very little in abundance at relatively unaffected locations (Table 2.7), thereby representing taxa most susceptible to disturbances caused by *A. planci*. One of these groups, the soft coral genera *Sinularia*, actually increased in abundance over the period of the study (Figure 2.9). Each of the remaining taxa (*Pocillopora*, *Stylophora*, *Montipora*, *Acropora robusta* grp., *A. formosa* grp., *A. aspera* grp., *A. selago* grp., *A. hyacinthus* grp., *A. nasuta* grp., Oculinidae, *Lobophyllia*, *Merulina*, *Favites*, *Goniastrea*, and *Echinopora*) declined in abundance, in accordance with increases in the abundance of *A. planci*.

**Table 2.7.** Temporal variation in the abundance of sessile invertebrates at severely affected and relatively unaffected locations. Data presented are F-ratios from univarate ANOVA. '*' denote significant changes in the abundance of taxa (*p<0.05, **p<0.01, ***p<0.001, Bonferroni corrected 95% significance level = 0.0012).

| TAXA | | Severely affected | Relatively unaffected |
|---|---|---|---|
| Family Pocilloporidae | *Pocillopora* | 3.36** | 0.82 |
| | *Seriatopora* | 0.95 | 2.85* |
| | *Stylophora* | 4.41*** | 0.19 |
| Family Acroporidae | *Montipora* | 7.50*** | 0.74 |
| | *Isopora* | 0.69 | 0.29 |
| | *Acropora humilis* Group | 1.52 | 0.41 |
| | *Acropora robusta* Group | 3.74*** | 0.79 |
| | *Acropora formosa* Group | 7.81*** | 1.44 |
| | *Acropora aspera* Group | 2.52* | 0.84 |
| | *Acropora selago* Group | 3.35* | 0.56 |
| | *Acropora hyacinthus* Group | 3.88*** | 0.19 |
| | *Acropora latistella* Group | 3.03* | 2.85* |
| | *Acropora nasuta* Group | 6.83*** | 0.11 |
| | *Acropora loripes* Group | 1.27 | 0.74 |
| | *Acropora florida* Group | 0.91 | 0.49 |
| Family Poritidae | *Porites* | 0.78 | 0.40 |
| | *Goniopora* | 0.93 | 0.41 |
| Family Agariciidae | *Pavona* | 1.53 | 0.62 |
| | *Leptoseris* | 0.86 | 0.57 |
| | *Coleoseris* | 1.53 | 1.00 |
| | *Pachyseris* | 1.88 | 1.09 |
| Family Fungiidae | Fungiidae | 0.92 | 1.33 |
| Family Oculinidae | Oculinidae | 2.90* | 0.65 |
| Family Pectiniidae | *Mycedium* | 0.90 | 0.41 |
| Family Mussidae | *Lobophyllia* | 2.78* | 2.07 |
| | *Symphyllia* | 0.92 | 1.17 |
| Family Merulinidae | *Merulina* | 2.53* | 1.69 |
| Family Faviidae | *Favia* | 1.65 | 0.90 |
| | *Favites* | 2.22* | 1.89 |
| | *Goniastrea* | 3.14* | 0.19 |
| | *Platygyra* | 0.83 | 0.26 |
| | *Leptoria* | 1.63 | 1.02 |
| | *Diploastrea* | 0.45 | 0.22 |
| | *Cyphastrea* | 1.11 | 6.32*** |
| | *Echinopora* | 2.79* | 1.39 |
| Family Dendrophyllidae | *Turbinaria* | 1.09 | 0.33 |
| Family Helioporidae | *Heliopora* | 0.38 | 0.46 |
| Family Milleporidae | *Millepora* | 0.68 | 0.30 |
| Family Alcyoniidae | *Lobophytum* | 1.68 | 0.37 |
| | *Sarcophyton* | 1.81 | 0.72 |
| | *Sinularia* | 2.94* | 1.63 |

The scleractinian coral taxa most affected by the infestations of crown-of-thorns starfish, were from the families Pocilloporidae (*Stylophora*), and Acroporidae (*Montipora*, *Acropora robusta* grp., *A. aspera* grp., *A. formosa* grp., *A. hyacinthus* grp., and *A. nasuta* grp) (Table 2.7). Each of these taxa declined in abundance by 55-95% across the five severely affected locations (Figure 2.9). Prior to infestations of *A. planci*, several of these taxa (*Acropora robusta* grp., *A. formosa* grp., and *A. hyacinthus* grp.) were among the most dominant coral taxa at Lizard Island. The staghorn acroporids (*Acropora robusta* grp. and *A. formosa* grp) initially dominated scleractinian coral communities at both Corner Beach and Casuarina, accounting for 41-45% of scleractinian coral cover at these locations. Following infestations of *A. planci* (in January 1999) the abundance of staghorn acroporids (*A. robusta* grp., and *A. formosa* grp.) had declined to <5%, and in turn, contributed greatly to massive reductions in overall coral cover at both Casuarina and Corner Beach (Figure 2.7). Tabular acroporids (*Acropora hyacinthus* group) once dominated the shallow water (3 metre) coral communities at North Reef, Lizard Head and South Island, accounting for 45-52% of scleractinian coral cover. However, the abundance of tabular acroporids declined rapidly during infestations of *A. planci* (Figure 2.9). At North Reef the average cover of tabular acroporids corals declined by 50% in just 9 months, from a mean of 18.1% cover (± 2.5SE) in October 1996, down to 8.8% cover (± 1.2SE) in June 1997. Declines in the abundance of tabular acroporids (*Acropora hyacinthus* grp.), along with declines in the abundance of both *A. nasuta* grp. and *Montipora* were primarily responsible for temporal changes in the community composition of benthic assemblages North Reef, Lizard Head and South Island (Table 2.6).

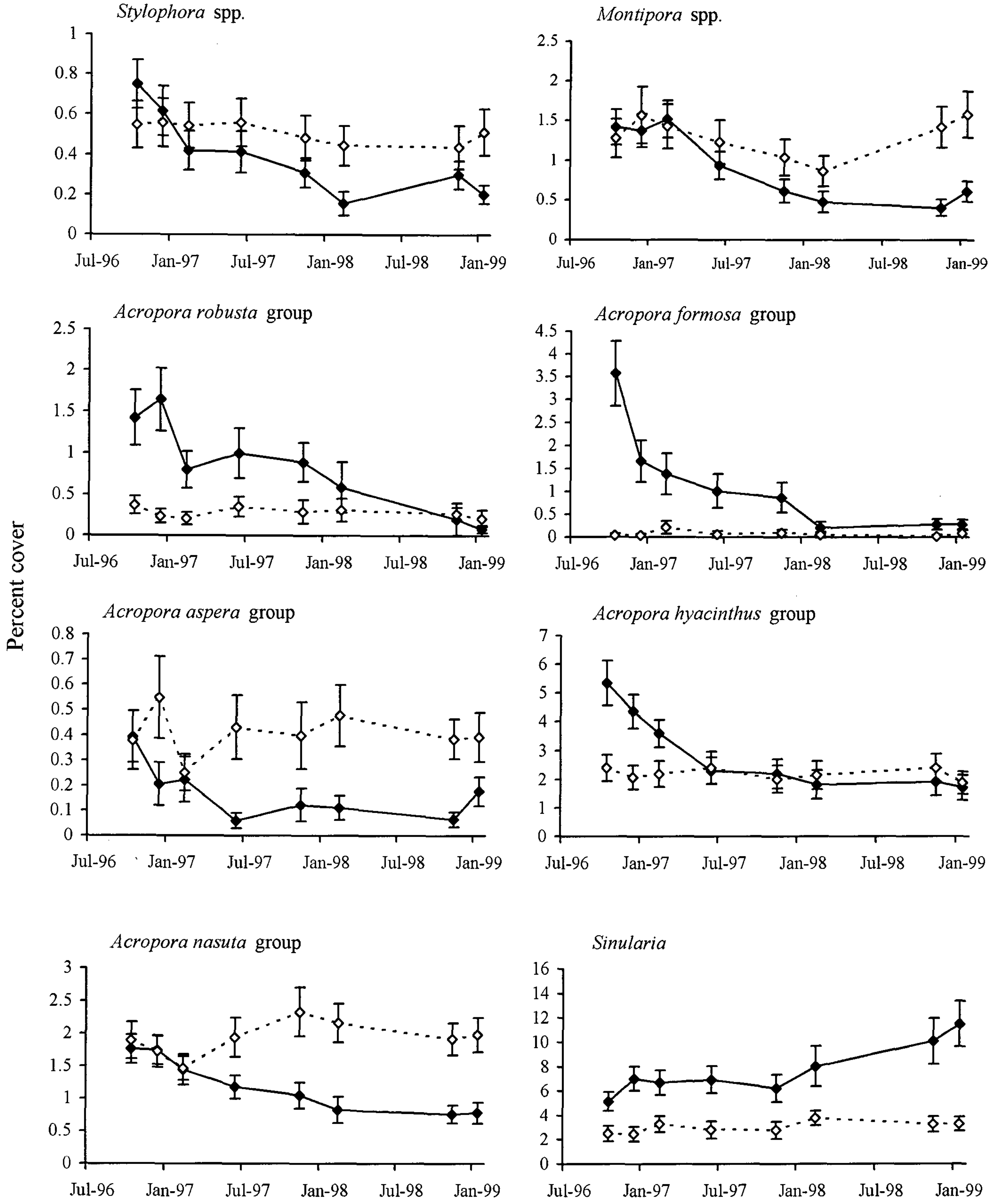

**Figure 2.9.** Temporal variation in the mean cover (+/- SE) of eight different coral taxa at both severely affected locations (solid lines) and relatively unaffected locations (dashed lines). Data pooled across all severely affected locations (North Reef, Lizard Head, South Island, Casuarina and Corner Beach), and across relatively unaffected locations (Washing Machine, Coconut Beach, South Bay, East Palfrey and Middle Lagoon).

## 2.5 DISCUSSION

### Population dynamics of *A. planci*

Overall densities of *A. planci* recorded at Lizard Island from December 1996 to February 1998 significantly exceeded the upper threshold density of 40 starfish.ha$^{-1}$ (0.8 starfish per 200m$^2$), considered indicative of crown-of-thorns outbreaks on the GBR, following Moran and De'ath (1992). These findings are consistent with those of Sweatman et al. (1998) who surveyed starfish populations at Lizard Island and many other reefs (>74 reefs) throughout the GBR, at regular intervals (mostly annually) from 1986 to 1999. Using manta tow surveys to estimate the abundance of *A. planci*, Sweatman et al. (1998, 2000) reported that active outbreaks of *A. planci* were apparent at Lizard Island in 1996 and 1998. At the same time, outbreaks of *A. planci* were also reported from 18 other reefs on the GBR (see also Engelhardt et al. 1999). These data indicate that the outbreak of *A. planci* observed at Lizard Island was not an isolated incident, but a regional phenomenon (Stump 1996). Initial outbreaks of *A. planci* occurred on reefs within the immediate vicinity of Lizard Island (Linnet, Lizard Island, North Direction, Rocky Islet) (Sweatman et al. 1998). However, by 1998 outbreaks of *A. planci* were also apparent on reefs situated up to 400-500km south of Lizard Island (Sweatman et al. 1998, Engelhardt et al. 1999). The southward progression of outbreaks from their initial origin within the vicinity of Lizard Island is consistent with the sequence of crown-of-thorns outbreaks observed on the GBR in 1962-1977 (Kenchington 1976, 1977), and 1982-1989 (Reichelt et al. 1990, Moran et al. 1992). It is possible therefore, that outbreaks of *A. planci* observed within the vicinity of Lizard Island represent 'seed' areas of primary outbreaks (Reichelt et al. 1990, James and Scandol 1992, Johnson 1992), leading to secondary outbreaks on reefs to the south (Reichelt et al. 1990).

The outbreak of *A. planci*, at Lizard Island, resulted from a steady and prolonged build-up in starfish numbers over several consecutive years (Figure 2.2, see also Stump 1996, Sweatman et al. 1998). This finding is a stark contrast to most previous studies (e.g. Chesher 1969, Branham et al. 1971, Moran et al. 1985, Zann et al. 1987, Stump 1992, 1994) which have shown that outbreaks generally result from sudden and dramatic increases in the abundance of *A. planci* (but see Zann et al. 1990). For example, at Tutuila Island, American Samoa, the overall abundance of *A. planci* increased from 1-2 starfish in 1976 to more than 200,000 starfish by late 1977 (Birkeland and Randall 1979, in Birkeland and Lucas 1990). Rapid increases in the abundance of *A. planci* are almost certainly the result of a single massive influx of recruits, probably spawned by large aggregations of adult starfish on upstream reefs (reviewed by Moran 1986), thereby representing secondary outbreaks. By contrast, the slow and progressive accumulation of crown-of-thorns starfish, as observed at Lizard Island, may represent a mechanism by which primary outbreaks occur (Johnson 1992, Stump 1996). The sizes of starfish collected from around Lizard Island ranged from 11-62cm (total diameter), representing at least four different cohorts. There was also further evidence that recruitment occurred in each year from 1992-1998. This continual recruitment of *A. planci* over several consecutive years, combined with increased persistence of older individuals, could lead to outbreak densities of *A. planci* without any substantial increase in the recruitment of *A. planci* (cf. Vine 1973, Lucas 1973, Birkeland 1982), although the two processes (continual recruitment over several years versus marked increases in the size of an individual recruitment events) are not necessarily mutually exclusive (Johnson 1992).

The source of starfish recruits settling at Lizard Island is not known, but they may represent the progeny of the adult starfish that were already present on reefs around

Lizard Island prior to the outbreak (*sensu* Endean 1973). It is becoming increasingly apparent that pelagic larvae from various coral reef organisms can, and often do, settle on natal reefs (e.g. reef fishes, Meekan et al. 1993, Swearer et al. 1999, Jones et al. 1999; scleractinian corals, Ayre and Hughes 2000, Hughes et al. 2000 [Appendix 4]). Where conditions enhance self-seeding, outbreaks of *A. planci* may result from incremental increases in the reproductive output of the initial reproductive population and all of their subsequent progeny, leading to exponential growth in consecutive recruitment events (Stump 1997). It is very rare however, that outbreak populations of crown-of-thorns starfish comprise several successive cohorts. In some instances, outbreak populations have comprised individuals of two distinct size classes, caused by a secondary influx of starfish recruits to reefs already supporting high density adult populations (e.g. Endean 1973, Birkeland 1982, Moran et al. 1985). However, most studies have found that outbreak populations comprise individuals with only a very narrow range of sizes (typically 25-35cm), representing essentially only one year class (e.g. Chesher 1969, Branham et al. 1971, Goreau et al. 1972, Glynn 1973, Sakai 1985, Zann et al. 1987, Stump 1992, 1994, but see also Stump 1996, Engelhardt et al. 1999). The majority of these outbreaks (*ibid*) are likely to represent secondary outbreaks, caused by massive influxes of new recruits spawned by outbreak populations on upstream reefs; most (if not all) of the crown-of-thorns outbreaks that have been studied in the last three decades almost certainly represent secondary outbreaks (Johnson 1992, Moran et al. 1992, Keesing and Halford 1992). By contrast, primary outbreaks of *A. planci* have never (knowingly) been observed (Johnson 1992), and it remains to be seen whether primary outbreaks result from self-seeding of local populations (e.g., Fisk 1992), or a persistent flow of recruits from upstream reefs.

Spatial variation in the size structure of starfish populations provide insights into settlement patterns of *A. planci* around Lizard Island. Smaller starfish (<20cm) were generally found only in the northern and western locations (North Reef, Casuarina and Corner Beach), suggesting that starfish may recruit primarily to sheltered back reef sites, and then move to more exposed locations as they grow larger. This pattern of settlement would be consistent with self-seeding of *A. planci* populations, whereby larvae could be retained in back-reef eddies until ready to settle (e.g., Gay et al. 1991). However, other studies which have explored temporal and spatial patterns in the abundance of *A. planci* (e.g., Laxton 1974, Moran et al. 1985, Sakai 1985, Engelhardt et al. 1999) have found that aggregations of *A. planci* initially develop on front reef slopes, and starfish then move *en masse* to more sheltered back reef zones. Settlement patterns of *A. planci* may be controlled by i) settlement preferences of larval starfish, ii) patterns of larval supply (Black et al 1990, Black and Moran 1991), iii) spatial variation in prey availability (Lucas 1975), or iv) differential rates of post-settlement mortality (Engelhardt et al. 1999). Current evidence suggests that the growth and survival of juvenile starfish is highly constrained by food availability (e.g., Keesing and Halford 1992), and so starfish would be expected to settle preferentially in areas which provide greatest access to prey resources. Optimal areas for settlement will not necessarily be in the same location on all reefs. Also, patterns of larval supply are likely to vary among reefs, and through time, with variation in currents (Black et al 1990, Dight et al. 1990).

Repeated surveys of starfish populations, conducted in quick succession revealed that localised distributions of *A. planci* were highly variable, and changed very rapidly. Increases in the abundance of starfish at one location were often associated with corresponding declines at a nearby location (e.g., North Reef versus Washing Machine), which may indicate that starfish moved between locations. However, the sequence of outbreaks did not indicate any systematic movement of starfish aggregations across the reef, as has been noted previously (reviewed by Birkeland and Lucas 1990). Densities of *A. planci* were always highest on the more sheltered western side of the island (see also Ormond and Campbell 1971, Laxton 1974, Sakai 1985). Crown-of-thorns starfish face considerable risk of dislodgment (and death) in turbulent environments, so they tend to aggregate in sheltered habitats, particularly during rough weather (Endean and Stablum 1973). The avoidance of exposed positions may also explain why starfish tended to occur mostly on the reef slope (rather than the exposed reef crest) at more exposed locations (Chesher 1969, Colgan 1982, Moran et al. 1985). Environmental characteristics cannot however, completely explain fine scale distributions of *A. planci*. For example, crown-of-thorns starfish were almost never found within the Lizard Island lagoon, which is very protected from wind and wave action. Starfish densities also varied greatly among locations (< 500m apart) which did not appear to differ in either physical or biological structure.

At the end of the outbreak at Lizard Island, there was a precipitous decline in the abundance of *A. planci*. This is a conspicuous feature of most crown-of-thorns outbreaks (e.g. Endean 1969, Chesher 1969, Pearson and Endean 1969, but see also Keesing 1992). In many cases (e.g. Endean 1969, Colgan 1967, Chesher 1969, Pearson and Endean 1969) rapid declines in starfish populations followed the almost total depletion of scleractinian corals, prompting suggestions that either the starfish die from starvation, or move *en masse* to find alternate sources of prey (Endean 1969). At Lizard Island, however, declines in starfish densities occurred despite the presence of substantial cover of living sclaractinian corals (>25%) at many locations. It is unlikely therefore, that rapid declines in starfish populations were caused by a lack of prey resources (see also Zann et al. 1987, 1990). It is also unlikely that rapid declines in starfish populations at Lizard Island were attributable to simultaneous senescence of large numbers of starfish, because declines in abundance were seen across starfish with a very wide range of ages (from 1 year old recruits to 6+ year old adults). Simultaneous senescence of numerous crown-of-thorns starfish may cause rapid population declines where outbreaks comprise only a single cohort of *A. planci* (e.g. Chesher 1969, Branham et al. 1971, Goreau et al. 1972, Glynn 1973, Sakai 1985, Zann et al. 1987, Stump 1992, 1994). However, most authors confer that the maximum age of *A. planci* is between 8-12 years (e.g. Chesher 1969, Lucas 1984), while outbreaks of *A. planci* usually last only 1-5 years (reviewed by Moran 1986).

An alternative explanation for rapid declines in the abundance of *A. planci* following outbreaks, is that high-density populations of *A. planci* are subject to some form of disease (Zann et al. 1989, Pratchett 1999 [Appendix 1], Glazebrook et al. Unpublished Manuscript). Pratchett (1999) demonstrated that dead and dying starfish collected from Lizard Island in January 1999 contained a highly infectious pathogen, causing rapid mortality (within 4 days) in seemingly healthy starfish brought into contact with the necrotic tissues of affected starfish (Pratchett 1999[Appendix 1]). The symptoms of this disease were very similar to those observed during mass-mortalities of *A. planci* on reefs in Fiji (Zann et al. 1987, 1990), and in captive starfish collected from the GBR (Sutton et al. 1988). Echinoderms, generally, are highly susceptible to disease (Jangoux and Lawrence 1982), and disease has been implicated in mass-mortalities of numerous echinoderm species (e.g. Menge 1979, Dungan et al. 1982, Lessios et al. 1984, Williams et al. 1986). Considerable research is still required to resolve the potential role of disease in prematurely ending starfish outbreaks, but this could be an extremely fruitful avenue of future research. Most notably, the operation of disease (independent of any other regulatory mechanisms) can lead to predictable fluctuations in the abundance of the host animal (May & Anderson 1979, and references therein), possibly accounting for cyclical outbreaks of *A. planci* on the GBR.

### Effects of *A. planci* on coral communities

Outbreak populations of *A. planci* caused significant reductions in the abundance of scleractinian corals around Lizard Island, killing approximately 32% of scleractinian corals across all locations. Numerous other factors (e.g., coral disease, predation by other corallivores, and/ or bleaching) may have contributed to coral mortality. However, there was no significant change in coral cover at locations (e.g., Washing Machine, East Palfrey, and Middle Lagoon) where *A. planci* were rarely found. Therefore, any additional coral mortality (caused by factors other than coral predation by *A. planci*) is likely to be negligible. Among locations that were severely affected (North Reef, Lizard Head, South Island, Casuarina and Corner Beach), coral cover declined by 45-72%. Although significant, these reductions in coral cover are still much less severe than have been observed elsewhere on the GBR (e.g. Pearson and Endean 1969, Done 1985), and elsewhere throughout the Indo-Pacific (e.g. Chesher 1969, Colgan 1987). For example, in 1969, at Tanguisson Point Guam, outbreak populations of *A. planci* killed >90% of corals along a 34km stretch of coastline, such that surface cover by scleractinian corals was reduced to less than 1%. In contrast, even at the most severely affected location around Lizard island (Corner Beach), scleractinian corals still occupied >10% of hard substrates after outbreaks of *A. planci* had passed.

Despite causing only minor change in total live coral cover, crown-of-thorns starfish concentrated their feeding on very few highly abundant coral taxa (specifically, *Acropora formosa* grp., and *A. hyacinthus* grp.), thereby causing marked shifts in the community structure of coral assemblages (see also Glynn 1976, Ormond et al. 1976, Colgan 1987). Effects of *A. planci* were not sufficient to cause the local extinction of any coral species. However, the overall cover of acroporid corals (all taxa combined) declined by 50-80% at each of the five severely affected locations. In turn, the community structure, at these locations, shifted from being dominated by *Acropora* corals, to one in which normally insignificant corals, such as *Porites* and *Goniastrea*, predominated. The selective removal of acroporid corals is consistent with studies on the feeding preferences of *A. planci* (e.g., Keesing 1992, De'ath and Moran 1998), which have shown that crown-of-thorns starfish tend to favour acroporids (particularly, branching *Acropora* spp.), over virtually all other coral species. However, *A. planci* also consumed a considerable proportion of pocilloporid corals (*Pocillopora* and *Stylophora*), which are generally thought to be protected from crown-of-thorns attack. Glynn (1974, 1976) showed that highly aggressive coral symbionts, contained within most colonies of *Pocillopora, Stylophora* and *Seriatopora*, attack *A. planci* and deter them from feeding on their host corals. This research, conducted in the eastern Pacific, showed that coral symbionts were the main reason why common pocilloporid corals were under-represented in the diet of *A. planci* (see also Pratchett et al. 2000 [Appendix 3]). Pocilloporid corals are, however, eaten quite readily by crown-of-thorns starfish on the GBR (Keesing 1990, De'ath and Moran 1998, this study), suggesting that there may be a geographical difference in the effectiveness with which coral symbionts defend their host colonies from *A. planci*.

In contrast to scleractinian corals, *A. planci* will only very rarely eat soft corals, even when alternate prey is extremely scarce (Keesing 1992). As a consequence, the predominance (if not the absolute abundance) of soft corals in benthic reef assemblages tends to increase after outbreaks of *A. planci* (e.g., Nishihira and Yamazato 1974, Chou and Yamazato 1990). At Lizard Island, increases in the abundance of soft-corals were restricted mainly to sheltered back-reef habitats, where the physical environment is known to enhance both the growth and survivorship of alcyonacean soft corals (Fabricius 1997). Over the period of the study, the structure of benthic assemblages at back-reef locations (Casuarina and Corner Beach) shifted from being dominated by scleractinian corals, to one where alcyonacean soft corals predominated. Shifts to soft coral-dominated assemblages, following the extensive depletion of scleractinian corals by outbreaks of *A. planci*, have also been observed in Japan (Nishihira and Yamazato 1974, Chou and Yamazato 1990). In contrast, Fabricius (1997), did not find increased abundances of soft corals on reefs affected by outbreaks of *A. planci*, compared to nearby unaffected reefs, in the central section of the GBR (see also Ninio et al. 2000). The specific response of soft corals to reductions in the abundance of scleractinian corals will vary depending on what regulates their abundance. Often, soft corals are competitively superior to scleractinian corals (e.g. Sammarco et al. 1985, Alino et al, 1992), such that their abundance is unlikely to be constrained by space occupancy by scleractinian corals. Fabricius (1997) suggested that populations of alcyonacean soft corals are more likely to be limited by their slow growth and very low levels of recruitment (Fabricius 1995). However, there are situations where soft corals are sub-ordinate to scleractinian corals (e.g. Benayahu and Loya 1981, Dai 1990) whereby temporary reductions in hard coral cover may enhance soft coral abundance (Endean et al. 1988). This response will be most pronounced if reductions in hard coral cover coincide with high recruitment and/ or rapid growth by soft corals.

Despite significant changes in both coral cover and composition, the recovery of coral communities around Lizard Island is likely to be very rapid (*sensu* Done 1985). Estimates of the time required for coral communities to recover from outbreaks of *A.*

*planci* (and other major disturbances) are highly varied, ranging from <5 years to >1000 years (Pearson 1981, Done and DeVantier 1990, Lourey et al. 2000). In extreme cases, coral communities may never regain their initial structure, though live coral cover will, more than likely, return to pre-disturbance levels (e.g., Endean and Cameron 1985, Endean et al. 1988). The rate and extent of recovery in coral communities depends primarily on the amount of damage that has occurred. For example, completely denuded reefs recover much more slowly than reefs in which at least some corals have survived to grow and reproduce (Connell et al. 1997). At Lizard Island, effects of *A. planci* were comparatively mild (discussed previously), and some colonies of all coral taxa survived. Recovery also depends on the types of corals affected. In instances where effects are restricted to fast growing branching corals (e.g. *Acropora* spp.), as opposed to slow-growing massive species (e.g. *Porites* spp.), as was observed at Lizard Island, coral communities quickly attain (within 10 years) both their initial structure and initial levels of species abundances (Pearson 1981, Done 1985).

In summary, this study has shown that the distribution and abundance of crown-of-thorns starfish can vary quite considerably at small spatial scales, within reefs. Furthermore, localised distributions of starfish aggregations changed very rapidly through time. This had significant implications for fine-scale patterns in the effects of *A. planci* on coral communities; this being the first ever study to successfully relate differences in the extent of coral depletion, observed between depths and among locations, to spatial variation in the abundance of *A. planci*. The effects of *A. planci* were very patchy, with declines in coral cover ranging from 0-72% among locations. However, substantial cover of scleractinian corals (>10% cover) remained at all locations after outbreaks had passed, suggesting that subsequent recovery of coral communities is likely to be very rapid.

# CHAPTER 3. Influence of coral symbionts on feeding preferences of *Acanthaster planci*[†]

## 3.1 ABSTRACT

The crown-of-thorns starfish *Acanthaster planci* (L.) is well adapted to feed on a wide range of different corals, but often exhibit striking preference for a small suite of the available prey species. Numerous hypothese have been forwarded to explain the feeding preferences of crown-of-thorns starfish, but many of these hypotheses have not been tested. In this study, I test whether coral symbionts significantly affect the feeding preferences of crown-of-thorns starfish, by removing symbionts from replicate colonies of six different coral species. Crown-of-thorns starfish had a clearly defined hierarchy of preference for the six different corals when they contained symbionts (*Acropora gemmifera* > *A. nasuta* = *A. loripes* > *Seriatopora hystrix* > *Pocillopora damicornis* > *Stylophora pistillata*). However, when coral symbionts were removed, then starfish readily consumed all six corals and did not exhibit any significant selectivity. Further manipulation of symbiont assemblages showed that the trapeziid crabs (*Tetralia* and *Trapezia*) were the most effective of the various coral symbionts in deterring starfish from feeding on their host colony. Moreover, those corals that were least preferred by crown-of-thorns starfish contained the largest and most powerful species of *Trapezia* (*Tr. cymodoce*), whereas the most preferred corals contained only very small *Tetralia* crabs. Further experimentation is required to assess the generality of these results, but for the six coral species tested, it is clear that coral symbionts (and particularly trapeziid crabs) do have a marked influence on the feeding preferences of crown-of-thorns starfish.

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## 3.2 INTRODUCTION

Outbreaks of the crown-of-thorns starfish, *Acanthaster planci* (L.) represent the most significant biological disturbance on tropical coral reefs throughout much of the Indo-Pacific region. Aside from their potential to cause widespread coral destruction (e.g., Guam; Chesher 1969, Great Barrier Reef; Pearson & Endean 1969, Japan; Yamaguchi, 1986), selective feeding by *A. planci* causes differential mortality among coral species, and can exert a major influence on coral community structure. In the eastern Pacific, Glynn (1974, 1976) found crown-of-thorns starfish fed mostly on rarer coral species, increasing the dominance of the abundant coral species, *Pocillopora damicornis* (see also Branham et al. 1971). Elsewhere, *A. planci* tend to feed mostly on relatively abundant coral species (eg. *Acropora* and *Montipora*) and thereby increase the prevalence of non-preferred corals (eg. Ormond et al. 1976, Colgan 1987, Keesing 1992, De'ath and Moran 1998, see also Chapter 2).

*Acanthaster planci* is adapted to feed on a wide range of different corals and it is not known why they consistently target a small suite of available prey species. In general, *A. planci* appears to favour corals of the family Acroporidae (see reviews by Potts 1981, Moran 1986, Birkeland & Lucas 1990). However, Moran (1986) and more recently De'ath & Moran (1998) have pointed out that few studies of the feeding habits of *A. planci* have employed methodologies necessary to determine feeding preference (see also Potts 1981). Most studies compare the proportion of a particular coral eaten to its proportional availability at the community or reef level (e.g. Branham et al. 1971, Glynn 1974, Keesing 1992). Such studies clearly show that *A. planci* are very selective in their choice of prey, but often fail to identify the actual prey species that are preferred. Identifying preferred prey in the field is difficult because feeding preferences are confounded by differences in the relative size, abundance and accessibility of different corals (De'ath & Moran 1998).

General models of optimal diet theory predict that *A. planci* choose prey which maximise energetic return (Ormond et al. 1976). However, Keesing (1990) explored the relationship between the nutritional value of corals and prey preferences of *A. planci*, and although the most highly preferred corals (eg. *Acropora*) had the highest energy content, feeding preferences were not altogether consistent with theoretical predictions of optimal foraging. Principally, non-preferred corals from the family Faviidae had similar nutritional value to preferred acroporid corals (Keesing 1990). In reviewing feeding habits of *A. planci*, Potts (1981) suggested that coral prey which are readily consumed by *A. planci* may represent the least avoided species, rather than those which are most actively sought. Defensive mechanisms of scleractinian corals, including nematocysts, mesenterial filaments, secondary metabolites, and the antagonostic behaviour of coral symbionts, all may deter starfish from feeding on certain corals (Potts 1981). In the best documented example, Glynn (1974, 1976) showed that coral symbionts attack *A. planci* and deter them from feeding on pocilloporid corals. This research, conducted in the eastern Pacific, showed that coral symbionts were the main reason why common pocilloporid corals were under-represented in the diet of *A. planci*.

Although it has never been explicitly tested, coral symbionts are thought to have comparatively little influence on the feeding habits of *Acanthaster planci* in the western Pacific (particularly on the Great Barrier Reef). This theory came about because both *Pocillopora* and *Stylophora*, which both contain highly agnostic coral symbionts, are among the most highly preferred coral prey of *A. planci* on the Great Barrier Reef (e.g. Keesing 1990, De'ath & Moran 1998, see also Chapter 2). The purpose of the present study was to test whether coral symbionts do influence the feeding preferences of crown-of-thorns starfish on the Great Barrier Reef. The influence of coral symbionts was tested by examining feeding preferences of *A. planci* for various corals with their symbionts removed, and comparing feeding preferences of starfish for the same corals which contained symbionts. Further manipulative experiments were also conducted to assess the relative efficacy with which different symbionts deter *A. planci* from feeding on their respective host colonies.

