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# Factors affecting community dynamics of scleractinian corals: Competition, succession, keystone species and history.

Thesis submitted by

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in July 1995

for the degree of Doctor of Philosophy
in the Department of Marine Biology
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# Abstract

A major focus of ecology is to determine the causes of community structure. In this thesis, I examine the role of interactions between sessile organisms, primarily scleractinian corals and algae, in structuring the benthic assemblage of a coral reef. Specifically, I look at four main factors: competition, succession, keystone species, and the role of history or ecological memory. While competition among corals has received a certain amount of attention to date, its consequences for the individuals involved, and for the community, have not yet been ascertained. The other three processes that I investigate have all been virtually ignored on coral reefs, with very few exceptions. This is the first time that the effect of competition on the fitness of scleractinian corals has been examined, and is also the first detailed investigation of succession, keystone species and the effects of history in coral reef benthic assemblages.

There have been few reports on the intensity of competition experienced by coral colonies in their natural habitat. I examined the frequency with which competitive encounters occurred between corals, and between corals and algae, at three sites around Heron Island and Wistari reefs. Intensity of competition was found to be linearly related to coral cover, with a mean encounter rate of 1 per colony once cover reached approximately 50%.

Competition was found to have a significant negative impact on the fitness of competing colonies. Colonies engaged in competition with other scleractinian corals experienced a decreased growth rate compared to non-competing controls, and a localised decrease in fecundity. Mortality rates of corals were not affected by competition however. Competition with macroalgae was also found to cause a decrease in growth rate, and caused a decline in whole colony fecundity by approximately 50%. Again, survivorship was not affected to any significant extent.

Patterns of succession and community dynamics of three reef crest coral assemblages were further investigated by the use of matrix models. The pattern of succession observed most closely fits the tolerance model. Interactions between species groups almost always occurred in a reciprocal fashion, with no species clearly dominating the rest. It was found that the model community structure took greater than 20 years to equilibrate, much longer than the time between cyclones, supporting the non-equilibrium nature of coral reefs. Sensitivity analysis of the model communities failed to show up any keystone species, although this technique is likely to be a powerful means for identifying the presence of such species in complex communities.

To examine the role of history in determining the structure of these coral assemblages, the models were extended to incorporate a knowledge of the communities past. I found no evidence that history was having any effect at the community level, although the probabilities of transition between different species did show a marked effect of history. The lack of an effect of history at the community level is likely to be due to the highly disturbed nature of the reef crest at Heron Island, with other more sheltered areas possibly not showing the same results.

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# Chapter 1

# Introduction.

One of the main focuses of ecology is to determine what causes communities to be structured in the way that they are. The processes which determine community structure can be divided up into biotic and abiotic. Biotic processes include competition, predation, succession and dispersal abilities, while abiotic factors include physical disturbance, climate, resource availability and substrate characteristics. In coral reef benthic ecosystems, a great deal of attention has been paid to the role of disturbance, primarily through cyclones (e.g. Connell 1978, Woodley et al. 1981) and anthropogenic events (e.g. Smith et al. 1981, Hawkins & Roberts 1993), and to predation from organisms such as *Acanthaster* (Colgan 1987, Done 1988), and *Drupella* (e.g. Turner 1994). The role of climate, especially in relation to El Nino events and global warming, is also coming under increasing attention (e.g. Brown 1990). Much less attention has been paid to the role of interactions between members of the sessile benthos, including competition, succession, the presence of keystone species, and the effects of history or ecological memory. These four processes are investigated in this thesis to extend our knowledge of the role that biological interactions play in structuring coral assemblages.

## Competition:

Intraspecifc competition has been found to be an important structuring process in many different communities, and has often received detailed study to determine in what way it influences not only communities, but populations and individuals as well (reviewed in Connell 1983, Schoener 1983, Gurevitch et al. 1992). However, there has been a degree of controversy as to the importance of competition in structuring coral assemblages, with several investigators proposing that it has little or no significance (e.g. Bradbury & Young 1981, 1983), while others suggest that, like in many other communities, competition is extremely important. The diversity of mechanisms by which scleractinian corals, and other major benthic organisms such as alcyonacean corals and algae, can compete with each other, however, points to competition being highly important in these assemblages. Connell (1973) proposed splitting up these mechanisms into two fundamentally different categories, direct and indirect. Direct competition involves actual physical contact between the opponents, and includes such forms as extracoelenteric digestion (e.g. Lang 1971, 1973), sweeper tentacles and polyps (e.g. Richardson et al. 1979, Sheppard 1979, Wellington 1980), direct overgrowth (Rinkevich & Loya 1983, Yamazato & Yeemin 1986), histoincompatability (Hildemann et al. 1977, Hidaka 1985) and mucous smothering (Chadwick 1986, 1988). The first two of these mechanisms are restricted to scleractinian corals, while the later may also be employed by other groups such as alcyonacean corals and/or algae. Abrasion of coral soft tissues by algae brushing against the colony is another direct mechanism (e.g. Coyer et al. 1993). Indirect competition does not involve any physical contact between the competitors, but rather operates at a distance, and is generally not targeted at specific individuals, unlike direct mechanisms of competition. The main mechanism of indirect competition employed by scleractinians is overtopping (Connell 1973, Stimson 1985), although it has been suggested, but not proven, that some species may also be capable of allelopathy (Sheppard 1979, Rinkevich & Loya 1983, Rinkevich et al. 1992). Allelopathy has been demonstrated in both the Alcyonacea and in algae, with scleractinian corals being targeted by at least some of the chemicals released (e.g. Coll et al. 1982, Maida et al. 1995).

In coral assemblages, competition is generally thought to be for space (Lang & Chornesky 1990). Two dimensional space is especially important for reef corals, which are almost exclusively zooxanthellate, thus requiring light to survive (e.g. Falkowski et al. 1990). Competition may also be for food, as has been demonstrated in several other colonial organisms (e.g. Buss 1979, Buss & Jackson 1981), although it has not been shown in the Scleractinia. While both inter- and intra-specific competition are important in many communities, in this thesis I will only be dealing with intraspecific competition.

While competition among corals has received a fair degree of attention, most of this has focused on determining competitive hierarchies amongst a suite of species which are all competing by a single mechanism (e.g.

Lang 1973, Chornesky 1989, Tanner 1993). Given the diversity of competitive mechanisms available to corals, and the significant role that factors such as water movement, temperature, competitor size etc. play in determining the outcome of any given encounter (e.g. Johnston et al. 1981, Bak et al. 1982, Lang & Chornesky 1990, Alino et al. 1992, Genin et al. 1994), these hierarchies cannot by themselves tell us a great deal about community structure, or how competition actually affects the corals involved. To determine if competition really is important, we must first know how frequent it is. There are in fact very few published estimates on the number of competitive encounters experienced by an average coral, with the few reports in the literature on how common competition is generally being on a per square meter basis (e.g. Bak et al. 1982, Logan 1984, Sheppard 1985), rather than per colony. Most surveys of competition in the field fail to report the area covered, or the number of colonies examined, as the work was carried out to examine competitive hierarchies, or determine whether competitive encounters occur randomly etc. Before anything can be said about how competition affects community structure, it must be determined just how common it is; after all, if only one in a hundred colonies is competing, competition is probably going to be irrelevant at the community level, even if it does severely affect the colonies involved.

A second question that has received inadequate attention in the study of competition among corals is 'What are the costs of competition for those individuals competing?' (Lang & Chornesky 1990). The main question of interest here is to determine how competition affects the fitness of colonies. One possible reason for the scant attention paid to this question is the difficulty of measuring fitness in species which broadcast their gametes into the water column, with subsequent planktonic development and possible long-distance dispersal of the larvae. Even in those species which brood their larvae, following larval dispersal and recruitment is extremely difficult, although under the right conditions it can be done (Best pers. com.). To measure fitness, reproductive success must be known, which would necessitate tracking gametes and larvae from a known individual, to determine their survival rates and recruitment success. This is not possible with current technology, however, a number of surrogate measures of relative fitness are still available. If growth, survivorship, number of gametes and size of gametes of competing corals are all measured and compared to non-competing corals, then a fair idea of the fitness effects of competition can be gained, although the results may be difficult to interpret if some of these variables increase while others decrease. Interpretation of the results of studies examining these four life-history variables becomes easier if mathematical models of population dynamics are constructed. If Leslie matrix models or one of their extensions (see Caswell 1989) are employed, the population growth rate, $\lambda$, can be directly equated to fitness (e.g. Lande 1982, Caswell 1989). Thus, if a population of competing corals has a lower $\lambda$ than a population of non-competing corals, then competing corals are less fit than non-competing corals. It is also possible to calculate confidence limits for $\lambda$, allowing statistical comparisons of fitness to be made (e.g. Alvarez-Buylla & Slatkin 1991, 1993, 1994).

To determine how important competition with a certain species (or species group) is in determining community structure, the species can be removed from certain areas and subsequent community development followed. If areas with the species removed behave identically to areas where it is still present, then it is very unlikely that it is a vigorous competitor. If the community does change in response to the removal of a species, the change may be simple or complex. A simple change would involve an increase in all the removed species' competitors in proportion to their original abundance, resulting from the freed resources (i.e. space) being shared equally amongst the rest of the community. This, however, will only be true if the freed resources are equally important to all competitors, as is likely to be at least approximately true for corals if they are only competing for space. More complex changes would result if there are indirect interactions (i.e. when species A has an effect on species B, which in turn then has an effect on species C) within the community, when some species would gain more than others from the elimination of a competitor, and some may even suffer.

### Succession:

Different species within a community may also interact to determine community structure through the process of succession. Competition itself is an important component of succession in many circumstances

(Anderson 1986), but it is by no means the only one. Connell and Slatyer (1977) have proposed several models of succession, these being the facilitation model, the inhibition model, and the tolerance model. The later two models hold that competition is important, and slows or prevents species change, but the first is based on pioneering species benefiting later arrivals, while changing the environment to such an extent that they themselves can no longer survive. There have been a few studies which have examined coral succession (e.g. Grigg & Maragos 1974, Pearson 1974, Loya 1976, Connell 1978, Grigg 1983, Hughes 1985, Colgan 1987), although these have tended to be descriptive, and have not paid a great deal of attention to what is causing the observed succession. The very early stages of succession in coral assemblages are likely to be characterised by facilitative interactions, as coralline algae promote coral settlement (Morse et al. 1988, 1994), and bacterial films are often needed before many other invertebrates can settle (e.g. Keough & Raimondi 1995). Once corals have become established, the inhibition and tolerance models are more likely to describe the form of succession that occurs. Previous studies on succession in coral assemblages have relied on either long-term monitoring of changing coral communities, or the examination of communities on substrata of known age, such as lava flows. Another possible way of examining succession is through the use of mathematical models of community dynamics. Such models have been largely confined to studies of succession in plant communities (e.g. Horn 1975, Enright & Ogden 1979, Acevedo 1981, Lough et al. 1987), although Usher (1979) has also applied them to insect communities.

## Keystone Species:

It has been proposed that in some communities, one or two species play a disproportionately large role in establishing community structure, with these species being known as keystone species (e.g. Paine 1969, 1974, Menge et al. 1994). One of the best known examples of a keystone species is the starfish *Pisaster* on intertidal shores of western North America. *Pisaster* plays an important role in preventing these shores from becoming dominated by mussels, allowing numerous other species to flourish, completely changing the community composition

(Paine 1969, 1974). While the original definition of a keystone species only encompassed predators, it has since been broadened to include species at other trophic levels (e.g. Roughgarden 1983). Several examples of possible keystone species on coral reefs include coral inhabiting crustaceans which defend their hosts from *Acanthaster* (Glynn 1990), and territorial damselfish (e.g. Williams 1980, Hixon & Brostoff 1983). Currently it is not known if any corals act as keystone species.

It can be extremely difficult to identify a keystone species without an enormous amount of experimental manipulation, or a great deal of luck (Bender et al. 1984, Mills et al. 1993). Experimental identification would require that the species be removed from certain areas, and the community followed to see if any major changes occur compared to areas where the species has been left. Removal would have to be repeated for a large number of species to have any certainty of finding a keystone species in a diverse community such as a coral reef, if one was present. Alternatively, mathematical models of community dynamics have a potential for identifying keystone species, as well as for examining patterns and mechanisms of succession. Using sensitivity analysis, the effect of slight changes in each model parameter can be identified. These sensitivities can then be examined to determine whether the parameters associated with any one species are consistently high. If so, this species has a disproportionately large influence on the community structure, and can be said to be a keystone species.

### History:

The consequences that an organisms history has for its ecology have been largely ignored, as have the effects of history at the population and community levels. By history, I mean events that happened in the past which have left no visible effect, but which change the way an individual, population or community responds to other events. This has been alternatively defined as ecological memory (e.g. Hendry & McGlade 1995). A number of studies have addressed the importance of the order of species arrival in determining the final structure of experimental communities (e.g. Wilbur & Alford 1985, Robinson & Dickerson 1987, Butler & Chesson 1990, Drake et al. 1993), with the general conclusion being that order of arrival is extremely important to the eventual success of many species. Thus whether a newly introduced species becomes established or not may not only depend on what species were present before it arrived, but also on what order they arrived in. Several studies of natural communities have also shown that disturbances can interact across time to substantially alter community structure (e.g. Hughes 1989, 1994, Dublin et al. 1990). Like succession, the effects of history can also be examined using mathematical models of community dynamics. To do this, a hierarchical series of models must be constructed, each model containing more information about the past than the last. A comparison of model outputs will then show up where history is having an influence. If all models produce much the same output, then history has little or no effect on the community. However, if there are major differences in output between the different models, this must be due to the differing amounts of history that they incorporate, and thus the past must be having an effect on the community dynamics.

## Chapter Outlines:

I start by determining how frequent competitive encounters really are in chapter 2. Competitive encounters in belt transects at three different sites around Heron Island and Wistari reefs are examined to determine how successful each of nine species groups are at competing using each of three types of competition. I also examine the relationship between coral cover in each transect, and the mean number of competitive encounters each colony experiences. Before anything can be said about the importance of competition in any community, it is important to know how commonly competitive encounters occur, which species are involved, what mechanisms of competition are employed most frequently, and which species are best at each mechanism.

In chapter 3, I go on to examine how interspecific competition between scleractinian corals affects the fitness of the competitors. To do this, I followed growth, survivorship, and reproductive output in experimentally competing and non-competing colonies of *Acropora hyacinthus*, and growth and survivorship in *Pocillopora damicornis*. The population level consequences of competition are also examined using matrix population models. This is the first time that the effect of competition on growth, survivorship and reproductive output for scleractinian corals engaged in interspecific competition has been determined, allowing the effect on fitness to be inferred.

Chapter 4 extends the examination of the consequences of competition for fitness in corals to encounters between scleractinian corals and macroalgae. This chapter also looks a bit more closely at how competition affects community structure. A series of natural coral outcrops was followed in this experiment to determine the effect that the removal of approximately 95% of macroalgae had on the corals growing on each outcrop. Again, I follow growth, survival and reproduction of individual colonies, and I also examine changes in relative cover and number of colonies of each species (i.e. community structure), and the number of fission events.

The role of succession and keystone species in coral assemblages is examined in chapter 5. Using matrix models of community dynamics constructed from data from a 30 year study of three shallow reef crest coral assemblages at Heron Island, I examined changes in species abundances following a major disturbance. I also determined which species groups had the greatest influence on how the community recovered from a major disturbance, using sensitivity analysis. This chapter also examines the role that competitive networks play in determining community structure.