## 3.2 METHODS

### Feeding Trials

Feeding preferences of *A. planci* were examined during feeding trials conducted in large tanks at Lizard Island (14°40'S, 145°27'E), on the northern Great Barrier Reef (GBR), Australia. Feeding trials were conducted using six coral species from two different families (Acroporidae; *Acropora gemmifera, Acropora loripes* and *Acropora nasuta* and Pocilloporidae; *Pocillopora damicornis, Seriatopora hystrix* and *Stylophora pistillata*). Both *Acropora* and pocilloporid corals were used because of known differences in their symbiotic fauna (e.g., Garth 1964). However, the particular coral species were selected during a 3-day preliminary investigation of symbiotic fauna among 42 species of tightly branching scleractinian coral. The six coral species selected were highly abundant, easily collected and nearly always occupied by coral symbionts.

To conduct feeding experiments, forty small (900-1200cm$^3$) colonies of each of the six coral species (*A. gemmifera, A. loripes, A. nasuta, P. damicornis, S. hystrix* and *S. pistillata*) were collected from within the Lizard Island lagoon and then transported to the Lizard Island research station. All coral colonies were collected and transported in separate containers to retain their coral symbionts. Two colonies of each coral species were then arranged haphazardly in each of 20 large (1.1 metre diameter) circular tanks, giving a total of 12 coral colonies per tank. To test the influence of coral symbionts on feeding preferences of *A. planci*, symbionts were removed from all coral colonies in half (10/20) of the tanks. Symbionts were removed using plastic forceps, and then fixed in 5% seawater formalin to be identified. Symbionts within coral colonies in the remaining ten tanks (the control tanks) were identified *in situ* prior to the experiment, but then removed at the termination of the experiment to confirm species identification.

Twenty-four hours after the corals were collected, which allowed both the corals and their symbionts to acclimatise, crown-of-thorns starfish of approximately equal size (36cm ± 1.3 SE total diameter) were introduced into each of the twenty coral tanks. To counter potential differences in the recent feeding history of the individual starfish, they had been held for five days without food before being used in the feeding trials, following Keesing (1990). At the start of the feeding trials, a single starfish was placed directly in the centre of each tank and observations were then made every three to four hours for a total of 10 days to determine the sequence in which coral colonies were consumed. The experiment was terminated after 10 days to ensure that the experiment was ended before corals and their symbionts began to suffer the effects of captivity. Few colonies (at most three in one tank) were uneaten after this period.

### Analysing feeding preference

Analyses of feeding preferences of *A. planci* were based on the order in which coral colonies were consumed. Every coral colony within each of the tanks was assigned a rank (from 1-12) according to the order in which it was eaten. All colonies that were not eaten at the end of the experiment (after 10 days) were given an equal rank, equal to the mean of remaining ranks (ie when 2 out of 12 colonies were left they were both given a rank score of 11.5). Where the starfish feed selectively then preferred prey species would have significantly lower ranks than less preferred species. To analyse differences in the ranks for each coral species I used Friedman's test, which compares the mean ranks of each coral species across all replicate tanks (n=10). These analyses were carried out separately for the control tanks (symbionts removed) and the experimental tanks (symbionts retained). Where there were significant differences in the mean ranks among coral species, this indicated that starfish were feeding selectively.

Separate analyses, using Kendall's coefficient of concordance, were carried out to test that the patterns of prey preference were consistent among starfish in separate tanks. Kendall's coefficient of concordance was used firstly, to test for differences in feeding preferences of *A. planci* across all control and experimental tanks (following Zar 1984). Where there was a significant difference across all tanks (n=20), I then tested whether there were significant differences among control tanks (n=10), and among experimental tanks (n=10). If symbionts had a significant influence on the feeding preferences of starfish, I would expect significant differences across experimental and control tanks, but concordance (no difference in the feeding preferences of starfish) among control tanks and among experimental tanks.

### Coral symbionts

Differences in the symbiont assemblages of the six coral species were analysed to assess whether variation in the symbiont fauna reflected differences in the feeding preferences of *A. planci*. Symbiont assemblages of the six coral species were described using the 40 colonies of each coral species that were collected for use in the aforementioned feeding trials. Variation in symbiont assemblages was analysed using multivariate analysis of variance (MANOVA), which simultaneously compares the abundance of all symbiont taxon among the six coral species. Where there were significant differences in the symbiont assemblages of the six coral species, I used canonical discriminate analysis (CDA) to show the relative similarity of symbiont assemblages from each coral species. To assist with interpretation of the CDA, structural coefficients of the most significant response variables were plotted as vectors, which identify the symbionts that are primarily responsible for differences between each coral species.

### Manipulating symbionts

To compare the efficacy with which symbionts deter *A. planci* from feeding on their host corals, further feeding trials were conducted in which I modified the symbiont composition in replicate coral colonies. In each of 20 large circular tanks, I placed a total ten coral colonies (all of the same species and of approximately equal size). I then selected colonies at random and modified their symbiont assemblages, so that there were two colonies in each tank that were subject to each of five different experimental regimes; (1) no symbionts, (2) gobies only, (3) shrimps only, (4) crabs only, and (5) gobies, shrimps, and crabs. All colonies used in the experiment were collected from the Lizard Island lagoon, and transported back to the research station in separate containers to maintain their symbiont assemblages.

Twenty-four hours after the experiment had been set-up, a single crown-of-thorns starfish (ca 36cm ± 1.3 SE total diameter), which had been starved for five days, was then placed in to the centre of each tank. The subsequent order in which coral colonies were consumed was recorded over a period of ten days. These trials were conducted using *Pocillopora damicornis* and *Acropora nasuta*, in ten replicate tanks with each coral species. Feeding preferences of *A. planci* were analysed by comparison of combined ranks for colonies in each treatment, using Friedman's test (described above). I then tested whether feeding preferences of *A. planci* were consistent between the two coral species, and across replicate tanks using Kendall's coefficient of concordance (described above).

## 3.4 RESULTS

### Coral symbionts

A total of 18 symbiont taxa were recorded across the 240 coral colonies examined. These included three species of *Tetralia*, four species of *Trapezia*, five different species of *Gobiodon*, two species of *Paragobiodon*, *Cymo* sp., *Coralliocaris* sp., *Periclimenes* sp., and *Alpheus* sp. (Figure 3.1). The symbiont assemblages varied greatly between the six coral species (*A. gemmifera, A. loripes*, *A. nasuta P. damicornis, S. hystrix* and *S. pistillata*). Most notably, there was a clear distinction in the symbiont assemblages between acroporid and pocilloporid corals. Essentially, *Tetralia*, *Gobiodon*, *Periclimenes* and *Coralliocaris* occurred only in acroporid corals, whereas *Trapezia*, *Paragobiodon*, and *Alpheus* occurred only in pocilloporid corals (Figure 3.1).

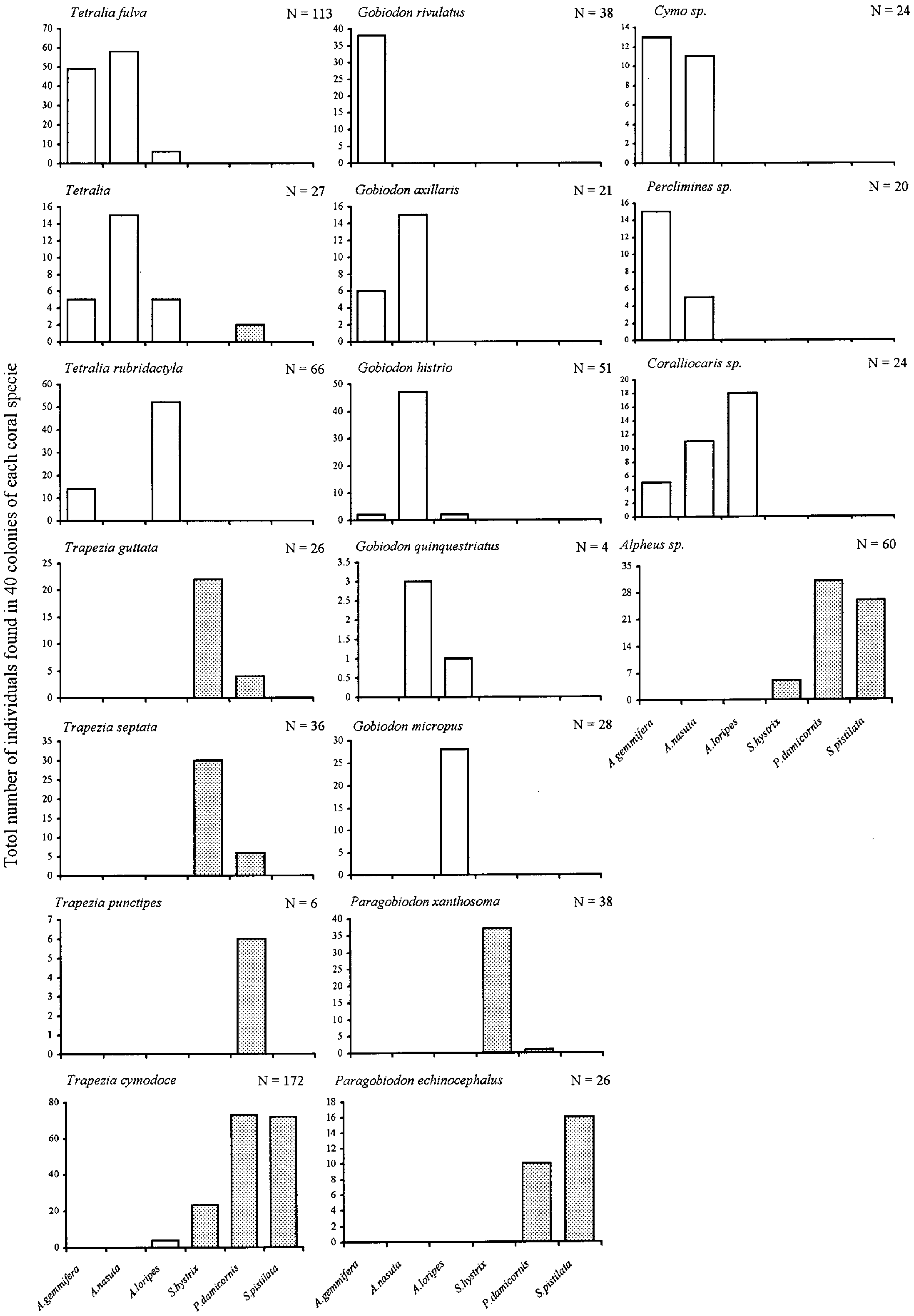


**Figure 3.1.** Variation in the distribution of coral symbionts among six different coral species, from two different families; Acroporidae (clear columns) and Pocilloporidae (shaded columns). Data respresent the number of each symbiont found in 40 colonies of each coral species. The total number of each symbiont (N) is also provided.

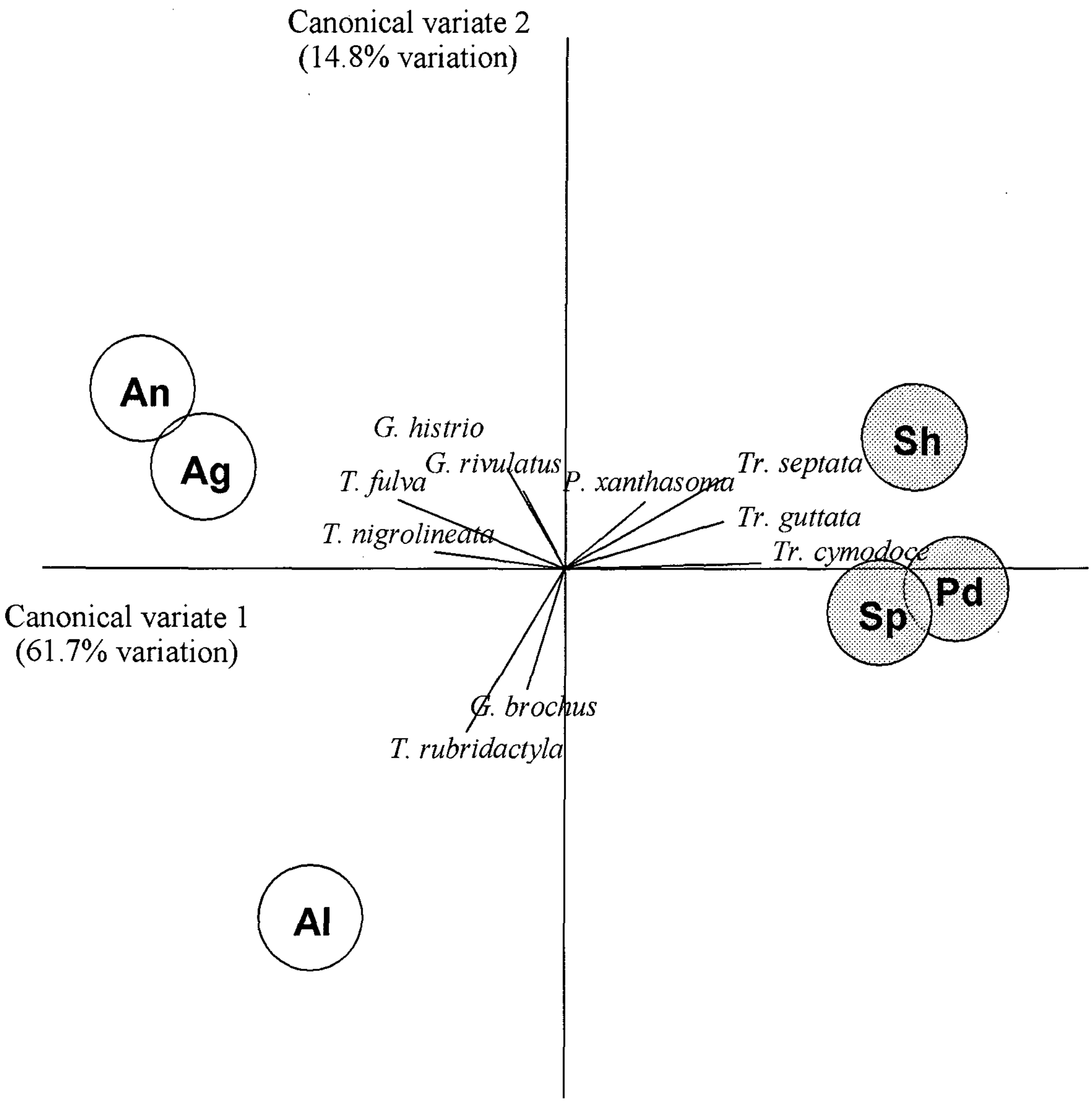


**Figure 3.2a.** CDA of the community structure of symbionts from 3 *Acropora* (clear circles) and 3 pocilloporid corals (shaded circles), showing canonical variates 1 and 2. Canonical variates 1 and 2 represent 76.5% of variation and emphasise differences among *Acropora* corals. Circles plotted represent 95% confidence limits around the centroids for each coral species. Vectors are structural coefficients of response variables, indicating the relative abundance of each coral symbiont within different coral species.

Al- *Acropora loripes*, Ag- *A. gemmifera*, An- *Acropora nasuta*, Sh- *Seriatopora hystrix*, Pd- *Pocillopora damicornis*, Sp- *Stylophora pistillata*.

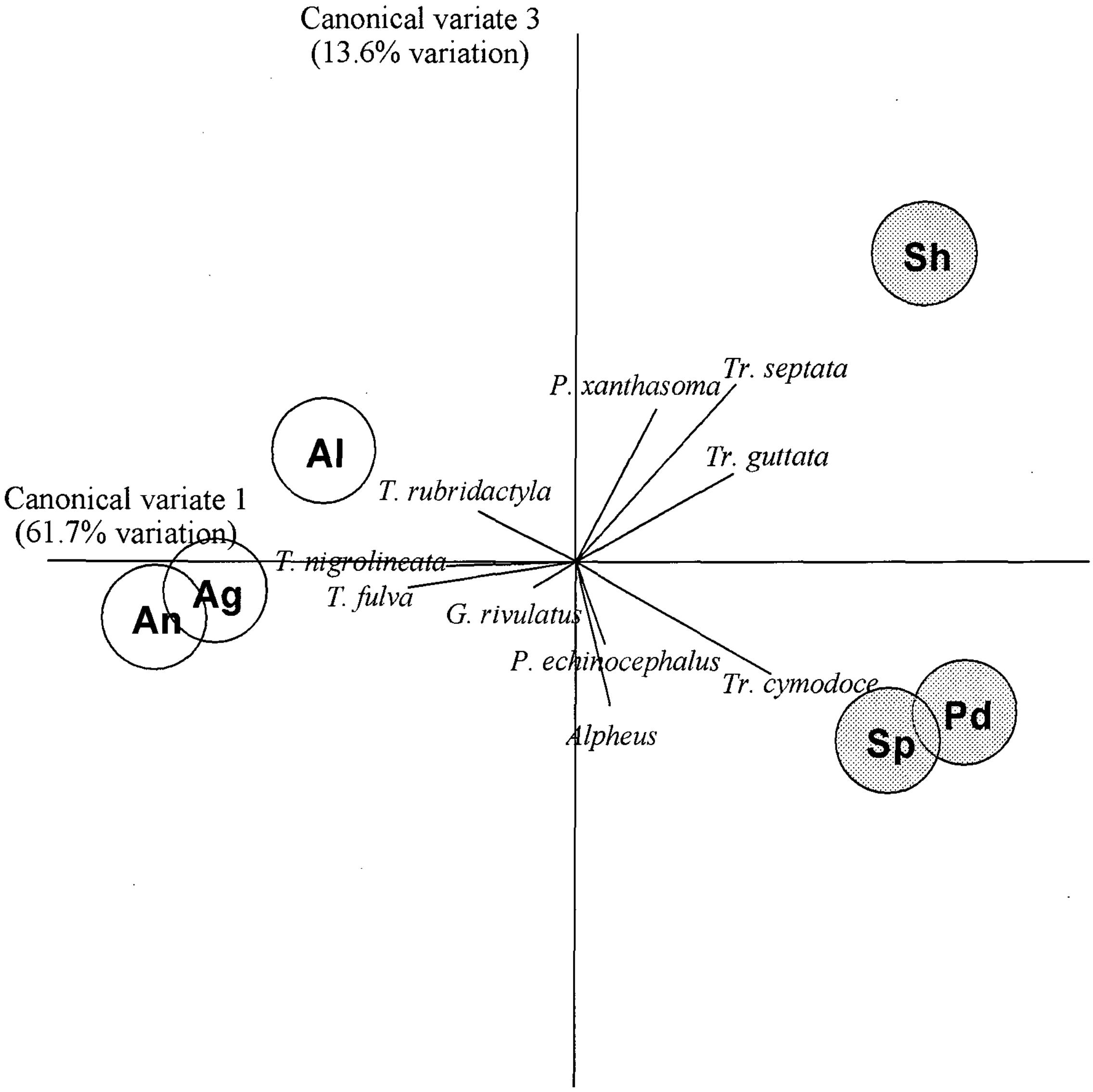


**Figure 3.2b.** CDA of the community structure of symbionts from 3 *Acropora* (clear circles) and 3 pocilloporid corals (shaded circles), showing canonical variates 1 and 3. Canonical variates 1 and 3 represent 75.3% of variation and emphasise differences among pocilloporid corals. Circles plotted represent 95% confidence limits around the centroids for each coral species. Vectors are structural coefficients of response variables, indicating the relative abundance of each coral symbiont within different coral species.

Al- *Acropora loripes*, Ag- *A. gemmifera*, An- *Acropora nasuta*, Sh- *Seriatopora hystrix*, Pd- *Pocillopora damicornis*, Sp- *Stylophora pistillata*.

Only two of the 18 symbiont species identified (*Tetralia nigrolineata*, and *Trapezia cymodoce*) were found in colonies from both coral families (Figure 3.1). Overall, there were significant differences in symbiont assemblages across all six coral species (Pillai's Trace = 2.95, F = 17.61, df = 90, P <0.01). In the CDA, acroporid corals were clearly separated from the pocilloporids along the primary canonical variate, which accounted for the vast majority (61.7%) of the variation in symbiotic assemblages (Figure 3.2a). The second and third cannonical variates which both accounted for similar proportions of the variance (14.8% and 13.6%, respectively) clearly showed variability in the symbiont assemblages among the acroporids and among the pocilloporids, respectively (Figure 3.2b).

Within the acroporids, the symbiont assemblages of *A. nasuta* and *A. gemmifera* were relatively similar, whereas *A. loripes* had the most distinct symbiont fauna (Figure 3.2a). The predominant crab species found in both *A. gemmifera* and *A. nasuta* was *Tetralia fulva*, whereas most colonies (75%) of *A. loripes* contained only *Tetralia rubridactyla* (Figure 3.2a). *Cymo* crabs and *Perclimines* shrimps were also common to both *A. gemmifera* and *A. nasuta*, but were never found in colonies of *A. loripes*. The most prevalent goby, *G. histrio*, occupied all three *Acropora* species but most individuals (92%) were found in *A. nasuta* (Figure 3.1). *Gobiodon rivulatus* was the second most commonly occuring goby, but it was found only in *A. gemmifera*, while *G. brochus* was only found in colonies of *A. loripes* (Figure 3.2a).

Among pocilloporid corals, *P. damicornis* and *S. pistillata* were very similar in their symbiotic communities, whereas *S. hystrix* had a very distinct symbiont fauna (Figure 3.2b). *Trapezia cymodoce* was prevalent in 95% of *P. damicornis* colonies and 97.5% of *S. pistillata*, but were only rarely found is *S. hystrix* (Figure 3.1). Most *S.*

*hystrix* colonies (52.5%) contained the smaller variegated crab, *Tr. septata*. *Alpheus* shrimps were found in all three pocilloporid corals, but they were much more abundant in *P. damicornis* and *S. pistillata*, compared to *S. hystrix* (Figure 3.1). The goby *P. echinocephalus* only occurred in *P. damicornis* and *S. pistillata*, whereas *P. xanthasoma* was most commonly found in colonies of *S. hystrix* (Figure 3.1).

## Feeding trials

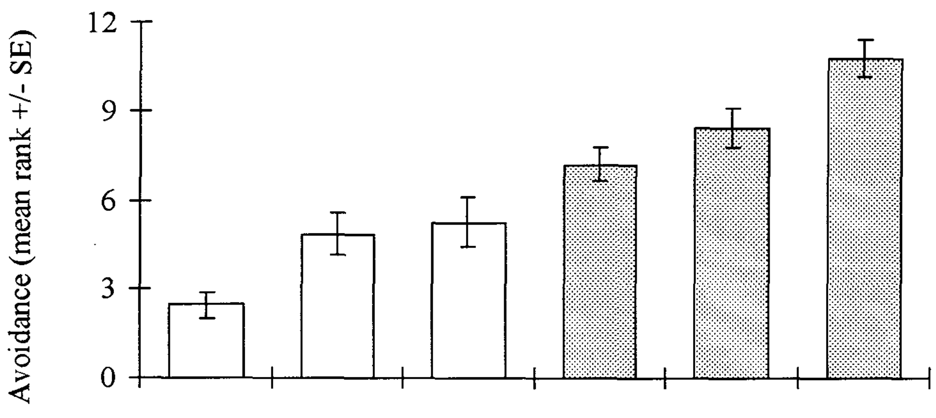
Crown-of-thorns starfish exhibited strong and consistent feeding preferences among corals containing symbiotic fauna. *Acropora gemmifera* was the most highly preferred coral species, and was the first coral eaten in nine (of 10) treatment tanks. After *A. gemmifera*, the starfish tended to consume either *A. nasuta* or *A. loripes*, which were equally preferred (Figure 3.3). All acroporid species were significantly preferred over pocilloporid species. Among pocilloporid corals, *Seriatopora hystrix* was usually eaten first, followed by *Pocillopora damicornis* and then *Stylophora pistillata* (Figure 3.3). *Stylophora pistillata* was clearly the least preferred of the six coral species and was only rarely (4/20 colonies) consumed. The combined ranks for each coral species were significantly different ($\chi^2 = 44.17$, df = 5, $P < 0.01$). Also, the order in which corals were consumed was essentially the same across all replicate tanks ($W = 0.52$, df = 9, $P < 0.01$) showing strong patterns of feeding preference among *A. planci*.

The removal of symbionts from coral colonies did not alter the overall pattern of feeding preferences of *A. planci*; within the control tanks *A. gemmifera* was still the most preferred coral species, and *S. pistillata* was the least preferred (Figure 3.3). However, when symbionts were removed, starfish consumed *A. nasuta*, *A. loripes*, *S. hystrix* and *P. damicornis* with apparently equal preference (Figure 3.3). The least preferred coral species, *S. pistillata*, was also eaten far more readily where symbionts had been removed. In tanks where corals contained symbionts, starfish consumed only 20% (4/20) of *S. pistillata* colonies, but where symbionts had been removed, starfish consumed 80% (16/20) of the *S. pistillata* colonies. Statistically, there was no significant difference in the combined ranks of the six coral species with their symbionts removed ($\chi^2 = 4.11$, df = 5, P = 0.53). Moreover, the order in which coral species were eaten differed greatly between replicate tanks (W = 0.09, df = 9, P = 0.39), further suggesting that starfish had no clear preference for one coral species over another. The feeding preferences of starfish in tanks where all coral symbionts were removed were significantly different from starfish in control tanks (W = 0.18, df = 19, p = 0.60), suggesting that coral symbionts do have a significant influence on the feeding preferences of *A. planci*.

### Manipulating symbionts

Experimental alteration of the symbiotic fauna in replicate colonies of the same coral species had a great impact on the feeding preferences of crown-of-thorns starfish. Differences in the feeding preferences of *A. planci* for *P. damicornis* colonies with different symbiont assemblages were highly significant ($\chi^2 = 30.74$, df = 4, $P < 0.01$), and the order in which different colonies were consumed was consistent across replicate tanks (W = 0.74, df = 9, $P < 0.01$). The most preferred colonies of *P. damicornis* were those containing either no symbionts or only the goby *P. ecinocephalus*. The least preferred colonies were those containing *Tr. cymodoce* (Figure 3.4). Starfish also tended to avoid colonies containing only *Alpheus* shrimps, but these colonies were always consumed before those containing *Tr. cymodoce*.

(a) with commensals



(b) without commensals

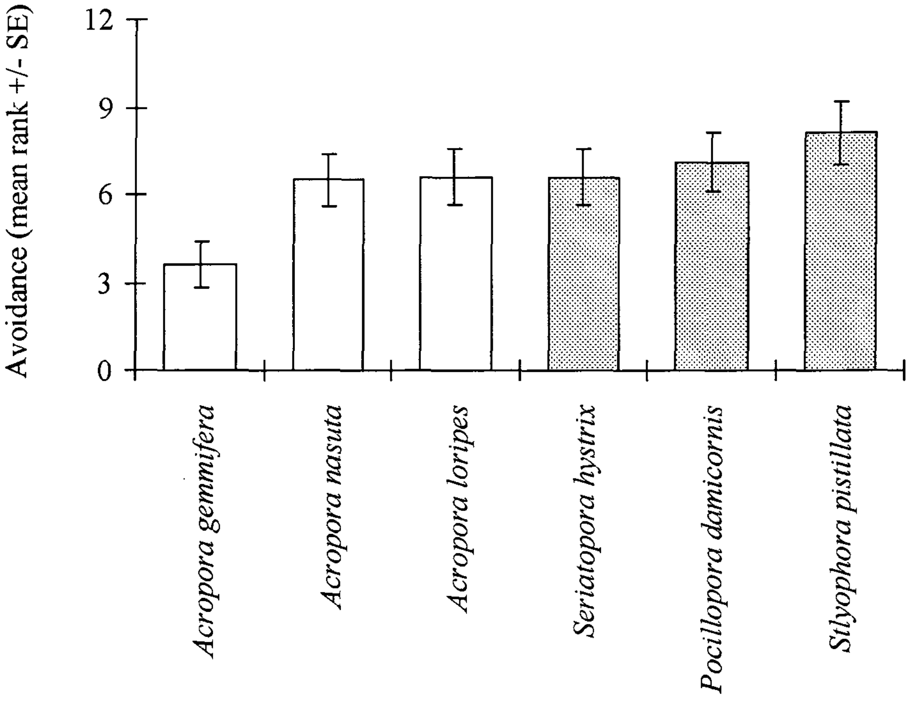
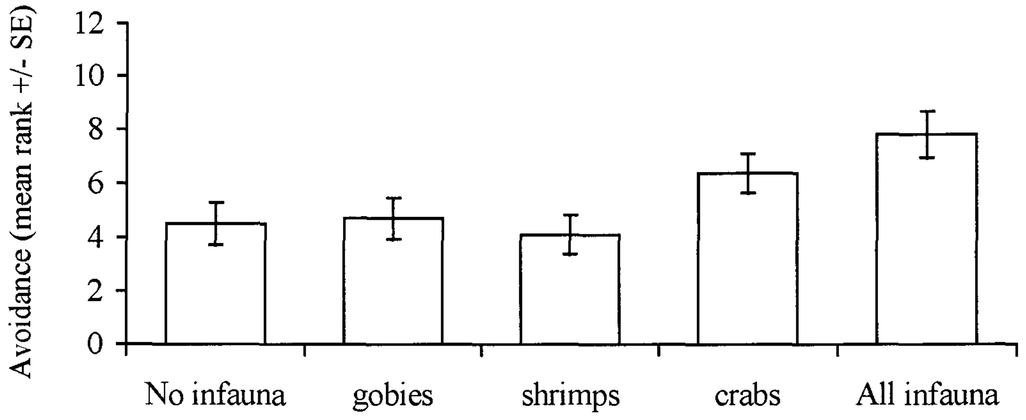


**Figure 3.3.** Variation in the average rank score (± SE) for different coral species showing relative avoidance by crown-of-thorns starfish in controlled feeding trials. Feeding preferences of starfish were compared firstly (a) between colonies which contained natural symbiont assemblages (with symbionts), and (b) between colonies with symbionts removed (without symbionts).

In trials using *A. nasuta*, colonies which contained only *G. histrio* or *Coralliocaris* sp. were consumed with equal preference by *A. planci,* to those colonies that did not contain any symbionts (Figure 3.4). However, starfish avoided colonies which contained *Tetralia fulva* (individually and with other symbionts). Colonies containing all symbionts (*T. fulva*, *Coralliocaris* sp. and *G. histrio*) were less preferred than colonies containing just *T. fulva* (Figure 3.4). Overall, there was a significant difference in the rank scores for *A. nasuta* colonies in each treatment ($\chi^2 = 10.98$, df = 4, P <0.05) and the order that colonies were eaten was consistent across replicate tanks (W = 0.52, df = 9, P <0.01).

The influence of coral symbionts on feeding preferences of *A. planci* were similar for both *A. nasuta* and *P. damicornis* in so much that colonies containing no symbiotic fauna were significantly preferred over those containing Trapeziidae crabs. Also, colonies of both coral species containing just coral gobies (*G. histrio* and *G. echinocephalus* respectively) were equally preferred to colonies containing no symbionts. However, starfish were significantly more selective in trials using *P. damicornis* than *A. nasuta* (W = 0.30, df = 19, p = 0.08). Clearly, starfish avoided *P. damicornis* colonies containing *Tr. cymodoce* (rank score = 8.5 ± 0.53 SE) far more than *A. nasuta* colonies containing *T. fulva* (rank score = 6.37 ± 0.72 SE). In addition, *A. planci* avoided *P. damicornis* colonies containing only *Alpheus* snapping shrimps, whereas they readily consumed *A. nasuta* colonies containing only *Coralliocaris* snapping shrimps.

(a) *Acropora nasuta*



(b) *Pocillopora damicornis*

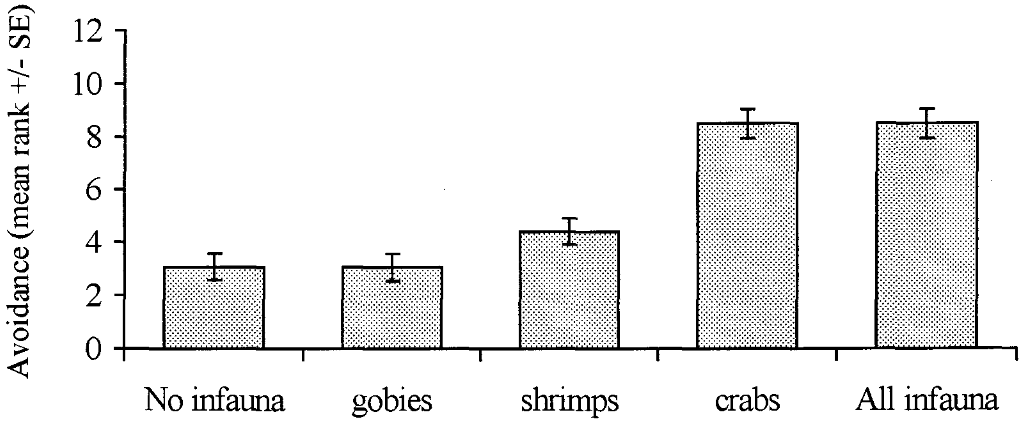


**Figure 3.4.** Variation in the average rank score (± SE) for colonies of each coral species which contained different symbiont assemblages, showing relative avoidance by crown-of-thorns starfish during controlled feeding trials. Feeding preferences of starfish were assessed using (a) *Acropora nasuta* and (b) *Pocillopora damicornis*.

## 3.5 DISCUSSION

Feeding preferences of crown-of-thorns starfish were very apparent from the well-defined and consistent sequence (across replicate tanks) in which they consumed the six coral species provided (*A. gemmifera* > *A. nasuta* = *A. loripes* > *S. hystrix* > *P. damicornis* > *S. pistillata*). Whereas previous studies have looked only at differences across broad taxonomic groups (e.g., acroporids versus pocilloporids versus poritids; Brauer et al. 1970, Collins 1975, Ormond et al. 1976, De'ath & Moran 1998), this study is the first to show that *A. planci* have very strong feeding preferences among closely related and morphologically quite similar coral species. This study has also used controlled feeding experiments to largely eradicate many of the factors (such as variation in the size, distribution and abundance of different corals) which may have confounded previous estimates of feeding preference (*sensu* Moran 1986) and re-affirms that *A. planci* do have strong feeding preferences.

The lack of feeding selectivity among coral species when coral symbionts were removed implies that feeding preferences of *A. planci* were determined to a large extent, by the differences in the effectiveness with which coral symbionts defended their particular host species (see also Glynn 1982, 1987). Given that feeding selectivity of *A. planci* for corals with their symbionts removed was not significant, any influence that other factors, such as the nutritional value, nematocyst defences, or chemical properties of these corals may have, must be very weak. Even so, *A. planci* do exhibit strong selectivity for chemical extracts of different coral species (Brauer et al. 1970), which must be caused by differences in either their nutritional value or chemical properties. Similarly, coral nematocysts have been shown to repel *A. planci* (Barnes et al. 1972). Rather than these finding being contradictory, it is likely that the importance of different factors in determining the feeding preferences of *A. planci* depends greatly on the coral species being considered.

*Acanthaster planci* consistently prefer *Acropora* corals over pocilloporids (e.g., Ormond et al. 1976, Keesing 1990, De'ath and Moran 1998) probably because of differences in the symbionts associated with these corals. In this study, coral symbionts from both *A. nasuta* and *P. damicornis* repelled starfish, but symbionts from the latter were much more effective. Differences in the symbiont assemblages of *Acropora* versus pocilloporids are consistent across a wide range of coral species (Knudsen 1967, Tsuchiya 1992). Most notably, *Acropora* species always contain *Tetralia* crabs (Sin 1999, Abele and Patton 1976) whereas pocilloporids usually contain *Trapezia* species (Abele and Patton 1976). The larger size (of both the carapace and chelipeds) of *Trapezia* species, compared to *Tetralia* crabs, may account for their increased efficacy in repelling *A. planci* (Glynn 1987). Moreover, behavioural observations have revealed that *Trapezia* crabs often attack the thorns of the starfish breaking them off at the pedicel, whereas *Tetralia* pinch mainly at the tube feet and, unlike *Trapezia*, do not cause any lasting damage to the starfish (Glynn 1982, Pratchett et al. 2000). The efficacy with which *Tetralia* and *Trapezia* crabs defended their respective host colonies also varied among species. This observation, together with findings that many commensal species exhibit a high degree of host specificity (Munday et al. 1997, Sin 1999, this study), accounts for observed differences in the feeding preferences of *A. planci* among individual coral species. The least preferred coral species, *Stylophora pistillata*, was nearly always occupied by *Trapezia cymodoce* which was the largest and most aggressive of the *Trapezia* crabs. *Trapezia cymodoce* were also found in *Pocillopora damicornis* but, individuals found in *P. damicornis* were much smaller than those found in *S. pistillata*. This difference in the size of crabs occupying different coral hosts may be related to the size of spaces between branches, whereby the smaller space between branches of *P. damicornis*, compared to *S. pistillata*, may limit the size of crabs that can occupy *P. damicornis* (Vytopil and Willis, In Press).

Individually, trapeziid crabs were far more effective at repelling crown-of-thorns starfish than either coral gobies or snapping shrimps. Even so, *Gobiodon histrio* and/or *Coralliocaris* did contribute to the defence of *Acropora nasuta*; *Acanthaster planci* avoided colonies containing all symbionts more strongly than colonies with only *Tetralia*. The synergistic effect of crabs with gobies and/or shrimp in defending *A. nasuta* from crown-of-thorns may be related to cooperation among symbionts, as proposed by Lassig (1977, 1981), whereby the gobies and/ or shrimps alert crabs to any potential intruders or corallivores (see also Vannini 1985). This hypothesis is supported from the findings of this study because neither *Gobiodon histrio* or *Coraliocaris* could repel *A. planci* themselves. In pocilloporid corals, both *Trapezia* crabs and *Alpheus* shrimps attack crown-of-thorns (Glynn 1980) and as shown in this study, both deter starfish from feeding on *P. damicornis*. Contrary to Lassig's (1981) suggestions, however, there was no synergistic effect of symbionts from *P. damicornis*, perhaps because *Trapezia* crabs can effectively detect approaching *A. planci* in small colonies of this coral species and effectively defend colonies without the assistance of other symbionts. There was also no evidence that *Paragobiodon echinocephalus* contributed to the defence of *P. damicornis* (but see Lassig 1981).

The species of *Trapezia* found in pocilloporid corals on the Great Barrier Reef include many of the same species (except for a few uncommon endemic species) as those which protect pocilloporids in the eastern Pacific (Garth 1974). Moreover, the effectiveness of *Trapezia* crabs in repelling *A. planci* appears to be consistent across broad geographical boundaries. In Guam, *A. planci* consume *Pocillopora eydouxi* and *Stylophora mordax* 2-3 times more if symbionts (including *Trapezia*) are removed (Glynn 1982). Similarly on the Great Barrier Reef, *P. damiconis* colonies with symbionts removed were preferred 2.8 times over colonies containing *Trapezia* (Figure 3.4). In Panama, however, the protection provided by coral symbionts, combined with outbreaks of *A. planci*, has increased the dominance of pocilloporid corals (Glynn 1974, 1976). Whereas, on the GBR, *Pocillopora* are commonly consumed during starfish outbreaks (see Keesing 1990, De'ath & Moran 1998) and *Acropora* corals virtually always dominate shallow-water coral communities (Done 1982). Increased consumption of pocilloporid corals by *A. planci* on the GBR, may relate to the higher intensity of outbreaks, compared to reefs elsewhere in the Pacific, because at higher densities crown-of-thorns starfish increasingly feed on less preferred coral species (reviewed by Birkeland & Lucas 1990).

Despite the protection provided by coral symbionts, *Acropora* and pocilloporid corals appear to be among the most highly preferred prey of *Acanthaster planci*, compared to other corals such as poritids and favids which are strongly avoided (see reviews by Potts 1981, Moran 1986, Birkeland & Lucas 1990). Poritids also contain symbiotic organisms (*Pedum spondyloideum* and *Spirobranchus giganteus*), but rather than preventing *A. planci* from eating their host colony, these organisms enhance the survivorship of only a few adjacent coral polyps which may enable subsequent regeneration of the colony (Devantier et al. 1986, DeVantier & Endean 1988). The avoidance of poritids by *A. planci* is currently ascribed to their low nutritional value and/ or the presence of chemical deterrents to feeding (De'ath & Moran 1998). Controlled experiments, like the one conducted in this study, will be required to resolve why *Porites* (and faviids) are avoided by *A. planci*, but whatever the reason(s), it is clear that many coral species are avoided far more than either *Acropora* or pocilloporids. Therefore, the size, abundance, accessability, the nematocyst or chemical defences, morphology (texture, shape, tissue thickness etc.) or the nutritional value of corals, may be far more important than symbiont defence in determining the overall feeding preferences (across the broad range of different coral species) for *A. planci*.

This study has demonstrated that the feeding preferences of *A. planci*, for the six coral species examined, are influenced primarily by differences in their symbiotic assemblages. Although coral symbionts effectively deter starfish from feeding on their host corals, these corals are not totally immune to crown-of-thorns attack and are readily eaten when coral prey is limited. Consequently, coral symbionts are most likely to influence the feeding preferences and ecological impacts of *A. planci* when starfish are below outbreak densities or coral prey is abundant.

# CHAPTER 4. Variable responses to resource depletion in a guild of corallivorous fishes[†]

## 4.1 ABSTRACT

Benthic communities on tropical coral reefs are subject to frequent and often catastrophic disturbances, resulting from human impacts, cyclones, or infestations of crown-of-thorns starfish (*Acanthaster planci* L.). Despite a close association between reef fish and benthic habitats, there has been little consideration for how disturbances to benthic reef habitats affect reef fishes. This study examined long-term changes (over 5 years) in the structure and dynamics of a guild of corallivorous butterflyfish at a reef infested by crown-of-thorns starfish. Depletion of scleractinian corals by *A. planci* caused significant reductions in the abundance of seven butterflyfish species (*Chaetodon auriga*, *C. citrinellus*, *C. kleinii*, *C. plebeius*, *C. rainfordi*, C. *trifascialis*, and *C. unimaculatus*), whereas there was no change in the abundance of *C. aureofasciatus*, C. *baronessa*, *C. ephippium*, *C. lunulatus*, *C. melannotus* or *C. vagabundus*. *Chaetodon s*pecies affected by coral depletion had a high dependence on live coral either for food (*C. citrinellus*, *C. kleinii*, *C. plebeius* and *C. trifascialis*) or habitat (*C. auriga*). However, impacts of coral depletion on corallivorous butterflyfish varied with their degree of feeding specialisation. For example, declines in the abundance of the coral-feeding specialist *C. trifascialis* were much more pronounced than declines in the abundance of the generalist coral feeding species *C. baronessa*. *Chaetodon baronessa* responded to the depletion of prey resource by expanding both the range of prey it consumed and also its depth distribution, thereby mediating impacts of resource depletion on its population size. This study demonstrates that disturbances to benthic habitats can impact on populations of reef fishes, but the extent of the impact varies among fish species in accordance with differences in their feeding, population and behavioural ecology.

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[†] Results of this study form the basis of a manuscript titled "Niche partitioning and resource depletion in a guild of corallivores" being prepared for submission to the journal *Oecologia*.

## 4.2 INTRODUCTION

Disturbances have a pervasive influence on the structure and dynamics of ecological communities in a wide range of environments (e.g., Sousa 1984, Pickett and White 1985, Karlson and Hurd 1993). This is particularly apparent on tropical coral reefs, which are subject to many and varied forms of disturbance operating across a wide range of temporal and spatial scales (see reviews by Stoddart 1969, Connell and Keough 1985, Karlson and Hurd 1993, Brown 1996). Chronic small scale disturbances (e.g. tidal exposure, wave action and predation) generate fine-scale (within reef) patterns in the distribution and abundance of many coral reef organisms (Done 1982, 1983, Huston 1985, Acevedo and MorLock 1988). Whereas, acute and often catastrophic disturbances (e.g., severe tropical storms, freshwater plumes, and unseasonal temperature extremes) generate over-riding patterns in the composition and structure of coral reef communities, particularly among benthic assemblages of sessile invertebrates (Loya 1976, Porter et al. 1982, Kaufman 1983, Hughes 1989, Dawson-Shepherd et al. 1992, Bythell et al. 1993, Connell et al. 1997). Importantly, catastrophic disturbances may contribute to increased diversity by freeing up space for subsequent colonisation and thereby preventing competitive exclusion of subordinate species (Rogers 1993, Tanner et al. 1994). Such disturbances may also affect the distribution and/ or abundance of mobile animals living in close association with coral reef substrates (e.g., Kaufman 1983, Lassig 1983, Dawson-Shepherd et al. 1992). However, despite considerable research of disturbance related changes in the structure and dynamics of benthic assemblages of sessile invertebrates (e.g. Connell and Keough 1985, Done 1992, Connell et al. 1997, Hughes and Connell 1999), very little attention has been given to the impacts of natural disturbances on mobile reef animals, such as coral reef fishes (Williams 1986).

Aside from being impacted directly by major disturbance events (e.g., Lassig 1983, Walsh 1983), mobile reef organisms may feel the effects of major disturbances through alterations to coral reef substrates (Syms and Jones 2000). There is considerable correlative evidence linking the distributions and abundances of coral reef fish with variation in the biological composition and/ or physical structure of coral reef substrates (e.g., Caley and St. John 1996, Ault and Johnson 1998b, Öhman and Rajasuriya 1998, Munday 2000, Holbrook et al. 2000). In the most recent example, Holbrook et al. (2000) demonstrated that spatial variation in the abundance of certain scleractinian corals (defined as coarse branching corals) accounted for up to 78% of variation in adult abundance of the coral-dwelling damselfish, *Dascyllus aruanus* (family Pomacentridae). These correlations suggest, but do not demonstrate, that benthic habitats have an important influence on distributions and abundances of coral reef fishes. The best evidence that benthic habitats are important in structuring reef fish assemblages, come from studies showing that changes in benthic habitats are reflected in changes in the distribution and/ or abundance of specific fish species (e.g., Williams 1986, Clarke 1996, Munday et al. 1997). Temporal variation in the biological and physical structure of benthic communities is, however, generally very conservative (Connell et al. 1997), and so such studies are very rare. Experimentally induced disturbances (e.g., Tricas 1985, Lewis 1997, Syms 1998, Syms and Jones 2000) have proved useful in showing the influence of habitat structure on fish assemblages. In particular, these experiments provide valuable insights into the mechanisms involved in the habitat structuring of reef fish assemblages (*ibid*), but they are necessarily limited in scale and may have little ecological relevance to natural processes. Studies of large-scale natural disturbances that dramatically alter the habitat structure of coral reef environments, but do not impact directly on reef fish populations (e.g. bleaching events and infestations of *A. planci*), will provide invaluable information on the processes affecting community structure of coral reef fishes (e.g., Williams 1986).

Outbreaks of the crown-of-thorns starfish, *Acanthaster planci* represent one of the most significant biological disturbances on tropical coral reefs, not only killing large areas of reef corals, but also drastically altering the biological and physical structure of reef environments (Pearson 1981, Moran et al. 1988). Outbreaks of *A. planci* have been recorded on many reefs throughout the Indian and Pacific oceans, and almost invariably caused significant declines in the abundance of scleractinian corals (reviewed by Moran 1986). In extreme cases, outbreak populations of *A. planci* have killed more than 90% of scleractinian corals over expansive areas (e.g., Pearson and Endean 1969, Chesher 1969, Randall 1973, Colgan 1987). At Green Island (northern GBR), for example, outbreak populations of *A. planci* killed approximately 80% of scleractinian corals across the entire reef, from the shallow reef crest (<2 metres depth), down to a depth of 40 metres (Pearson and Endean 1969). Following attack by *A. planci*, the exposed skeleton of scleractinian corals are highly susceptible to biological erosion (Hutchings 1986), which may eventually (after several years) cause the complete collapse of coral structures (e.g. Sano et al. 1987). At Irimote Island, Japan, outbreaks of *A. planci* reduced entire areas of once prolific coral growth to wide expanses of dead coral rubble (Sano et al. 1987). Not surprisingly, Sano et al. (1987) found that there were significantly fewer fishes living on these rubble banks, compared to nearby reefs where coral cover was in excess of 80%. Even short-term reductions in live coral cover, caused by outbreaks of *A. planci*, are likely to impact on coral reef fishes, particularly those fish species with a direct reliance on scleractinian corals (Sano et al. 1984, Bouchan-Navaro et al. 1985, Williams 1986).

Among those fishes with the greatest reliance on scleractinian corals are butterflyfish from the genus *Chaetodon* (family Chaetodontidae), many of which, feed almost exclusively on scleractinian corals (Birkeland & Neudecker 1981). *Chaetodon* butterflyfish, generally, feed on a wide variety of different prey, including zooplankton, polychaetes, small crustaceans, algae, soft corals, scleractinian corals and gorgonians (Hobson 1974, Anderson *et al.* 1981). However, most butterflyfish feed, at least in part, on scleractinian corals (e.g., Reese 1975, 1977, Neudecker 1977, 1979, 1985, , Harmelin-Vivien & Bouchan-Navaro 1981, 1983, Gore 1984, Anderson et al. 1981). Trophic analysis of 20 different *Chaetodon* species from the Great Barrier Reef by Anderson et al. (1981), revealed that eight of the species (40%) were obligate corallivores, feeding almost exclusively on scleractinian corals. A further eight species (40%) were facultative corallivores, feeding mostly, but not exclusively on scleractinian corals, while only four (20%) of the species did not consume any scleractinian coral (Anderson et al. 1981). Given their reliance on corals for food, as well as evidence suggesting that butterflyfish may be food limited (e.g., Tricas 1985, Irons 1989), many authors have argued that spatial and temporal patterns in the abundance of butterflyfish should be tightly correlated with the availability of coral prey (e.g., Hourigan et al. 1988, Crosby and Reese 1996, Öhman et al. 1998). Both, local and regional scale distributions of *Chaetodon* butterflyfish have been correlated with the abundance of live coral cover (Birkeland and Neudecker 1981, Bouchan-Navaro et al. 1985, Findley & Findley 1985, Bouchan-Navaro & Bouchan 1989, Cadoret et al. 1999; but see Bell et al.

1985, Fowler 1990). Previous studies (e.g., Bouchan-Navaro et al. 1985, Williams 1986) have also shown that abundances of specific butterflyfish species (particularly, obligate coral feeding species) are significantly reduced on reefs affected by crown-of-thorns starfish (see also Sano et al. 1984, 1987). Williams (1986) proposed that these declines are caused by reductions in the availability of prey corals. However, temporal declines in the abundance of butterflyfish species have never been explicitly related to changes in the abundance of their specific prey corals.

This study examines changes in the distribution and abundance of *Chaetodon* butterflyfish, associated with the natural depletion of scleractinian corals caused by outbreak populations of *A. planci*. The specific purpose of this study was to test whether densities of butterflyfish reflect changes in the availability of their specific prey corals. Therefore, it was first necessary to assess the dietary composition and specific feeding preferences of different butterflyfish species. Sampling of both butterflyfish and coral assemblages was then undertaken at regular intervals throughout the entire course of an outbreak of *A. planci*. If distributions and abundances of *Chaetodon* butterflyfish are strongly influenced by the availability of their prey corals, densities of *Chaetodon* butterflyfish would be expected to decline in direct response to any reductions in the availability of their prey coral. Impacts of *A. planci* in coral reef environments are, however, very patchy (Moran 1986). Most notably, the impacts of *A. planci* are unequally apportioned among different coral species (e.g., Glynn 1974, 1976, Ormond et al. 1976, Colgan 1987, De'ath and Moran 1998). Furthermore, corals within specific reef zones (mostly on the reef flat) are generally protected from crown-of-thorns starfish by physical limitations (e.g., wave action) to the distribution of starfish (Endean and Stablum 1973, Moran et al. 1985 see also Chapter Two). *Chaetodon* butterflyfish could, therefore, mediate the potential impacts of local coral depletion either by moving to areas that are relatively unaffected by *A. planci,* and/ or by utilising prey species which are generally not eaten by crown-of-thorns starfish.

Previous studies on the feeding behaviour of butterflyfish (e.g., Birkeland & Neudecker 1981,Tricas 1985, Irons 1989, Pratchett 1995), have shown that corallivorous butterflyfish often exhibit specific preferences for particular coral species (but see Gore 1984, Hourigan 1987). In general, butterflyfish favour corals of the family Acroporidae, and also Pocilloporidae (Randall 1974, Irons 1989, Pratchett 1995), which are also the among the most preferred prey of crown-of-thorns starfish (see Chapter Three). As a consequence, outbreaks of crown-of-thorns starfish are likely to have a significant impact on availability of coral prey for corallivorous butterflyfish (see Williams 1986). However, not all butterflyfish exhibit specific prey preferences (Gore 1984, Hourigan 1987). Birkeland and Neudecker (1981) divided corallivorous butterflyfish into two groups; i) specialist species, which consistently favour certain corals whether these corals are common or rare, and ii) generalist species which eat a wider range of different corals, mostly in accordance with their proportional availability in the environment. The impacts of disturbances on sympatric species are likely to vary between specialists and generalists, as has been demonstrated in a number of environments (reviewed by MacNally 1995). Specialist butterflyfish species would be expected to be disproportionately impacted by reductions in the availability of their preferred corals (Hourigan et al 1988). Whereas, generalist species may be able to switch feeding from one coral species to another, with changes in the relative abundance of different corals (Hourigan et al. 1988). As a consequence, the local abundance of generalist species is likely to be affected only in cases where there is extensive reductions in the availability of all corals species (e.g., Sano et al. 1987). This paper tests the prediction that specialist species are impacted disproportionately more than generalist butterflyfish, examining temporal variation in not only the abundance of different butterflyfish, but also in their patterns of prey preference.

## 4.3 METHODS

This study was conducted from February 1995 until February 1999, at Lizard Island (14°40'S, 145°27'E), on the northern Great Barrier Reef (GBR) Australia. Sampling was carried out at each of four locations (North Reef, Washing Machine, Lizard Head and South Island), separated by 0.5-8 kilometres along the exposed (south-east) side of Lizard Island (Figure 4.1). Four distinct physiognomic reef zones (the reef flat, reef crest, reef slope and reef base) were apparent at each of the four locations (Figure 4.1). The reef flat zone (1-3m depth) represented an area of low relief comprised predominantly of carbonate pavement, which extended seaward for 20-200 metres from the low water mark ending in a slightly raised reef crest. The reef crest zone (1-3m depth) represented a 5-8m wide strip of topographically complex habitat extending along the seaward edge of the shallow reef front. The reef slope (3-11m depth) represented the almost vertical reef face, which ended where the contiguous reef matrix met the loose substrate at the reef base. The reef base (8-16 m depth) was a gently sloping area, comprised of sand or coral rubble, where occasional corals had become established to form isolated bombies.

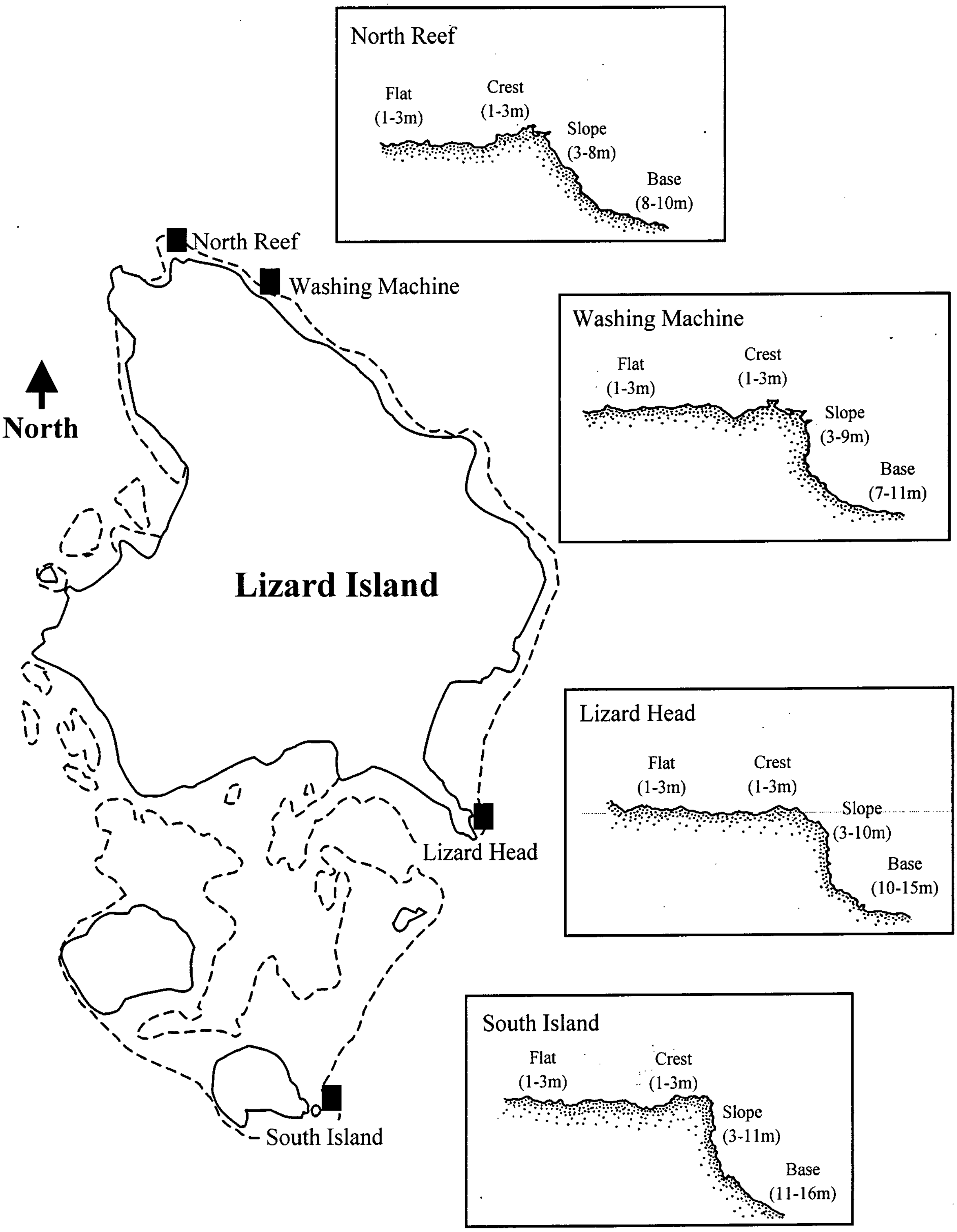

**Figure 4.1.** Map of Lizard Island showing reef profiles at each of the four locations used to assess temporal variation in the abundance of *Chaetodon* butterflyfish.

## Sampling design

To document temporal variation in the distribution and abundance of *Chaetodon* butterflyfish, detailed surveys were conducted in January or February of each year from 1995 to 1999. During each survey, I recorded the abundance of butterflyfish at each of the four reef zones (flat, crest, slope and base), within each of the four different locations (North Reef, Washing Machine, Lizard Head and South Island). To measure the distribution and abundance of butterflyfish I used replicate 50m × 4m belt transects. Five replicate transects were run in each zone, at every location, in each year. Transects were orientated parallel to the reef crest, and run from a haphazardly selected starting point within each zone. To census butterflyfish I swam slowly (~0.2 metres/ second) along the centre of the transect and recorded all butterflyfish species seen within a four metre wide path, following Brock (1982), However, recently settled butterflyfish are generally cryptic and usually require much more intensive searching (Fowler 1988), and therefore, in this study I counted only butterflyfish that were greater than 50 mm in total length.

Variation in the community structure of butterflyfish assemblages, among zones, among locations and among years, was analysed using multivariate analysis of variance (MANOVA). Significant variation in the structure of benthic assemblages was then displayed using canonical discriminant analysis (CDA), but instead of using traditional bi-plots, I plotted variation in the first canonical variate along a time series (see also Syms and Jones 2000), thereby explicitly showing temporal variation in the structure of butterflyfish assemblages at each depth and each location. Having shown there was significant variation in community structure, I then examined temporal variation in the individual abundance of each butterflyfish species, to reveal their individual responses to disturbances caused by infestations of *A. planci*.

To relate spatial and temporal variation in the abundance of butterflyfish to variation in benthic assemblages, I also quantified changes in the abundance of sessile invertebrates (scleractinian corals, alcyonaceans, gorgonians and hydrozoans) among zones, locations and years. Benthic assemblages were sampled using replicate 10 metre line intercept transects, with 10 replicate transects run in each reef zone, at each location, in every year. On each transect (n = 800 transects), every sessile invertebrate underlying the transect tape was identified, and the intercept length was measured to the nearest centimetre. Variation in the abundance of *Chaetodon* butterflyfish was then compared to changes in the abundance and species composition of benthic reef assemblages using linear regression.

**Patterns of prey use**

The range of prey types eaten by *Chaetodon* butterflyfish, and their proportional use of each prey type, was ascertained from patterns of feeding during field observations of individual fish, following Hourigan (1987). Most butterflyfish continued to feed despite the divers presence, but observations were aborted when ever fish fled from the diver or sought shelter within the reef matrix. A total of thirty replicate fish of each of eight different species were observed during each of three different sampling occasions (1995, 1997 and 1999). The specific butterflyfish species (*Chaetodon auriga*, *C. baronessa*, *C. citrinellus*, *C. kleinii*, *C. lunulatus*, *C. plebeius*, *C. trifascialis*, and *C. vagabundus*) were selected based on their high abundance in 1995.

During feeding observations, I followed each individual fish for three minutes at a distance of 2-3 metres, recording the total number of bites taken from each species of scleractiniain coral, alcyonacean, gorgonian or hydrozoan. I also recorded the number of bites taken from substrates that were not obviously occupied by any macro-invertebrates, which are hereafter referred to as “bare substrate”. Previous studies (e.g., Purcell 1996) have demonstrated that bare substrates are extensively occupied by small turfing algae, which support small motile invertebrates, microbes and/ or detritus. No attempt was made to identify the specific source of prey for butterflyfish feeding on "bare substrate" though it was assumed that they were targeting small non-coral invertebrates (e.g., polychaetes and crustaceans), following Hobson (1974), Birkeland & Neudecker (1981) and Motta (1988).

Temporal variation in the feeding patterns of each butterflyfish species were analysed using multivariate analysis of variance (MANOVA), to specifically test whether the proportional use of different prey categories varied among years. I also assessed whether butterflyfish exhibited significant feeding selectivity, using the log-likelihood statistic ($X^2_{L2}$), calculated using the formula

$$X^2_{L2} = 2\sum_{j=1}^{n}\sum_{i=1}^{I} u_{ij} Ln\{u_{ij} / E(u_{ij})\}$$

where $u_{ij}$ is the proportional use of each prey type ($i$) by each individual ($j$), and $E(u_{ij})$ is the expected number of bites taken from prey type $i$ by the $j$th individual if use is proportional to availability (Manly et al. 1993). The resulting value of $X^2_{L2}$ was compared to the chi-squared distribution with $n(I-1)$ degrees of freedom to determine the significance of selectivity exhibited by each butterflyfish species. Where log-likelihood statistics revealed that butterflyfish were feeding selectively, I then used resource selection functions (Manly et al. 1993) to determine which prey categories were used more or less frequently than expected.

Resource selection functions ($w_i$) were calculated for each prey category ($i$) used by each species of butterflyfish, using the formula:

$$w_i = u_i / \pi_i$$

which compares the proportional use ($u_i$) of each prey category ($i$) with the proportional availability of that prey category ($\pi_i$) within the local area (at North Reef). I also calculated Bonferroni corrected 95% confidence intervals around each selection function, following Manly et al. (1993), whereby the use of a particular habitat was only deemed to be disproportionate to its availability if the 95% confidence interval did not encompass 1 (Manly *et al.* 1993). Selection functions significantly greater than 1 indicated that corals were consumed more than expected from their availability, while selection functions significantly less than 1 indicated that corals were consumed significantly less than expected.

### Butterflyfish abundance and prey availability

To test whether variation in the abundance of butterflyfish was related to variation in the availability of prey, I used multiple linear regression to compare the abundance of each of the eight *Chaetodon* species (*C. auriga*, *C. baronessa*, *C. citrinellus*, *C. kleinii*, *C. lunulatus*, *C. plebeius*, *C. trifascialis*, and *C. vagabundus*) with each of 12 different prey categories (*Acropora cytherea*, *A. nasuta*, *A. florida*, *A. gemmifera*, *A. hyacinthus*, *A. intermedia*, *A. millepora*, *Goniastre retiformes*, *Montipora* spp., *Pocillopora damicornis*, *Porites* spp. and bare substrate). Best subsets multiple regression was used to assess which combination of the 12 prey categories accounted for most variation in the abundance of each butterflyfish species, using Mallow's $C_p$ as the test statistic. Using the best subset of habitat variables for each butterflyfish species, I then measured the proportion of variation in the abundance of butterflyfish that could be attributed to variation in prey availability.

## 4.4 RESULTS

At the time this study was initiated (January 1995), very few crown-of-thorns starfish were seen anywhere around Lizard Island. However, reef wide surveys conducted in November 1994, by Sweatman et al. (1996), revealed that densities of *A. planci* ($\bar{x}$ = 0.25 starfish per 200m$^2$) were several orders of magnitude higher than had been recorded at any time since 1986. Furthermore, densities of *A. planci* continued to increase from July 1995 to December 1996, by which time elevated starfish densities were apparent at several locations around Lizard Island (Chapter Two). At the four locations considered during this study (North Reef, Washing Machine, Lizard Head and South Island), mean densities of starfish ranged from 0.19 (± 0.07 SE) starfish per 200m$^2$ at Washing Machine, up to 0.88 (± 0.27 SE) starfish per 200m$^2$ at South Island. At three (out of 4) of the locations (North Reef, Lizard Head and South Island), starfish densities significantly exceeded the threshold density of 0.8 starfish per 200m$^2$ (or 40 starfish ha$^{-1}$) that is considered to be the maximum sustainable density of *A. planci* on reefs in the GBR (Moran and De'ath 1992). These outbreak densities persisted for several months, causing dramatic declines in the abundance of scleractinian corals (Table 4.1), and also significantly altering the biological structure of coral communities (Table 4.2). In contrast, at Washing Machine, starfish densities of *A. planci* were consistently less than 0.8 starfish per 200m$^2$ throughout the entire course of the study, and as a consequence, there was little observable impact of *A. planci* on coral communities (Figure 4.2).