I further extend the models of community dynamics in chapter 6, where I ask what influence history has in shallow reef crest communities. I do this by examining the output of a hierarchical series of models built from the same data, but incorporating different amounts of knowledge about the past. These models also allow the effect of history to be examined for each species group individually, by comparing the transition probabilities in the different models.

# Chapter 2

## Intensity and mechanisms of competition among scleractinian corals.

### Abstract:

Competition is widely regarded as an important structuring force in coral assemblages, however there have been few reports on the intensity of competition experienced by corals in the field. The frequency of competitive encounters between scleractinian corals at Heron Island and Wistari reefs was examined to determine how likely competition is to be important in structuring these assemblages. It was found that on average, each colony was engaged in between 0.58 and 1 encounter, with the major determinant of variability being coral cover. Overtopping was the most common competitive mechanism employed, followed by direct contact and then overgrowth. As expected, different species competed successfully using different mechanisms, although some, such as soft corals, performed well in all forms of competition while others, such as pocilloporids, fared poorly with all forms.

### Introduction:

The sessile nature of the vast majority of scleractinian corals, and their requirement for light in order to grow, mean that competition for space is likely to be important in structuring coral assemblages in areas or times of high cover and diversity. The importance of competition is further suggested by the large number of direct and indirect mechanisms which corals have evolved for use in competing against each other (reviewed in Lang & Chornesky 1990). Direct mechanisms involve soft tissue contact, and include: extracoelenteric digestion, where mesenterial filaments are extruded over a neighbour (e.g. Lang 1971, 1973, Wellington 1980); sweeper tentacles, which are specially modified tentacles with high numbers of nematocysts (e.g. Richardson et al. 1979, Chornesky 1983); and histoincompatability or tissue rejection (e.g. Rinkevich & Loya 1983, Hidaka 1985). Overgrowth is another direct mechanism, which involves one coral growing directly on or immediately above (< 1 cm) the skeleton of another (Rinkevich & Loya 1983, Yamazato & Yeemin 1986), but may be preceded by other forms of competition which first kill off the soft tissues (Lang & Chornesky 1990). Indirect mechanisms of competition do not involve contact between the participants, with overtopping generally being considered the only form of indirect competition employed by scleractinian corals (Lang & Chornesky 1990). Overtopping occurs when one coral grows above another, blocking its access to light and water flow (Connell 1973, Stimson 1985). A second form of indirect competition, allelopathy, has been postulated to occur in scleractinian corals (Sheppard 1979, Rinkevich & Loya 1983), although no firm evidence has so far been found. Allelopathy has, however, been demonstrated in the Alcyonacea (Coll et al. 1982, Maida et al. 1995), and other benthic invertebrate taxa.

With the diversity of competitive mechanisms available to corals, it is not always possible to predict the winner of any given encounter based solely on a knowledge of the species competing. Competitive hierarchies for any one mechanism of competition are generally well defined (e.g. Lang 1973, Chornesky 1989, Chadwick-Furman & Rinkevich 1994, Tanner 1993). However, these hierarchies may break down when multiple mechanisms of competition occur (Lang & Chornesky 1990). The mechanisms of competition being employed between two colonies are important in determining the final outcome, but it is also possible for the role of winner to oscillate back and forth between the two colonies as they switch back and forth between different forms of competition (Chornesky 1989). The outcome of any particular encounter can also be affected by the relative position of the competing colonies. For example, if a favid and a tabular *Acropora* meet edge to edge, the favid can hold off the *Acropora*. However, if the favid is lower than the *Acropora*, it will be overtopped (e.g. Lang & Chornesky 1990). Other potential factors which could influence the outcome of an encounter include colony health, size, competitive history and environmental conditions such as light regime and water flow etc. (e.g. Johnston et al. 1981, Bak et al. 1982, Lang & Chornesky 1990, Alino et al. 1992, Genin et al. 1994).

Despite the widespread acknowledgment that competition plays an important role in structuring many coral communities, especially those with high diversity and cover, little effort has been made to determine the frequency of naturally occurring competitive encounters (but see Bak et al. 1982, Logan 1984, Sheppard 1985). To assess the potential role of coral competition in structuring the benthic community at Heron Island and neighbouring Wistari reef, I quantify the occurrence of each of three forms of competition, direct contact, overgrowth and overtopping. In addition, I examine which species groups are participating in each of the above types of competition, and how successful they are. It should be noted that the data presented in this chapter are static measures of competitive outcome, and that they do not necessarily indicate the final winner, if one colony does in fact eventually end up dominating.

## Methods:

To quantify the rates of natural encounters between different coral species in the vicinity of Heron Island on the southern Great Barrier Reef (23° 26'S, 151° 55'E), 5 randomly placed permanent 10 x 2 m belt transects were established between 5 and 10 m depth at each of three sites in September 1992. Two of these sites were on Heron Island reef itself, one on the southern side and the other on the northern, while the third was located on the northern side of nearby Wistari reef. Use of the three sites allowed competition to be examined over a range of values of coral cover, from approximately 10% to almost 50% . The two north facing sites are exposed to the full force of cyclones, and their coral communities were severely damaged by cyclone Fran in March 1992, while the southern site is fairly protected and suffered little damage from this cyclone.

Each belt transect was divided up into 1m$^2$ quadrats, and each encounter between corals, or between corals and algae, was recorded. Encounters with other sessile taxa (e.g. *Millepora*, sponges), were extremely rare. Each record consisted of the species involved, the form of encounter (direct contact, overgrowth, overtopping or standoff), and which species, if any, was winning at the time of the census. Colonies not apparently competing with any other colony were also recorded, in order to estimate per colony encounter rates. Direct contact was defined as the death of the margin of one colony within five centimetres of another, presumably through the actions of the sweeper tentacles or mesenterial filaments of its neighbour, and was only scored if there was no skeletal damage, and if the injury was confined to the vicinity of a neighbour. Overgrowth occurred when one colony grew directly over another, apparently without the prior death of the inferior coral through the use of sweeper tentacles, mesenterial filaments or other mechanisms. Overtopping involved one coral growing over the top of another without any physical contact occurring between the two colonies. A standoff was scored when two colonies were in contact with one another, either without any apparent negative effects to either colony, or else with equivalent damage to both colonies. Designation of an encounter as a standoff does not imply that it will remain so, but only that at the time of the survey there was no apparent winner.

To investigate the presence of any yearly variation in encounter rates, each transect was censused twice, first in September 1992, and then again ten months later in July 1993. In addition to the number and types of competitive encounters occurring, the percent cover of corals for each belt transect was also visually estimated, so that encounter rates could be related to coral cover. Each quadrat was divided into 100 $cm^2$ sections to aid cover estimation for each 1 $m^2$ in each belt transect. To reduce the complexity of the data set, the 135 species of hard and soft corals and algae recorded in the transects were grouped into nine species groups (Table 2.1), based on taxonomic and morphological criteria (see Chapter 5, Tanner et al. 1994). Without this grouping, there would be a potential for encounters between $n(n+1)/2 = 29403$ species pairs, each with four different encounter types, making analysis at the species level impossible.

**Results:**

The number of naturally occurring encounters between coral colonies was relatively high compared to previously published values (e.g. Logan 1984, Sheppard 1985), especially at the south slope site, where there were over 10 encounters per square meter. The most common form of encounter was overtopping, which accounted for approximately 50% of the encounters at each site and in each year (Figure 2.1). Direct contact and overgrowth both formed about 20% of encounters, with standoffs forming only a minor proportion (around 10%) (Figure 2.1). On average, every colony at the south slope site was engaged in competition with one other colony (Figure 2.1). The north slope and Wistari had fewer encounters, with approximately 5 encounters per square meter at each, corresponding to 0.58 and 0.76 encounters per colony. At the north slope 50% of colonies were not engaged in competition, while this decreased to 33% at Wistari and 12% at the south slope. The number of competitive encounters, excluding standoffs, is highly correlated between years ($r^2=0.79$, $P< 0.0001$), however, the number of standoffs is not correlated ($r^2=0.14$, $P=0.19$). Because there was very little difference in the patterns of competition between years, only the results for 1992 are presented.

The reason for the high encounter rate on the south slope becomes clear when the effect of coral cover is examined. Two way ANOVA shows that there is a highly significant effect of site on coral cover ($F_{2,23}=15.38$, $P<0.0001$), but no effect of year ($F_{1,23}=0.07$, $P=0.79$) and no interaction effect ($F_{2,23}=0.24$, $P=0.79$). Tukey's test shows that the south slope has significantly higher cover (about 42%) than either the north slope (23%) or Wistari (28%). A regression of number of encounters per colony on percent coral cover is highly significant (Figure 2.2, $P<0.0001$), with coral cover explaining 86% of the variance in the number of encounters per colony.

As was expected, different species groups competed successfully using different mechanisms (Table 2.2). The most successful overtoppers were the plate, staghorn and bushy *Acropora*, and soft corals - particularly gorgonians (groups B, D, C and E respectively). The worst overtoppers were massive corals (G), and algae (F), both of which remain fairly low on the substrate. However, massive corals are the most successful competitors using direct contact, with soft corals (E) being close behind. All corals show at least moderate competitive success using contact, with the encrusting Acroporids (A) being the worst, but still winning 25% of encounters they were involved in with this mechanism. The best groups at overgrowth are algae, soft corals, and encrusting Acroporids (F, E, A), with most other groups being fairly poor at overgrowth, especially Pocilloporid corals (H). When competitive success is examined over all mechanisms, tabular *Acropora* (B) dominate, winning 83% of their encounters, with the next most successful being soft corals (E, 67%).

The only particularly poor group are the pocilloporids (H), which only won 25% of their encounters, with most other groups winning between 40 - 60%.

## Discussion:

Average encounter rates of 1 per colony, even when coral cover is only 50%, indicate that competition has the potential to play a major role in structuring scleractinian coral communities. As this figure only includes encounters which caused external physical damage, and overtopping, the encounter rate is likely to be even higher. For example, newly established encounters that had not yet resulted in damage are not included, nor are most allelopathic interactions. Although corals are competing, it is not axiomatic that competition is important in determining community structure. Competition must impact differentially on different species if it is to be important at the community level. Not enough is known about the effects of competition on the colonies involved to be able to state what the community level consequences are from a knowledge of encounter rates, even when it is obvious that some species (e.g. Tabular *Acropora*) win most of their encounters while others (e.g. Pocilloporids) lose most of theirs. Competition does generally appear to involve a cost to the competitors (Rinkevich & Loya 1985, Romano 1990, Tanner 1995 a, b, Chapters 3, 4), but this cost cannot be predicted just from knowing the winner. Romano (1990), for instance, has shown that the physiological winner of an encounter may actually turn out to be the ecological loser as its growth is decreased more than its opponents growth.

The linear nature of the relationship between coral cover and number of competitive encounters suggests that corals do not generally settle and grow in such a way as to avoid each other (e.g. Romano 1990). If this were to occur, the number of encounters would only increase slowly at low levels of cover, but would start increasing rapidly at higher levels as it became more difficult to find vacant space without nearby neighbours. Some corals do respond to competition by redirecting growth away from the competitor, however, contact is still usually maintained in this situation (Romano 1990). It has also been demonstrated that some soft corals can depress recruitment in their immediate vicinity (Maida et al. 1995), and also that recruitment is inhibited under table *Acropora* (e.g. Fisk & Harriott 1993, Baird 1994), however, on a community level, these processes do not appear to cause recruitment to occur away from neighbours in general.

Coral colonies involved in competition often have substantially reduced growth rates and fecundities compared to non-competing colonies (Rinkevich & Loya 1985, Romano 1990, Tanner 1995 a, b, Chapters 3, 4), indicating that the levels of competition reported here are capable of having a major impact on the fitness of competing corals. At higher levels of cover, up to 88% of corals in the censused transects were engaged in competition with at least one other colony, so there are probably few colonies which do not experience a decline in fitness from competing with other corals, or other organisms such as algae, sponges etc. How much fitness is decreased by competition has not yet been determined, but in areas of high cover where colonies are totally surrounded by near neighbours, it is likely to be fairly substantial (Tanner 1995 b, Chapter 3).

The inability of any one species group to consistently win encounters provides evidence for the complex nature of competitive networks on coral reefs (Lang & Chornesky 1990, Tanner et al. 1994, Chapter 5). Even species (rather than species group), is not a very good indicator of which coral will win an encounter, even when only a single mechanism of competition is employed (e.g. Lang 1973, Cope 1982, Logan 1984, Tanner 1993). In fact, there were a number of instances in this study, especially involving closely related species, of one colony winning at one point along the competition boundary and the other further along, even when both colonies were employing the same mechanism of competition (unpublished data). Similar patterns have been found by studying species replacements over time, with transitions between most species groups occurring in both directions (Connell 1976, Jackson 1979, Chornesky 1989, Tanner et al. 1994, Chapter 5). Factors such as encounter angle, water movement, relative colony size etc. (e.g. Johnston et al. 1981, Bak et al. 1982, Lang & Chornesky 1990, Alino et al. 1992, Genin et al.

1994), are thus probably at least as important as species identity in determining the outcome of any specific encounter. This variability and complexity in competitive outcome, along with frequent disturbances such as cyclones, probably results in competitive exclusion being a fairly uncommon event in most high diversity coral assemblages (e.g. Tanner et al. 1994, 1995, Chapters 5, 6).

The frequency of competitive encounters found at the south slope site compares with that found by Sheppard (1985) at two reefs in the central Great Barrier Reef. On a per square meter basis, I found approximately 10 encounters on the south slope, with a coral cover of nearly 50%, while Sheppard (1985) found approximately 11 encounters $m^{-2}$, in areas with coral cover ranging from 57 to 83 %. In contrast, on the north slope and at Wistari where coral cover was much lower (20 - 30%), the number of competitive encounters was around 4.5 $m^{-2}$ (Figure 2.1). This is comparable to values found by Logan (1984) in Bermuda in areas of 13 - 25% cover. These results suggest that the form of the relationship between coral cover and number of encounters may be fairly consistent geographically, although this hypothesis is only very preliminary given the low number of sites from which data are available.

The results of this study show that competition in coral assemblages is extremely complex. This complexity is probably due to the common occurrence of competitive networks (*sensu* Jackson & Buss 1975), and reversals in competitive outcome (e.g. Chornesky 1989). The result of any encounter between two corals cannot be determined by a knowledge of the species alone, with the environment and the history of the encounter both playing important roles in determining the apparent winner at any point in time. Simple linear hierarchies of competitive dominance thus cannot be used to predict competitive displacement, nor the course of community development. Instead, a complex array of species transitions are needed, as employed by Tanner et al. (1994, 1995, Chapters 5, 6).

**Table 2.1:** Species groups formed on the basis of taxonomic and morphological considerations.

| Code | Species Group |
|---|---|
| A | Encrusting Acroporid corals |
| B | Tabular *Acropora* |
| C | Bushy *Acropora* |
| D | Staghorn *Acropora* |
| E | Soft Corals |
| F | Algae |
| G | Massive corals |
| H | Pocilloporid corals |
| O | Other scleractinia |

**Table 2.2:** Interspecies-group competitive abilities by mechanism. Numbers indicate the frequency of wins by the species group in the top row over the species group in the left column. Numbers in brackets indicate the total number of competing colonies in each category.

Overtopping

| | A | | B | | C | | D | | E | | F | | G | | H | | O | | Total lost | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 22 | (44) | 41 | (41) | 59 | (68) | 111 | (135) | 22 | (32) | 0 | (2) | 15 | (47) | 24 | (43) | 4 | (10) | 298 | (422) |
| B | 0 | (41) | 4 | (8) | 2 | (12) | 4 | (15) | 1 | (8) | 0 | (2) | 4 | (28) | 0 | (21) | 1 | (6) | 16 | (141) |
| C | 9 | (68) | 10 | (12) | 16 | (32) | 30 | (43) | 6 | (12) | 0 | (3) | 1 | (22) | 2 | (23) | 1 | (6) | 75 | (221) |
| D | 24 | (135) | 11 | (15) | 13 | (43) | 23 | (46) | 7 | (22) | 0 | (1) | 2 | (36) | 1 | (30) | 0 | (11) | 81 | (339) |
| E | 10 | (32) | 7 | (8) | 6 | (12) | 15 | (22) | 4 | (8) | 0 | (0) | 1 | (37) | 0 | (12) | 1 | (5) | 44 | (136) |
| F | 2 | (2) | 2 | (2) | 3 | (3) | 1 | (1) | 0 | (0) | 0 | (0) | 0 | (2) | 0 | (0) | 0 | (0) | 8 | (10) |
| G | 32 | (47) | 24 | (28) | 21 | (22) | 34 | (36) | 36 | (37) | 2 | (2) | 6 | (12) | 10 | (15) | 2 | (2) | 167 | (201) |
| H | 19 | (43) | 21 | (21) | 21 | (23) | 29 | (30) | 12 | (12) | 0 | (0) | 5 | (15) | 1 | (2) | 0 | (1) | 108 | (147) |
| O | 6 | (10) | 5 | (6) | 5 | (6) | 11 | (11) | 4 | (5) | 0 | (0) | 0 | (2) | 1 | (1) | 0 | (0) | 32 | (41) |
| Total won | 124 | (422) | 125 | (141) | 146 | (221) | 258 | (339) | 92 | (136) | 2 | (10) | 34 | (201) | 39 | (147) | 9 | (41) | 829 | (1658) |

Table 2.2. Continued

Direct Contact

| | A | | B | | C | | D | | E | | F | | G | | H | | O | | Total lost | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 5 | (10) | 4 | (5) | 14 | (19) | 28 | (71) | 5 | (5) | 0 | (0) | 87 | (88) | 9 | (20) | 14 | (14) | 166 | (232) |
| B | 1 | (5) | 0 | (0) | 0 | (0) | 3 | (6) | 0 | (0) | 0 | (0) | 3 | (3) | 1 | (5) | 0 | (1) | 8 | (20) |
| C | 5 | (19) | 0 | (0) | 8 | (16) | 8 | (17) | 2 | (4) | 0 | (0) | 12 | (13) | 4 | (25) | 4 | (4) | 43 | (98) |
| D | 43 | (71) | 3 | (6) | 9 | (17) | 35 | (70) | 7 | (10) | 0 | (0) | 23 | (27) | 10 | (34) | 15 | (16) | 145 | (251) |
| E | 0 | (5) | 0 | (0) | 2 | (4) | 3 | (10) | 0 | (0) | 0 | (0) | 6 | (8) | 2 | (4) | 1 | (1) | 14 | (32) |
| F | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (1) | 0 | (1) |
| G | 1 | (88) | 0 | (3) | 1 | (13) | 4 | (27) | 2 | (8) | 0 | (0) | 16 | (32) | 4 | (25) | 2 | (8) | 30 | (204) |
| H | 11 | (20) | 4 | (5) | 21 | (25) | 24 | (34) | 2 | (4) | 0 | (0) | 21 | (25) | 2 | (4) | 2 | (5) | 87 | (122) |
| O | 0 | (14) | 1 | (1) | 0 | (4) | 1 | (16) | 0 | (1) | 1 | (1) | 6 | (8) | 3 | (5) | 2 | (4) | 14 | (54) |
| Total won | 66 | (232) | 12 | (20) | 55 | (98) | 106 | (251) | 18 | (32) | 1 | (1) | 174 | (204) | 35 | (122) | 40 | (54) | 507 | (1014) |

Table 2.2. Continued.

Overgrowth

| | A | | B | | C | | D | | E | | F | | G | | H | | O | | Total lost | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 47 | (94) | 0 | (1) | 3 | (40) | 3 | (45) | 37 | (57) | 10 | (11) | 8 | (26) | 3 | (30) | 4 | (26) | 115 | (327) |
| B | 1 | (1) | 1 | (2) | 1 | (1) | 1 | (2) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 4 | (6) |
| C | 37 | (40) | 0 | (1) | 1 | (2) | 6 | (7) | 2 | (2) | 1 | (1) | 1 | (3) | 0 | (1) | 0 | (0) | 48 | (57) |
| D | 42 | (45) | 1 | (2) | 1 | (7) | 15 | (30) | 8 | (11) | 0 | (0) | 3 | (3) | 0 | (1) | 1 | (2) | 71 | (96) |
| E | 20 | (57) | 0 | (0) | 0 | (2) | 3 | (11) | 1 | (2) | 0 | (0) | 4 | (14) | 0 | (3) | 1 | (4) | 29 | (94) |
| F | 1 | (11) | 0 | (0) | 0 | (1) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (1) | 0 | (0) | 0 | (0) | 1 | (13) |
| G | 18 | (26) | 0 | (0) | 2 | (3) | 0 | (3) | 10 | (14) | 1 | (1) | 4 | (8) | 0 | (1) | 3 | (7) | 38 | (57) |
| H | 27 | (30) | 0 | (0) | 1 | (1) | 1 | (1) | 3 | (3) | 0 | (0) | 1 | (1) | 0 | (0) | 0 | (0) | 33 | (36) |
| O | 22 | (26) | 0 | (0) | 0 | (0) | 1 | (2) | 3 | (4) | 0 | (0) | 4 | (7) | 0 | (0) | 0 | (0) | 30 | (35) |
| Total won | 212 | (327) | 2 | (6) | 9 | (57) | 25 | (96) | 65 | (94) | 12 | (13) | 19 | (57) | 3 | (36) | 5 | (35) | 352 | (704) |

Table 2.2. Continued.

All Mechanisms

| | A | | B | | C | | D | | E | | F | | G | | H | | O | | Total lost | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 74 | (148) | 45 | (47) | 76 | (127) | 142 | (251) | 64 | (94) | 10 | (13) | 110 | (161) | 36 | (93) | 22 | (50) | 579 | (981) |
| B | 2 | (47) | 5 | (10) | 3 | (13) | 8 | (23) | 1 | (8) | 0 | (2) | 7 | (31) | 1 | (26) | 1 | (7) | 28 | (167) |
| C | 51 | (127) | 10 | (13) | 25 | (50) | 44 | (67) | 10 | (18) | 1 | (4) | 14 | (38) | 6 | (49) | 5 | (10) | 166 | (376) |
| D | 109 | (251) | 15 | (23) | 23 | (67) | 73 | (146) | 22 | (43) | 0 | (1) | 28 | (66) | 11 | (65) | 16 | (29) | 297 | (686) |
| E | 30 | (94) | 7 | (8) | 8 | (18) | 21 | (43) | 5 | (10) | 0 | (0) | 11 | (59) | 2 | (19) | 3 | (10) | 87 | (262) |
| F | 3 | (13) | 2 | (2) | 3 | (4) | 1 | (1) | 0 | (0) | 0 | (0) | 0 | (3) | 0 | (0) | 0 | (1) | 9 | (24) |
| G | 51 | (161) | 24 | (31) | 24 | (38) | 38 | (66) | 48 | (59) | 3 | (3) | 26 | (52) | 14 | (41) | 7 | (17) | 235 | (462) |
| H | 57 | (93) | 25 | (26) | 43 | (49) | 54 | (65) | 17 | (19) | 0 | (0) | 27 | (41) | 3 | (6) | 2 | (6) | 228 | (305) |
| O | 28 | (50) | 6 | (7) | 5 | (10) | 13 | (29) | 7 | (10) | 1 | (1) | 10 | (17) | 4 | (6) | 2 | (4) | 76 | (130) |
| Total won | 402 | (981) | 139 | (167) | 210 | (376) | 389 | (686) | 175 | (262) | 15 | (24) | 227 | (462) | 77 | (305) | 54 | (130) | 1688 | (3376) |

**Figure 2.1.** The mean number of encounters per colony between corals occurring in $20m^2$ belt transects at Heron Island.

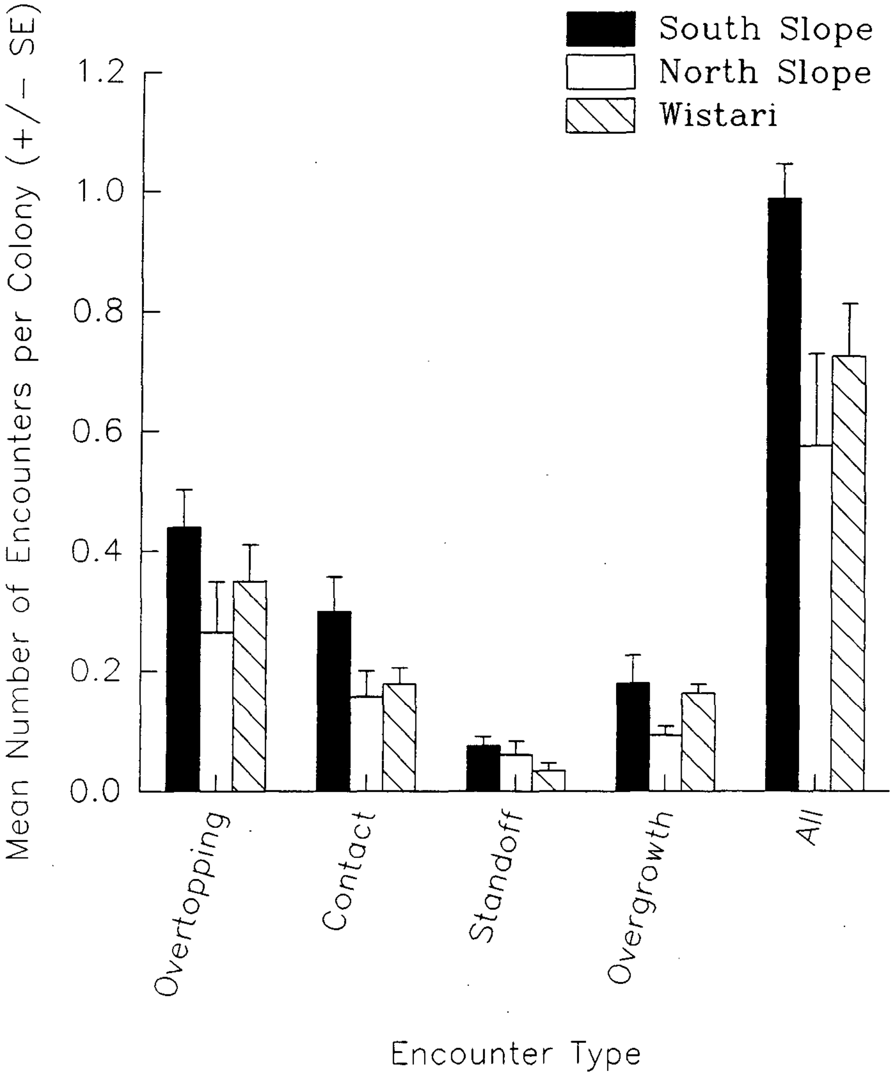
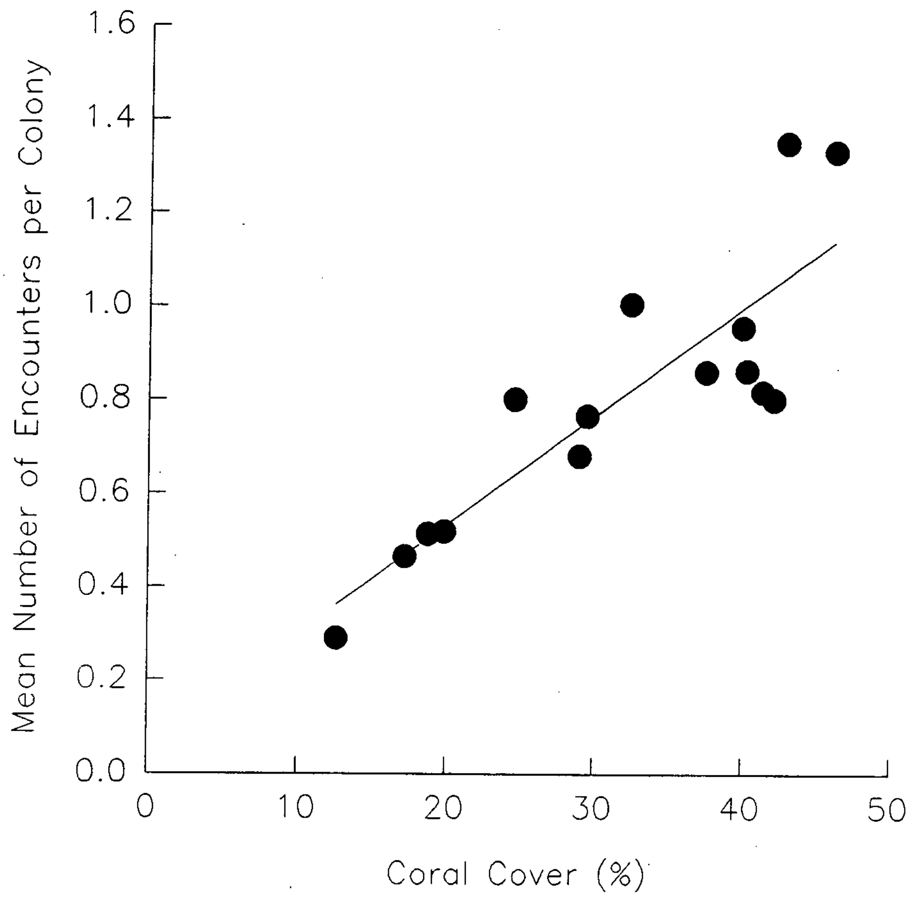

South Slope
North Slope
Wistari
Mean Number of Encounters per Colony (+/- SE)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Overtopping
Contact
Standoff
Overgrowth
All
Encounter Type

**Figure 2.2.** Regression between number of competitive encounters per colony and percent coral cover in each transect (all sites pooled). The regression is significant with $P<0.01$.


Mean Number of Encounters per Colony
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
Coral Cover (%)

# Chapter 3

## Interspecific Competition Reduces Fitness in Scleractinian Corals.

Reference: Tanner, J.E. Interspecific competition reduces fitness in scleractinian corals. J. Exp. Mar. Biol. Ecol. In Review.

### Abstract:

Competition is widely regarded as an important structuring mechanism in coral reef benthic communities, yet there is little evidence available to determine what impact it has on the fitness of individual colonies. Fitness has been shown to decline in scleractinian corals engaged in competition with macroalgae, and in intraspecific competition, but the only attempts to investigate the costs of interspecific competition between scleractinian corals have examined either growth or reproduction, but not both. In this paper I show, by establishing experimental contacts and monitoring them over time, that competition between several species of scleractinian coral has major consequences for colony fitness.