Overall, the mean cover of scleractinian corals (averaged across all locations and zones) declined by 31%, from a mean of 25.1% cover (± 1.3 SE) in January 1995 down to 17.3% cover (± 0.7 SE) in January 1999. However, variation in the extent of coral depletion varied significantly among locations, and also among reef zones (Table 4.1). Among locations, the greatest declines in live coral cover were seen at South Island and North Reef, where coral cover (for all zones combined) declined by 42% between 1995 and 1999. In contrast, live coral cover declined by just 26% at Lizard Head over the same period. At Washing Machine, live coral cover was very constant throughout the course of the study (Figure 4.2). Variation in the extent of coral depletion observed among reef zones varied with respect to locations. At North Reef, proportional declines in coral cover were fairly similar across all reef zones, ranging from 30% on the reef flat to 53% on the reef base. In contrast, at South Island, the extent of coral depletion varied greatly among reef zones. Proportional declines in the abundance of corals were always greatest on the reef base (consistently >50%, even at Washing Machine), but absolute changes in live coral cover were very small because coral cover was very low on the reef base from the start (Figure 4.2).

**Table 4.1.** Three way ANOVA to explore variation in the availability of live coral cover. Data was arcsine transformed prior to analysis, "*" indicates significant effects (*p<0.05, **P<0.01, ***p<0.001).

| Source | df | MS | F |
|---|---|---|---|
| Year | 4 | 1764.62 | 20.82*** |
| Location | 3 | 1639.29 | 19.34*** |
| Zone | 3 | 13556.03 | 159.96*** |
| Year × Location | 12 | 159.23 | 1.88* |
| Year × Zone | 12 | 189.45 | 2.23** |
| Location × Zone | 9 | 331.41 | 3.91*** |
| Year × Location × Zone | 36 | 94.95 | 1.12 |
| Error | 640 | 84.75 | |

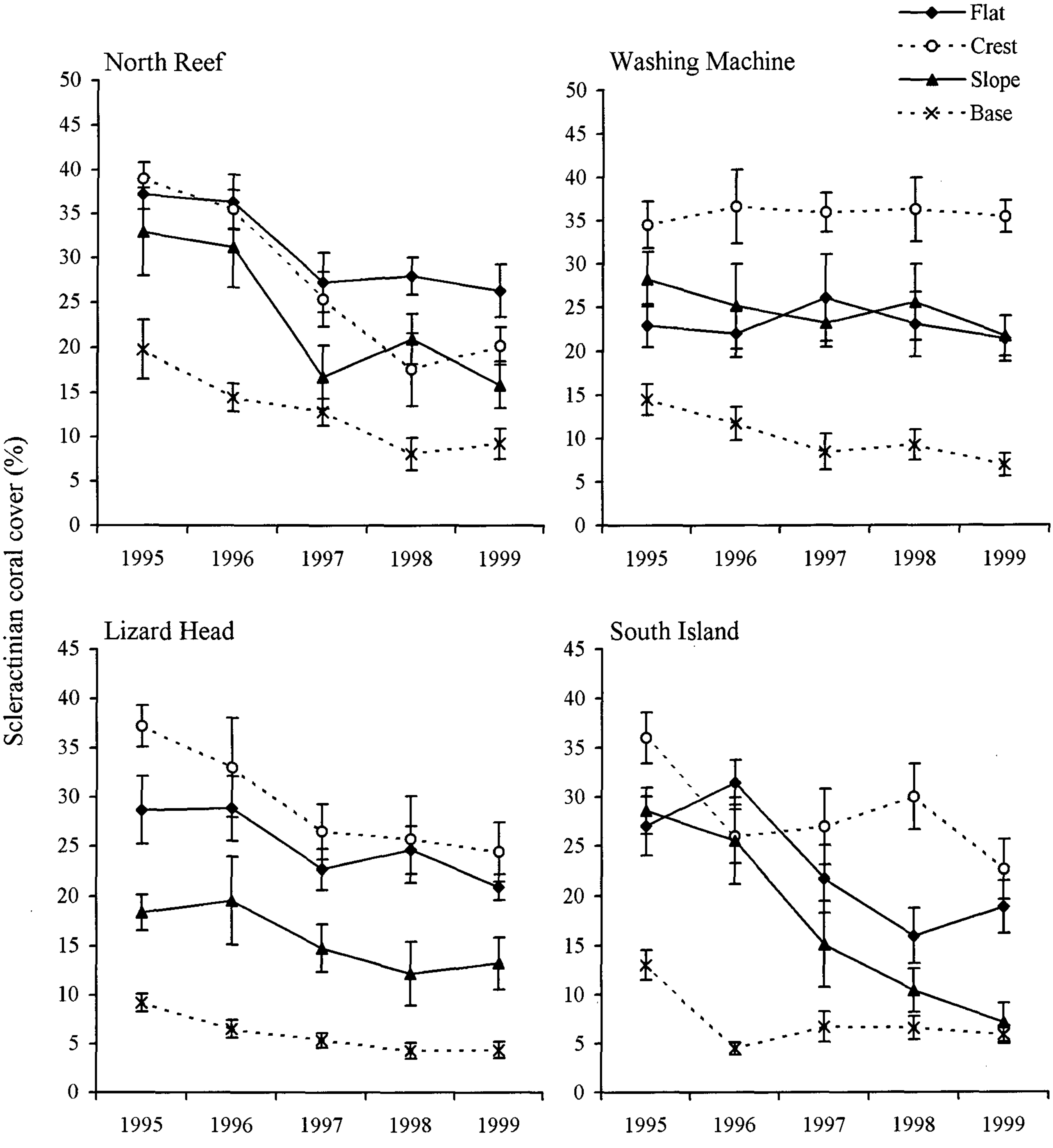

**Figure 4.2**. Temporal variation in mean area cover of scleractinian corals (+/- SE) at each zone, at every location, n = 10 transects in each year.

In addition to changes in the total abundance of scleractinian corals, there was also significant temporal variation in the composition and structure of coral assemblages (Table 4.2). CDA revealed that temporal variation in the community structure of benthic communities was greatest at North Reef and South Island, and varied relatively little at Lizard Head or Washing Machine (Figure 4.3). Temporal variation in the structure of coral communities also varied among zones within each location (Table 4.3). However, there was a fairly consistent downward trend of changes in community structure (relative to the first canonical variate), suggesting that *A. planci* had similar affects in all zones. Temporal variation in the structure of benthic communities was due primarily to declines in abundances of *Acropora hyacinthus*, *Montipora* spp. *A. nasuta* grp, *A. formosa* grp., *A. cytherea*, and *Pocillopora damicornis*, and increases in the relative abundances of the soft corals *Sinularia* spp., *Sarcophyton* spp. and the massive coral *Diploastrea heliopora* (Table 4.3). Each of the former species (*A. hyacinthus*, *Montipora* spp. *A. nasuta* grp, *A. formosa* grp., *A. cytherea*, and *P. damicornis*) are readily eaten by *A. planci* and exhibited significant declines in abundance during this study.

**Table 4.2.** Three way MANOVA to explore temporal and spatial variation in the relative abundance of benthic taxa. Data was arcsine transformed prior to analysis, "*" indicates significant effects (*p<0.05, **P<0.01, ***p<0.001).

| Source | Pillai's Trace | df | F |
|---|---|---|---|
| Year | 2468 | 104 | 3.21*** |
| Location | 1848 | 78 | 4.25*** |
| Zone | 1848 | 78 | 16.73*** |
| Year × Location | 7500 | 312 | 1.61*** |
| Year × Zone | 7500 | 312 | 1.84*** |
| Location × Zone | 5598 | 234 | 3.28*** |
| Year × Location × Zone | 16614 | 936 | 1.36*** |

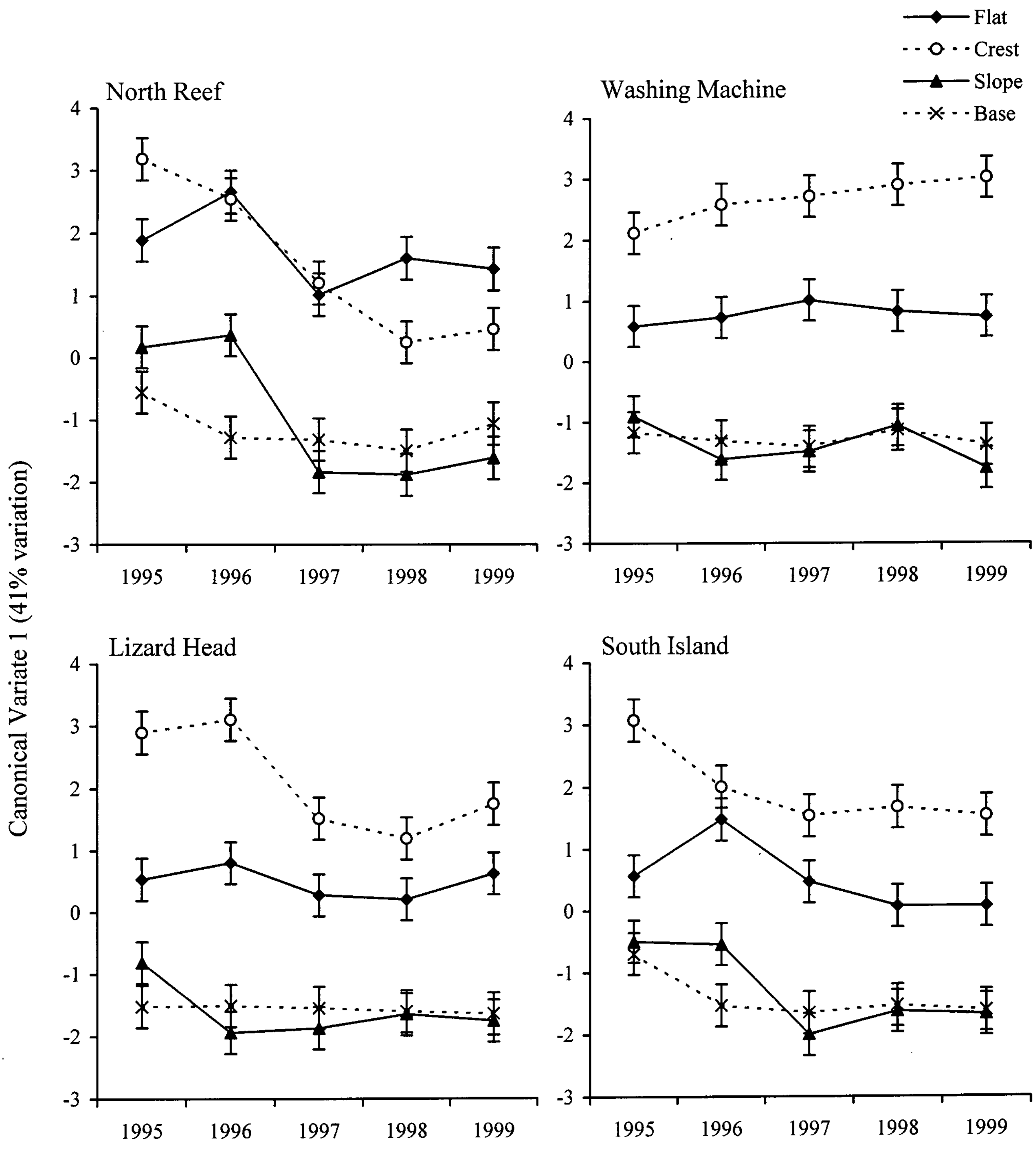

**Figure 4.3**. Canonical discriminant analysis (CDA) showing temporal variation in the structure of coral communities. Only the first canonical variate (explaining 41.2% of variation) is presented to emphasise the temporal aspect of the data. Error bars represent 95% confidence limits around canonical scores.

**Table 4.3.** Structure coefficients of benthic categories used in CDA of benthic communities. Coral species are ranked according to their correlation with the first canonical axis. Coefficients greater than ±0.22 are considered significant ($\propto = 0.05$) and are shown in bold. F-statistics are provided as an indication of relative variation seen in the abundance of each taxon among years, among locations and among zones (*p<0.05, **p<0.01, ***p<0.001).

| Taxa | Correlation with first canonical variate | F-statistic |
|---|---|---|
| ***Acropora hyacinthus*** | **0.61** | **2.02***** |
| ***Montipora* spp.** | **0.42** | **1.63*** |
| ***Acropora nasuta* grp** | **0.29** | **1.77**** |
| ***Acropora formosa* grp** | **0.23** | **1.96**** |
| ***Acropora cytherea*** | **0.23** | **1,26** |
| ***Pocillopora damicornis*** | **0.23** | **2.28***** |
| Other *Pocillopora* spp. | 0.19 | 1.53 |
| *Seriatopora hystrix* | 0.10 | 2.37*** |
| *Acropora aspera* grp | 0.09 | 1.18 |
| *Favites* spp. | 0.08 | 2.54*** |
| *Goniastrea* spp. | 0.05 | 1.79** |
| *Acropora latistella* grp | 0.05 | 1.81** |
| *Acropora robusta* grp | 0.05 | 1.63* |
| *Acropora formosa* grp | 0.04 | 1.71** |
| *Astreopora* spp. | 0.04 | 1.04 |
| *Acropora loripes* grp | 0.04 | 0.92 |
| *Stylophorai pistillata* | 0.03 | 0.62 |
| *Favia* spp. | -0.01 | 1.65 |
| *Acropora florida* grp | -0.02 | 0.69 |
| *Acropora divaricata* grp | -0.03 | 0.86 |
| *Goniopora* spp. | -0.05 | 0.84 |
| *Porites* spp. | -0.06 | 1.23 |
| *Symphyllia* spp. | -0.10 | 0.63 |
| *Lobophyllia* spp. | -0.11 | 0.98 |
| *Sarcophyton* spp. | -0.14 | 0.95 |
| *Sinularia* spp. | -0.19 | 1.09 |
| ***Diploastrea* spp.** | **-0.22** | **0.60** |

## Temporal variation in butterflyfish abundance

Corresponding with the declines in the abundance of scleractinian corals, this study revealed significant temporal declines in the abundance *Chaetodon* butterflyfish (Table 4.4). From 1995 to 1999, overall densities of butterflyfish (all species combined) almost halved, declining from a mean of 13.6 (± 0.6 SE) fish per $200m^2$ in 1995, down to 8.6 (± 0.5 SE) fish per $200m^2$ in 1999. Declines in butterflyfish abundance, particularly among locations, closely followed changes in live coral cover (Figure 4.4). For example, declines in the butterflyfish abundance were most pronounced at North Reef and South Island (Figure 4.4), as was the case for live coral cover. Also, at Washing Machine, where there were only very slight changes in the abundance of scleractinian corals, there was also very little change in the abundance of *Chaetodon* butterflyfish (Figure 4.4). In all, there was a very strong and positive relationship between the butterflyfish abundance and live coral cover ($r^2 = 0.78$, $n = 20$), whereby changes in the mean densities of *Chaetodon* butterflyfish, at each location, were directly proportional to changes in live coral cover (Figure 4.5).

**Table 4.4.** Three way ANOVA to explore variation in the total abundance of *Chaetodon* butterflyfish. Count data was $Log_{10}$ transformed prior to analysis, "*" indicates significant effects (*p<0.05, **P<0.01, ***p<0.001).

| Source | df | MS | F |
|---|---|---|---|
| Year | 4 | 261.94 | 21.85*** |
| Location | 3 | 580.56 | 48.44*** |
| Zone | 3 | 587.84 | 49.04*** |
| Year × Location | 12 | 25.54 | 2.13* |
| Year × Zone | 12 | 17.31 | 1.44 |
| Location × Zone | 9 | 28.25 | 2.35 |
| Year × Location × Zone | 36 | 15.81 | 1.32 |
| Error | 320 | 11.98 | |

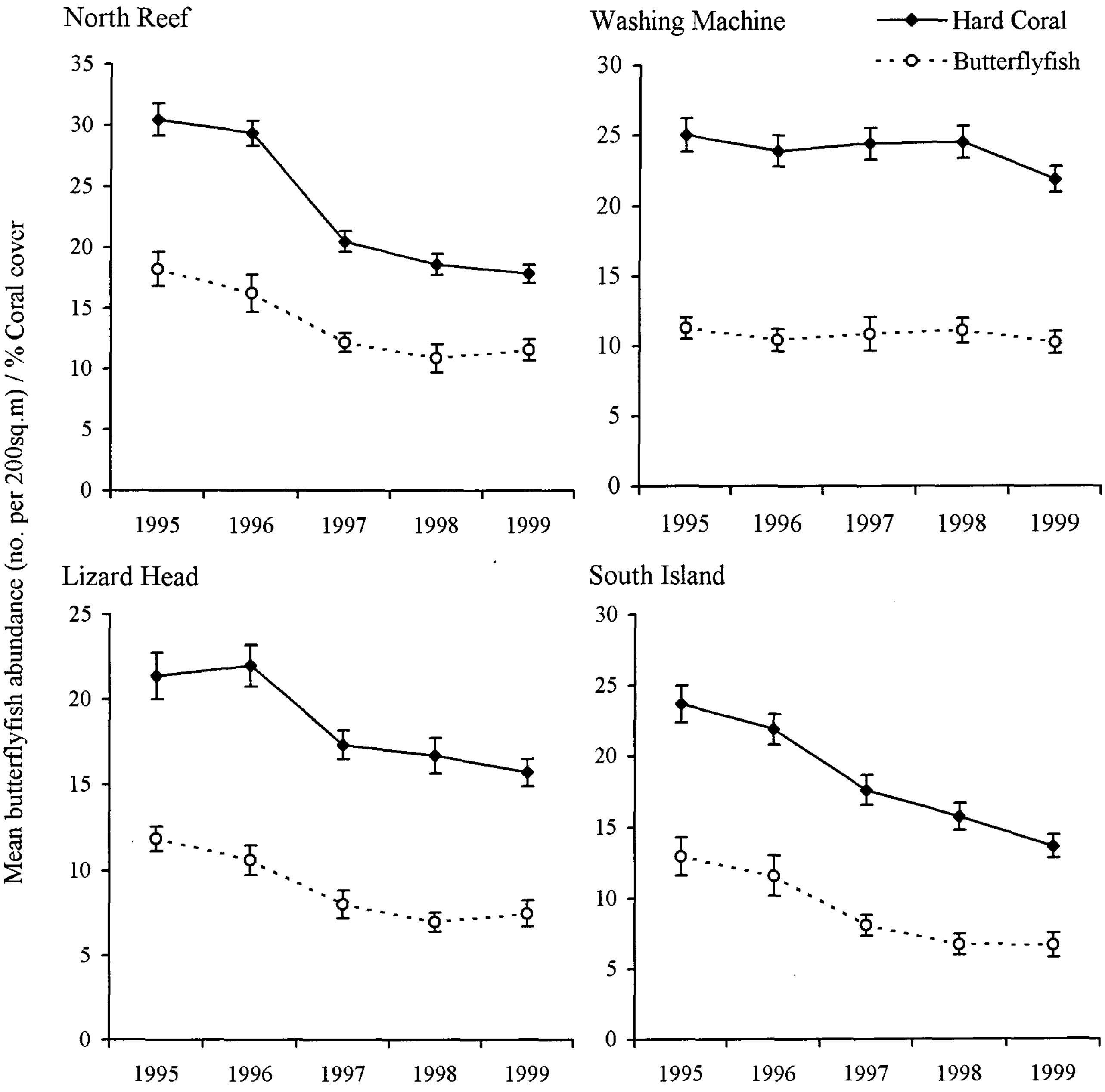

**Figure 4.4.** Temporal variation in the mean abundance (+/-SE) of *Chaetodon* butterflyfish at each location, compared to overall declines in live coral cover. Data was pooled across reef zones within each location, n = 20 transects at each location in each year.

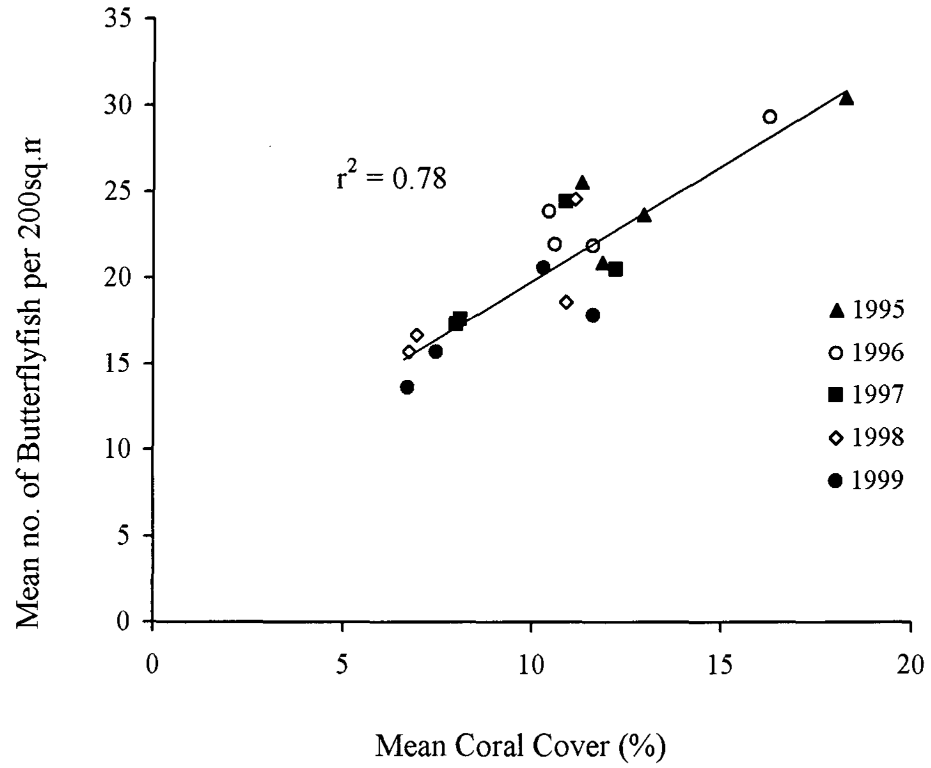

**Figure 4.5.** Relationship between the mean area cover of scleractinian corals and average densities of *Chaetodon* butterflyfish. Data represent temporal changes (from 1995-1999) in both coral cover and butterflyfish densities at each location, n = 20.

The community structure of butterflyfish assemblages also varied significantly among years (Table 4.5), indicating that not all butterflyfish were equally affected by changes in scleractinian coral cover. CDA showed that the structure of butterflyfish assemblages varied very little among years at Washing Machine, but varied quite considerably at North Reef, South Island and Lizard Head (Figure 4.6). At each of these latter locations (North reef, South Island, and Lizard Head) the structure of butterflyfish assemblages tended to converge across reef zones, through time (Figure 4.6). This trend may be caused by disproportionate declines in the abundance of the dominant butterflyfish at each reef zone. Alternately, one or more butterflyfish species may have expanded their distribution among zones. Temporal changes in the structure of butterflyfish assemblages were due mainly to declines in the abundances of *Chaetodon citrinellus*, *C. plebeius*, *C. trifascialis*, *C. baronessa*, and increases in the relative abundance of *C. kleinii* (Table 4.6).

**Table 4.5.** Three way MANOVA to explore variation in the relative abundance of 13 butterflyfish species (listed in table 4.6). Data was $Log_{10}$ transformed prior to analysis, "*" indicates significant effects (*p<0.05, **P<0.01, ***p<0.001).

| Source | Pillai's Trace | df | F |
|---|---|---|---|
| Year | 0.41 | 56 | 2.50*** |
| Location | 0.99 | 42 | 10.83*** |
| Zone | 1.44 | 42 | 20.33*** |
| Year × Location | 0.51 | 168 | 1.00 |
| Year × Zone | 0.75 | 168 | 1.52*** |
| Location × Zone | 0.91 | 126 | 2.52*** |
| Year × Location × Zone | 1.30 | 504 | 0.91 |

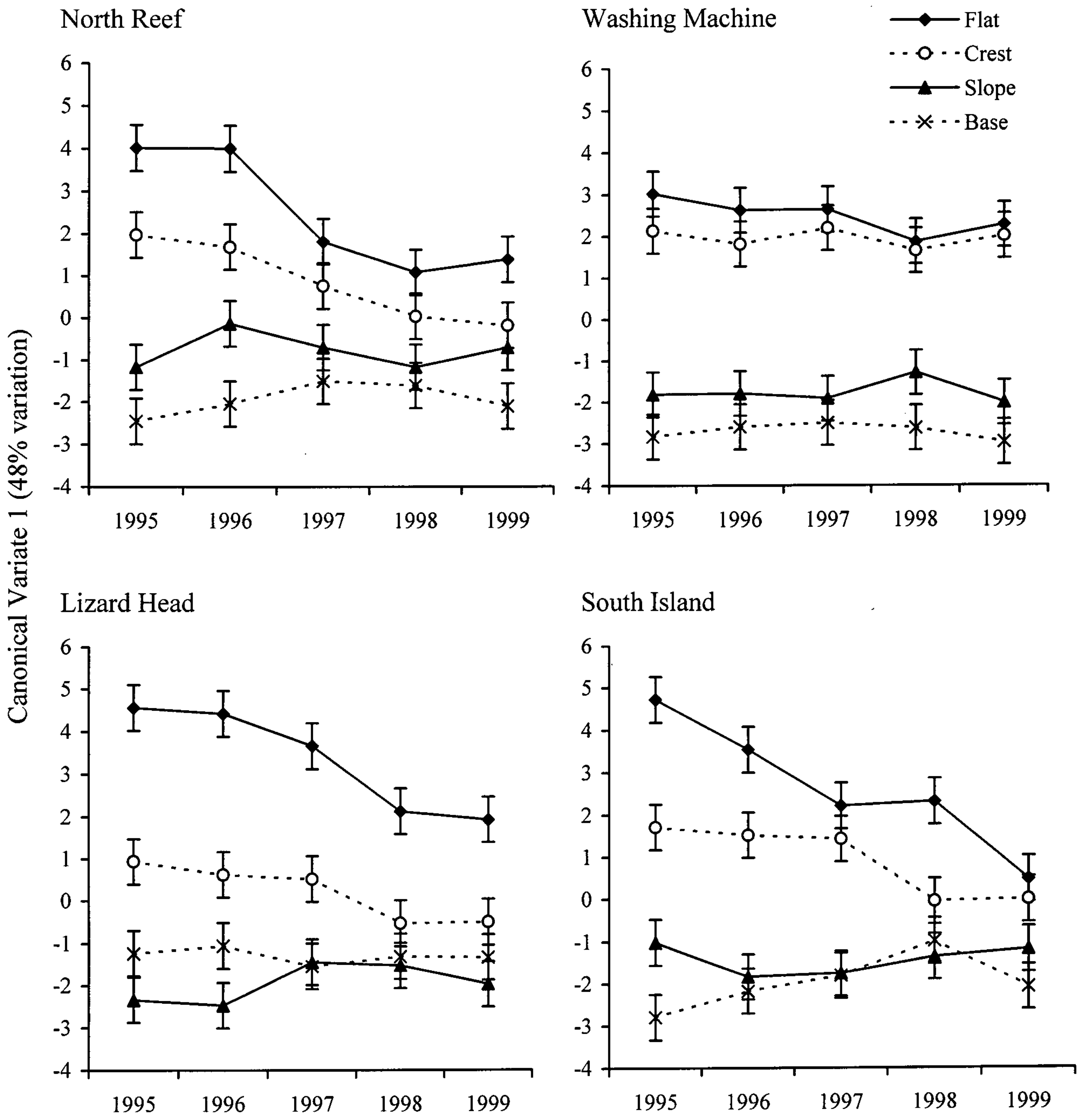

**Figure 4.6.** Canonical discriminant analysis (CDA) showing variation in the community structure of butterflyfish assemblages. Only the first canonical variate (explaining 48.3% of variation) is presented to emphasise the temporal aspect of the data. Error bars represent 95% confidence limits around canonical scores.

**Table 4.6.** Structure coefficients for *Chaetodon* species used in the CDA of butterflyfish assemblages. Species are ranked according to their correlation with the first canonical axis. Coefficients greater than ±0.22 are considered significant (∝= 0.05), and are shown in bold.

| Species | Correlation with first canonical variate |
|---|---|
| ***Chaetodon citrinellus*** | **0.69** |
| ***Chaetodon plebeius*** | **0.37** |
| ***Chaetodon trifascialis*** | **0.29** |
| ***Chaetodon baronessa*** | **0.23** |
| *Chaetodon lunulatus* | 0.12 |
| *Chaetodon vagabundus* | 0.02 |
| *Chaetodon rainfordi* | 0.01 |
| *Chaetodon unimaculatus* | 0.01 |
| *Chaetodon melannotus* | -0.01 |
| *Chaetodon ephippium* | -0.04 |
| *Chaetodon aureofasciatus* | -0.07 |
| *Chaetodon auriga* | -0.10 |
| ***Chaetodon kleinii*** | **-0.22** |

To further explore changes in the community composition of butterflyfish assemblages, I examined temporal variation in the individual abundance of each butterflyfish species (Table 4.7). Only five species (*C. trifascialis, C. plebeius, C. citrinellus, C. kleinii, C. auriga,*) exhibited statistically significant declines in their overall abundance among years (Table 4.7). Notably, declines in the abundance of all these species occurred only at North Reef, South Island and Lizard Head, but not Washing Machine (Figure 4.7). Given the limited impact of outbreak populations of *A. planci* on coral communities at Washing Machine (see Figure 4.2, 4.3), this location essentially served as a control for the effects of coral depletion (Figure 4.7). In this way, I was more able to differentiate natural variation in the abundance of butterflyfish, from temporal declines caused by extensive and widespread coral depletion. Interestingly, those species which exhibited significant temporal declines were not all obligate corallivores. Rather, there were only two species of obligate corallivores (*C. trifascialis, C. plebeius*), two facultative corallivores (*C. citrinellus*, *C. kleinii*), and one non-coral feeding species (*C. auriga*) (Table 4.7).

Other butterflyfish species (*Chaetodon unimaculatus*, and *C. rainfordi*) also exhibited declines in abundance at severely affected locations (North Reef, South Island and Lizard Head), while maintaining fairly constant population sizes at Washing Machine (Figure 4.7). However, temporal declines in the abundance of these two species (*C. unimaculatus*, and *C. rainfordi*) were not significant (Table 4.7). For *C. baronessa*, there was no significant decline in overall abundance among years. However, the mean abundance of *C. baronessa* with each reef zone varied significantly among years (Table 4.7). In February 1995, *C. baronessa* was found predominantly on the reef crest, with 63% of individuals found on the reef crest, as opposed to 24%, 10% and 3% on the slope, flat, and base, respectively. However by 1999, the distribution of *C. baronessa* among reef zones was much more even, changing to reflect the extensive depletion of scleractinian corals on the reef crest. In 1999, only 36% of individuals were found on the reef crest, whereas 22%, 25% and 17% of individuals were found on the slope, flat, and base, respectively.

For the majority of species (*C. aureofasciatus*, *C. ephippium*, *C. lunulatus*, *C. melannotus, C. rainfordi*, *C. unimaculatus* and *C. vagabundus*) there was no significant variation in either their overall abundance or zonal distribution among years (Table 4.7).

**Table 4.7a.** Three-way ANOVAs used to explore variation in the individual abundance of obligate coral feeding butterflyfish. Data was $\mathrm{Log}_{10}$ transformed prior to analysis, "*" indicate significant effects (*p<0.05, **P<0.01, ***p<0.001), after Bonferroni correction.

| Species | Source | df | MS | F | P |
|---|---|---|---|---|---|
| *C. aureofasciatus* | Year | 4 | 0.54 | 1.80 | 0.129 |
| | Location | 3 | 9.67 | 31.97 | 0.000** |
| | Zone | 3 | 3.22 | 10.63 | 0.000** |
| | Year × Location | 12 | 0.22 | 0.73 | 0.718 |
| | Year × Zone | 12 | 0.23 | 0.75 | 0.701 |
| | Location × Zone | 9 | 2.22 | 7.34 | 0.000** |
| | Year × Location × Zone | 36 | 0.19 | 0.62 | 0.958 |
| *C. baronessa* | Year | 4 | 7.62 | 2.49 | 0.043 |
| | Location | 3 | 101.40 | 33.14 | 0.000** |
| | Zone | 3 | 141.09 | 46.11 | 0.000** |
| | Year × Location | 12 | 2.146 | 1.70 | 0.750 |
| | Year × Zone | 12 | 11.11 | 3.63 | 0.000** |
| | Location × Zone | 9 | 17.39 | 5.68 | 0.000** |
| | Year × Location × Zone | 36 | 4.51 | 1.47 | 0.044 |
| *C. lunulatus* | Year | 4 | 6.08 | 1.71 | 0.147 |
| | Location | 3 | 69.62 | 19.60 | 0.000** |
| | Zone | 3 | 9.36 | 2.64 | 0.050 |
| | Year × Location | 12 | 2.18 | 0.62 | 0.829 |
| | Year × Zone | 12 | 4.09 | 1.15 | 0.318 |
| | Location × Zone | 9 | 11.23 | 3.16 | 0.001* |
| | Year × Location × Zone | 36 | 4.72 | 1.33 | 0.105 |
| *C. plebeius* | Year | 4 | 4.61 | 4.96 | 0.001* |
| | Location | 3 | 13.88 | 17.24 | 0.000** |
| | Zone | 3 | 20.41 | 25.35 | 0.000** |
| | Year × Location | 12 | 1.93 | 2.40 | 0.006 |
| | Year × Zone | 12 | 1.00 | 1.24 | 0.256 |
| | Location × Zone | 9 | 3.56 | 4.43 | 0.000** |
| | Year × Location × Zone | 36 | 0.93 | 1.16 | 0.256 |
| *C. rainfordi* | Year | 4 | 1.78 | 3.83 | 0.005 |
| | Location | 3 | 3.95 | 8.49 | 0.000** |
| | Zone | 3 | 1.56 | 3.36 | 0.019 |
| | Year × Location | 12 | 1.01 | 2.18 | 0.012 |
| | Year × Zone | 12 | 0.53 | 1.13 | 0.332 |
| | Location × Zone | 9 | 0.47 | 1.01 | 0.433 |
| | Year × Location × Zone | 36 | 0.32 | 0.69 | 0.914 |
| *C. trifascialis* | Year | 4 | 5.64 | 8.40 | 0.000* |
| | Location | 3 | 3.78 | 5.64 | 0.001* |
| | Zone | 3 | 27.27 | 40.62 | 0.000** |
| | Year × Location | 12 | 1.18 | 1.75 | 0.055 |
| | Year × Zone | 12 | 1.72 | 2.56 | 0.003* |
| | Location × Zone | 9 | 3.82 | 5.70 | 0.000** |
| | Year × Location × Zone | 36 | 0.73 | 1.09 | 0.343 |

**Table 4.7b.** Three-way ANOVAs used to explore variation in the individual abundance of facultative corallivores[1] and non-coral feeding butterflyfish[2]. Data as per Table 4.7a.

| Species | Source | df | MS | F | P |
|---|---|---|---|---|---|
| *C. auriga*[2] | Year | 4 | 2.78 | 4.07 | 0.003* |
| | Location | 3 | 3.66 | 5.34 | 0.001* |
| | Zone | 3 | 5.88 | 8.59 | 0.000** |
| | Year × Location | 12 | 0.79 | 1.16 | 0.308 |
| | Year × Zone | 12 | 0.99 | 1.44 | 0.143 |
| | Location × Zone | 9 | 0.62 | 0.90 | 0.524 |
| | Year × Location × Zone | 36 | 0.58 | 0.85 | 0.715 |
| *C. citrinellus*[1] | Year | 4 | 5.58 | 3.62 | 0.007 |
| | Location | 3 | 13.10 | 8.50 | 0.000** |
| | Zone | 3 | 305.95 | 198.51 | 0.000** |
| | Year × Location | 12 | 0.88 | 0.57 | 0.863 |
| | Year × Zone | 12 | 7.57 | 4.91 | 0.000** |
| | Location × Zone | 9 | 4.08 | 2.65 | 0.006 |
| | Year × Location × Zone | 36 | 0.91 | 0.59 | 0.971 |
| *C. ephippium*[1] | Year | 4 | 0.17 | 0.23 | 0.920 |
| | Location | 3 | 0.22 | 0.30 | 0.823 |
| | Zone | 3 | 1.30 | 1.81 | 0.145 |
| | Year × Location | 12 | 0.72 | 1.01 | 0.438 |
| | Year × Zone | 12 | 0.39 | 0.55 | 0.879 |
| | Location × Zone | 9 | 1.07 | 1.49 | 0.149 |
| | Year × Location × Zone | 36 | 0.70 | 0.99 | 0.497 |
| *C. kleinii*[1] | Year | 4 | 4.10 | 4.66 | 0.001* |
| | Location | 3 | 10.16 | 11.53 | 0.000** |
| | Zone | 3 | 50.40 | 57.19 | 0.000** |
| | Year × Location | 12 | 0.58 | 0.65 | 0.794 |
| | Year × Zone | 12 | 2.64 | 3.00 | 0.001* |
| | Location × Zone | 9 | 3.38 | 3.84 | 0.000** |
| | Year × Location × Zone | 36 | 0.69 | 0.79 | 0.804 |
| *C. melannotus*[1] | Year | 4 | 0.30 | 0.45 | 0.772 |
| | Location | 3 | 2.70 | 4.00 | 0.008 |
| | Zone | 3 | 0.11 | 0.17 | 0.918 |
| | Year × Location | 12 | 0.16 | 0.24 | 0.996 |
| | Year × Zone | 12 | 0.77 | 1.15 | 0.322 |
| | Location × Zone | 9 | 0.54 | 0.80 | 0.620 |
| | Year × Location × Zone | 36 | 0.35 | 0.52 | 0.991 |
| *C. unimaculatus*[1] | Year | 4 | 1.68 | 3.72 | 0.006 |
| | Location | 3 | 1.58 | 3.50 | 0.016 |
| | Zone | 3 | 0.43 | 0.95 | 0.417 |
| | Year × Location | 12 | 0.60 | 1.33 | 0.200 |
| | Year × Zone | 12 | 0.82 | 1.82 | 0.044 |
| | Location × Zone | 9 | 1.16 | 2.57 | 0.007 |
| | Year × Location × Zone | 36 | 0.65 | 1.43 | 0.058 |
| *C. vagabundus*[2] | Year | 4 | 1.69 | 1.07 | 0.369 |
| | Location | 3 | 2.86 | 1.82 | 0.143 |
| | Zone | 3 | 2.35 | 1.50 | 0.215 |
| | Year × Location | 12 | 1.89 | 1.21 | 0.277 |
| | Year × Zone | 12 | 1.87 | 1.19 | 0.287 |
| | Location × Zone | 9 | 0.51 | 0.33 | 0.966 |
| | Year × Location × Zone | 36 | 1.70 | 1.08 | 0.351 |

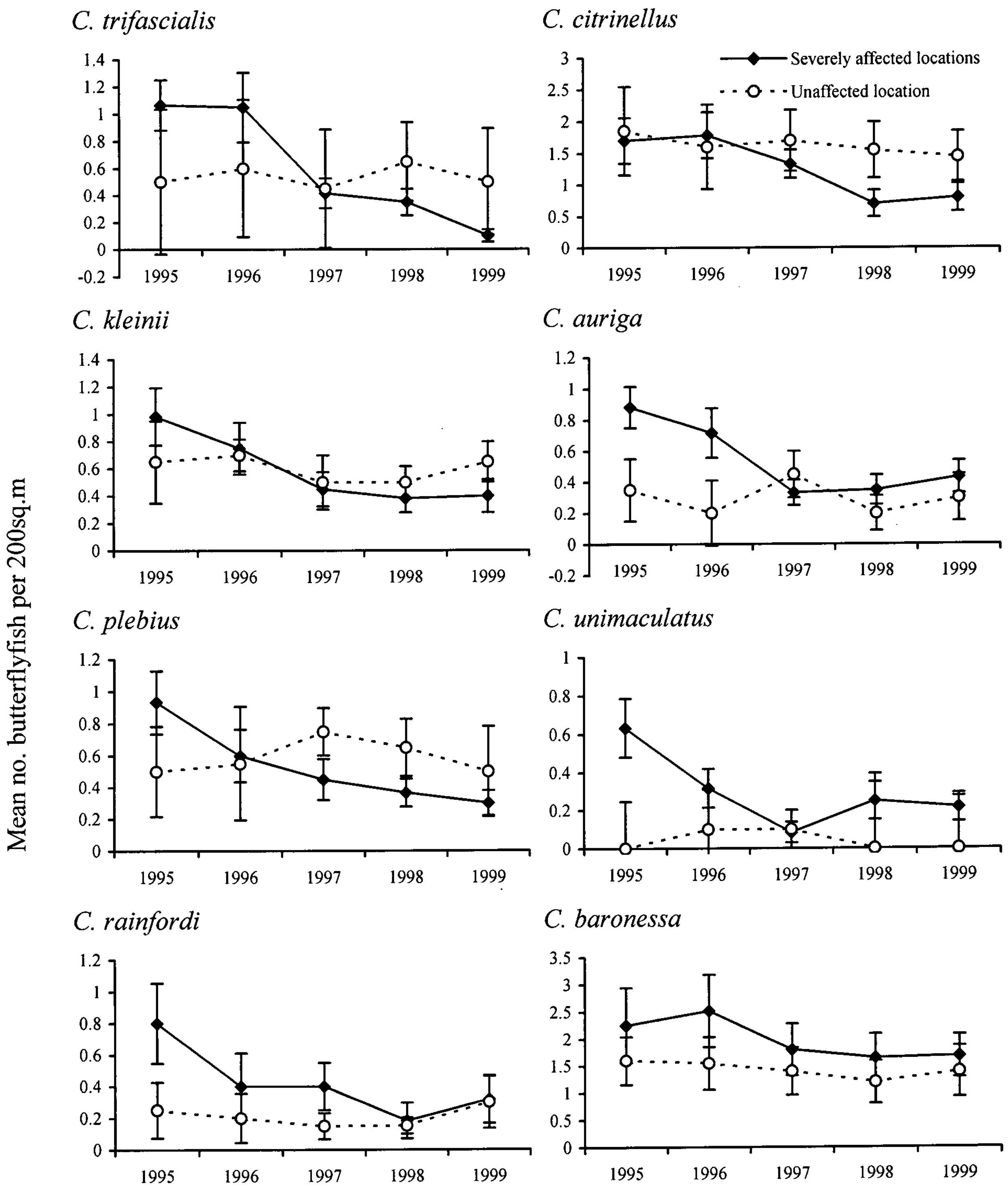

**Figure 4.7.** Temporal variation in the mean abundance (+/-SE) of six *Chaetodon* butterflyfish, associated with impacts of outbreak populations of *A. planci*. Data was pooled across three locations (North Reef, Lizard Head and South Island) all of which, were severaly affected by *A. planci*. In contrast there was one location (Washing Machine) which was essentially unaffected .

## Patterns of prey use

*Chaetodon* butterflyfish fed on a wide variety of different benthic substrates, including various scleractinian corals, soft corals, gorgonians, hydrozoans and bare substrate (Table 4.8). However, most of the eight butterflyfish species, for which feeding observations were conducted, fed predominantly on scleractinian corals. Four of the species (*C. baronessa*, *C. plebeius*, *C. lunulatus* and *C. trifascialis*) were obligate corallivores, taking more than >95% of bites on scleractinian corals. A further two species (*C. citrinellus* and *C. kleinii*) were facultative corallivores, taking most of their bites from scleractinian corals (74% and 58% respectively). However, both these butterflyfish species (*C. citrinellus* and *C. kleinii*) also fed on soft corals, gorgonians, hydrozoans and bare substrates (Table 4.8). In contrast to the other six butterflyfish species, both *C. auriga* and *C. vagabundus* very rarely grazed on scleractinian corals, rather most of their bites (96% and 98% respectively) were taken from bare substrate (Figure 4.8).

Each butterflyfish species used between 9-48 different prey categories (Table 4.8), although most butterflyfish species fed predominantly on just one or two different prey categories. The obligate corallivores (*C. trifascialis*, *C. baronessa*, *C. lunulatus*) fed predominantly on *Acropora hyacinthus* and/ or *Pocillopora damicornis*, though both these coral species declined in availability as a result of feeding activities of *A. planci*. In contrast, the facultative coral feeders (*C. citrinellus* and *C. kleinii*) and non-coral feeders (*C. auriga* and *C. vagabundus*) fed predominantly on bare substrates, although *C. citrinellus* frequently consumed *A. hyacinthus* and *C. kleinii* frequently consumed *P. damicornis* (Figure 4.8).

**Table 4.8.** Range of prey categories used by each of eight species of *Chaetodon* butterflyfishes. All prey categories used by each butterflyfish are indicated by "*". Data was pooled across all individuals from all years.

| | Butterflyfish species | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Prey Categories | *C. auriga* | *C. baronessa* | *C. citrinellus* | *C. kleinii* | *C. lunulatus* | *C. plebeius* | *C. trifascialis* | *C. vagabundus* |
| **ACROPORIDAE** | | | | | | | | |
| *Acropora aculeus* | | * | | | | * | * | |
| *Acropora aspera* | | | | * | * | * | | |
| *Acropora cerealis* | * | * | * | * | | * | * | |
| *Acropora cytherea* | | * | * | * | * | * | * | |
| *Acroproa digitifera* | | * | | | * | | | * |
| *Acropora divaricata* | | | | * | | | * | |
| *Acropora donei* | | | | * | * | | | |
| *Acropora florida* | | * | * | * | * | * | * | |
| *Acropora formosa* | | * | * | * | * | * | | |
| *Acropora gemmifera* | | * | * | * | * | * | * | |
| *Acropora humilis* | | * | * | * | * | * | | |
| *Acropora hyacinthus* | | * | * | * | * | * | * | * |
| *Acropora intermedia* | | * | * | * | * | * | * | |
| *Acropora loripes* | | * | | | * | * | | |
| *Acropora millepora* | * | * | * | * | * | * | * | |
| *Acropora monticulosa* | | * | * | | | * | | * |
| *Acropora nasuta* | | * | * | * | * | * | * | * |
| *Acropora robusta* | | * | * | | * | * | * | |
| *Acropora sarmentosa* | * | * | | * | * | * | | |
| *Acropora secale* | | * | * | * | * | * | | |
| *Acropora tenuis* | | * | * | * | * | * | * | |
| *Acropora valenciennesi* | | * | | * | | * | | |
| *Acropora valida* | | * | * | * | * | * | * | |
| *Acropora yongei* | | * | | | | | | |
| *Astreopora* spp. | | | * | * | * | * | | |
| *Isopora cuneata* | | * | * | | * | * | | |
| *Montipora* spp. | * | * | * | * | * | * | | * |
| **POCILLOPORIDAE** | | | | | | | | |
| *Pocillopora damicornis* | * | * | * | * | * | * | * | * |
| *Pocillopora eydouxi* | | * | * | * | | * | * | |
| *Pocillopora meandrina* | | * | * | * | * | | * | |
| *Pocillopora verrucosa* | * | * | * | * | * | * | * | * |
| *Seriatopora hystrix* | | * | * | * | * | * | | |
| *Stylophora pistillata* | * | * | * | * | * | * | | |
| **AGARICIIDAE** | | | | | | | | |
| *Coeloseris mayeri* | | | | | * | * | | |
| *Pavona varians* | | | * | * | | | | |
| *Pachyseris speciosa* | | | | | * | | | |

**Table 4.8.** Continued

| | Butterflyfish species | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Prey Categories | *C. auriga* | *C. baronessa* | *C. citrinellus* | *C. kleini* | *C. lunulatus* | *C. plebeius* | *C. trifascialis* | *C. vagabundus* |
| **FAVIIDAE** | | | | | | | | |
| *Cyphastrea seriala* | | | | | * | | | |
| *Diploastrea heliopora* | | | | | * | * | | |
| *Echinopora lamellosa* | | * | * | * | * | * | | |
| *Echinopora mammiformis* | | * | | * | | * | | |
| *Favia favus* | | | * | | * | | | |
| *Favia pallida* | | | * | * | * | * | | |
| *Favites abdita* | | * | * | | * | * | | |
| *Favites halicora* | | | | | * | | | |
| *Goniastrea aspera* | | * | | | | * | | |
| *Goniastrea edwardsi* | | | * | | * | | | |
| *Goniastrea retiformes* | | * | * | * | * | * | | |
| *Platygyra daedalea* | | * | * | | | * | | |
| *Leptoria phrygia* | | * | * | | * | * | | |
| *Leptastrea purpurea* | | | | * | * | | | |
| **MUSSIDAE** | | | | | | | | |
| *Lobophyllia hemprichii* | * | * | | | | | | * |
| *Symphyllia recta* | | * | | * | | * | | |
| **Other Scleractinian corals** | | | | | | | | |
| *Fungia* spp. | | * | | * | * | * | | |
| *Galaxea astreata* | | * | | * | * | * | | |
| *Galaxea fascularis* | | * | | * | * | | | |
| *Hydonophora microconos* | | | | * | | | | |
| *Merulina ampliata* | | | | | * | | | |
| *Psammacora contigua* | * | * | | | * | | | |
| *Porites* spp. | | * | * | * | * | * | | |
| **Soft Corals** | | | | | | | | |
| *Lobophyton* spp. | | | * | * | | | | |
| *Sarcophytum* spp. | | | * | * | | | | |
| *Sinularia* spp. | | | * | * | | | | |
| *Dendronephthya* spp. | | | | * | | | | |
| *Nepthea* spp. | | | | * | * | | | |
| **Gorgonians** | | | | | | | | |
| *Hisksonella* spp. | | | | * | | | | |
| *Isis* spp. | | | | * | * | | | |
| **Hydrozoans** | | | | | | | | |
| *Aglaophenia* spp. | | | | * | | | | |
| *Lytocarpus* spp. | | | | * | | | | |
| **Bare Substrate** | * | * | * | * | * | * | * | * |
| **No. categories used** | 10 | 44 | 37 | 48 | 48 | 43 | 18 | 9 |

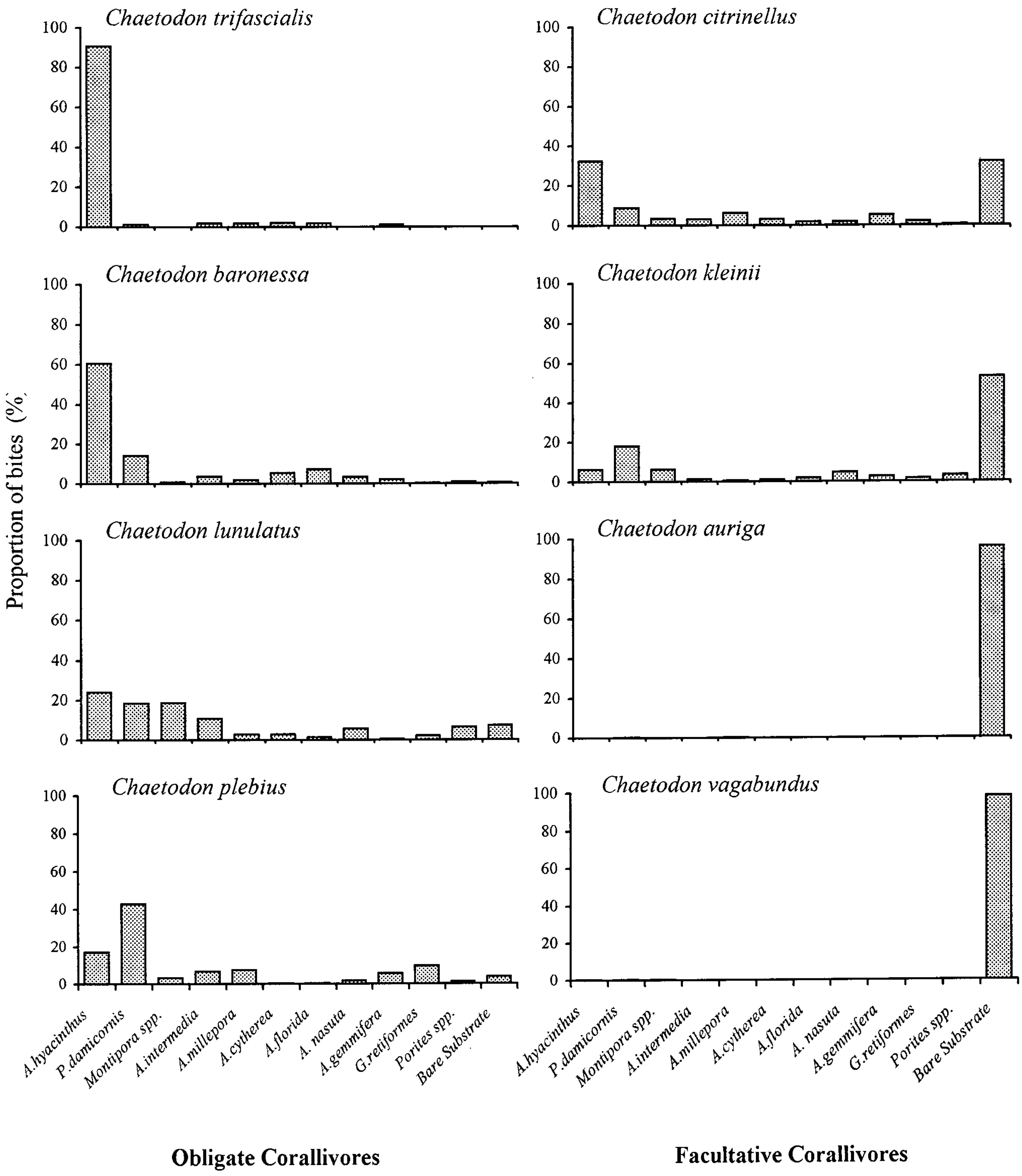

**Figure 4.8.** Variation in dietary composition among eight butterflyfish species. Data shown is the proportion of bites taken on each of the 12 most frequently consumed prey categories (A- *Acropora*, P- *Pocillopora*, G- *Goniastrea*. Data pooled across years, n = 90 feeding observations.

The relative use of different prey corals by most butterflyfish species (7/8 species) was very consistent among years (Table 4.9), despite significant changes in both coral cover (Table 4.1) and composition (Table 4.2). In case of *C. baronessa*, however, dietary composition varied significantly through time (Table 4.9). In 1995, *C. baronessa* appeared to represent an extreme specialist, feeding almost exclusively on *Acropora hyacinthus* (Figure 4.9). In subsequent years (1997 and 1999) *C. baronessa* continued to feed predominantly on *Acropora hyacinthus*, but the proportion of bites taken from *A. hyacinthus* declined dramatically, from 84% in 1995, down to 51% and 38% in 1997 and 1999, respectively (Figure 4.9). Temporal declines in the proportional consumption of *A. hyacinthus* by *C. baronessa*, followed massive reductions in the abundance of this coral species; At North Reef, where feeding observations were conducted, the mean cover of *A. hyacinthus* declined by 44%, from 4.7% cover (±0.9 SE) in 1995 down to 2.6% cover (±0.4 SE) in 1999. In response to wide-spread depletion of *A. hyacinthus*, *C. baronessa* fed increasingly on *Pocillopora damicornis*, and *Acropora florida* (Figure 4.9).

**Table 4.9.** Temporal variation in the dietary composition of each of eight *Chaetodon* butterflyfish. Patterns of prey use were analysed using MANOVA to compare relative proportions of each of 12 different prey categories (listed in Table 4.3) in the diet of each butterflyfish species, among years (1995, 1997 and 1999) .

| Species | Pillai's Trace | F | df | p |
|---|---|---|---|---|
| *C. auriga* | 0.23 | 1.05 | 20 | 0.40 |
| ***C. baronessa*** | **1.22** | **1.80** | **86** | **<0.01** |
| *C. citrinellus* | 0.83 | 1.14 | 70 | 0.27 |
| *C. kleinii* | 0.96 | 1.00 | 86 | 0.49 |
| *C. lunulatus* | 1.20 | 1.36 | 96 | 0.07 |
| *C. plebeius* | 1.20 | 1.38 | 92 | 0.07 |
| *C. trifascialis* | 0.61 | 1.32 | 34 | 0.14 |
| *C. vagabundus* | 0.32 | 1.31 | 22 | 0.17 |

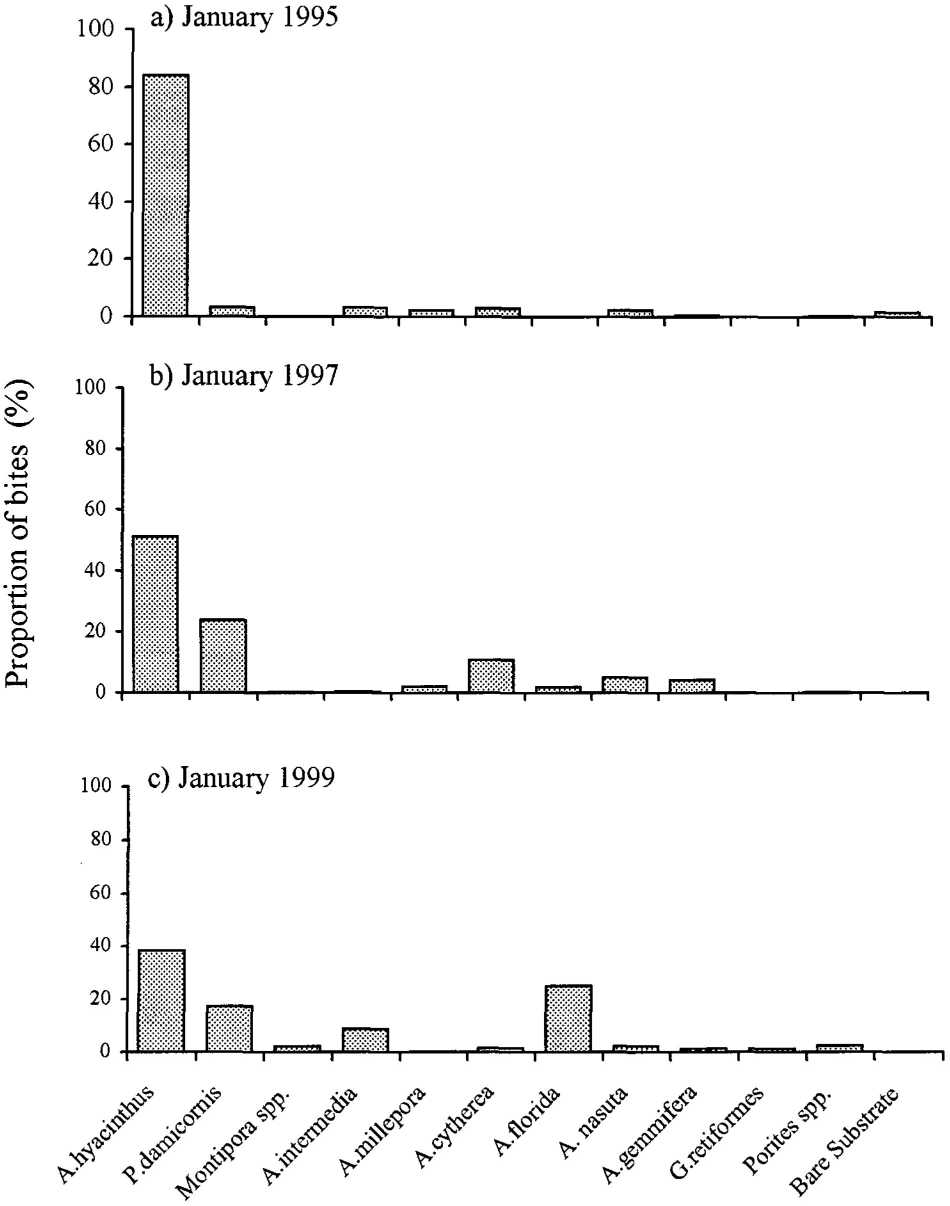

**Figure 4.9.** Temporal variation in the dietary composition of *Chaetodon baronessa*. Data shown are the proportion of bites taken on each of the 12 most frequently used prey categories, in each year (1995, 1997 and 1999), n = 30 observations for each year.

All eight butterflyfish species exhibited significant selectivity in their pattern of feeding, using particular prey categories disproportionately more or less than predicted by their availability (Table 4.10). Resource selection functions showed that every butterflyfish species used at least one prey category significantly more than predicted by its availability, consumed a range of different prey types significantly less than expected, and consumed a number of prey types in approximate accordance with their availability (Table 4.10).

**Table 4.10.** Patterns of feeding selectivity for each of eight butterflyfish species (n = 90 fish with data pooled across all years). All eight butterflyfish species exhibited significant ($P<0.01$) feeding selectivity ($X^2_{L2}$). "+" = coral species used significantly more than expected, "-" = corals used significantly less than expected, and "0" = prey categories which were used in approximate accordance with their availability (i.e. neither selected or avoided).

| | | Prey Categories | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | $X^2_L$ 2 | *A. hyacinthus* | *P. damicornis* | *Montipora* spp. | *A. intermedia* | *A. millepora* | *A. cytherea* | *A. florida* | *A. nasuta* | *A. gemmifera* | *G. retiformes* | *Porites* spp. | Bare substrates |
| *C. trifascialis* | 1334 | + | – | – | 0 | – | 0 | – | – | – | – | – | – |
| *C. baronessa* | 956 | + | + | – | 0 | – | 0 | + | 0 | 0 | – | – | – |
| *C. plebeius* | 889 | + | + | 0 | 0 | + | – | – | 0 | + | + | 0 | – |
| *C. citrinellus* | 867 | + | + | + | 0 | + | 0 | 0 | 0 | + | 0 | – | – |
| *C. lunulatus* | 824 | + | + | + | + | + | 0 | 0 | 0 | 0 | 0 | + | – |
| *C. vagabundus* | 576 | – | – | – | – | – | – | – | – | – | – | – | + |
| *C. auriga* | 496 | – | – | – | – | – | – | – | – | – | – | – | + |
| *C. kleinii* | 482 | 0 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*Chaetodon trifascialis* exhibited the greatest degree of feeding selectivity, consuming *Acropora hyacinthus* to the exclusion of almost all other prey types (Table 4.10). *Chaetodon baronessa* also exhibited considerable selectivity, despite showing a marked shift in its feeding habits through time (Figure 4.9). The feeding selectivity exhibited by *C. citrinellus*, *C. lunulatus*, C. *plebeius*, *C. auriga*, *C. vagabundus* and *C. kleinii* was much lower than that of *C. trifascialis* or *C. baronessa*. *Chaetodon citrinellus*, *C. lunulatus* and *C. plebeius* all consumed 5-6 different coral species significantly more than expected, including *Acropora hyacinthus*, *A. millepora* and *Pocillopora damicornis*. Meanwhile, both *C. auriga* and *C. vagabundus* used bare substrate significantly more than expected and tended to avoid all scleractinian corals. *Chaetodon kleinii* exhibited the least feeding selectivity of the eight *Chaetodon* species, using virtually all prey categories (including bare substrates) in approximate accordance with their availability (Table 4.10).

Temporal and spatial variation in the abundance of seven (out of 8) butterflyfish species was significantly associated with the availability of their preferred prey (Table 4.11). The only butterflyfish species which was not significantly associated with availability of it's preferred prey was *C. vagabundus*. In the remaining species, the proportion of variation in butterflyfish abundance explained by prey availability varied from 24% for *C. citrinellus* up to 62% for *C. trifascialis* (Table 4.11). The strongest associations with prey availability were shown for butterflyfish with the highest degree of feeding selectivity (*C. trifascialis* and *C. baronessa*). For *C. trifascialis*, the availability of prey corals, and particularly the availability of *Acropora hyacinthus*, accounted for 62% of variation in abundance. Similarly, the abundance of prey corals, and again particularly *Acropora hyacinthus*, accounted for 47% of variation in the abundance of *Chaetodon baronessa* (Table 4.11).

**Table 4.11.** Multiple linear regression of butterflyfish abundance and prey availability. Best-subsets multiple regression was conducted for each butterflyfish species to assess the proportion of variation in abundance explained (adjusted $r^2$) by variation in prey availability. Regression coefficients shown for all coral species used in each regression model. Positive correlations with preferred prey categories are shown in bold.

| | Butterflyfish species | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Variables | *C. trifascialis* | *C. baronessa* | *C. kleinii* | *C. citrinellus* | *C.lunulatus* | *C. plebeius* | *C.auriga* | *C.vagabundus* |
| *A. hyacinthus* | **0.67** | **0.60** | -0.22 | | | | | |
| *P. damicornis* | 0.21 | | **0.18** | | | **0.21** | | |
| *Montipora* spp. | | 0.17 | | **0.33** | **0.20** | | -0.18 | |
| *A. intermedia* | | 0.14 | | | **0.31** | | | |
| *A. millepora* | | | | | | **0.42** | -0.24 | |
| *A. cytherea* | | | | | | | | |
| *A. florida* | -0.16 | **0.20** | | -0.13 | | -0.18 | -0.19 | -0.16 |
| *A. nasuta* | | | | 0.33 | 0.18 | 0.36 | 0.22 | |
| *A. gemmifera* | -0.18 | -0.21 | -0.35 | | | | 0.20 | |
| *G. retiformes* | | | -0.21 | 0.18 | | | | -0.21 |
| *Porites* spp. | | -0.16 | | -0.15 | 0.21 | | | |
| Non-coral substrates | -0.22 | -0.14 | | | | | **0.21** | |
| Mallow's $C_P$ | 0.74 | 4.81 | 1.00 | 3.04 | 3.10 | 5.20 | 3.88 | -2.82 |
| Adjusted $r^2$ | 0.62 | 0.47 | 0.26 | 0.24 | 0.32 | 0.28 | 0.30 | 0.06 |
| Significance | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 |

## 4.5 DISCUSSION

### Coral cover and butterflyfish abundance

The acquisition of prey resources is fundamental to the existence of most living organisms. Accordingly, variation in the availability of prey may influence the distribution and abundance of organisms in time and space (e.g., Hunter and Price 1992, Menge 1992). If prey availability is limiting, then the abundance of consumers is likely to vary in direct response to fluctuations in prey availability. In this study, declines in the abundance of scleractinian corals were followed almost immediately by corresponding declines in the combined abundance of *Chaetodon* butterflyfish (Figure 4.5). This finding is consistent with previous studies which have shown declines in butterflyfish abundance following declines in the abundance of scleractinian corals, during small-scale disturbance experiments (Tricas 1986, Lewis 1997) and after extensive coral depletion by outbreak populations of crown-of-thorns starfish (Bouchan-Navaro et al. 1985, Williams 1986, Sano et al. 1987). In addition, many other studies have demonstrated spatial correlations in the distribution and abundance of butterflyfish with distributions and abundances of scleractinian corals (e.g., Reese 1977, 1981, Birkeland & Neudecker 1981, Bouchan-Navaro et al. 1985, Findley & Findley 1985, Bouchan-Navaro & Bouchan 1989, Roberts et al. 1988, Pratchett 1995, but see also Bell et al. 1985, Fowler 1990). These findings suggest that *Chaetodon* butterflyfish are not only dependent on scleractinian corals, but that the abundance of corals is potentially limiting to their distribution and abundance.