Both *Pocillopora damicornis* and *Acropora hyacinthus* experienced substantial declines in growth rates when competing against other corals compared to non-competing controls, although mortality was not affected. Growth in *A. hyacinthus* decreased from 120% to 35%, while in *P. damicornis* it decreased from 45% to -16% (i.e. one group of competing colonies shrank in size on average). An examination of the effects of competition on reproduction of *A. hyacinthus* showed that at the polyp level, there is no detectable response. This conclusion is reversed at the colony level, as the reduction in growth rate leads to smaller colonies which are less fecund. This reduction in colony fecundity due to a decrease in size is somewhat compensated for by a decrease in the number of non-reproductive polyps in the colony. Size-classified matrix models of cohort dynamics show that competition has a major impact on cohort survival for *A. hyacinthus*, but this impact, while still present, is much less for *P. damicornis*. Overall, even though the target colonies did not appear to be greatly affected by competition on first examination, when their growth and reproduction were examined, it became obvious that competition does impose a significant fitness cost.

## Introduction:

Competition is ubiquitous in many communities (see reviews in Connell 1983, Schoener 1983, Gurevitch et al. 1992), including high diversity coral reef benthic assemblages. Competition for space and other resources is often cited as a major mechanism influencing the community structure of coral reefs (Connell 1978, Lang & Chornesky 1990, Karlson & Hurd 1993, Rogers 1993). Several of the most spectacular examples of how important competition for space can be in coral reefs come from anthropogenically disturbed systems, where algae and/or sponges have proliferated, decimating the pre-existing coral communities (Hawaii: Smith et al. 1981, Jamaica: Hughes 1994). The diversity of mechanisms by which corals compete (reviewed in Lang & Chornesky 1990), and the high degree of variability in a species' success when competing with different mechanisms, have been proposed to be highly important in maintaining the high diversity seen in many coral reef benthic assemblages (e.g. Connell 1978, Karlson & Hurd 1993). Despite this acknowledged importance of competition at the community level, how the individuals involved are affected by prolonged interaction with one-another is poorly understood. A few studies on scleractinian corals have examined how interspecific competition affects growth

(Romano 1990), and reproduction (Chadwick 1991), and Rinkevich & Loya (1985) have examined how intraspecific competition in *Stylophora pistillata* affects both reproduction and growth. In all cases, it was found that competition was energetically costly, and Romano (1990) proposed that corals only deployed competitive structures against inferior competitors, in order to minimise the costs associated with competition. However, there has been no single integrated study to examine the effects that interspecific competition has on the fitness of scleractinian corals.

The first priority of any long-lived iteroparous organism, such as a scleractinian coral, when faced with a competitor, should be to survive. Obviously if a colony fails to survive a competitive encounter, it has zero future reproduction, whereas if it survives by sacrificing other functions, it may still have the opportunity to reproduce again at a later date. Energy should thus be diverted to survival from other functions, such as growth and reproduction, unless the coral has an energy surplus. For colonial organisms such as corals, a decrease in growth equates to a decrease in future reproduction and survivorship, as fecundity generally increases with size while mortality decreases (e.g. Hughes 1984, Lasker 1990, Hall & Hughes 1996). Thus the tradeoff between sacrificing growth or current reproduction in order to survive competition can be viewed as a tradeoff between current and future reproduction. These trade-offs are further complicated by the different levels that reproduction can be examined at. Measurements of fecundity can be performed either at the polyp level, or at the colony level, and changes found at one level may not necessarily reflect changes at the other level. For example, if there is no change in polyp level fecundity, but growth decreases, then colony level fecundity will be reduced relative to a similar colony which does not experience reduced growth. To calculate colony fecundity from polyp fecundity, the number of reproductive polyps in the colony must be known. This number will be a function of three variables, the size of the colony itself, the density of polyps, and the proportion of nonreproductive polyps. Most of the nonreproductive polyps are located around the periphery of the colony, in what is generally termed the sterile zone (e.g. Wallace 1985, Harrison & Wallace 1990). This term is somewhat of a misnomer, however, in that the polyps in this area are generally considered to be pre-reproductive, probably having been budded after the commencement of gametogenesis, rather than sterile (Harrison & Wallace 1990).

Here I report on how long-term contact among corals (and some other invertebrates), influences their survivorship, growth, and reproduction, three major components of fitness. A decrease in any of these three demographic factors will decrease lifetime reproductive output, provided there is no compensatory increase in another. Unless this decrease in fecundity is compensated for by an increase in larval survival and subsequent recruitment, which is unlikely to occur, especially if egg size remains constant, fitness will then be reduced. I also construct and analyse population dynamics models for the different levels of competition employed, in order to determine the population level consequences that competition has for scleractinian corals. The effects of competition can be determined by comparing the analysis and simulations of competing populations to non-competing populations, and also by a direct comparison of the underlying transition matrices used in the models. The transition matrices can be compared using either log-linear analysis (Caswell 1989), or a chi-square test (Anderson & Goodman 1957, Bierzychudek 1982), although the log-linear approach is preferable for population matrices as it incorporates mortality as well as the frequency of transitions between the different classes (Caswell 1989). These models allow the effects of growth and mortality to be integrated into a single measure of fitness, the population growth rate ($\lambda$). In closed populations, reproduction can also be incorporated into this measure by including terms for fecundity. However, scleractinian corals, like most other colonial organisms, have open populations at all but the largest scales, and it is not realistic to incorporate reproduction into models which describe dynamics at the scale of an individual reef or less. This is the first time that the consequences of competition have been examined at the population level in coral reef colonial invertebrates.

Previous mathematical models of coral population dynamics show that population growth rate, and individual fitness, is influenced more by growth into larger size classes, which increases future reproduction and survivorship, than it is by current reproduction (e.g. Gotelli 1991, Lasker 1991). This can be seen by examining the elasticities of population matrices, which describe how a change in any transition will affect population growth relative to a similar change in any other transition (DeKroon et al. 1986). In general, corals have a high elasticity for growth and survival of large size classes, meaning that slight changes in these processes will have a large affect on population growth and individual fitness. Reproduction, on the other hand, tends to have very low elasticities, due to the very low survival rates of coral larvae and juveniles, meaning that large changes in reproduction will have little affect on population growth and colony fitness. Colony growth should thus be maintained in favour of current reproduction when a coral faces an energy drain, such as that imposed by competition, if the colony is to maximise its fitness.

## Methods:

### Mortality & Growth:

To examine the effect that competition has on the mortality and growth of scleractinian corals, experimental contacts between *in situ* target colonies and transplanted fragments were established at Heron Island (23°26'S, 151°55'E), on Australia's Great Barrier Reef. The target species for these experiments were *Acropora hyacinthus* (Dana), a large tabulate species that broadcast spawns during the mass spawning in late spring (Harrison & Wallace 1990), and *Pocillopora damicornis* (Linnaeus), a smaller brooding species that releases planulae several times a year (Tanner 1996). Fragments of other species were tied to the margins of all experimental colonies, in such a fashion as to mimic competition which occurs when fragments either fall onto neighbours, or when a young coral grows up into the overhanging branches of another. For *P. damicornis*, the competitors were *A. formosa* Dana (n = 99) and the confamilial *Stylophora pistillata* Esper (n = 105), with 86 non-competing controls, while *A. formosa* (n = 120) and encrusted coral branches (n = 106) were used against *A. hyacinthus*, with 130 non-competing controls. The encrusted branches used were covered with algae, sponges, bryozoans and ascidians, all of which are potential competitors of scleractinian corals. These encrusting organisms provide a moderate level of active competition, and thus encrusted branches do not act as controls for the passive effects associated with the branch blocking light, and inhibiting water flow. In the context of this study, any reduction in light levels or water flow caused by the attached competitors is regarded as a part of the competitive effect. In all cases, the non-competing control colonies had an identification tag tied to them, but were otherwise undisturbed.

To follow the growth and survivorship of the above corals, all colonies were photographed approximately once every 8 months, with *Acropora hyacinthus* being followed for 15 months, and *Pocillopora damicornis* for 24. All photographs were traced onto maps and subsequently digitised in order to determine their planer area, which was then used to calculate growth rates. A total of 6 colonies of *A. hyacinthus*, and 13 of *P. damicornis* could not be relocated at the end of the study, and were excluded from analysis, thus probably resulting in a slight underestimate of mortality rates.

Reproduction:

To determine how competition affected reproduction in *Acropora hyacinthus*, 100 colonies were established in competition with *A. formosa*, in the same way as described above, in March 1992, with a further 100 having all potential competitors removed. Just prior to the mass spawning (Harrison & Wallace 1990), in November 1992, all colonies were photographed to determine their size, and had small (~30-50 $cm^2$) samples taken from them. Non-competing control colonies had the sample removed from a haphazardly chosen area, while the competing colonies were sampled both near the site of competition (near samples), and on the opposite side of the colony to the competitive encounter (far samples). All samples were taken from the periphery of the colony, and extended in from the colony margin for approximately 10 cm. This allowed reproductive polyps past the edge of the lateral sterile zone, a zone of non-reproductive polyps around the periphery of the colony (Wallace 1985, Harrison & Wallace 1990), to be collected, and the size of the sterile zone to be determined. All samples were initially preserved in 10% formalin in seawater for at least 1 week, after which they were transferred to a solution of 5% HCl and 10% formalin in seawater for decalcification.

Due to minor colony mortality, and the loss of some samples, only 86 control colonies and 86 treatment colonies were examined for fecundity. Five polyps from each of the 86 samples in each of the three groups (i.e. control, near and far), randomly selected from the inner 1-2 cm of the sample, were dissected, and the number of eggs and testes in each counted. The volume of one randomly chosen egg and testis from each polyp was also determined by measuring the length of the three orthogonal axes and approximating volume as that of an ellipsoid. The lengths of the lateral and vertical sterile zones were measured for each sample. All statistical comparisons for reproductive variables were by ANCOVA with colony area as a covariate.

Modelling:

The dynamics and fate of cohorts of competing and non-competing corals were modelled using the standard size-classified variant of the Leslie matrix model (Caswell 1989). Due to the open nature of coral populations, fecundity estimates cannot be linked to recruitment, and it is not realistic to incorporate reproduction into these models, so instead of modelling population dynamics, I modelled cohort dynamics. To allow for the size specific nature of coral growth and mortality, colonies of each species were divided up into four size classes (see Table 3.2), and the fate of each colony determined for each census interval as a function of size class. Log-linear models (Caswell 1989) were used to determine if the fate of a colony was determined by either the time interval or the competition treatment it experienced. Transition probability matrices were then constructed for each treatment after pooling (=adding) the transition matrices for the different time intervals, and simulations run according to the equation:

$$x(t+1) = \mathbf{A}\, x(t)$$

where **A** is the transition probability matrix, and x(t) is a vector describing the composition of the cohort by size class at time t. In all simulations, I began with x(0) having 1000 new recruits in size class I, and no individuals in the other size classes. Matrix eigenanalysis (Caswell 1989), was performed to calculate cohort extinction rates, and the stable size composition of cohorts.

## Results:

### Outcome of Competition:

The apparent outcome of the competitive encounters varied greatly for both species, and was not closely related to the species against which it was competing. Overall, there were very few instances of large portions of the colony dying around the encounter, with the most common result being an infilling reaction, where both corals deposit a pad of relatively undifferentiated skeleton along the area of contact, creating a weak bond between them, and with no colony obviously dominating the other (Lang & Chornesky 1990). There were also many instances of overgrowth in the encounters involving *Acropora hyacinthus*, although never by more than about 2cm, and with no consistent winner.

### Mortality:

As predicted, competition had little effect on the survivorship of either *Acropora hyacinthus* or *Pocillopora damicornis*, with control colonies of both species having only marginally lower mortality than colonies in contact with encrusted or living branches. Over the fifteen month study period, 22% of control *A. hyacinthus* colonies died, while 28% of colonies in each of the experimental treatments died ($\chi^2_2 = 1.47$, $P > 0.5$). Mortality was higher in *P. damicornis*, which experienced a cyclone a few weeks after the experiment was set up. Over twenty-four months, 63% of control *P. damicornis* died, 69% of colonies competing with *A. formosa* died, and 76% competing with *Stylophora pistillata* died ($\chi^2_2 = 1.46$, $P > 0.5$).

### Growth:

In contrast to survivorship, the growth rate of *Acropora hyacinthus* was significantly reduced by competition (Fig 3.1a, Kruskal-Wallis test $\chi^2_2$ = 16.3, P=0.0003). Over the fifteen month study period, control colonies not engaged in competition increased their size by an average of 120 ± 18 (SE)%. In contrast, colonies in contact with encrusted branches and live *A. formosa* grew by 60 ± 11% and 35 ± 10% respectively. This pattern also occurred with *Pocillopora damicornis*, where non-competing control colonies grew by 45 ± 19% in twenty four months, while colonies competing against *A. formosa* grew 14 ± 20%, and colonies competing against the confamilial *Stylophora pistillata* shrank by 16 ± 9% of their original size (Fig 3.1b, Kruskal-Wallis test $\chi^2_2$ = 6.1, P=0.047).

### Reproduction:

Unexpectedly, while competition had a significant effect on growth, its direct effect on reproduction was minimal, with none of the polyp level variables measured being significantly affected (Table 3.1). Total gonad volume per polyp in *Acropora hyacinthus* was 1.06 ± 0.02 (SE) mm$^3$ for control colonies, 1.05 ± 0.02 mm$^3$ for far samples (i.e. samples from competing colonies, but on the opposite side of the colony to the site of competition), and 0.99 ± 0.02 mm$^3$ for near samples (i.e. samples from adjacent to the site of competition).

The width of the lateral sterile zone (LSZ), the zone of non-reproductive polyps around the periphery of the colony, decreased significantly with the imposition of competition (ANOVA $F_{2,251} = 8.3$, P=0.0003). Control colonies had a mean LSZ of 26.4 ± 1.0 (SE) mm, far samples 23.6 ± 0.9 mm and near samples 20.4 ± 1.2 mm. Tukey's test showed that the only significant pairwise difference at $\alpha = 0.05$ was between near and control samples. Vertical sterile zone (VSZ) length showed the same trend as LSZ, although in this case it was not significant (ANOVA $F_{2,118}=0.73$, $P=0.49$). Control colonies had a mean VSZ of 8.0 ± 0.4 mm, far samples 7.9 ± 0.5 mm and near samples 7.4 ± 0.5 mm.

### Transition Matrices:

There was no difference in the transition matrices for *Pocillopora damicornis* over time, nor between competition treatments, while for *Acropora hyacinthus*, time was also not significant, but the competition treatment was marginally significant (Table 3.2). The non-significance of time for both species allowed the transition matrices for each time interval to be pooled, giving a single matrix, with a larger sample size, for each competition treatment. Once this was done, competition level became significant for *A. hyacinthus* (Table 3.2), but still wasn't significant for *P. damicornis*. I then converted the pooled transition matrices to transition probability matrices (Table 3.3). Examination of the transition probability matrices shows that while the diagonal elements (stasis) tend to remain fairly constant across treatments, the elements above the diagonal (colony shrinkage) tend to increase, and those below the diagonal (colony growth) tend to decrease, in the competition treatments compared to the controls. This is in agreement with the decrease in colony growth due to competition (Fig 3.1).

### Model Analysis:

The differences found between the transition matrices for the different treatments for *Acropora hyacinthus*, but not *Pocillopora damicornis* (Table 3.2), are borne out by the results of the simulations carried out using these matrices. A cohort of control *A. hyacinthus* shows a much slower rate of decline than do cohorts that are competing (Fig 3.2a), while the difference between control and competing cohorts of *P. damicornis* is only very slight (Fig 3.2b). Despite the apparently minor differences between treatments for *P. damicornis* in the simulations, the cohort survival rate (λ, which is equivalent to the population growth rate), is in fact much higher for the non-competing controls than it is for the competing colonies (Table 3.4). It also takes 53 years for the non-competing cohort to decline from 1000 recruits to less than 1 individual, compared to 18 and 20 years for the two competing cohorts. For all categories of competition, *A. hyacinthus* shows a higher cohort survival rate than does *P. damicornis* (Table 3.4), although this result must be interpreted with caution as it may simply be an artefact of the different size classes used for the two species. For both species, control cohorts have a much larger proportion of large individuals than do competing cohorts (Fig 3.3). For both *P. damicornis* and *A. hyacinthus*, the two competition treatments result in cohort structures more similar to each other than to the cohort structure of the controls (Fig 3.3a).

## Discussion:

Previous studies which have examined the costs of competition to scleractinian corals have tended to find negative effects on growth and reproduction (Rinkevich & Loya 1985, Romano 1990, Chadwick 1991, Tanner 1995). However, it is not axiomatic that competition will decrease both growth and reproduction. Romano (1990), found that *Pocillopora damicornis* did not experience reduced growth rates when competing with *Cyphastrea ocellina*, even though it was the inferior competitor, but that it instead reoriented growth away from its competitor. Similarly, in this study, I found no effect on polyp level fecundity, although growth did slow down substantially. Contrary to Romano's (1990) finding that growth of *P. damicornis* was not affected by competition, I did find a substantial decrease in growth rates of competing colonies of this species.

The results found in this study were not entirely as expected for maximisation of fitness, although the hypothesis that survival would not be affected by competition was borne out. However, instead of reproduction being more affected than growth, as originally predicted, I found that reproduction was minimally affected, while growth was substantially reduced by competition. In fact, the only significant direct effect on reproduction, the decrease in lateral sterile zone width, was in the opposite direction to what was expected, suggesting that reproduction may actually increase marginally in colonies experiencing competition. A decrease in sterile zone width is what would be expected with a decrease in growth rate if sterile zones are only formed of those polyps which were budded off after gametogenesis commenced and are thus to young to be reproductive (Wallace 1985, Harrison & Wallace 1990). If the width of the sterile zone was influenced directly by the presence of a competitor, it is more likely that it would increase, with energy being drawn from reproduction for competition and increased maintenance costs.

One possible explanation for the lack of effect on reproduction could be that polyp fecundity is only decreased in a very localised area around the site of competition - a result which would not have been picked up in this study as all polyps dissected were taken from 5-7 cm inside the edge of the lateral sterile zone so as to avoid areas of naturally low fecundity. The lack of an impact on reproduction may also be related to the timing of the experiment. Experimental contacts were established in March, approximately at the time oogenesis commences in most broadcast spawning corals (Harrison & Wallace 1990). If the energy commitment to reproduction is low at this time, while the major cost of competition occurs when the contact is initially established, there may have been no large energy demand when energy was required for reproduction. It is also possible that the resources required for competition do not overlap sufficiently with the resources required for reproduction for competition to limit polyp level reproduction.

If we extrapolate the results on polyp level fecundity to determine the effect that competition has on colony level fecundity, however, we obtain a different result. The decrease in colony growth rate means that total colony fecundity will in fact be reduced by competition, as fecundity is directly related to colony size (e.g. Hall & Hughes 1996). Such a decrease in fecundity strongly suggests that competition reduces fitness, unless larval survival increases for competing colonies. Such an increase is unlikely, as egg size did not change, and thus there is presumably no difference in the resources available to larvae from competing versus non-competing colonies, although egg quality was not examined.

The decrease in LSZ only near the site of competition, but not far from it, suggests that the effects of competition may only be localised, and that the energy for competition is coming predominantly from the polyps close to the encounter, and not from those on the other side of the colony. Examination of the direction of growth of competing colonies would provide further evidence to test this hypothesis. If corals keep growing on the opposite side of the colony to where a competitive encounter occurs as though they were not in competition, (as suggested by the decrease in LSZ only near the site of competition but not far from it), this would further show that energy is only being drawn from polyps near the competitive interaction. Such asymmetric growth has been observed in *Pocillopora damicornis* competing against *Cyphastrea ocellina*, although the *C. ocellina* displayed reduced growth over the whole colony (Romano 1990). Similarly, physical injury affects the reproductive status of polyps a short distance from the site of injury, but not on the other side of the colony (Van Veghel & Bak 1994).

When translated to the population level, the reduction in growth caused by competition appeared to have little impact on *Pocillopora damicornis*, which experienced a rapid rate of decline in cohort size regardless of whether it was competing or not. However, even though there is a minimal difference between the three groups, if we take extinction time as being the time for the cohort of 1000 individuals to be reduced to below 1 individual, the control cohort survives for more than twice as long as the competing cohorts, albeit at very low numbers. This of course assumes that the benthic assemblages which these corals occur in are at equilibrium, which they are not (Tanner et al. 1994, 1996), with cyclones causing major disruptions approximately every five years. However, even though coral assemblages are non-equilibrium in nature, this result still indicates that non-competing colonies do have a longer life expectancy than competing colonies. For *Acropora hyacinthus*, however, the non-competing population performed fairly well after passing through the early period of heavy mortality of small colonies, and maintained a much higher cohort size than did the two competing populations. These two contrasting results show that an examination of the consequences of competition, or any other factor, for individual colonies will not necessarily allow us to estimate the effects at the population level simply by extrapolation, but that we must employ some means of looking at population dynamics specifically. Size-classified models of population dynamics, as employed here, provide a simple means of extending results to the population level. The lack of reproduction in the models used does not hinder comparisons in this case, because reproduction was not affected by competition.

This study shows that competition can significantly decrease the growth rate, and thus future fecundity, of scleractinian corals. Considering that many naturally growing colonies are in contact with more than one competitor (pers. obs.), and that many corals are much more aggressive than the transplanted competitors used (Tanner 1993), it becomes likely that most if not all species of coral suffer reduced fitness when in contact with neighbours. Any coral which can in some way reduce its exposure to competitors is thus likely to experience a substantial gain in fitness, and indeed a number of such mechanisms have been recognised. Corals can avoid competition by growing up and then over potential competitors (Connell 1978, Lang & Chornesky 1990), by growing away from other corals (Romano 1990), or in some cases, such as the non-attached fungids, by actively moving away from neighbours (e.g. Chadwick 1988). Competition may also be avoided if larvae choose to settle away from other corals. Overall, the fitness of colonies of *Acropora hyacinthus* and *Pocillopora damicornis* engaged in competition appears to be substantially reduced compared to those not competing with other colonies. Thus, even if there is no clear winner (Chornesky 1989), competition between scleractinian corals can still have major ecological and evolutionary consequences for the competitors.

Acknowledgments:

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**Table 3.1**: The effect of competition on the reproduction of *Acropora hyacinthus*. All tests are ANCOVA's with colony area as covariate.

| Variable | F Ratio | df | Probability |
|---|---|---|---|
| Total gonad volume | 0.645 | 2, 254 | 0.526 |
| Total egg volume | 0.289 | 2, 254 | 0.749 |
| Total testes volume | 1.190 | 2, 254 | 0.306 |
| Number of eggs | 0.850 | 2, 254 | 0.429 |
| Number of testes | 0.519 | 2, 254 | 0.596 |
| Individual egg size | 1.696 | 2, 254 | 0.186 |
| Individual testis size | 1.259 | 2, 254 | 0.286 |

**Table 3.2**: Log-linear analyses for the effects of time and competitive regime on population transition matrices. State refers to the initial size class and fate to the final size class. The interpretation is with respect to fate.

| Model | $\chi^2$ | df | Prob | Interpretation |
|---|---|---|---|---|
| *Pocillopora damicornis* | | | | |
| (State*Time*Competition)<br>+(State*Fate*Time) | 64.3 | 62 | 0.40 | Competition NS |
| (State*Time*Competition)<br>+(State*Fate*Competition) | 65.3 | 62 | 0.36 | Time NS |
| *Acropora hyacinthus* | | | | |
| (State*Time*Competition)<br>+(State*Fate*Time) | 89.4 | 71 | 0.07 | Competition marginal |
| (State*Time*Competition)<br>+(State*Fate*Competition) | 49.8 | 56 | 0.71 | Time NS |
| *A. hyacinthus*<br>(Time pooled) | | | | |
| (State*Fate)<br>+(Fate*Competition) | 58.2 | 39 | 0.025 | Competition significant |

**Table 3.3**: Transition probability matrices for different competition levels for *Acropora hyacinthus* and *Pocillopora damicornis* pooled over time. The size classes for *A. hyacinthus* are: I 0-200, II >200-800, III >800-2000, IV >2000, and for *P. damicornis*: I 0-50, II >50-100, III >100-200, IV >200. N indicates the total number of colonies originally present in the size class.

| | *Acropora hyacinthus* | | | | *Pocillopora damicornis* | | | |
|---|---|---|---|---|---|---|---|---|
| | No competition | | | | No competition | | | |
| | I | II | III | IV | I | II | III | IV |
| I | 0.382 | 0.064 | 0.022 | 0.125 | 0.605 | 0.333 | 0.088 | 0.056 |
| II | 0.393 | 0.670 | 0.333 | 0.063 | 0.066 | 0.303 | 0.175 | 0.037 |
| III | 0 | 0.170 | 0.622 | 0.188 | 0 | 0.273 | 0.474 | 0.148 |
| IV | 0 | 0 | 0.178 | 0.688 | 0 | 0.061 | 0.228 | 0.833 |
| Dead | 0.225 | 0.106 | 0.089 | 0 | 0.355 | 0.121 | 0.035 | 0.019 |
| N | 89 | 94 | 45 | 32 | 76 | 33 | 57 | 54 |

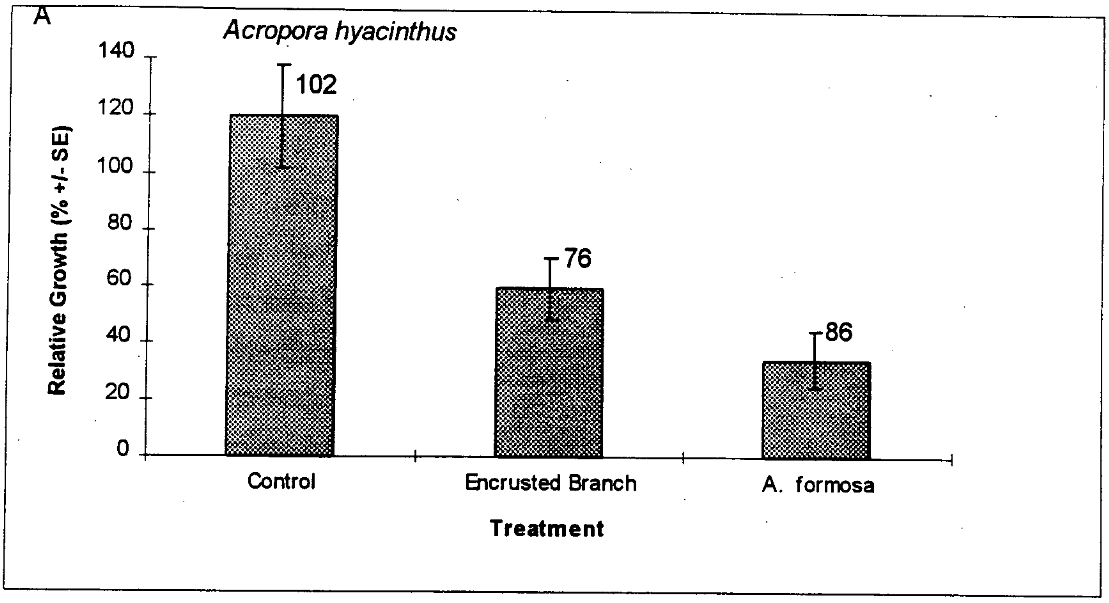
**Table 3.3.** (cont).

| | Competition vs *A. formosa* | | | | Competition vs *A. formosa* | | | |
|---|---|---|---|---|---|---|---|---|
| I | 0.531 | 0.291 | 0.149 | 0.233 | 0.473 | 0.340 | 0.250 | 0.089 |
| II | 0.188 | 0.671 | 0.191 | 0.133 | 0.121 | 0.320 | 0.333 | 0.067 |
| III | 0 | 0.076 | 0.638 | 0.167 | 0.022 | 0.300 | 0.350 | 0.311 |
| IV | 0 | 0 | 0.064 | 0.767 | 0 | 0 | 0.083 | 0.600 |
| Dead | 0.302 | 0.127 | 0.085 | 0 | 0.407 | 0.160 | 0.067 | 0 |
| N | 96 | 79 | 47 | 30 | 91 | 50 | 60 | 45 |
| | Competition vs encrusted branches | | | | Competition vs *S. pistillata* | | | |
| I | 0.59 | 0.064 | 0.19 | 0.056 | 0.54 | 0.30 | 0.21 | 0.11 |
| II | 0.14 | 0.65 | 0.12 | 0.17 | 0.060 | 0.43 | 0.19 | 0.075 |
| III | 0 | 0.088 | 0.62 | 0.33 | 0.024 | 0.17 | 0.56 | 0.25 |
| IV | 0 | 0 | 0.19 | 0.67 | 0 | 0 | 0.057 | 0.68 |
| Dead | 0.289 | 0.143 | 0 | 0 | 0.373 | 0.149 | 0.086 | 0.038 |
| N | 76 | 91 | 26 | 18 | 83 | 47 | 70 | 53 |

**Table 3.4:** The effect of competition on the cohort survival rate (λ, equivalent to population growth rate).

| Treatment | *Pocillopora damicornis* | *Acropora hyacinthus* |
|---|---|---|
| No competition | 0.95 | 0.99 |
| A. formosa | 0.84 | 0.93 |
| S. pistillata / encrusted branch | 0.83 | 0.96 |

**Figure 3.1:** The effect of competition on relative growth rates. Numbers above the bars indicate sample size.


A
Acropora hyacinthus
Relative Growth (% +/- SE)
140
120
100
80
60
40
20
0
102
76
86
Control
Encrusted Branch
A. formosa
Treatment