Declines in the abundance of *Chaetodon* butterflyfish following coral depletion are generally ascribed to starvation and subsequent mortality, resulting from drastic reductions in prey availability (Hourigan et al. 1988, Williams 1986). However, not all

*Chaetodon* butterflyfish rely on scleractinian corals for prey (Birkeland and Neudecker 1981, Anderson et al. 1981, Motta 1988). Of the 13 butterflyfish species examined during this study, only six species (*C. aureofasciatus*, *C. baronessa*, *C. lunulatus*, *C. plebeius*, *C. rainfordi*, and *C. trifascialis*) were obligate corallivores, depending entirely on scleractinian corals for food. A further five species (*C. citrinellus*, *C. ephippium*, *C. kleinii*, *C. melannotus*, and *C. unimaculatus*) were facultative corallivores, and two species (*C. auriga* and *C. vagabundus*) were non corallivores. Similarly, in Moorea (French Polynesia), Harmelin-Vivien and Bouchan-Navaro (1983) found that only five (out of 14) *Chaetodon* butterflyfish were obligate corallivores; a further five species were facultative corallivores, and the remaining species (4/14) only very rarely consumed scleractinian corals (see also Anderson et al. 1981, Bouchan-Navaro 1986). These findings demonstrate that only 30-45% of butterflyfish species depend entirely on scleractinian corals for food, whereas most butterflyfish species (>55% of species) are theoretically capable of using alternate sources of prey (e.g., soft corals, gorgonians, or motile invertebrates) when scleractinian corals are scarce. Therefore, the affects of coral depletion on *Chaetodon* butterflyfish are likely to vary among species, and broad scale reductions in the overall abundance of butterflyfish are effected by declines in only a few individual species (see Bouchan-Navaro et al. 1985, Williams 1986, Sano et al. 1987).

Massive reductions in scleractinian coral cover, due to crown-of-thorns outbreaks or any other major disturbances (e.g., freshwater plumes or unseasonal temperature extremes, or anthropogenic disturbances) would be expected to have greatest impacts on obligate coral feeding butterflyfish (Hourigan et al 1988, Crosby and Reese 1996). In comparison, those butterflyfish species with little, or no reliance on corals for food (i.e. facultative and non-coral feeding species, respectively) would be expected to be much less affected (if at all) by coral depletion (see Bouchan-Navaro et al 1985). In this study, however, there were several obligate coral feeding species (*C. aureofasciatus*, *C. baronessa*, *C. lunulatus*, and *C. rainfordi*) that were ostensibly unaffected by declines in coral cover. Over the same period, there were two facultative coral feeding butterflyfish (*C. citrinellus* and *C. kleinii*) that exhibited significant declines in abundance following coral depletion by crown-of-thorns starfish (Table 4.12). Similarly, Williams (1986) found that two obligate coral feeding butterflyfish (*C. lunulatus* and *C. trifascialis*) were apparently unaffected by outbreaks of *A. planci*, while there was at least one facultative corallivore (*C. melannotus*) that declined in abundance during infestations of *A. planci* on reefs in the central Great Barrier Reef (Table 4.12). These findings suggest that the proportion of scleractinian corals in the diet of *Chaetodon* butterflyfish is not necessarily a true indication of their dependence on scleractinian corals (cf. Bouchan-Navaro et al 1985). While obligate coral feeding butterflyfish must have access to at least some coral species, facultative coral feeding species may be equally reliant on scleractinian corals to provide essential nutrients and/ or provide a mixed diet to maximise assimilation efficiency (*sensu* Birkeland and Neudecker 1981). In the extreme, both facultative and obligate corallivores will be unable to persist in areas devoid of all scleractinian corals. For example, Sano et al. (1987) reported a complete absence of all coral-feeding butterflyfish (facultative and obligate corallivores) on a ‘rubble reef’ in southern Japan, where crown-of-thorns starfish had not only decimated coral cover, but subsequent erosion of coral skeletons resulted in the complete collapse of coral structures. It is likely that a greater range of different butterflyfish species, including those species with only a partial reliance on scleractinian corals, will be affected with increasing severity of coral depletion.

**Table 4.12**. Contrasting results of four different studies (Bouchan-Navaro et al 1985[1], Williams 1986[2], Sano et al. 1987[3], this study[4]) exploring changes in the abundance of *Chaetodon* butterflyfish on reefs affected by outbreak populations of *A. planci*. "↓" = moderate declines in abundance, "↓↓" = severe declines in abundance, "0" = no change.

| | French Polnesia[1] | Central GBR[2] | Southern Japan[3] | Northern GBR[4] |
|---|---|---|---|---|
| Obligate Corallivores | | | | |
| *C. aureofasciatus* | | ↓↓ | | 0 |
| *C. baronessa* | | ↓ | ↓↓ | 0 |
| *C. lunulatus* | ↓ | 0 | ↓↓ | 0 |
| *C. plebeius* | | ↓ | ↓↓ | ↓ |
| *C. rainfordi* | | ↓↓ | | 0 |
| *C. trifascialis* | ↓↓ | 0 | ↓↓ | ↓↓ |
| Facultative corallivores | | | | |
| *C. citrinellus* | ↓ | 0 | | ↓ |
| *C. ephippium* | 0 | | | 0 |
| *C. kleinii* | | | ↓ | ↓ |
| *C. melannotus* | | ↓↓ | ↓ | 0 |
| *C. unimaculatus* | ↓ | | ↓↓ | 0 |
| Non-coral feeders | | | | |
| *C. auriga* | ↓ | | 0 | ↓ |
| *C. vagabundus* | 0 | 0 | 0 | 0 |

## Patterns of prey preference

Most studies which have examined feeding habits of *Chaetodon* butterflyfish have tended to categorise butterflyfish species into one of several broad-feeding categories; i) obligate corallivores, ii) facultative corallivores or iii) non-corallivores (e.g., Neudecker 1977, 1979, Anderson et al. 1981, Harmelin-Vivien and Bouchan-Navaro 1981, 1983, Bouchan-Navaor et al. 1985). While these broad feeding categories are useful in underlining broad similarities in the feeding habits of different butterflyfish species, they obscure significant differences in the patterns of prey use among individual species within each category (Hourigan et al. 1988). For example, among obligate coral feeding species there were both specialist coral feeders (e.g., *C. trifasicalis*) and generalist coral feeders (e.g., *C. lunulatus*), following Birkeland and Neudecker (1981). All *Chaetodon* butterflyfish exhibited significant feeding selectivity (see also Hourgian et al. 1988), but the degree of dietary specialisation varied greatly among species (Table 4.10). Furthermore, variation in the dietary specialisation of different butterflyfish species appeared to have a significant influence on their individual responses to coral depletion by crown-of-thorns starfish. Notably, three out of four of the most specialised coral feeding butterflyfish (*C. trifascialis*, *C. plebeius* and *C. citrinellus*) all declined in abundance during the recent outbreak of *A. planci* at Lizard Island.

The results of this study provide empirical evidence for the ecological tenet that specialist species are more prone to disturbances, than are generalist species. In the most extreme example, *C. trifascialis* was driven to virtual extinction as its' preferred prey (*Acropora hyacinthus*) was rapidly depleted during initial stages of the starfish outbreak. In contrast, *C. baronessa*, which also fed preferentially on *Acropora hyacinthus* (especially in 1995), mediated potential impacts of resource depletion by altering both its' depth zonation and dietary composition to utilise a broader range of habitats and prey types. Generalist species, which can utilise a wide range of different prey species, are much less likely to be affected by reductions in the availability of coral prey (Hourigan et al. 1988), especially where impacts are unequally apportioned among different coral species, as is generally the case during outbreaks of *A. planci* (Moran 1986) and other major disturbances (e.g., Jokiel 1993, Marshall and Baird 2000). It is not known why *C. trifascialis* was unable to exploit alternate prey corals, following depletion of *Acropora hyacinthus*. However, Motta (1980) found that *C. trifascialis* (along with *C. multicinctus*) is among the most highly evolved of the coral feeding *Chaetodon* species, with highly modified jaws for nipping at small polyped corals. It may be, therefore, that highly specialised coral feeding butterflyfish have coevolved with particular coral species, such that they now exhibit an obligate association with these prey corals (Reese 1981). In support of coevolution between *C. trifascialis* and *A. hyacinthus*, Reese (1981) found that *C. trifascialis* will not feed in captivity unless *A. hyacinthus* is made available. Moreover, *C. trifascialis* are always associated with tabular acroporids (and mostly A. *hyacinthus*) in the field (reviewed by Reese 1981).

While many corallivorous butterflyfish exhibit significant feeding selectivity (e.g., Reese 1977, Cox 1986, Hourigan 1987, as well as this study), it is not known what determines their particular prey preferences. Two separate studies (Tricas 1985, Pratchett 1995) have attempted to relate the preference patterns of corallivorous butterflyfish to the nutritional value of different coral species. Tricas (1985) examined the calorific content of different coral species in Hawaii, while Pratchett (1995) measured lipid, protein and carbohydrate content in various coral species from Great Barrier Reef. Both these studies (Tricas 1985, Pratchett 1995) found that prey preferences of *Chaetodon* butterflyfish were largely unrelated to the nutritional content of different coral species. Therefore, feeding preferences of corallivorous butterflyfish may be structured by the physical defences of corals (e.g., the size and density of nematocysts), or the presence of feeding deterrents in less preferred coral species (*sensu* Alino et al. 1988, Baird et al. 2001 [Appendix 7]). Detailed examination of the feeding preferences of corallivorous butterflyfish at Lizard Island, revealed that all six butterflyfish species (C. *baronessa*, *C. citrinellus*, *C. kleinii*, *C. lunulatus*, *C.* plebeius and C. *trifascialis*) essentially preferred the same species of corals; *Acropora hyacinthus*, and *Pocillopora damicornis*. This overlap in the preferred coral prey of sympatric *Chaetodon* species suggests that there is likely to be very strong inter-specific competition for food (Tricas 1985, Pratchett 1995). More importantly, however, the preferred prey corals of *Chaetodon* butterflyfish (*Acropora hyacinthus* and *Pocillopora damicornis*) are also among the most highly preferred prey corals of crown-of-thorns starfish (Kessing 1990, De'ath and Moran 1998, see also Chapter Three). Often, *Acropora hyacinthus* and *Pocillopora damicornis* are among the first coral species eaten by outbreak populations of *A. planci* (e.g., Chapter Two). Therefore, even relatively mild outbreaks of crown-of-thorns starfish (causing only moderate declines in total coral cover) are likely to exert considerable influence on the distribution, abundance and/ or feeding habits of coral-feeding butterflyfish.

Although this study found no significant decline in the abundances of generalist butterflyfish species (C. *aureofasciatus, C. baronessa*, *C. ephippium*, C. *lunulatus*, *C. melannotus* and *C. unimaculatus*), this does not necessarily mean that these species are entirely unaffected by infestations of *A. planci*. Rather impacts might be more subtle and not, therefore, appreciable over the time frame of this study (Williams 1986). For example, the consumption of less preferred coral species may yield less energy, leading to subsequent declines in growth, survivorship and/ or reproductive output, with long term consequences for the population size (e.g., Jones 1986, Kerrigan 1997). Local recruitment of *Chaetodon* butterflyfish may also decline on reefs affected by *A. planci*, as most butterflyfish species recruit preferentially to areas with high coral cover (Williams 1986). Moreover, the recent infestation of *A. planci* at Lizard Island caused only relatively minor reductions in scleractinian coral cover (0-42% coral mortality) compared to previous outbreaks of *A. planci* on the GBR (see reviews by Moran et al. 1988, Riechelt et al. 1990), and elsewhere throughout the western Pacific (e.g., Chesher 1969, Colgan 1987). More severe disturbances, which greatly reduce the availability of all coral species, are likely to have a much more pronounced affect on butterflyfish, affecting both specialist and generalist species (e.g., Sano et al. 1987).

Temporal and spatial variation in the individual abundance of corallivorous butterflyfish species (*C. baronessa*, *C. citrinellus*, *C. kleinii*, C. *lunulatus*, *C. plebeius*, and *C. trifascialis*), was significantly associated with variation in the availability of their most highly preferred coral prey (Table 4.11). Therefore, depletion of prey resources was almost certainly the mechanism causing declines in butterflyfish abundance during the outbreak of *A. planci*. However, there was at least one non-coral feeding butterflyfish species, namely *C. auriga*, that also declined in abundance during the course of this study (see also Bouchan-Navaro et al. 1985). Hourigan et al. (1985) suggested that close associations between *Chaetodon* butterflyfish and scleractinian corals are not restricted to requirements for prey resources, but rather scleractinian corals may represent essential habitat for newly settled fish recruits (e.g., Bouchan-Navaro et al. 1985), and also provide predator refuges for adult butterflyfish. Spatial and temporal variation in the abundance of *C. auriga* was closely associated with availability of tightly branching *Acropora* spp. (*A. nasuta* grp., *A. gemmifera* grp.). Consistent with this finding previous studies have shown that *C. auriga* settle almost exclusively into tightly branching *Acropora* spp. In tank experiments where larval butterflyfish were given the choice of live branching coral, dead branching coral, coral rubble and bare sand, *C. auriga* always settled into live coral (Nangle, unpubl. data). Further, early post-settlement individuals of *C. auriga* are always closely associated with tightly branching *Acropora* spp. in the field (Nangle, unpubl. data). Reductions in the availability of suitable settlement habitat (specifically, branching acroporids) may, therefore, have caused a reductions in recruitment success over several consecutive years, leading to the gradual declines in the overall abundance of *C. auriga* (Bouchan-Navaro et al. 1985).

In conclusion, this study has shown that coral depletion by outbreak populations of crown-of-thorns starfish can effect reef associated fish species, particularly those species with a specific reliance on scleractinian corals for either food or shelter. Marked reductions in scleractinian coral cover caused significant declines in the overall abundance of *Chaetodon* butterflyfish and also substantially altered the structure of butterflyfish assemblages. These findings suggest that certain populations of *Chaetodon* butterflyfish (particularly highly specialised coral feeding species) are limited by the availability of coral prey. It remains to be seen whether butterflyfish communities will retain their former structure after recovery of coral communities (e.g., Sano 2000). If so, this will further reinforce the role of benthic habitats in structuring reef fish assemblages (Syms and Jones 2001). Therefore, annual monitoring of butterflyfish assemblages around Lizard Island is continuing.

# CHAPTER 5. Effects of coral host depletion on fish commensals[†]

## 5.1 ABSTRACT

Many species of reef fish live in very close association with live colonies of scleractinian corals, and consequently, declines in coral cover may lead to corresponding declines in the abundance of reef fish. This study explores changes in the abundance and habitat associations of six coral-dwelling damselfish species on a reef affected by outbreak populations of crown-of-thorns starfish (*Acanthaster planci* L.). Coral-dwelling damselfish occupied a very limited suite of available habitat categories, showing strong preference for only a limited range of habitat types (mostly specific coral species). Patterns of habitat use by coral-dwelling damselfish were also very consistent among locations and between years, despite significant variation in both the total abundance of corals and the relative abundance of different coral species. Coral cover declined by 16-59% at locations affected by *A. planci*, causing declines in the abundance of *Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus* and *Pomacentrus moluccensis*, but not *C. atripectoralis* or *P. amboinensis*. Species not affected (*C. atripectoralis* and *P. amboinensis*) often inhabited skeletons of dead corals, whereas all other species were strongly dependent on live coral as shelter. Variation in the abundance of obligate coral-dwelling species (*C. viridis*, *D. aruanus*, *D. reticulatus* and *P.moluccensis*) was strongly associated with variation in the abundance of corals that they most frequently occupied. This study demonstrates that infestations of *A. planci* can significantly effect the distributions and abundances of reef fishes with strong dependence on live corals.

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[†] This study was conducted in collaboration with Philip L. Munday and Geoffrey P. Jones and forms the basis of a manuscript submitted to the *Oecologia*, titled "Impacts of *A. planci* on coral reef fish: effects of coral host depletion on fish commensals"

## 5.2 INTRODUCTION

The distribution and abundance of organisms in time and space is often related to the availability of particular habitats that provide increased access to resources and increase individual fitness (e.g., Pulliam 1989, Rosenzweig 1991, Orians and Wittenberger 1991). On coral reefs, distributions and abundances of many reef fish are related to the distribution and abundance of scleractinian corals. This is particularly true for fish that explicitly use scleractinian corals for food or shelter (e.g., Bell and Gazlin 1984, Bouchan-Navaro et al. 1985, Kuwamurra et al. 1994, Jennings et al. 1996, Munday et al. 1997, Holbrook et al. 2000). For coral-feeding butterflyfish of the genus *Chaetodon* (family Chaetodontidae), the availability of prey corals can account for up to 70% of variation in their population abundance among reef zones and among locations separated by 0.5 – 1.0 kilometres (Pratchett 1995). Similarly, the abundance of host corals can account for more than half of the variation in the abundance of coral-dwelling gobies (family Gobidae), within reefs (Munday et al. 1997, Munday 2000), and across geographical regions separated by thousands of kilometres (Munday, In press). Temporal and spatial variation in the abundance of many other reef-fish, including those that have no direct reliance on scleractinian corals, has also been related to changes in the abundance of live coral (e.g., Sano et al. 1984, Dawson-Shepherd et al. 1992, Jennings et al. 1996, Syms and Jones 2000; but see also Findley and Findley 1985, Roberts et al. 1988, Fowler 1990, Cox 1994). Consequently, large-scale and increasingly prevalent disturbances to coral communities (e.g., Hughes 1994, Sebens 1994) are likely to impact greatly on populations, or communities, of coral reef fishes.

Coral communities are subject to frequent, and often catastrophic disturbances, caused by a variety of factors, including severe tropical storms, freshwater plumes, unseasonal temperature extremes, or infestations of the corallivorous crown-of-thorns starfish, *Acanthaster planci* (reviewed by Brown 1996). Such disturbances can drastically reduce the abundance of scleractinian corals (Dollar and Tribble 1993), but may or may not affect reef fish assemblages. Several studies have shown that natural disturbances to coral communities can have a major effect on reef fish assemblages (Kaufman 1983, Lassig 1983, Dawson-Shepherd et al. 1992, but see also Walsh 1983, Wellington and Victor 1985, Glynn 1985, Guzman and Robertson 1989). To date, the most significant impacts of habitat alteration on reef fish assemblages have been reported during severe tropical storms, which reduce the abundance of scleractinian corals, but also reduce heterogeneity and topographic complexity of reef habitats (e.g., Harmelin-Vivien and Laboute 1986). Such events can reduce the abundance of coral reef fishes by up to 60% (e.g., Letourneur et al. 1993), but it is not clear whether changes in fish abundance are due to reductions in live coral cover, alterations to habitat structure, or both. Disturbance events that reduce coral cover, but do not immediately alter the physical structure of reef habitats (e.g., severe bleaching events, infestations of *A. planci*) appear to have much less dramatic impacts on reef fish assemblages (e.g., Wellington and Victor 1985, Glynn 1985, Guzman and Robertson 1989), which may indicate that most reef fish depend on the structure provided by corals (i.e., their carbonate skeleton) rather than live coral *per se* (but see Sano et al. 1984).

Outbreaks of *A. planci* have occurred on many reefs throughout the Indo-West Pacific since the 1960's, and have almost invariably caused extensive mortality of scleractinian corals (reviewed by Moran 1986). In extreme cases, outbreaks of *A. planci* have killed 90% of scleractinian corals across expansive reef areas (e.g., Green Island on the Great Barrier Reef, Pearson and Endean 1969; Guam, Chesher 1969). Perturbations of this magnitude are likely to have significant implications for all manner of reef associated organisms, including reef fishes (Moran 1986). However, relatively few studies (Bouchan-Navaro et al. 1985, Williams 1986, Sano et al. 1984, 1987, Hart et al. 1996, Munday et al. 1997) have explored changes in the abundance of fish on reefs affected by *A. planci*. Moreover, these studies have considered only a few different reef fish species (but see Williams 1986). Even so, it is clear that coral depletion caused by infestations of *A. planci* can impact on abundances of reef fishes, although effects may be restricted to only a few specialised species (Williams 1986). Williams (1986) examined changes in the abundance of 69 reef fish species from five major families (Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, and Scaridae) on reefs affected by *A. planci*, but only coral-feeding butterflyfish (family Chaetodontidae) showed changes in abundance that could be ascribed to impacts from *A. planci* (see also Bouchan-Navaro et al. 1985, Chapter Four). Another group of reef fish that has been shown to be significantly affected by infestations of *A. planci* are obligate coral-dwelling gobies (family Gobidae), which declined in abundance in accordance with declines in the abundance of coral colonies at Lizard Island on the Great Barrier Reef, due to localised infestations of *A. planci* (Munday et al. 1997).

In this study, we consider the affect of *A. planci* on a suite of small damselfishes (family Pomacentridae) that are typically found living in close association with live coral colonies. These coral-dwelling damselfish, from the genera *Chromis*, *Dascyllus*, and *Pomacentrus* tend to live within the immediate vicinity of a single branching coral colony, in which they seek shelter at the approach of danger (Sale 1971, Robertson and Lassig 1980). The abundance of some coral-dwelling damselfish is directly proportional ($r^2 \geq 0.83$) to the availability of specific coral habitats (Holbrook et al. 2000), and consequently we might expect these fishes to be negatively affected by coral depletion caused by infestations of *A. planci*. Previously, Williams (1986) failed to detect any significant decline in the abundance of coral-dwelling damselfish on reefs affected by *A. planci*. However, Sano et al. (1987) showed that coral-dwelling damselfish were significantly less abundant at a reef that was heavily impacted by *A. planci*, compared to an adjacent but unaffected reef, though these spatial comparisons may be confounded by natural variation in the abundance of damselfish (*sensu* Doherty and Williams 1988). Even if there are not direct effects on damselfish abundance, the reduction in habitat availability may influence patterns of habitat use, which further influence growth, survival and/ or reproductive success. Also, the impacts of *A. planci* are likely to vary among damselfish species according to differences in their dependence on scleractinian corals, and specific patterns of habitat use.

Patterns of habitat use by coral-dwelling damselfish, specifically *Dascyllus aruanus* and *Pomacentrus moluccensis*, have been explored previously (Forrester 1990, 1991, Holbrook et al. 2000). However, their degree of habitat specialisation and their specific dependence on live corals as habitat is largely unknown. Sufficient evidence exists to suggest that coral-dwelling damselfish exhibit preferences among different coral species (Ault and Johnson 1998a, Holbrook et al. 2000), but it is not known whether these patterns of habitat use are consistent across spatial gradients, or whether habitat use varies in response to habitat alterations. In this study we document spatial and temporal patterns of habitat use by six species of coral-dwelling damselfish, *Chromis atripectoralis*, *C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis* and *P. moluccensis* at Lizard Island, on the Great Barrier Reef. We then compared the abundance of these fishes with the availability of the coral species they occupied. Finally, we assessed whether the abundance and/ or patterns of habitat use of coral-dwelling damselfish changed in response to the depletion of scleractinian corals caused by localised infestations of crown-of-thorns starfish, over a 12 month period.

## 5.3 METHODS

### Study locations

This study was initiated in February 1998, at Lizard Island (14°40'S, 145°27'E), on the northern Great Barrier Reef, Australia. At this time, the Lizard Island fringing reefs were experiencing declining coral cover due to the feeding activities of large populations of crown-of-thorns starfish. Starfish densities were greatest on the north-eastern side of the island, though elevated numbers of starfish could also be found all along the southern and eastern margins of the island. Conversely, *A. planci* were mostly absent from within the lagoon (Chapter 2). To assess the effect of *A. planci* on coral-dwelling damselfish, sampling was conducted at locations along the southern and eastern margins of Lizard Island (North Reef, Washing Machine, Coconut Beach, Lizard Head, South Island, South Bay), as well as within the lagoon (East Palfrey and Middle Lagoon). These eight locations (Figure 5.1) differed in their recent history of crown-of-thorns disturbances (Chapter 2), but all locations had reasonable cover (>30%) of scleractinian corals when this study was initiated. Preliminary sampling was also conducted at Corner Beach and Casuarina, but crown-of-thorns starfish had already severely depleted coral communities at these locations (Chapter 2), and all coral-dwelling damselfish were extremely rare (<5 damselfish per $40m^2$). As a consequence, these locations (Corner Beach and Casuarina) were not considered in this study.

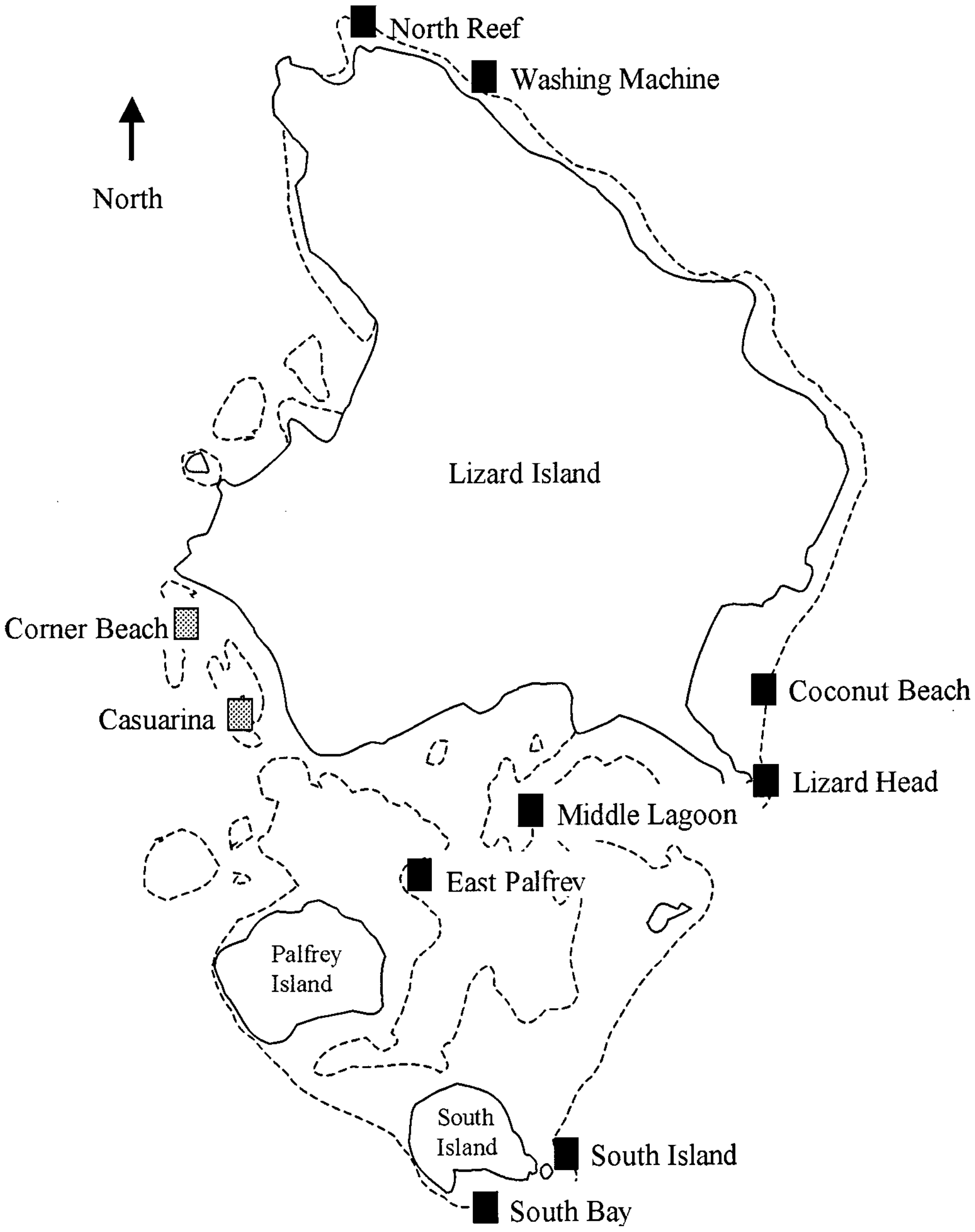

**Figure 5.1.** Map of Lizard Island showing locations (black boxes) used to assess abundance of coral-dwelling damselfish. Additional locations (grey boxes) were censused during preliminary sampling, but scleractinian corals and coral-dwelling damselfish were so rare that sampling was not continued. Solid lines delineate land and dashed lines delineate approximate outline of reefs.

## Sampling design

Patterns of abundance and habitat use of coral-dwelling damselfish were assessed in two reef zones (the reef crest and reef base) at each of the eight locations (Figure 5.1). To census coral-dwelling damselfish we used replicate 20 × 2 metre belt transects. Ten replicate transects were run on both the reef crest and reef base at each site, giving a total of 80 transects and a total sample area of 3,200m$^2$. Each transect was orientated parallel to the reef crest, and run from a haphazardly selected starting point within each zone. A 20m tape was placed along the centre of the transect and a 1m measuring bar was used to mark the transect width. Every scleractinian coral, located at least half within the transect and with a diameter greater than 10cm, was identified to species and its size was recorded by measuring the maximum diameter and perpendicular diameter. We also identified and counted any damselfish that sheltered within each colony at the divers approach. To accurately count the damselfish sheltering within each colony, divers moved 1-2 metres away from the colony and counted fish as they emerged from within the colony. Counts were repeated several times where there was any uncertainty, and whenever colonies contained more than ten individuals. The few damselfish (<5%) that were not clearly associated with one particular coral colony were included in the total densities for each transect, but excluded from analyses of habitat association.

All locations were resurveyed after approximately one year, in January 1999, to determine if there had been any changes in the abundance of coral-dwelling damselfish, and whether these changes reflected the extent of disturbance caused by local starfish populations. The sampling design employed in this study enabled comparisons of damselfish abundance and habitat availability (the number and size of suitable coral colonies) between zones, among locations and between years. Additionally, we were able to explore associations between coral-dwelling damselfish and particular coral species, and assess whether the abundance of damselfish varied in response to changes in the abundance of their most frequently used coral species.

## Analysis of habitat use

Log-linear analysis was used to determine whether each damselfish used particular corals disproportionately to their availability, and also whether patterns of habitat use were consistent among locations and between years. Log-linear models were fitted to the observed data based on the frequency with which the damselfish used particular habitats relative to the proportional availability of these habitats at each site, and in each year. To perform the analyses, a series of models with increasing complexity (Table 5.1) were tested sequentially (1→ 4) until there was no significant improvement in the goodness-of-fit statistic from one model to the next, thereby indicating the simplest combination of factors which could account for patterns of habitat use, following Munday (2000). The number of habitat categories used in the analysis was necessarily restricted, and so the habitats chosen were those which were used most often by coral-dwelling damselfish (*Acropora divaricata, A. millepora, A. valida, , Echinopora lamellosa, Pocillopora. damicornis, P. eydouxi Porites cylindrica, Seriatopora hystrix, Stylophora pistillata*, and Dead Corals). To ensure independence of observations, analyses were based on the presence/ absence of each damselfish species in each colony, rather than number of damselfish per colony (see Thomas and Taylor 1990, Munday 2000). Data were pooled across replicate transects to provide adequate cell counts and analyses were conducted separately for each of the two different zones (crest and slope), because many of the damselfish species were restricted mostly to a single reef zone.

**Table 5.1.** Log-linear models used to test patterns of habitat use (adapted from Munday 2000). Hierarchical models were tested sequentially until there was no further improvement in the fit of the model to the data. Two models were considered as alternative conditional models (3a and 3b) in the progression from model 2 → 4.

| Model | Factors included | Hypothesis tested |
|---|---|---|
| 1 | site*year | coral use is proportional to availability |
| 2 | coral + site*year | corals used disproportionately to availability and the pattern uniform among locations and years |
| 3a | coral*year + site*year | corals used disproportionately to availability, but the pattern changes between years |
| 3b | coral*site + site*year | corals used disproportionately to availability, but the pattern changes between locations |
| 4 | coral*year + coral*site + site*year | corals used disproportionately to availability, but the pattern changes between locations and between years |

Where log-linear analyses indicated that a damselfish used habitats disproportionately to their availability, we used resource selection functions (Manly et al. 1993) to determine which habitats were used more or less frequently than expected. Resource selection functions ($w_i$) were calculated using the formula

$$w_i = u_i / \pi_i$$

which compares the proportional use ($u_i$) of each habitat type ($i$) with the proportional availability of that habitat ($\pi_i$) within the local area. Selection functions were calculated for all habitat categories used in log-linear analyses, and estimates of the proportional use and proportional availability of different coral species were pooled among locations and/ or between years wherever log-linear analyses showed there were no significant differences in habitat use among locations or between years. To aid in the interpretation of selection functions, we calculated Bonferroni corrected 95% confidence intervals around each selection function, using the formula:

$$Z_{\alpha/2k}\sqrt{\{u_i(1-u_i)/(u_+\pi_i^2)\}}$$

where $Z_{\alpha/2k}$ is the critical value of the standard normal distribution corresponding to the upper tail probability of $\alpha/2k$, $\alpha = 0.05$, k = the total number of habitat categories, and $u_+$ is the total number of colonies of all different types used by each damselfish species ($u_i$ and $\pi_i$ are as defined previously). Consequently, the use of a particular habitat was only deemed to be disproportionate to its availability if the 95% confidence interval did not encompass 1 (Manly *et al.* 1993). Selection functions significantly greater than 1 indicated that corals were used more than expected from their availability, while selection functions less than 1 indicated that corals were used less than expected.