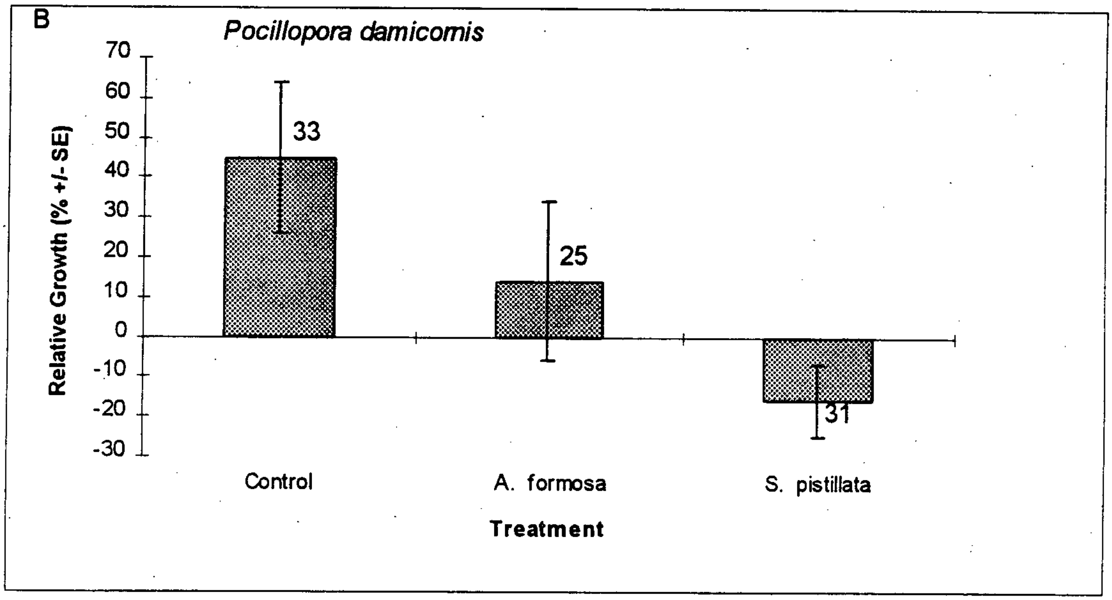
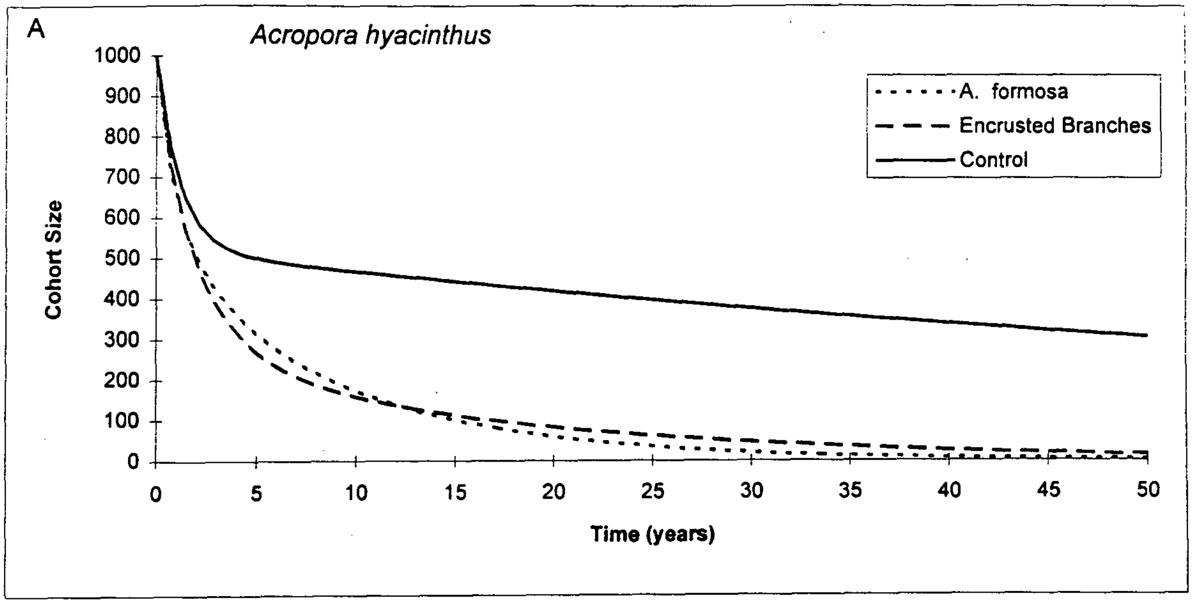

B
Pocillopora damicornis
Relative Growth (% +/- SE)
70
60
50
40
30
20
10
0
-10
-20
-30
33
25
31
Control
A. formosa
S. pistillata
Treatment

**Figure 3.2:** Simulations of cohort dynamics under the three different competition regimes.


A
Acropora hyacinthus
1000
900
800
700
600
500
400
300
200
100
0
Cohort Size
0
5
10
15
20
25
30
35
40
45
50
Time (years)
A. formosa
Encrusted Branches
Control

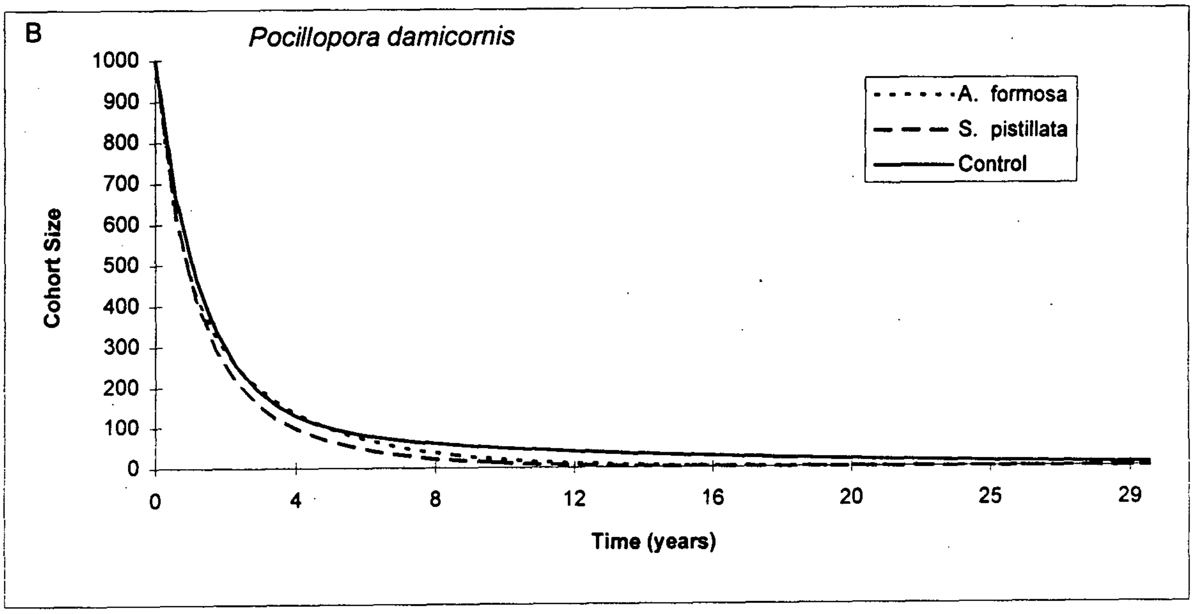
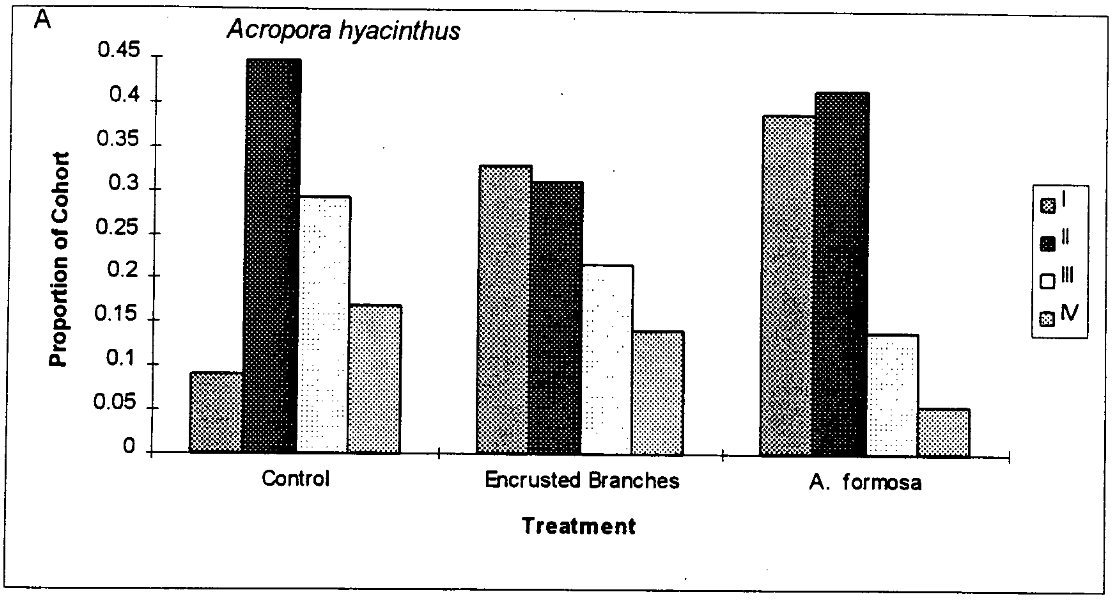
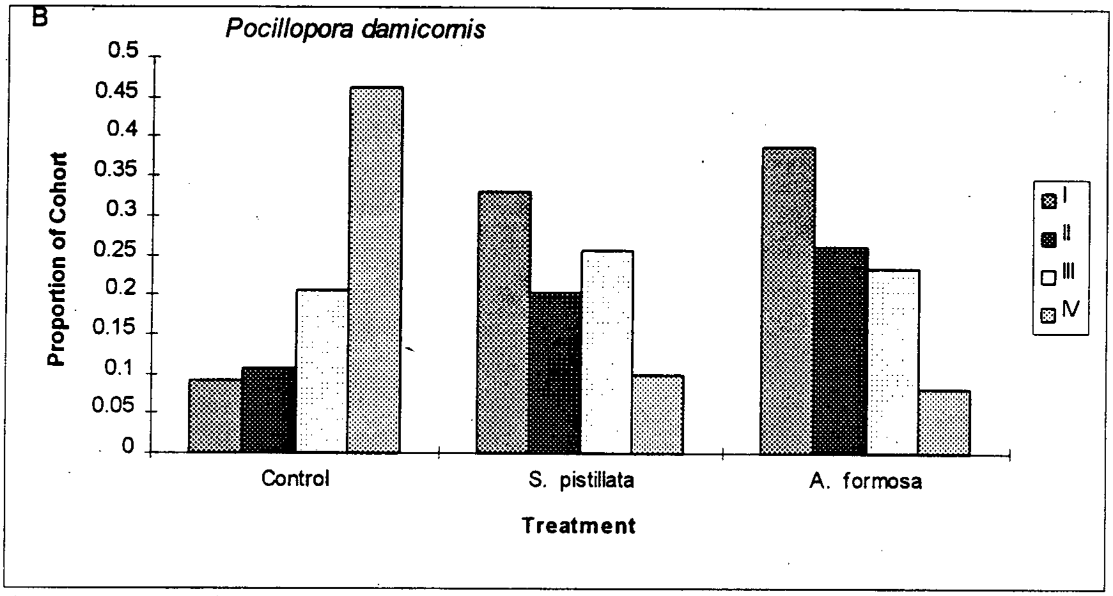

B
Pocillopora damicornis
1000
900
800
700
600
500
400
300
200
100
0
Cohort Size
0
4
8
12
16
20
25
29
Time (years)
A. formosa
S. pistillata
Control

**Figure 3.3:** Stable size composition of cohorts under different competition regimes. The legend indicates size classes which are given in Table 3.


A
Acropora hyacinthus
Proportion of Cohort
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Control
Encrusted Branches
A. formosa
Treatment
I
II
III
IV


B
Pocillopora damicornis
Proportion of Cohort
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Control
S. pistillata
A. formosa
Treatment
I
II
III
IV

# Chapter 4

# Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction.

Reference: Tanner, J.E. 1995. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. J. Exp. Mar. Biol. Ecol. 190:151-168.

**Abstract:**

Macroalgae are a major component of many coral reef flat communities, and are potentially major competitors with corals. I examined the influence of macroalgae on several demographic parameters of four species of scleractinian coral by means of an algal clearance experiment. Specifically, I tested to see if macroalgae are affecting coral cover, growth, fecundity, fission, survivorship and recruitment. I also investigated patterns of natural encounters between corals and algae.

Algal cover at the study site ranged from 41 to 56 %, and coral cover from 8 to 10 %. In total, 92 +/- 4 (SE) % of coral colonies were in contact with one or more species of macroalgae. Changes in coral cover were significantly affected by the presence of macroalgae, with cover of *Acropora* species increasing faster in areas from which algae had been cleared compared to control areas where algae had not been removed, although this pattern did not occur for *Pocillopora damicornis*. Similarly, growth of individual colonies was faster when macroalgae were absent for three *Acropora* species but not for *P. damicornis*. There were no differences detected in rates of fission or survivorship of corals between algal clearance and control treatments, although there were high levels of variability in both of these parameters. Fecundity of *Acropora palifera*, the only species examined, was approximately double in colonies in cleared plots compared to those in control plots with macroalgae present. As no recruitment occurred throughout the two year study, it remains to be determined how macroalgae effect the settlement of coral larvae. The

results show that macroalgae can have a major influence on the demography of scleractinian corals.

## Introduction:

Competition is an important factor in structuring many communities, and has been studied in detail in many systems to determine how it affects individuals, populations and communities (see reviews in Connell 1983, Schoener 1983, Gurevitch et al. 1992). In coral reef assemblages dominated by scleractinian corals, the major focus of investigation into competition has been on elucidating the competitive dominance hierarchy among the assemblage's constituent species (e.g. Lang 1973, Chornesky 1989, Lang & Chornesky 1990, Tanner 1993). The interest has thus been on which species outcompetes which other species and by what mechanisms, emphasising the role of competition in determining patterns of species abundances and distributions. These studies have shown that corals have many ways of competing with each other (reviewed in Lang & Chornesky 1990), and that competition tends to be transitive when only one competitive mechanism is employed. For example, if corals compete solely by extracoelenteric digestion, the outcome is highly predictable based on taxonomy and morphology. However, if the competing species are given time to develop other competitive structures such as sweeper tentacles, or to change their growth patterns, this transitive hierarchy breaks down, and a complex competitive network is formed, with the outcome of any encounter being dependent both on characters of the competing species and the environment (e.g. Chornesky 1989).

The effects of competition on the demography and fitness of individual coral colonies have received little attention (but see Rinkevich & Loya 1985, Romano 1990, Chadwick 1991). In fact, this area has been largely ignored for colonial invertebrates as a whole. It is important to study this large group of organisms as they have different life history strategies compared to the more commonly studied animals such as birds, mussels and fish (e.g. Jackson & Hughes 1985, Sebens 1987, Stearns 1992). Colonial invertebrates display much greater morphological plasticity than do unitary organisms (e.g. Sebens 1987), and may have the option of sacrificing unproductive parts of their colony in favour of growth in other areas. Hence they may reduce the impact of competition by continuing growth along margins which are not in close proximity to potential competitors (Lang & Chornesky 1990, Romano 1990). This strategy is intermediate between that of mobile organisms, which may move away from sites of high competition, and unitary sessile organisms, which have no ability to avoid competition once they are attached to the substrate (e.g. Buss 1979).

The few studies that have been conducted to determine how competition affects the demography of individual coral colonies have shown that it significantly reduces both their growth and fecundity (Rinkevich & Loya 1985, Romano 1990, Chadwick 1991). Romano (1990) studied competitive interactions between bushy *Pocillopora damicornis* and massive *Cyphastrea ocellina*, and found that while *C. ocellina* won in the short term, it experienced a long-term reduction in growth relative to non-competing controls, whereas *P. damicornis* did not experience reduced growth. This presumably occurred because the slower growing *C. ocellina* redirected its energy from growth to fighting its faster growing opponent, which would otherwise have overgrown it, while *P. damicornis* invested minimal resources in defending itself, but continued to grow rapidly along non-competing margins. In contrast, Rinkevich & Loya (1985), found that colonies of different morphs of *Stylophora pistillata* involved in intraspecific competition showed a decline in growth rate irrespective of their position in the dominance hierarchy. They also showed that competition decreased the overall fecundity of both competitors, as has Chadwick (1991) for temperate water corals.