## Habitat availability and damselfish abundance

Variation in the abundance and species composition of scleractinian corals was analysed to assess temporal and spatial variation in the availability of coral habitats for coral-dwelling damselfish. Area cover, rather than the number of colonies, was used to assess availability of coral habitats thereby accounting for variation in both the number and size of coral colonies. Area cover of individual coral colonies was estimated from the mean of the maximum diameter and perpendicular diameter using the equation:

$$Area = \pi(d_{max} + d_p / 4)^2$$

where $d_{max}$ is the maximum diameter, and $d_p$ is the perpendicular diameter. The total area of all colonies of each coral species (excluding colonies with $d_{max} < 10$cm) was then calculated for each replicate transect, and the data were analysed to assess variation in total coral cover between zones, among locations and across years.

In addition to total availability of coral habitats, we also analysed variation in the species composition of coral habitats, using Multivariate Analysis of Variance (MANOVA). However, due to limited replication ($n = 10$), it was not possible to include all coral species used by coral-dwelling damselfish (30 species) in a single analysis of habitat structure. To overcome this, we first ran a Principal Components Analysis (PCA) on the area cover of each coral species on each replicate transect, accounting for the maximum possible variation in a reduced number of variables. We then analysed the first nine Principal Components (which summarised 88% of the total variation within the data set) with MANOVA, using Pillai's trace as the test statistic. MANOVA was used to test for significant differences in the species composition of coral communities between zones, among locations and across years.

To test whether variation in the abundance of damselfish (between zones, among locations, and across years) was related to variation in habitat availability, we used multiple linear regression to compare the abundance of each of the six damselfish species (*Chromis atripectoralis*, *C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis* and *P. moluccensis*) with each of ten different habitat categories (*Acropora divaricata, A. millepora, A. valida, Echinopora lamellosa*, *Pocillopora damicornis*, *P. eydouxi*, *Porites cylindrica*, *Seriatopora hystrix*, *Stylophora pistillata*, and Dead Corals) used in log-linear analyses. Best subsets multiple regression was used to assess which combination of the ten habitat categories accounted for most variation in the abundance of each damselfish species, using Mallow's $C_p$ as the test statistic. Using the best subset of habitat variables for each damselfish species, we then measured the proportion of variation in the abundance of damselfish that could be attributed to variation in habitat availability.

Multiple linear regression accounted for only 4-52% of variation in the abundance of each of the six coral-dwelling damselfish (*Chromis atripectoralis*, *C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis* and *P. moluccensis*), leaving considerable unexplained variation in their patterns of abundance. Consequently, we took the residuals from the multiple linear regression and analysed them using ANOVA, following Munday (2000), which enabled us to explore variation in the abundance of damselfish between zones, among locations and between years, independently of changes in habitat availability. If variation in the abundance of damselfish is determined largely by habitat availability, then residuals should be comparable across all treatments (ie. no significant effects associated with zone, location or year). If however, the abundance of coral-dwelling damselfish is influenced to a large extent by any factors other than habitat availability (*sensu* Caley et al. 1996) we would expect to find significant variation in residuals from different zones, locations and/ or years.

## 5.4 RESULTS

### Patterns of habitat use

During the course of this study, we censused a total of 12,062 coral colonies including 64 different species of live corals, as well as algal covered skeletons of dead coral colonies (classified as a single category "Dead Coral" irrespective of the coral species). Within these various habitat categories we found a total of 8,193 coral-dwelling damselfish from six different species (*Chromis atripectoralis*, *C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis* and *P. moluccensis*). All damselfish species lived mostly (>50% of individuals observed) in close association with live coral colonies, although some individuals of each damselfish species were seen sheltering in algal-covered skeletons of dead branching corals. The proportion of individuals found living in dead corals varied, from <1% for *D. reticulatus* (n =226), up to 48% for *P. amboinensis* (n =675). Four species of damselfish, *Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus* and *Pomacentrus moluccensis*, only rarely used dead corals (<5% individuals found in dead corals) and are hereafter referred to as obligate coral-dwelling species. By contrast, *P. amboinensis* and *C. atripectoralis* both occupied dead coral colonies far more than any single coral species. For *P. amboinensis*, 40-45% of individuals occupied dead coral in both 1998 and 1999 (Figure 5.2). For *C. atripectoralis*, 19.2% of individuals were found living in dead corals in 1998 (n =292). However, the proportion of individuals of *C. atripectoralis* found living in dead coral colonies increased markedly between years, up to 31.6% in 1999 (n =307) (Figure 5.2). Although each of the six damselfish species used predominantly live coral colonies, only 7.6% (820/ 10,786 colonies) of live coral colonies, and only 47% (30/ 64 species) of coral species were actually occupied by coral-dwelling damselfish. Each damselfish species used between 9-31 different habitat categoreis (Table 5.2), although each damselfish species was predominantly found in just one or two different habitat categories (Figure 5.2). The specific habitat categories used most often by each damselfish species were the same in 1998 and 1999 (Figure 5.2).

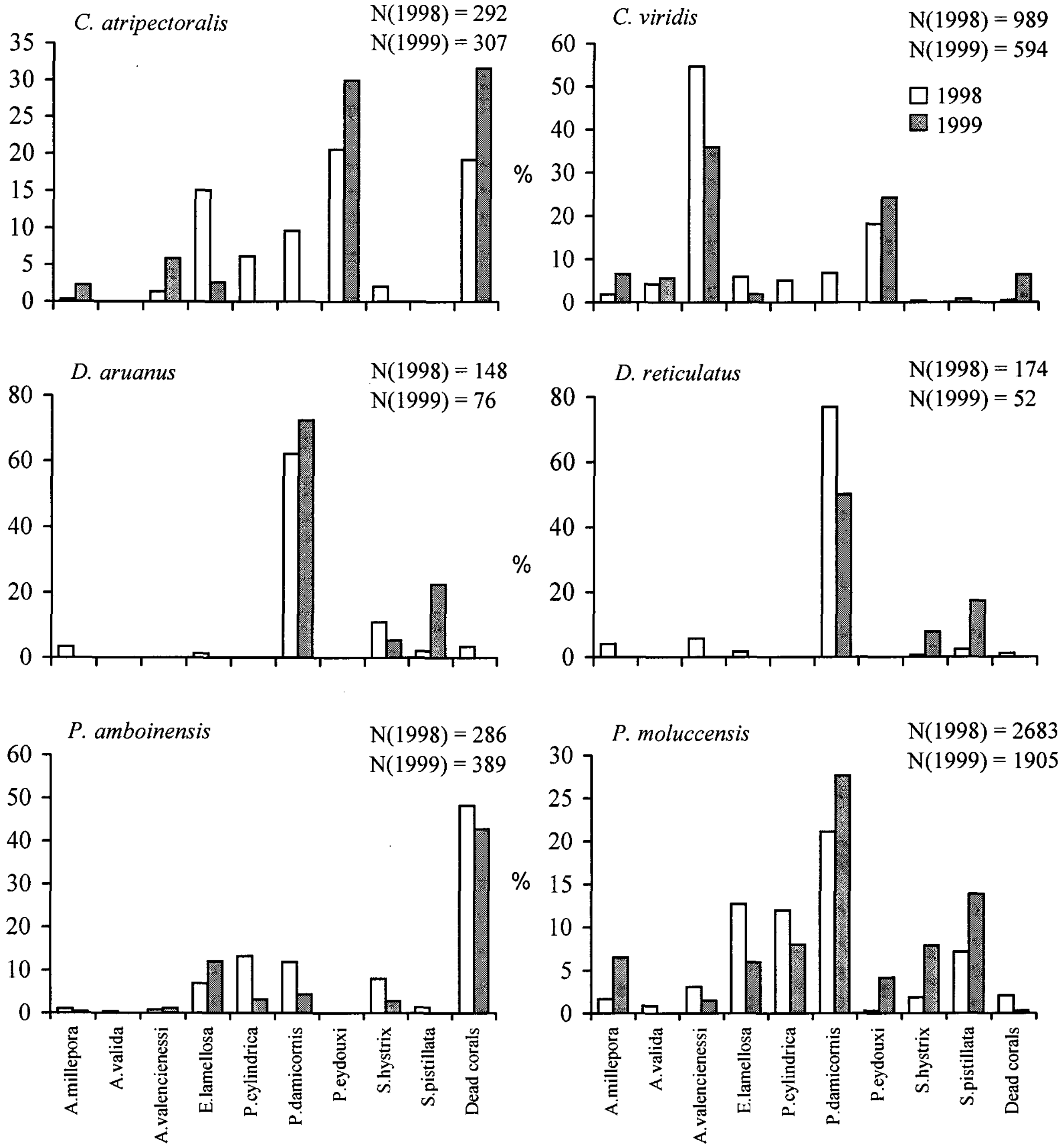

**Figure 5.2.** Temporal variation in the distribution of damselfish amongst 10 different habitat categories. The proportion of all individuals that occupied each habitat category was calculated in each year, but no account was made for variation in the relative abundance of different habitats.

**Table 5.2.** Occupation of different habitat categories by coral dwelling damselfish. All habitat categories used by each damselfish are indicated by "*" (* <10% of colonies occupied, ** 10-50% of colonies occupied, *** >50% of colonies occupied). Patterns of habitat use varied little between 1998 and 1999, so data was pooled across years.

| | | Damselfish species | | | | | |
|---|---|---|---|---|---|---|---|
| Habitat Categories | n | *C. atripectoralis* | *C. viridis* | *D. aruanus* | *D. reticulatus* | *P. amboinensis* | *P. moluccensis* |
| *Acropora aspera* | 12 | | | * | | | * |
| *Acropora cerialis* | 5 | | * | | | | * |
| *Acropora divaricata* | 10 | * | *** | | * | * | *** |
| *Acropora donei* | 8 | * | ** | | | | * |
| *Acropora echinata* | 8 | | * | | | | * |
| *Acropora formosa* | 24 | * | ** | | | * | ** |
| *Acropora gemmifera* | 124 | * | | | | * | * |
| *Acropora humilis* | 30 | | | | | | * |
| *Acropora loripes* | 177 | | * | * | * | | ** |
| *Acropora millepora* | 81 | | * | * | * | * | ** |
| *Acropora nasuta* | 142 | | * | | | * | * |
| *Acropora intermedia* | 22 | * | * | | | * | * |
| *Acropora robusta* | 21 | | * | | | | * |
| *Acropora sarmentosa* | 29 | | | | | | * |
| *Acropora tenuis* | 33 | | * | | | * | * |
| *Acropora valida* | 149 | | * | | | * | * |
| *Acropora yongei* | 5 | * | * | | | * | * |
| *Porites cylindrica* | 142 | | * | | | * | ** |
| *Porites nigrescens* | 86 | * | * | | | * | * |
| *Echinopora lamellosa* | 75 | * | * | * | * | ** | ** |
| *Echinopora horrida* | 40 | * | * | | | * | * |
| *Hydonophora rigida* | 8 | | | | | * | * |
| *Heliopora coerulea* | 76 | * | | | | * | ** |
| *Pavona cactus* | 4 | | | | | | * |
| *Pocillopora damicornis* | 348 | * | * | * | * | * | ** |
| *Pocillopora eydouxi* | 45 | ** | ** | | | | ** |
| *Pocillopora meandrina* | 48 | | | * | * | * | * |
| *Pocillopora verrucosa* | 100 | | | * | * | * | ** |
| *Seriatopora hystrix* | 237 | * | * | * | * | * | ** |
| *Stylophora pistillata* | 145 | | * | * | * | * | *** |
| Dead Corals | 1276 | * | * | * | * | * | * |
| # of habitat categories used | | 14 | 22 | 10 | 10 | 21 | 31 |

All six damselfish species used different habitat categories disproportionately to their availability (Table 5.3). For all damselfish species, except *P. moluccensis*, the proportional use of different habitat categories varied little among locations or between years, despite significant differences in coral cover among locations and between years (Table 5.5) as well as extensive changes in coral composition (Table 5.6). Resource selection functions showed that every damselfish species inhabited 1-3 habitat categories disproportionately more than predicted by the availability of different habitats (Table 5.4). *Chromis atripectoralis* used *Pocillopora eydouxi* significantly more than expected, while *Chromis viridis* used both *Acropora divaricata* and *Pocillopora eydouxi* more frequently than expected. *Dascyllus aruanus* and *D. reticulatus* both used *Pocillopora damicornis* and *Stylophora pistillata* far more than expected, and *Pomacentrus amboinensis* also used *Pocillopora damicornis* significantly more than expected. *Pomacentrus moluccensis* used *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata* more than expected on the reef crest in 1998, but patterns of habitat use varied between zones and also between years (Table 5.4). *Pomacentrus moluccensis* was the only species abundant enough to enable analysis of habitat use on both the reef crest and reef base (Table 5.3), and also the only species for which habitat use varied between years (Table 5.4). *Pomacentrus moluccensis* became less selective in its use of different habitat categories (using more coral species approximately in accordance with their availability) between years, as coral cover declined. *Pomacentrus moluccensis* also exhibited less selectivity for habitats on the reef base compared to the reef crest, in line with the reduced availability of live coral colonies on the reef base (Figure 5.3).

**Table 5.3.** Log-linear analysis of habitat use by coral-dwelling damselfish. Log-linear models (1→4) were tested sequentially until there was no significant improvement in deviance (*** = $p < 0.001$, ns = non-significant). The best model is highlighted for each species in each reef zone (see Table 5.1 for specific interpretation of models). *Pomacentrus moluccensis* was the only species abundant enough on both the reef crest and reef base for analysis of habitat use in more than one zone.

| Species | Zone | Model | Deviance | df | Improvement | df |
|---|---|---|---|---|---|---|
| *C. atripectoralis* | Crest | 1 | 239.39 | 144 | | |
| | | **2** | **39.79** | **135** | **253.60 *** ** | **9** |
| | | 3a | 34.05 | 126 | 5.74 ns | 9 |
| | | 4 | 5.54 | 63 | 28.51 ns | 63 |
| *C. viridis* | Crest | 1 | 293.39 | 144 | | |
| | | **2** | **39.79** | **135** | **253.60 *** ** | **9** |
| | | 3a | 34.05 | 126 | 5.74 ns | 9 |
| | | 4 | 5.54 | 63 | 28.51 ns | 63 |
| *D. aruanus* | Base | 1 | 402.56 | 144 | | |
| | | **2** | **45.98** | **135** | **356.58 *** ** | **9** |
| | | 3a | 30.16 | 126 | 15.82 ns | 9 |
| | | 4 | 0.55 | 63 | 29.61 ns | 63 |
| *D. reticulatus* | Base | 1 | 374.69 | 144 | | |
| | | **2** | **25.91** | **133** | **348.78 *** ** | **11** |
| | | 3a | 16.97 | 126 | 8.94 ns | 7 |
| | | 4 | 1.07 | 63 | 15.90 ns | 63 |
| *P. amboinensis* | Base | 1 | 362.67 | 144 | | |
| | | **2** | **85.46** | **133** | **277.21 *** ** | **11** |
| | | 3 | 68.57 | 126 | 16.89 ns | 7 |
| | | 4 | 20.56 | 63 | 48.01 ns | 63 |
| *P. moluccensis* | Base | 1 | 302.68 | 128 | | |
| | | 2 | 119.21 | 120 | 183.47 *** | 8 |
| | | **3a** | **74.91** | **112** | **44.30 *** ** | **8** |
| | | 4 | 12.74 | 56 | 62.17 ns | 56 |
| *P. moluccensis* | Crest | 1 | 160.49 | 128 | | |
| | | 2 | 94.83 | 120 | 65.66 *** | 8 |
| | | **3a** | **64.08** | **112** | **30.75 *** ** | **8** |
| | | 4 | 17.12 | 56 | 46.96 ns | 56 |

**Table 5.4.** Patterns of habitat use for coral-dwelling damselfish. "0" = habitat categories used in approximate proportion to their abundance, "+" = habitat categories used significantly more than expected, "-" = habitat categories used significantly less than expected, and "U" = habitat categories that were never used. Significance determined using Bonferroni 95% confidence intervals around resource selection functions. Data pooled across locations for all species.

| | | | Habitat Categories | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Zone | Year | *A. divaricata* | *A. millepora* | *A. valida* | *E. lamellosa* | *P. cylindrica* | *P. damicornis* | *P. eydouxi* | *S. hystrix* | *S. pistillata* | Dead Corals |
| *C. atripectoralis* | Crest | Both | – | 0 | – | – | – | 0 | + | – | U | – |
| *C. viridis* | Crest | Both | + | 0 | – | – | – | 0 | + | – | – | – |
| *D. aruanus* | Base | Both | U | – | – | 0 | – | + | – | 0 | + | – |
| *D. reticulatus* | Base | Both | – | – | – | – | – | + | – | 0 | + | U |
| *P. amboinensis* | Base | Both | 0 | 0 | – | 0 | 0 | + | – | 0 | 0 | – |
| *P. moluccensis* | Crest | 1998 | 0 | 0 | – | 0 | – | + | – | + | + | – |
| | | 1999 | 0 | 0 | 0 | 0 | – | + | – | 0 | 0 | – |
| | Base | 1998 | 0 | 0 | 0 | 0 | – | + | – | 0 | + | – |
| | | 1999 | 0 | 0 | 0 | 0 | – | 0 | – | 0 | 0 | – |

### Habitat availability and damselfish abundance

Many of the coral species utilised by coral-dwelling damselfish are among the most preferred coral prey of the crown-of-thorns starfish *Acanthaster planci* (see Chapter 2). As a consequence, localised infestations of *A. planci* at Lizard Island caused significant reductions in the availability of live coral hosts for coral-dwelling damselfish over the period of the study. The proportion of hard substrates occupied by the 30 coral species used by coral-dwelling damselfish (listed in Table 5.2) declined by 19.2%, from a mean of 8.2% cover (± 0.6SE) in February 1998, down to 6.6% cover (± 0.5SE) in January 1999. In terms of colony abundance, the average number of live colonies of all coral species used by coral-dwelling damselfish declined by 31.9%, from a mean of 37.9 (± 1.2SE) colonies per $200m^2$, down to 25.8 (± 0.7SE) colonies per $200m^2$. Declines in the overall abundance of corals used by coral-dwelling damselfish were highly significant. However, the extent of the impact varied among locations and also between reef zones (Table 5.5). The depletion of coral hosts was most pronounced at Coconut Beach, Lizard Head, South Island and South Bay, where the proportion of hard substrate occupied by the 30 coral species used by coral-dwelling damselfish declined by 34-59% from February 1998 to February 1999 (Figure 5.3). At North Reef and Washing Machine, the proportional cover of live corals used by coral-dwelling damselfish declined by 16-18%. However, there was no change in the abundance of these corals at either East Palfrey or Middle Lagoon (Figure 5.3). Declines in the abundance of coral hosts were also more severe on the reef base, compared to the reef crest (Figure 5.3).

**Table 5.5.** Three way ANOVA to explore variation in the proportion of hard substrates occupied by live colonies of all coral species used by coral-dwelling damselfish (coral species listed in Table 5.2). Data was arcsine transformed prior to analysis, "*" indicates significant effects (*p<0.05, **P<0.01, ***p<0.001).

| Source | df | MS | F |
|---|---|---|---|
| Year | 1 | 18.05 | 0.16 |
| Zone | 1 | 932.54 | 8.12** |
| Site | 7 | 752.44 | 6.55*** |
| Year × Zone | 1 | 663.55 | 5.78* |
| Year × Site | 7 | 262.12 | 2.28* |
| Zone × Site | 7 | 182.18 | 1.59 |
| Year × Zone × Site | 7 | 239.06 | 2.08* |
| Error | 288 | 114.88 | |

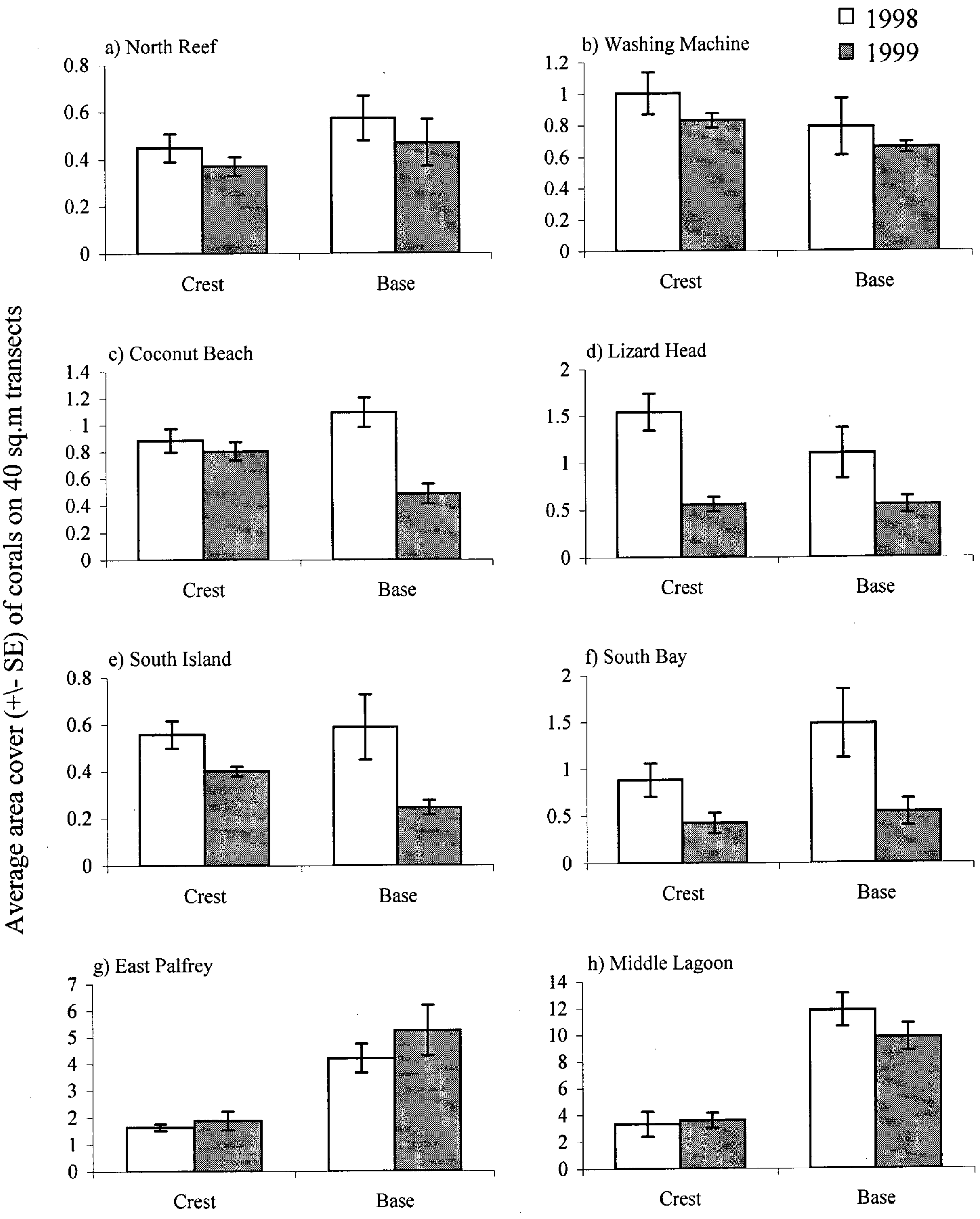

**Figure 5.3.** Temporal and spatial variation in habitat availability for coral-dwelling damselfish. The combined abundance of all coral species used by coral-dwelling damselfish (listed in Table 4) was compared between zones, among sites and between years.

There was also significant temporal variation in the relative abundance of the 31 different habitat categories used by coral-dwelling damselfish (Table 5.6), resulting from differential impacts by *A. planci* among different coral species. Only ten (out of 30) coral species used by coral-dwelling damselfish exhibited significant declines in area cover across all locations and depths. The coral species most affected by infestations of *A. planci* was *Pocillopora damicornis* (Table 5.7), which was also the most frequently used coral species by three (out of 6) species of coral-dwelling damselfish (Figure 5.2). The mean area cover of *P. damicornis* declined by 45% over the study period, from 0.77% cover (± 0.14SE) in 1998, down to 0.42% cover (± 0.06SE) in 1999. In terms of colony abundance, the average number of live colonies of *P. damicornis* declined by 31%, from a mean of 1.29 (± 0.12SE) colonies per $200m^2$, down to 0.89 (± 0.14SE) colonies per $200m^2$. Corresponding with declines in the abundance of many live coral species, there was a significant increase in the availability of Dead Corals (Table 5.7).

**Table 5.6.** Three-way MANOVA to explore variation in the relative abundance of habitat categories used by coral-dwelling damselfish. Analysis was performed using the first 9 principal components from a PCA of habitat availability, which together explained 88% of variation in habitat availability, '*' indicates significant effects (*p<0.05, **p<0.01, ***p<0.001).

| Source | df | Pillai's Trace | F |
|---|---|---|---|
| Year | 8 | 0.07 | 2.75** |
| Zone | 8 | 0.66 | 68.44*** |
| Site | 56 | 1.38 | 8.80*** |
| Year × Zone | 8 | 0.06 | 2.20* |
| Year × Site | 56 | 0.56 | 3.11*** |
| Zone × Site | 56 | 0.76 | 4.34*** |
| Year × Zone × Site | 56 | 0.31 | 1.70** |

**Table 5.7.** Temporal variation in the mean area cover (± SE) of each habitat category used by coral-dwelling damselfish. Data pooled between depths and across all locations. Significant changes in the cover of habitats are expressed as a proportion of initial cover, where *p<0.05, **p<0.01, ***p<0.001. Only Dead Corals increased significantly in cover over the study period.

| Habitat Categories | Initial cover - 1998 | Final cover - 1999 | Changes |
|---|---|---|---|
| *Acropora aspera* | 0.01 (± 0.00) | 0.02 (± 0.01) | |
| *Acropora cerialis* | 0.03 (± 0.02) | 0.08 (± 0.02) | |
| *Acropora divaricata* | 0.18 (± 0.08) | 0.08 (± 0.06) | - 0.56** |
| *Acropora donei* | 0.14 (± 0.08) | 0.09 (± 0.03) | |
| *Acropora echinata* | 0.03 (± 0.01) | 0.01 (± 0.01) | |
| *Acropora formosa* | 0.11 (± 0.07) | 0.15 (± 0.05) | |
| *Acropora gemmifera* | 0.18 (± 0.03) | 0.13 (± 0.03) | - 0.28* |
| *Acropora humilis* | 0.06 (± 0.02) | 0.03 (± 0.01) | |
| *Acropora loripes* | 0.16 (± 0.05) | 0.33 (± 0.06) | |
| *Acropora millepora* | 0.14 (± 0.03) | 0.17 (± 0.04) | |
| *Acropora nasuta* | 0.22 (± 0.04) | 0.12 (± 0.02) | - 0.45** |
| *Acropora intermedia* | 0.21 (± 0.07) | 0.11 (± 0.06) | - 0.48* |
| *Acropora robusta* | 0.09 (± 0.03) | 0.04 (± 0.02) | - 0.56** |
| *Acropora sarmentosa* | 0.03 (± 0.01) | 0.04 (± 0.01) | |
| *Acropora tenuis* | 0.02 (± 0.01) | 0.06 (± 0.02) | |
| *Acropora valida* | 0.18 (± 0.04) | 0.16 (± 0.03) | |
| *Acropora yongei* | 0.01 (± 0.00) | 0.01 (± 0.00) | |
| *Porites cylindrica* | 2.71 (± 0.82) | 2.19 (± 0.88) | |
| *Porites nigrescens* | 0.65 (± 0.15) | 0.72 (± 0.12) | |
| *Echinopora lamellosa* | 0.87 (± 0.11) | 0.70 (± 0.09) | - 0.20** |
| *Echinopora horrida* | 0.11 (± 0.07) | 0.21 (± 0.07) | |
| *Hydonophora rigida* | 0.05 (± 0.02) | 0.04 (± 0.01) | |
| *Heliopora coerulea* | 1.36 (± 0.19) | 1.19 (± 0.27) | |
| *Pavona cactus* | 0.09 (± 0.02) | 0.18 (± 0.04) | |
| *Pocillopora damicornis* | 0.77 (± 0.14) | 0.42 (± 0.06) | - 0.45*** |
| *Pocillopora eydouxi* | 0.26 (± 0.04) | 0.17 (± 0.05) | - 0.35* |
| *Pocillopora meandrina* | 0.05 (± 0.01) | 0.06 (± 0.01) | |
| *Pocillopora verrucosa* | 0.11 (± 0.03) | 0.13 (± 0.02) | |
| *Seriatopora hystrix* | 0.31 (± 0.07) | 0.25 (± 0.05) | - 0.19* |
| *Stylophora pistillata* | 0.42 (± 0.03) | 0.27 (± 0.06) | - 0.36** |
| Dead Corals | 5.51 (± 0.85) | 7.84 (± 1.01) | +0.42*** |

Declines in the availability of live coral hosts, caused by localised infestations of crown-of-thorns starfish, had a significant impact on densities of coral-dwelling damselfish. The overall abundance of coral-dwelling damselfish declined by 28.5% over the study period, from a mean of 29.8 fish per $40m^2$ (± 4.1SE) in 1998, down to 21.3 fish per $40m^2$ (± 2.3SE) in 1999. However, only the obligate coral-dwelling species (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, and *Pomacentrus moluccensis*) declined in abundance between years, whereas densities of *C. atripectoralis* and *P. amboinensis* remained remarkably constant between years, and varied only with respect to locations and zones (Table 5.7). Declines in the abundance of obligate coral-dwelling species (*C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, and *P. moluccensis*) occurred only at sites affected by *Acanthaster planci* (Figure 5.4). In contrast, there was no significant variation in the abundance of any damselfish species at unaffected locations (Figure 5.4). Declines in the abundance of obligate-coral dwelling damselfish were also more pronounced on the reef base, compared to the reef crest (Figure 5.4), which corresponds with previous findings that the depletion of live coral colonies, caused by *A. planci*, is more pronounced on the reef base, compared to the reef crest (see Figure 5.3).

Overall declines in the abundance of obligate coral-dwelling damselfish varied among species, with *Dascyllus reticulatus* being the most severely affected of the four species (Figure 5.4). Overall densities of *D. reticulatus* declined by 70% over the period of the study, whereas overall densities of other obligate coral-dwelling species (*C. viridis*, *D. aruanus*, and *P. moluccensis*) declined by just 21-30% during the same period. *Dascyllus reticulatus* was heavily impacted by infestations of *A. planci* because it lived primarily on the reef base, where *A. planci* had the greatest impact. Moreover, *D. reticulatus* was only found in locations along the southern and eastern margins of Lizard Island (North Reef, Washign Machine, Coconut Beach, Lizard Head, South Island and South Bay), that were all affected by *A. planci* (Figure 5.4).

**Table 5.8.** Three-way ANOVA to explore variation in the abundance of each species of coral-dwelling damselfish. Analyses were run firstly using the raw abundances of each damselfish, and then using residuals from regression analyses, to assess whether the abundance of damselfish varied independently of habitat availability. "*" denotes significant effects (*p<0.05, **p<0.01, ***p<0.001).

| | | | Raw abundance | | Residuals | |
|---|---|---|---|---|---|---|
| Species | Source | df | MS | F | MS | F |
| *C. atripectoralis* | Year | 1 | 0.19 | 0.17 | 2.41 | 0.04 |
| | Zone | 1 | 3.38 | 1.58 | 7.00 | 0.09 |
| | Location | 7 | 1.91 | 0.69 | 97.50 | 0.24* |
| | Year × Zone | 1 | 0.00 | 0.00 | 24.96 | 0.82 |
| | Year × Loc. | 7 | 1.16 | 2.15 | 66.40 | 1.66 |
| | Zone × Loc. | 7 | 2.14 | 3.97* | 79.10 | 1.97 |
| | Year × Zone × Loc. | 7 | 0.54 | 0.80 | 30.29 | 0.75 |
| *C. viridis* | Year | 1 | 3.52 | 6.92* | 0.02 | 0.01 |
| | Zone | 1 | 6.41 | 7.46* | 22.57 | 0.42 |
| | Location | 7 | 1.31 | 2.79 | 23.32 | 0.73 |
| | Year × Zone | 1 | 2.21 | 2.46 | 218.93 | 0.09 |
| | Year × Loc. | 7 | 0.51 | 0.57 | 18.12 | 0.84 |
| | Zone × Loc. | 7 | 0.86 | 0.96 | 32.16 | 0.53 |
| | Year × Zone × Loc. | 7 | 0.90 | 0.69 | 57.82 | 0.15 |
| *D. aruanus* | Year | 1 | 16.20 | 0.92 | 11.77 | 0.70 |
| | Zone | 1 | 143.11 | 4.47 | 38.74 | 0.94 |
| | Location | 7 | 30.07 | 0.66 | 27.08 | 3.72*** |
| | Year × Zone | 1 | 12.01 | 0.66 | 18.71 | 0.83 |
| | Year × Loc. | 7 | 17.53 | 0.97 | 16.71 | 2.29* |
| | Zone × Loc. | 7 | 31.98 | 1.77 | 41.14 | 5.65*** |
| | Year × Zone × Loc. | 7 | 18.08 | 2.31* | 22.54 | 3.09** |
| *D. reticulatus* | Year | 1 | 2.23 | 8.04* | 18.27 | 2.21 |
| | Zone | 1 | 9.56 | 18.94*** | 15.79 | 3.07 |
| | Location | 7 | 0.71 | 1.41 | 8.88 | 1.13 |
| | Year × Zone | 1 | 2.19 | 7.83* | 44.35 | 24.01** |
| | Year × Loc. | 7 | 0.28 | 0.99 | 8.23 | 1.06 |
| | Zone × Loc. | 7 | 0.50 | 1.80 | 5.13 | 0.66 |
| | Year × Zone × Loc. | 7 | 0.28 | 0.96 | 1.84 | 0.24 |
| *P. amboinensis* | Year | 1 | 0.02 | 0.04 | 18.08 | 2.61 |
| | Zone | 1 | 64.53 | 42.80*** | 128.91 | 2.93 |
| | Location | 7 | 1.99 | 1.13 | 49.41 | 3.76*** |
| | Year × Zone | 1 | 0.08 | 0.64 | 0.21 | 0.03 |
| | Year × Loc. | 7 | 0.37 | 3.10 | 6.91 | 0.53 |
| | Zone × Loc. | 7 | 1.51 | 12.61*** | 43.86 | 3.33** |
| | Year × Zone × Loc. | 7 | 0.12 | 0.21 | 6.99 | 0.53 |
| *P. moluccensis* | Year | 1 | 4.55 | 3.85 | 98.66 | 2.77 |
| | Zone | 1 | 72.39 | 15.79** | 487.93 | 2.86 |
| | Location | 7 | 17.31 | 6.63 | 180.15 | 7.82*** |
| | Year × Zone | 1 | 8.03 | 2.55 | 375.13 | 6.36* |
| | Year × Loc. | 7 | 1.18 | 0.37 | 35.51 | 1.54 |
| | Zone × Loc. | 7 | 4.58 | 1.45 | 170.76 | 7.41*** |
| | Year × Zone × Loc. | 7 | 3.15 | 2.66** | 58.97 | 2.56* |

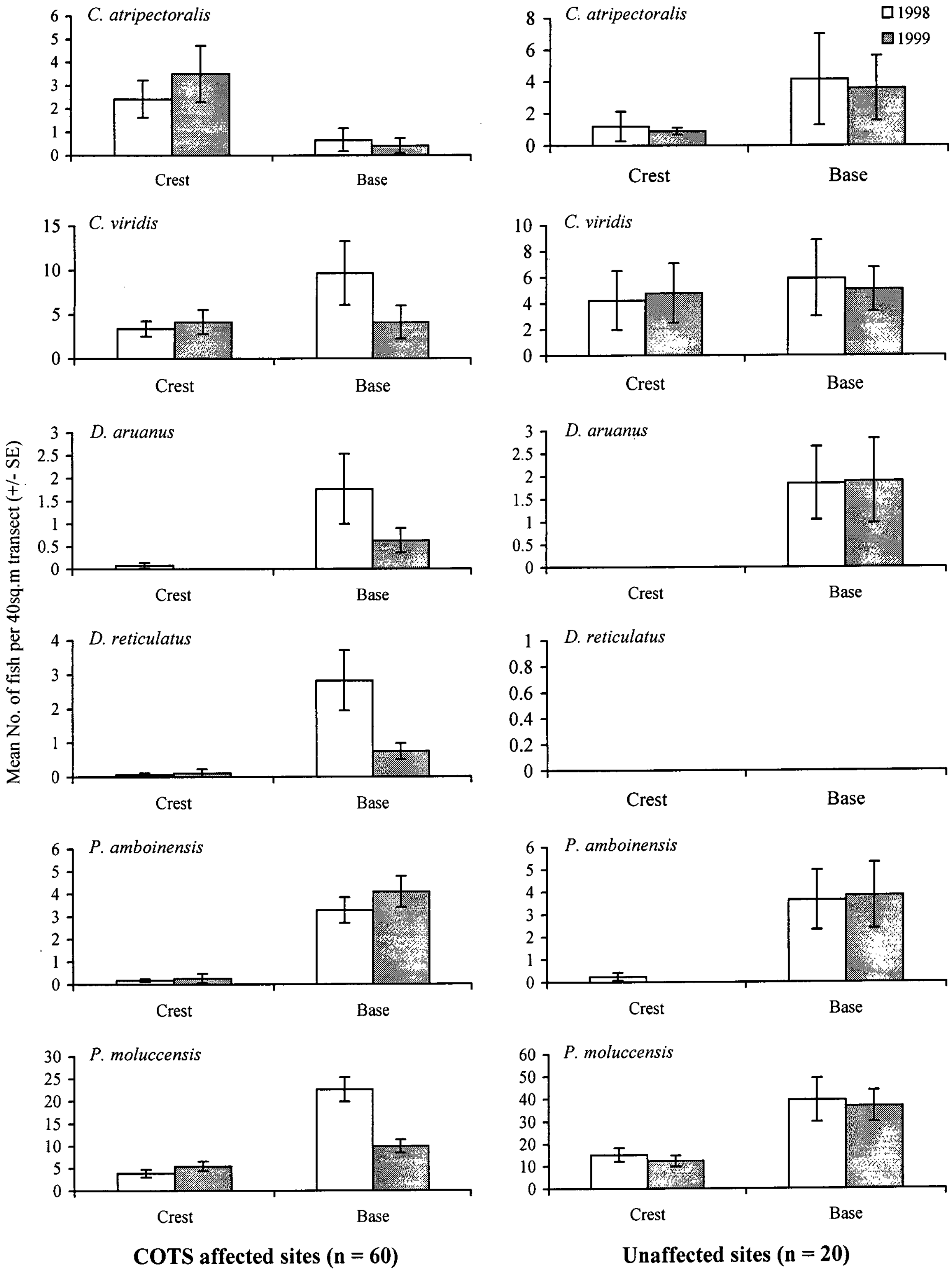

**Figure 5.4.** Variation in densities of coral-dwelling damselfish between zones, between years and between sites differentially affected by *A. planci*. Data was pooled across six sites affected by *A. planci* (North Reef, Washing Machine, Coconut Beach, Lizard Head, South Island and South Bay), and across two unaffected sites (East Palfrey and Middle Lagoon).

Variation in the abundance of all damselfish species was associated with the abundance of coral species they used disproportionately more than expected from their availability (Table 5.9). The abundance of *Chromis atripectoralis* was most strongly associated with the abundance of *Pocillopora eydouxi* (Table 5.9), which was the only coral it inhabited more than expected. The abundance of *C. viridis* was strongly associated with the abundance of both *Acropora divaricata* and *Pocillopora eydouxi*, which were the coral species it used most frequently. Variation in the abundance of both *Dascyllus aruanus* and *D. reticulatus* was most strongly associated with the abundance of *Pocillopora damicornis*, which they both occupied disproportionately more than expected. The abundance of *Pomacentrus amboinensis* was strongly associated with variation in the abundance of *Pocillopora damicornis*, which it inhabited more than expected. Further, the abundance of *Pomacentrus amboinensis* was strongly associated with the abundance of *Porites cylindrica* which it used in approximately equal proportions to its availability, and also varied in accordance with the abundance of non-coral substrates which it used more frequently than any given coral species. The abundance of *Pomacentrus moluccensis* was strongly associated with the availability of each of three coral species, *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata* (Table 5.9), all of which it used disproportionately more than expected from their availability (Table 5.4).

The abundance of all damselfish species was significantly associated with the abundance of particular habitat categories. However, the proportion of variation in the abundance of each damselfish species explained by habitat availability varied, from 4% for *C. atripectoralis*, up to 52% for *C. viridis* (Table 5.9). Variation in the abundance of *C. viridis* was determined largely by habitat availability, as there was no significant variation in the abundance of this species after accounting for variation in habitat availability (Table 5.8). In contrast, the abundance of *C. atripectoralis*, *D. aruanus*, *D. reticulatus*, *P. amoboinensis* and *P. moluccensis*, all showed significant temporal and spatial variation that was independent of changes in habitat availability (Table 5.8). Although habitat availability was important (Table 5.9), it is evident that additional factors (other than habitat availability) also generate temporal and/ or spatial variation in the abundance of these species.

**Table 5.9.** Habitat associations of coral-dwelling damselfish. Best-subsets multiple regression was conducted for each damselfish species to assess the proportion of variation in abundance explained by variation in habitat availability. Regression coefficients shown for all coral species used in each analysis. Adjusted $R^2$ was calculated for the best subset of habitat variables, and the significance of associations was assessed using ANOVA of regression (**p<0.01, ***p<0.001).

| | Coral-dwelling damselfish | | | | | |
|---|---|---|---|---|---|---|
| Variables | *C. atripectoralis* | *C. viridis* | *D. aruanus* | *D. reticulatus* | *P. amboinensis* | *P. moluccensis* |
| *A. divaricata* | 0.09 | 0.74 | | 0.08 | 0.08 | 0.09 |
| *A. millepora* | | -0.10 | | | | |
| *A. valida* | 0.08 | | | | | |
| *E. lamellosa* | 0.11 | | | | | 0.27 |
| *P. cylindrica* | | | | | 0.20 | |
| *P. damicornis* | | | 0.23 | 0.47 | 0.14 | 0.17 |
| *P. eydouxi* | 0.18 | 0.17 | | | | |
| *S. hystrix* | | 0.06 | | | | 0.24 |
| *S. pistillata* | | | | 0.08 | | 0.09 |
| Dead Corals | | | 0.13 | 0.11 | 0.34 | 0.13 |
| Mallow's $C_p$ | 1.44 | -0.32 | -2.02 | 0.61 | 2.34 | 5.38 |
| Adjusted $R^2$ | 0.04** | 0.52*** | 0.07** | 0.25*** | 0.14*** | 0.22*** |

## 5.5 DISCUSSION

### Habitat use

Many coral reef fish exhibit very specialised patterns of habitat use (e.g., Fautin and Allen 1992, Patton 1994, Kuwamurra et al. 1994, Munday et al. 1997). For example, one third of anemonefish of the genus *Amphiprion* (family Pomacentridae) have each been recorded from only one species of anemone (Fautin and Allen 1992). Also, many species of *Gobiodon* (family Gobidae) are found in obligate association with only one or two different species of branching corals, mostly from the genus *Acropora* (Munday et al. 1997, Munday 2000). Similarly, this study showed that the six species of coral-dwelling damselfish (*Chromis atripectoralis*, *C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, and *Pomacentrus moluccensis*, and *P. amboinensis*) all exhibit very specialised patterns of habitat use. All six damselfish species used only corals with branching or digitate morphologies, as opposed to massive or plate-like corals (see also Ault and Johnson 1998a, Holbrook et al. 2000). However, *Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, and *Pomacentrus moluccensis* exhibited habitat specificity beyond the level of broadly defined coral morphologies, showing preference for specific coral species (mostly *Pocillopora damicornis*). Patterns of habitat-use by each of the six damselfish species were also very consistent among sites and between years, despite significant differences in habitat availability and habitat composition, suggesting that selection for the most commonly used coral species is very strong.

There are a number of possible explanations for the distinct patterns of habitat-use exhibited by the six damselfish species (*sensu* Ault and Johnson 1998a). Firstly, patterns of habitat-use may be established by habitat selection at settlement (Booth 1992, Danilowicz 1996, Öhman et al. 1998). For example, when given the choice of live coral, dead branching coral, coral rubble and bare sand, *Chromis viridis* and *Pomacentrus moluccensis* consistently settled into live coral, whereas *P. amboinensis* selectively settled into both live coral and dead branching coral (Öhman et al. 1998). This is consistent with our observations on the habitat-use of post-settlement damselfish of these species (see also Holbrook et al. 2000). Settlement preferences of larval damselfish may also reinforce established patterns of habitat-use, because larvae from *C. viridis*, *D. aruanus*, *D. reticulatus* and *P. moluccensis* settle preferentially in the presence of conspecific adults (Sweatman 1985, Öhman et al. 1998). Secondly, patterns of habitat-use may be established by rearrangement of individuals sometime after settlement, resulting from either ontogenetic shifts in habitat-use (e.g., Booth 1992, Ault and Johnson 1998a) or inter-specific competition. Juveniles of the damselfish species considered in this study mostly cohabit the same coral species as adults (cf. Booth 1992), although post-settlement migration can occur between colonies separated by less than 12m (Sweatmean 1985, Jones 1987).

The conservative patterns of habitat use by each damselfish species among different sites and between years suggests that particular coral species offer considerable fitness benefits for coral-dwelling damselfish. Consistent with this hypothesis, Jones (1988) and Beukers and Jones (1997) showed that survivorship of coral-dwelling damselfish (specifically *D. aruanus*, *P. amboinensis* and *P. moluccensis*) was much high in *Pocillopora damicornis* compared to a less complex coral, *Acropora nibilis*. Similarly, Munday (2001) demonstrated fitness related advantages for coral gobies inhabiting specific coral species. There are also, strong parallels between the coral species selectively used by coral-dwelling damselfish, and those used by obligate coral-dwelling damselfish of the genus *Paragobiodon* (Kuwamurra et al. 1994, see also Chapter Three) and many crustacean symbionts (Knudsen 1967, Chapter Three). This suggests that certain corals, particularly *Pocillopora damicornis*, may offer selective advantages (such as increased survivorship) which extend across a range of different coral-dwelling organisms.

Despite clear preference for certain coral habitats, each of the six damselfish species used relatively few colonies (often <10%) of even the most frequently used coral species. This might indicate that i) coral-dwelling damselfish selectively use different coral colonies based on attributes beyond those which distinguish different coral species, or ii) coral colonies were in abundant supply. Holbrook et al. (2000) showed that the occupation of different coral colonies by *D. aruanus* was influenced by the basic morphology (branching versus plate etc.), colony size and also by the surrounding substrate (sand, reef pavement, or patch reef) of each coral colony. It is likely that damselfish would selectively use different colonies of the same species, if for example certain colonies, by virtue of their position, provided greater access to planktonic prey (Jones 1986, Forrester 1990). In this study, coral-dwelling damselfish tended to occupy colonies positioned closest to the seaward edge of the reef crest and reef base where access to planktonic prey may have been greatest.

### Habitat availability and damselfish abundance

Even though coral-dwelling damselfish may benefit from choosing between certain colonies of the same coral species, their selectivity is expected to decline when coral colonies are in short supply. For example, at One Tree Island, *Dascyllus aruanus* occupies all available colonies of particular coral hosts (e.g., Sale 1972, Holbrook et al. 2000). At such locations, the abundance of coral-dwelling damselfish may be limited by habitat availability (Sale 1972). However, at Lizard Island, the coral-dwelling damselfish (*Chromis atripectoralis*, *C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus* *amboinensis* and *P. moluccensis*) used only 4-55% of colonies of available coral hosts. From the limited use of available habitats at Lizard Island, it appears unlikely that populations of coral-dwelling damselfish would be limited by the supply of suitable corals (*sensu* Sale 1972). Localised infestations of *A. planci* at Lizard Island did not cause total depletion of any coral species, even on the reef base, so there were always other coral colonies available for damselfish to colonise. However, we found significant declines in the abundance of each of four obligate coral-dwelling damselfish species (*C. viridis*, *D. aruanus*, *D. reticulatus*, and *P. moluccensis*), associated with declines in the abundance of host corals. These findings indicate that the depletion of coral hosts may negatively impact on coral-dwelling damselfish even where alternate habitats are available. The fact that declines in the abundance of these damselfish occurred even though alternate coral habitats were locally abundant, suggests that damselfish may have migrated considerable distances to avoid areas affected by *A. planci*. Alternatively, displaced damselfish may have very limited success in colonising new habitats after their initial host colonies are killed. By residing in live coral colonies, coral-dwelling damselfish are afforded considerable protection from otherwise very high rates of predation (e.g., Beukers and Jones 1997), and so displaced individuals may be rapidly consumed when searching for, or moving directly to alternate habitats.

In contrast to obligate coral-dwelling damselfish species (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, and *Pomacentrus moluccensis*), we saw no change in the abundances of either *C. atripectoralis* or *P. amboinensis* at sites affected by *A. planci*. This probably reflects the limited dependence of these latter species on live coral colonies as habitat. Infestations of *A. planci* also impact differentially on different species of butterflyfish, whereby obligate-coral feeding butterflyfish are affected more often and more severely than either facultative coral feeders, or non-corallivorous butterflyfish

(Williams 1986, Bouchan-Navaro et al. 1985, Sano et al. 1987, see also Chapter Four). Although we found no change in the abundances of *C. atripectoralis* or *P. amboinensis*, this does not necessarily mean that these species are unaffected by infestations of *A. planci*. Wide spread reductions in coral cover may reduce the recruitment success of *C. atripectoralis* and/ or *P. amboinensis*, even though there was no direct affect on adult abundance. Further, the recent infestation of *A. planci* at Lizard Island caused only relatively minor disturbance to benthic reef habitats compared to previous infestations of *A. planci* on the GBR (see reviews by Moran et al. 1988, Riechelt et al. 1990), and elsewhere throughout the western Pacific (e.g., Chesher 1969, Colgan 1987). More severe disturbances are likely to have an even more pronounced effect on obligate coral-dwelling damselfish, and may also affect the abundances of *C. atripectoralis* and/ or *P. amboinensis*. Indeed this may account for the observed scarcity of all coral-dwelling damselfish (*C. atripectoralis*, *C. viridis*, *D. aruanus*, *D. reticulatus*, *P. amboinensis*, and *P. moluccensis*) on the western side of Lizard Island (Casurina and Corner Beach), where hard coral cover had been reduced to less than 5% by recent infestations of *A. planci* (see also Sano et al. 1987).

Variation in the abundance of all damselfish species between zones, among sites and across years was significantly associated with variation in the availability of their most frequently used habitats. This suggests that habitat availability has a significant influence on both the distribution and abundance of these coral-dwelling damselfish. Moreover, this influence extended across spatial scales, from 10's of metres (between replicate transects) up to 1000's of metres (between sites). Similarly, the abundance of several other reef fish with specialised patterns of habitat use is closely associated with the availability of specific habitats (e.g., Kuwamura et al. 1994, Buchheim and Hixon 1992, Clarke 1996, Munday et al. 1997, Munday 2000). These findings add to the increasing pool of evidence that reef fish populations (and assemblages) may exhibit a high degree of determinism (Ault and Johnson 1998b, Jones and Syms 1998 cf. Doherty 1991, Sale 1991, Doherty and Fowler 1994a,b). However, the importance of habitat availability in determining the distribution and abundance of reef fish varies considerably between species (reviewed by Munday and Jones 1998). Habitat availability explained between 4-52% of variation in the abundance of six different coral-dwelling damselfish. The apparent importance of habitat availability in determining the abundance of reef fish also varies between studies. Holbrook et al. (2000) found that the abundance of *D. aruanus* at Heron Island closely reflected the abundance of suitable habitat ($r^2 = 0.92$), whereas Sale (1972), as well as this study, failed to detect a strong relationship. Each of these studies used different categorisation of coral habitats, suggesting careful consideration must be made of the potential features that determine the suitability of particular habitats (see also Holbrook et al. 2000). However, the influence of habitat availability on fish abundance is also likely to vary spatially, due to differences in the abundance of fish relative to habitat availability (Sale 1972).

Temporal variation in the abundance of *D. aruanus*, *D. reticulatus*, and *P. moluccensis* occurred independently of variation in habitat availability. Specifically, the proportional declines in the abundance of these three damselfish species (56-73%), far exceeded proportional declines in the abundance of individual coral species (0-24%). This may indicate that reductions in habitat availability has secondary implications for coral-dwelling damselfish, whereby initial reductions in habitat availability lead to subsequent impacts on a much broader range of individual damselfish. However, a more likely explanation is that *A. planci* impacted disproportionately on the few coral colonies that were actually occupied by each of the three damselfish species. We noted that *D.*

*aruanus*, *D. reticulatus* and *P. moluccensis* mostly used colonies on the seaward edge of the reef base, which are the colonies most likely to be eaten by *A. planci*.

This study demonstrates that coral-dwelling damselfish (specifically *Chromis atripectoralis*, *C. viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis* and *P. moluccensis*) exhibit very specialised patterns of habitat use. Also, variation in the availability of specific habitats can have a significant influence on their patterns of abundance. These findings agree with similar work conducted on coral feeding butterflyfish (Chapter Four), coral-dwelling gobies (Munday et al. 1997), and also crustacean symbionts which maintain an obligate association with scleractinian corals (e.g., Sin 1999). Therefore, disturbances to benthic reef habitats caused by outbreak populations of *A. planci* and/ or any other factors which reduce the abundance of scleractinian corals (e.g., severe tropical storms, extreme changes in temperature and/ or salinity) are likely to influence both the distribution and abundance of many different coral reef organisms. These impacts will be most pronounced for species which maintain a strong association with scleractinian corals and have a high degree of habitat specialisation. However, more extensive disturbances to benthic reef habitats, such as caused by extreme outbreaks of *A. planci* (e.g., Pearson and Endean 1969, Chesher 1969, Colgan 1987) may have far-reaching impacts, extending to species with only very weak or partial reliance on scleractinian corals.

# CHAPTER 6. General Discussion

## 6.1. Population outbreaks of *A. planci*

Potts (1981) defined an 'outbreak' of crown-of-thorns starfish as "any large aggregation of many hundreds or thousands of individuals which persist at high densities for months or years and causes extensive mortality among coral over large areas of reef" (Potts 1981, pg 65). By this definition, there is little doubt that elevated densities of *A. planci* observed at Lizard Island, which persisted for a total of 20 months (December 1996 – July 1998) and caused significant declines in live coral cover (up to 72% coral mortality), represented an outbreak. However, Birkeland and Lucas (1990) argued that outbreaks of *A. planci* must be a sudden and eruptive occurrence. Contrary to their assertions, the outbreak of *A. planci* at Lizard Island resulted from a steady and prolonged build-up in starfish numbers over several consecutive years. Moreover, starfish populations comprised individuals from at least four different year classes, suggesting that the outbreak was caused by progressive accumulation of individuals from several consecutive year classes (Stump 1996). These findings are in stark contrast to most previous studies (e.g. Chesher 1969, Branham et al. 1971, Moran et al. 1985, Zann et al. 1987, Stump 1992, 1994) which have shown that outbreaks do generally result from sudden and dramatic increases in the abundance of *A. planci*, over the period of a few months (but see also Zann et al. 1990). Also, most studies have found that outbreak populations comprise individuals with only a very narrow range of sizes (typically 25-35cm), representing essentially only one year class (e.g. Chesher 1969, Branham et al. 1971, Goreau et al. 1972, Glynn 1973, Sakai 1985, Zann et al. 1987, Stump 1992, 1994).

Factors which cause slow and progressive increases in the abundance of *A. planci*, as observed in this study, are likely to be fundamentally different from those which cause rapid and dramatic increases in starfish densities, associated with sudden and eruptive outbreaks of *A. planci* (Johnson 1992). Most of the current hypotheses which attempt to explain the incidence of crown-of-thorns outbreaks (e.g., "Larval Recruitment hypothesis", Lucas 1973; "Terrestrial-Runoff hypothesis", Birkeland 1982, "Predator-Removal hypothesis", Endean 1969) were originally aimed at explaining sudden and eruptive outbreaks. However, some of these theories (e.g., "Predator-Removal hypothesis", Endean 1969) appear equally applicable, if not more so, in explaining more subtle but longer term changes in rates of starfish recruitment, and/ or post-settlement survivorship. Interestingly, the continual recruitment of *A. planci* over several consecutive years, combined with increased persistence of older individuals, could lead to outbreak densities of *A. planci* without any substantial increase in the annual recruitment rate of *A. planci* (Johnson 1992, cf. Vine 1973, Lucas 1973, Birkeland 1982). Therefore, the slow and progressive accumulation of crown-of-thorns starfish, as observed at Lizard Island, may represent a mechanism by which primary outbreaks could occur (Johnson 1992, Stump 1996). Although hesitant to suggest that recent aggregations of *A. planci* at Lizard Island represented a primary outbreak, the timing and location of the build-up in starfish numbers (relative to other outbreaks of *A. planci* along the GBR) was consistent with predictions for primary outbreaks (see Kenchington 1976, 1977, Reichelt et al. 1990, James and Scandol 1992, Johnson 1992, Chapter Two). Therefore, factors contributing to the gradual accumulation of successive starfish cohorts in specific locations (e.g. Zann et al. 1990, this study) should be considered as potential factors initiating primary outbreaks.

## 6.2. Impacts of *A. planci* on coral reef communities

In comparing the findings of this study with those of previous studies (e.g., Branham et al. 1971, Moran et al. 1985, Colgan 1987), it is apparent that population outbreaks of *A. planci* are highly variable, varying not only in their size and extent, but also in their impacts on coral reef communities. In extreme cases, outbreaks of *A. planci* can cause massive destruction of coral reef communities (e.g., Pearson and Endean 1969, Chesher 1969, Colgan 1987), but not all outbreaks cause such destruction (see Branham et al. 1971, Glynn 1974, 1976, this study). Most notably, the impacts of crown-of-thorns outbreaks vary among geographic regions, whereby incidences of very extensive coral destruction are essentially restricted to the Great Barrier Reef (Pearson and Endean 1969), Micronesia (Chesher 1969, Colgan 1987), and southern Japan (Nishihira and Yamzato 1974, Keesing 1992). The impacts of outbreaks of *A. planci* can also vary over much smaller spatial scales, within and between adjacent coral reefs (e.g., Endean and Stablum 1973, Moran et al. 1985, Reichelt et al. 1990).

In an attempt to explain small scale (within reef) variation in the impacts of *A. planci* on coral communities, Chapter Two examined correlative links between the abundance of *A. planci* and the extent of coral depletion observed at various locations around Lizard Island. This study showed that the effects of *A. planci* vary greatly within reefs, among locations (0.5-8 kilometres apart), and among reef zones (<5 metres apart). Also, spatial variation in the impacts of *A. planci* was strongly and positively correlated with patterns of starfish abundance ($R^2 = 56.9$, $df = 4$, $p<0.01$). Spatial variation in the size and abundance of crown-of-thorns starfish may further explain differences in the impacts of *A. planci* at larger scales (e.g., among reefs, among regions). However, geographic variation in the impacts of starfish outbreaks occurs irrespective of differences in starfish densities (reviewed by Moran 1986). A more promising explanation for these large-scale differences in the impacts of *A. planci* is related to geographical differences in coral composition (Birkeland 1996b), combined with well defined feeding preferences of *A. planci* (Chapter Three). The argument follows that in the eastern Pacific (e.g., Panama) coral communities are dominated by *Pocillopora damicornis*, which is only rarely eaten by *A. planci*, due to the presence of highly aggressive coral symbionts (Glynn 1976, Chapter Three). As a consequence, outbreak populations of *A. planci* in the eastern Pacific tend to feed mostly on rare coral species and have little effect on overall coral cover (Glynn 1976). In contrast, coral communities in the western Pacific, and throughout the Indian ocean, are dominated by highly preferred *Acropora* corals (e.g., Keesing 1990, Moran and De'ath 1992), and so here, outbreaks of *A. planci* cause rapid and dramatic declines in overall coral cover (Chapter Two).

In addition to causing massive reductions in the abundance of scleractinian corals, outbreaks of *A. planci* also had broad-scale impacts on a wide variety of other coral reef organisms; increasing the abundance of soft-corals (Chapter Two), while causing declines in the abundance of corallivorous butterflyfish (Chapter Four, see also Bouchan-Navaro Williams 1986), and coral-dwelling damselfish (Chapter Five). Among coral reef fishes, these impacts were most pronounced for individual species which maintain a strong association with scleractinian corals and have a high degree of dietary or habitat specialisation. However, more extensive disturbances to benthic reef habitats, such as those caused by extreme outbreaks of *A. planci* (e.g., Pearson and Endean 1969; Chesher 1969, Colgan 1987) are likely to have far-reaching impacts, extending to species with only very weak or partial reliance on scleractinian corals. These findings demonstrate the significant influence of outbreaks of crown-of-thorns starfish on coral reef ecosystems, further corroborating assertions by Pearson (1981) that crown-of-thorns outbreaks represent one of the most significant biological disturbances on tropical coral reefs.

## 6.3. Future directions

While most ecologists are now moving towards a systems approach to the study of coral reef ecology, *Acanthaster planci* is one of few organisms that is still worthy of individual attention (Birkeland and Lucas 1990). Importantly, crown-of-thorns starfish represent one of the most significant forces shaping the structure and dynamics of Indo-Pacific coral reef ecosystems (Pearson 1981, Birkeland 1996). In his review of especially influential species (potentially "keystone species") on tropical coral reefs, Birkeland (1996) devoted a considerable portion of his discussion to *Acanthaster planci*. The potentially significant role of crown-of-thorns starfish in coral reef environments is also reflected in the plethora of studies (>1200 published studies) that have considered various aspects of their biology and ecology (see reviews by Potts 1981, Moran 1986, Birkeland and Lucas 1990, and references therein). However, despite this considerable research effort, there is still very limited understanding of the population dynamics of *A. planci*, and the ultimate causes of outbreaks of *A. planci* are still not known.

In general, there is a critical lack of information on all aspects of the biology and ecology of crown-of-thorns starfish (see Moran 1986, Birkeland and Lucas 1990 for a complete review). In essence, however, there are two fundamental questions that encompass much of the mystery and controversy surrounding outbreaks of crown-of-thorns starfish. Firstly, and of primary importance, it needs to be ascertained whether outbreaks of *A. planci* are a natural phenomenon or caused by anthropogenic influences. This information is especially important in formulating appropriate management responses to crown-of-thorns outbreaks (Birkeland and Lucas 1990). Many hypotheses have been put forward linking crown-of-thorns outbreaks with anthropogenic effects such as overfishing, pollution, and coastal development (see reviews by Potts 1981, Moran 1986, Birkeland and Lucas 1990). However, the role of anthropogenic factors in the occurrence of outbreaks is far from certain (Birkeland and Lucas 1990, Kenchington and Kelleher 1992). Secondly, it needs to be ascertained whether outbreaks of *A. planci* are causing gradual degradation of coral reef ecosystems (e.g., Seymour and Bradbury 1999). While some authors regard crown-of-thorns outbreaks as a major tragedy, causing overall degradation of tropical coral reefs (e.g., Endean and Cameron 1985, Endean et al. 1988, Seymour and Bradbury 1999, Lourey et al. 2000), others view outbreaks as routine disturbances from which coral reef communities will usually recover (e.g., Newman 1970, Pearson 1981, Done 1985, Moran et al. 1985, Ninio et al. 2000). Arriving at satsifactory answers to these two questions will require considerable additional research.

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# *An infectious disease in crown-of-thorns starfish on the Great Barrier Reef*

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# Patterns of recruitment and abundance of corals along the Great Barrier Reef

**T. P. Hughes, A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj*, M. S. Pratchett, J. E. Tanner & B. L. Willis**

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**Different physical and biological processes prevail at different scales[1–4]. As a consequence, small-scale experiments or local observations provide limited insights into regional or global phenomena[5–8]. One solution is to incorporate spatial scale explicitly into the experimental and sampling design of field studies, to provide a broader, landscape view of ecology[1–8]. Here we examine spatial patterns in corals on the Great Barrier Reef, across a spectrum of scales ranging from metres to more than 1,700 km. Our study is unusual because we explore large-scale patterns of a**

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# *Coral crabs influence the feeding patterns of crown-of-thorns starfish*

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# SUPPLY-SIDE ECOLOGY WORKS BOTH WAYS: THE LINK BETWEEN BENTHIC ADULTS, FECUNDITY, AND LARVAL RECRUITS

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Coral Reefs (2001) 20: 13–17

REPORT

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# Consumption of coral propagules represents a significant trophic link between corals and reef fish

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Accepted for publication in the Proceedings of the 9th International Coral Reef Symposium

# Comparative palatability among eggs of mass-spawning corals

M.S. Pratchett[1], A.H. Baird[2] and C.P. Marquis[3]

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*Short Communication* *Mar. Freshwater Res.*, 2001, **52**, 865–8

# Variable palatability of coral eggs to a planktivorous fish

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# DETECTING REGIONAL VARIATION USING META-ANALYSIS AND LARGE-SCALE SAMPLING: LATITUDINAL PATTERNS IN RECRUITMENT

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