As well as competing among themselves, corals frequently come into contact with, and compete against, a wide range of other sessile organisms (e.g. Lang & Chornesky 1990, Chadwick 1991). Attention has particularly focussed on interactions between scleractinian and alcyonacean corals (e.g. LaBarre & Coll 1982, Sammarco et al. 1985), and between scleractinian corals and algae (e.g. Lewis 1986, Chadwick 1988, Hughes 1989, 1994, Coyer et al. 1993). Previous work has shown that macroalgae are capable of overgrowing scleractinian corals, and that encounters between the two groups usually result in the alga winning (e.g. Chadwick 1988, Hughes 1989). Algae can also adversely affect corals by abrasion (Coyer et al. 1993), and pre-emption of space (e.g. Hughes

1989). Allelopathy has been demonstrated to occur against alcyonacean corals (de Nys et al. 1991), but has not yet been shown to occur in interactions between algae and scleractinian corals. In contrast, De Ruyter van Steveninck et al. (1988) found that scleractinian corals were able to prevent overgrowth by the alga *Lobophora variegata*, and slow its growth in their vicinity, although they also found that *L. variegata* could occasionally overgrow corals.

The affect of algae on corals is becoming of increasing importance as concerns are raised about nutrient enhancement of coral reef waters, and how this will affect community structure and functioning (e.g. Tomascik & Sander 1987, Wittenberg & Hunte 1992). One of the major hypotheses related to nutrient enhancement is that algal growth rates will increase, enabling algae to outcompete corals and other sessile organisms (e.g. Birkeland 1977, 1988, Pastorok & Bilyard 1985). The ability of algae to flourish in high nutrient waters was dramatically shown in Kaneohe Bay in Hawaii, where sewage release into the bay resulted in dramatic increases in algal biomass and local extinction of corals (e.g. Smith et al. 1981). Severe overfishing may also release algae from the control of their major herbivores, allowing them to dominate areas where corals would otherwise be dominant (e.g. Hughes 1989, 1994). Grazers such as fish and sea urchins play a significant role in determining the distribution and abundance of most macroalgal species (e.g. Carpenter 1986, 1990, Hay 1991). The removal of grazers thus has a negative effect on coral cover due to an increase in algal biomass, and the subsequent overgrowth of corals by algae (Sammarco 1982, Lewis 1986). It is therefore obvious that man is substantially altering the community composition on many coral reefs, emphasising the importance of studying interactions between different components of coral reef communities, such as between corals and algae.

In this paper I examine the effects of macroalgae on the demography of scleractinian corals on a reef flat in the southern Great Barrier Reef, Australia. Specifically, I examine how algae affect growth, survivorship, fission, fecundity and recruitment of four species of coral at Heron Island. In addition, I quantify natural rates of encounter between corals and algae at the study site, and the coral and algal cover present.

## Materials and Methods:

### Study Site:

This study was conducted at Heron Island, Great Barrier Reef, Australia (23° 26' S, 151° 55' E). Heron Island is a coral cay located at the southern end of the GBR, approximately 70 km from the mainland. The study site on the reef flat remains submerged at low tide, although the tops of some coral colonies project out of the water for a few hours. The coral assemblage is dominated by the brooding species *Acropora cuneata* (Dana), *A. palifera* (Lamarck), *A. brueggemanni* (Brook), and *Pocillopora damicornis* (Linnaeus), which occur together on outcrops of coral rock located on a sandy bottom. Algal cover on these outcrops is approximately 50%, and is dominated by *Halimeda* spp., *Chlorodesmis fastigiata* (C. Ag.), *Peyssonnelia* spp., and *Turbinaria ornata* (Turn.).

### Natural Encounters:

The frequencies of competitive encounters between different species of scleractinian corals and macroalgae were assessed within five permanent 10 m x 2 m belt transects. Every colony in these transects was mapped, identified, and all encounters with algae were recorded. An encounter is defined as direct contact between a coral colony and neighbouring algae, and so does not take into account the potential for allelopathic interactions. Transects were set up in September 1992, and recensused approximately every three months until March 1994, eighteen months later. In addition to competitive encounters, the approximate percent cover of each algal and coral species was recorded for all but the first census. This was done by laying down a 1m$^2$ quadrat divided into 10 cm x 10 cm squares along the transect, and recording cover in each quadrat. All percent cover data are expressed as percentage of hard substratum, thereby eliminating variability due to different proportions of sand in different transects. To test if there was any change in the composition of the algal assemblage over time, a repeated measures ANOVA (Tabachnick & Fidell 1989) was conducted on the cover of each taxon at each census.

Growth, Survivorship and Recruitment:

To determine the effect that macroalgae have on growth, survival, and recruitment of scleractinian corals, an algal clearance experiment was set up in May 1992. Ninety nine naturally occurring outcrops of coral rock, each supporting one or more colonies of the study species, were tagged and randomly assigned to one of three treatments: algal clearance, disturbance control and unmanipulated control. All outcrops used in the study were 0.5 $m^2$ to 1.5 $m^2$ in area, although a much larger range of sizes was present at the site. Outcrops assigned to the clearance treatment had all macroalgae (not including turfing forms) scraped off them at the start of the experiment, and were recleared every six to eight weeks until the experiment was terminated after two years, in March 1994. Algal cover on these outcrops prior to reclearing was about 10 - 20 % of that present before the experiment commenced. Disturbance controls had the clearing action mimicked every time clearing was carried out, without removing more than 1-2 % of the algal biomass. This was done by lightly scraping along portions of the margins of each colony that were not in contact with macroalgae, and lightly stirring up the sediment in the vicinity of the outcrop. So as to control for the effects of any toxins released by damaged algae, specimens of species present on the outcrop were collected from nearby locations and lightly crushed over the outcrop. Unmanipulated control outcrops were left undisturbed with the exception of tying the tag to them, and conducting six monthly searches for new recruits.

To determine the linear growth rates of coral colonies, each outcrop was photographed at high tide from 1 to 2 meters directly overhead. This was done at the commencement of the experiment, and then every six to eight months afterward, for a total of four photographic censuses. The photographs were projected at a quarter to full life size, and colony outlines of all *A. cuneata*, *A. palifera*, *A. brueggemanni* and *P. damicornis* were drawn and then digitised to obtain their area. While this method does not account for three dimensional growth, it provides an easily measured index of coral size which does not result in disturbance to the colony being measured. *Acropora cuneata* and *A. palifera* are sibling species (Ayre et al. 1991), and were pooled because of difficulties in distinguishing them in the photographs. The tracings of colonies over time were also used to determine probabilities of survival and fission for each species in each treatment.

The null hypothesis that macroalgae had no effect on changes in total coral cover over the duration of the study was tested using a Model I ANOVA (Zar 1984), with the dependent variable being final cover of each species divided by initial cover for each outcrop. I similarly tested to determine if the presence of algae had an effect on the change in number of colonies and growth rate of surviving colonies. Data on fission and survival could not be transformed to meet ANOVA assumptions, and so I tested the null hypothesis that algae had no effect on either of these variables separately for each species using a Kruskal-Wallis test (Zar 1984).

### Reproduction:

A subsample of *A. palifera* from the above experiment were monitored immediately after the final census in March 1994 to determine colony fecundities. Mesh bags made of terylene cloth were placed around ten randomly selected 15 to 20 centimetre diameter colonies in each treatment, and the number of larvae released were counted at the daylight low tide every day for three weeks. The mesh size of the bags was approximately 500 µm, compared to a mean larval diameter for *A. palifera* at Heron Island of nearly 1500 µm (Kojis 1986). A Kruskal-Wallis test (Zar 1984) was used to determine if macroalgae had any effect on total larval output per colony.

## Results:

### Natural Encounters:

Total algal cover in the belt transects did not vary significantly over time (repeated measures ANOVA: $F=0.93$; $df=4,20$; $P=0.4688$). Cover was at a maximum in December 1992 at 56 ± 10 (SE)%, and reached a minimum of 41 ± 9 (SE)% in September 1993 (Figure 4.1). While differences in total algal cover were not significant, the composition of the algal assemblage did vary substantially over time (Table 4.1). During this period, there were only slight variations in coral cover, with a maximum of

10 ± 2 (SE)% and a minimum of 8 ± 1.9 (SE)% of hard substrate. The mean number of colonies in the transects also only fluctuated slightly (mean ± SE: 271 ± 7). In total, 92 ± 4 (SE)% of coral colonies were in contact with one or more species of macroalgae, with the major taxa being *Peyssonnelia* spp., *Turbinaria ornata*, *Chlorodesmis fastigiata*, and *Halimeda* spp. (Figure 4.2).

The number of coral colonies that each species of algae encountered was approximately proportional to the percent cover of that species. The only exception to this is *Halimeda* spp., which encountered corals one third as often as would be expected from its relatively high cover (Figure 4.2). When *Halimeda* spp. is excluded, 91% of the variation in encounter rates for macroalgae was explained by variation in percent cover amongst the different algal taxa. There was no relationship between percent cover of each coral species and the mean number of algal species that each colony encountered, however ($r^2 = 0.003$).

Growth, Survivorship and Recruitment of Corals:

The presence or absence of competing macroalgae had a major impact on coral cover (Table 4.2, Figure 4.3). For *A. brueggemanni* and *A. cuneata / palifera*, cover doubled over two years in the absence of macroalgae, while the unmanipulated and disturbance controls with macroalgae present only showed a 20 - 40 % increase. *Pocillopora damicornis*, however, did not show any differences between clearance and control treatments. Over all species, Tukey's test showed the clearance treatment to be significantly different from the two control treatments at $\alpha = 0.05$, but there was no difference between the two control treatments. While *P. damicornis* tended to show less of an increase in cover than the two *Acropora* species, this difference was not significant (Table 4.2).

Relative growth rates of coral colonies which survived for the two years of the study show similar responses to algal clearance as did total coral cover. Clearing macroalgae away from the two *Acropora* species resulted in increased growth rates, while *P. damicornis* actually showed a slight decrease in growth rate when algae were cleared (Table 4.3, Figure 4.4). *Acropora* colonies in the clearance treatment came close to doubling their size, while those in the controls increased in size 30 - 40 % (*A.*

*brueggemanni*), or failed to change size (*A. cuneata / palifera*). *Pocillopora damicornis* grew only slightly in all three treatments. Again, over all species, Tukey's test shows the difference between the clearance treatment and the two control treatments to be significant at $\alpha = 0.05$, while the two control treatments are similar.

In contrast to coral cover and growth, survivorship of individual coral colonies did not show any significant response to the clearing of macroalgae (Table 4.4, Figure 4.5). Approximately 85% of *A. brueggemanni* colonies survived through the study, with very little difference between treatments. Survival of *A. cuneata / palifera* was around 75% in the two control treatments, and 90% in the algal clearance treatment. *Pocillopora damicornis* showed a much broader range in survivorship, with 90% of colonies surviving in the disturbance control, 80% in the undisturbed control, and 60% in the clearance treatment.

Changes in the number of colonies present on each outcrop were not affected by the removal of competing macroalgae (Table 4.5, Figure 4.6). *Acropora cuneata / palifera* was the only species to display the expected trend of an increase in the number of colonies on outcrops with algae removed, and a decrease on the two control sets of outcrops. For the other two species, there were similar slight decreases in the number of colonies for all three treatments.

No new recruits were detected on any of the experimental outcrops during the two year study period, so the only source of new colonies for these populations was fission of pre-existing colonies. Fission rates for all three species were highly variable between outcrops (Figure 4.7), and there was no effect of macroalgae for any of the species (Table 4.6). For all species, however, the trend was towards increased rates of fission in the absence of macroalgae, especially for *A. cuneata / palifera*, which displayed 0.4 fission events per colony in the algal clearance treatment compared to less than 0.1 in the two control treatments. Overall, *P. damicornis* displayed the greatest rate of fission, approximately double that of the two *Acropora* species.

Reproduction:

Macroalgae had a significant effect on sexual reproduction in *Acropora palifera*, the only species examined (Kruskal-Wallis Test $\chi^2 = 15.959$; df = 2; P = 0.0003). Daily larval output for colonies on outcrops cleared of macroalgae was double that of colonies in the two control treatments with algae present. Mean daily larval output over 21 days for colonies in the algal clearance treatment was 6.8 ± 1.8 (SE), compared to 3 ± 0.7 for each of the control treatments.

## Discussion:

Natural Encounter Rates:

Ninety two percent of corals growing on the reef flat at Heron Island are in contact with at least one species of macroalgae. Macroalgae therefore have a large potential for impact on the scleractinian coral assemblage. While most species of algae did not actively overgrow the corals which they came in contact with, *Peyssonnelia* spp. did commonly extend over the margins of neighbouring corals, sometimes resulting in death of the underlying tissue (pers. obs.). Another potential negative effect is abrasion from brushing of algal thalli against living coral tissue. This causes the coral to remain with its tissues retracted almost continuously, allowing filamentous and encrusting coralline algae species to overgrow it (Coyer et al. 1993). De Nys et al. (1991) have also shown that contact between some species of algae and sessile organisms can result in tissue necrosis due to the transfer of allelopathic chemicals from the algae. Algae may also compete passively by the pre-emption of space, denying corals room in which to grow or settle (e.g. Hughes 1994).

Each species of algae encounters corals about as often as would be expected from its percent cover, with the exception of *Halimeda*, which has substantially fewer contacts than would be expected (Figure 4.2). This is probably because *Halimeda* forms dense monospecific stands which would be capable of completely overgrowing coral colonies in their midst, whereas the other algal species encountered were more dispersed. As a result of clumping, *Halimeda* also had less perimeter in proportion to its area than other species, restricting the potential for encounters with corals to occur. Encounters occur even at very low levels of algal cover (Figure 4.2), and so algae do not have to be a dominant component of the community to influence individual coral colonies.

Demographic Effects of Macroalgae:

The high encounter rate between corals and algae is having an obvious effect on the corals, with coral cover increasing three times as fast on outcrops without algae as compared to outcrops which had algae present (Figure 4.3). Most of this difference can be accounted for by differences in the growth rates of colonies in the algal clearance treatment compared to those in the control groups (Figure 4.4). However, corals grew and coral cover increased even in the treatments with macroalgae (Figures 4.3, 4.4), indicating that the study was conducted in a period which was highly favourable for coral growth. The lack of any effect of algae on the growth of *P. damicornis* (Figure 4.4), is most likely due to its morphology. While the *Acropora* species, which display large reductions in growth when exposed to competition with algae, are encrusting or semi-encrusting, *P. damicornis* is bushy, with a single relatively small attachment point. In general, encrusting species are more prone to space competition as they will come into contact with other organisms growing beside them. More upright species, including bushy ones, are able to avoid some encounters as they grow over the top of other organisms, including some algae, without actually coming into contact with them (Jackson 1979, Lang & Chornesky 1990). The susceptibility of encrusting species to space competition was shown by Hughes (1989), who found that encrusting corals in Jamaica suffered higher mortality rates due to algal overgrowth than did more three dimensional species.

Despite having a substantial impact on the growth of corals, algae did not appear to significantly affect their survival (Figure 4.5, Table 4.3). Examination of colonies which died, or which underwent substantial partial mortality suggested that algae were not actively displacing corals from areas which they already held, but rather slowing or preventing their growth into new territory (pers. obs.) In fact, there were very few instances of algal overgrowth seen, although on several occasions

*Peyssonnelia* sp. overgrew the bases of *P. damicornis* colonies, which could possibly make them more prone to bioerosion, and eventually to dislodgment from strong wave activity. Several overgrowth encounters were also seen between *Caulerpa racemosa* and *A. cuneata / palifera*, with the *Caulerpa* impinging on the border areas of the coral, but apparently without resulting in the death of even that part of the colony overgrown.

Algae also caused a major reduction in the fecundity of *A. palifera*, as was expected. A greater reduction in fecundity than growth of competing corals was expected because the fitness of long-lived colonial organisms with high fecundity and indeterminate growth is influenced much more by changes in growth rates and survival probabilities than it is by changes in fecundity (e.g. Gotelli 1991, Babcock, Hughes & Tanner unpublished data). Thus, a coral colony will achieve greater lifetime fitness if it sacrifices current fecundity instead of growth when a temporary demand for resources is placed upon it, such as would occur when it is competing with algae, or any other relatively ephemeral organism.

Algae obviously placed a drain on coral resources, even when they were not actively overgrowing the coral. While growth may be reduced simply through the unavailability of space that is occupied by neighbouring algae, the concomitant reduction in colony fecundity indicates that competition with algae requires the expenditure of energy, and has a significant energetic cost for the coral colony. It has been suggested previously that coral-coral competition places a significant energetic cost on at least one of the competitors (e.g. Romano 1990, Frank & Rinkevich 1994), but this is an area that requires further investigation. Costs to the coral may arise from the need to repair damage caused by algae, such as tissue abrasion (Coyer et al. 1993), or from energy expenditure in actively competing with the algae, and trying to prevent overgrowth (De Ruyter van Steveninck et al. 1988). Alternatively, abrasion by algae can cause chronic tissue retraction in corals (Coyer et al. 1993), which may then reduce the corals ability to meet its energy requirements, requiring it to expend a greater proportion of available energy on maintenance, and reducing that available for growth and reproduction.

Other studies which have examined the consequences of algal competition for coral cover have all found that corals are displaced when algal abundance is high (e.g. Smith et al. 1981, Lewis 1986, Birkeland 1988, Hughes 1989, 1994). These studies all focussed on the consequences of increased algal abundance, due either to grazer removal or nutrient enhancement, and algal cover was usually close to 100%. The current study focussed on the removal of algae at lower levels of algal cover (40-50%), in order to determine the consequences of competition with algae at lower levels of abundance, although this level of cover is still high in comparison to many other habitats such as the reef slope (e.g. Ogden 1976, Van den Hoek et al. 1978). As a consequence of this different approach, I found that while corals were experiencing significantly reduced growth and fecundity when in contact with macroalgae, they still managed to maintain or even increase cover levels on outcrops from which algae were not removed.

## Acknowledgments:

I thank T.P. Hughes, N. Moltschaniwskyj, V. Hall, A. Baird, A. Lewis and the James Cook University Coral Discussion Group for their comments on this work. I would also like to thank S.E. Stancyk and 2 anonymous reviewers for their contribution. Funding was provided by the Great Barrier Reef Marine Park Authority, Australian Coral Reef Society, and Heron Island Research Station to J.E. Tanner, and the Australian Research Council to T.P. Hughes. This work was conducted in partial fulfilment of the requirements for a PhD at James Cook University of North Queensland. This is contribution number 132 of the James Cook University Coral Ecology Group.

**Table 4.1:** Repeated measures ANOVA of algal composition over time in five unmanipulated belt transects.

| Souce of Variation | DF | Mean Square | F | P > F |
|---|---|---|---|---|
| Time | 4 | 0.0017 | 23.78 | 0.0001 |
| Time * Taxa | 40 | 0.0007 | 9.68 | 0.0001 |
| Error | 176 | 0.00007 | | |
| Total | 220 | | | |

**Table 4.2:** ANOVA on total coral cover in the algal clearance experiment.

| Source of Variation | DF | Mean Square | F | P > F |
|---|---|---|---|---|
| Treatment | 2 | 2.501 | 4.43 | 0.0139 |
| Species | 2 | 0.699 | 1.24 | 0.2938 |
| Treatment * Species | 4 | 0.676 | 1.20 | 0.3158 |
| Error | 123 | 0.565 | | |
| Total | 131 | | | |

**Table 4.3:** ANOVA on the effects of macroalgae on the growth of all colonies in the algal clearance experiment which survived the duration of the study.

| Source of Variation | DF | Mean Square | F | P > F |
|---|---|---|---|---|
| Treatment | 2 | 2.720 | 3.80 | 0.0240 |
| Species | 2 | 1.665 | 2.33 | 0.1003 |
| Treatment * Species | 4 | 1.356 | 1.89 | 0.1129 |
| Error | 198 | | | |
| Total | 206 | | | |

**Table 4.4:** Kruskal-Wallis Test results for the effect of treatment on probability of colony survival over two years in the algal clearance experiment.

| Species | $\chi^2$ | DF | $P > \chi^2$ |
|---|---|---|---|
| *A. brueggemanni* | 0.048 | 2 | 0.98 |
| *A. cuneata* | 4.94 | 2 | 0.085 |
| *P. damicornis* | 3.31 | 2 | 0.19 |

**Table 4.5:** ANOVA on relative final number of colonies on each outcrop in the algal clearance experiment.

| Source of Variation | DF | Mean Square | F | P > F |
|---|---|---|---|---|
| Treatment | 2 | 0.430 | 1.15 | 0.3194 |
| Species | 2 | 0.053 | 0.14 | 0.8676 |
| Treatment * Species | 4 | 0.324 | 0.87 | 0.485 |
| Error | 138 | 0.374 | | |
| Total | 146 | | | |

**Table 4.6:** Kruskal-Wallis Test results for the effect of clearing macroalgae on the probability of colony fission over two years.

| Species | $\chi^2$ | DF | $P > \chi^2$ |
|---|---|---|---|
| *A. brueggemanni* | 1.05 | 2 | 0.59 |
| *A. cuneata* | 2.6 | 2 | 0.27 |
| *P. damicornis* | 1.87 | 2 | 0.39 |

**Figure 4.1:** Mean live coral and algal cover (+/- standard error) over time expressed as a percentage of hard substrate (ie. area other than sand).

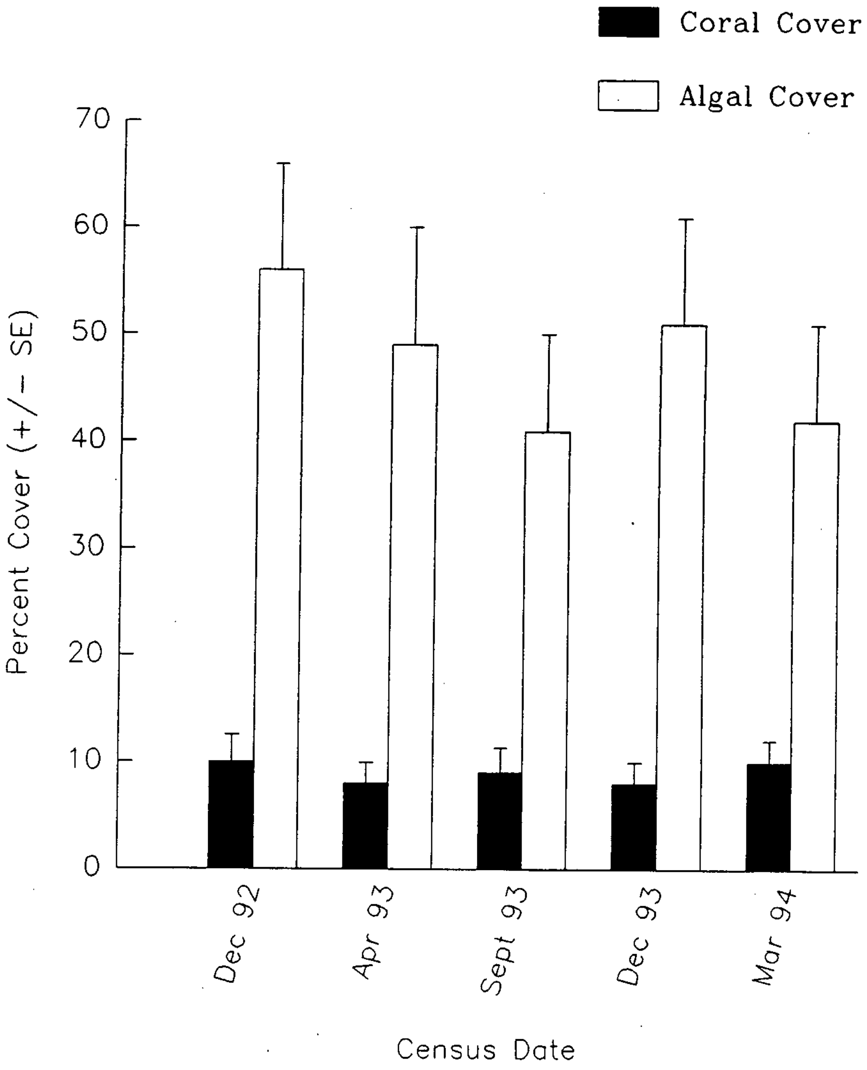
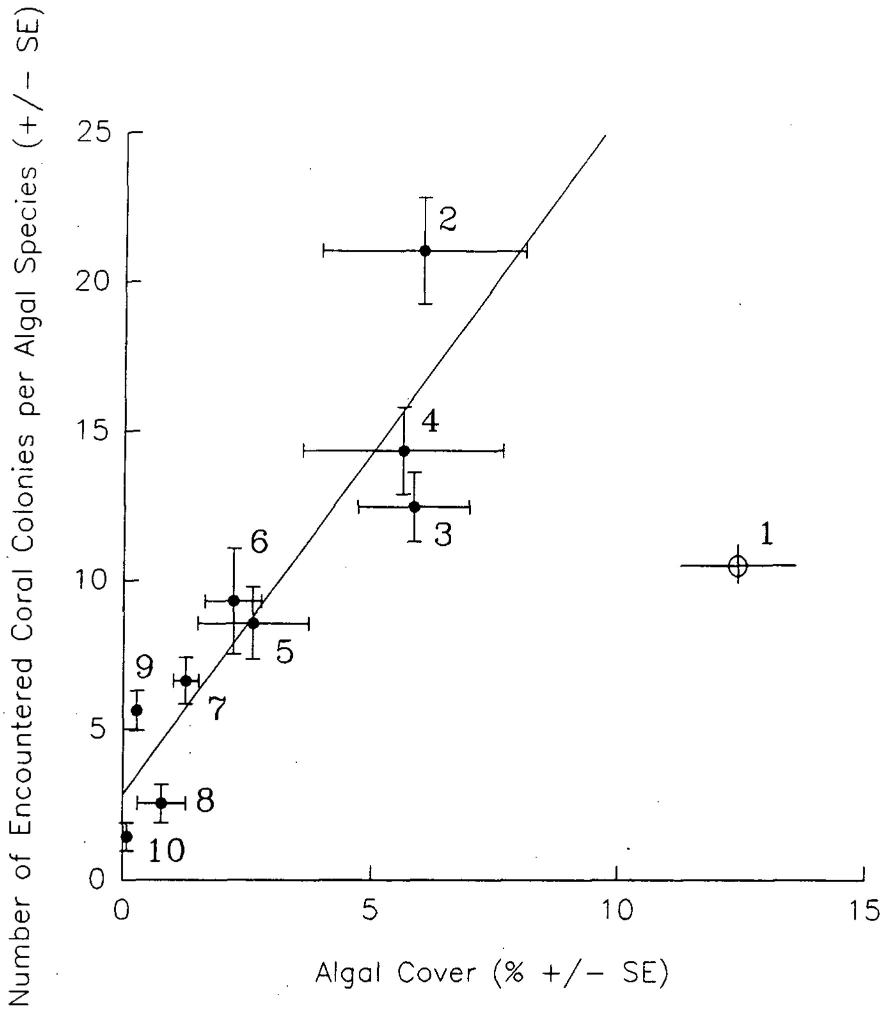

Coral Cover
Algal Cover
70
60
50
40
30
20
10
0
Percent Cover (+/- SE)
Dec 92
Apr 93
Sept 93
Dec 93
Mar 94
Census Date

**Figure 4.2:** Relationship between percent cover of each algal species and the number of coral colonies which it competed against ($r^2 = 0.91$). Percent cover is expressed as a percentage of hard substrate. *Halimeda* spp. was treated as an outlier and not used in calculating the regression line.



1 *Halimeda* spp
2 *Peyssonnelia* spp
3 *Chlorodesmis fastigiata*
4 *Turbinaria ornata*
5 *Sargassum* spp
6 *Amphiroa* spp
7 *Caulerpa* spp
8 *Hypnea* spp
9 *Enteromorpha* spp
10 *Padina* spp

**Figure 4.3:** Change in coral cover over two years for corals in the algal clearance treatment versus controls. Treatment differences are significant (Table 4.2). Numbers above the columns indicate the number of outcrops used in calculating each mean.

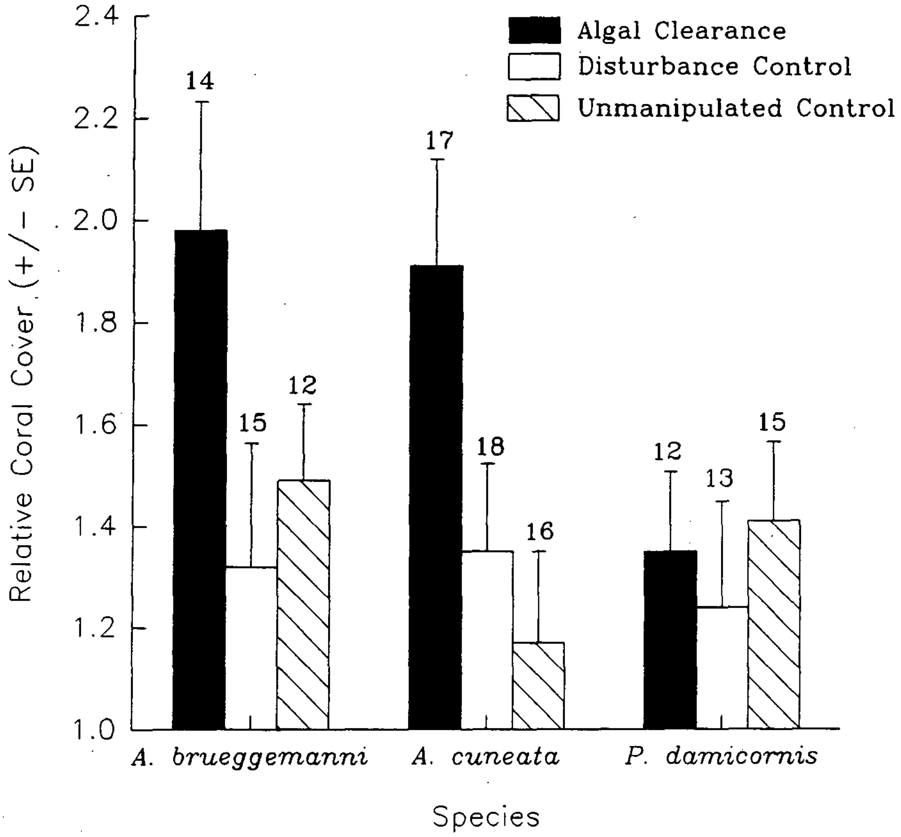

Algal Clearance
Disturbance Control
Unmanipulated Control
Relative Coral Cover (+/- SE)
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
14
15
12
17
18
16
12
13
15
A. brueggemanni
A. cuneata
P. damicornis
Species

**Figure 4.4:** Comparison of relative growth rates of coral colonies in the algal clearance experiment. These growth rates are based only on those colonies which survived until the end of the two year study. Treatment differences are significant (Table 4.3). Numbers above the columns indicate the number of colonies used in each treatment.

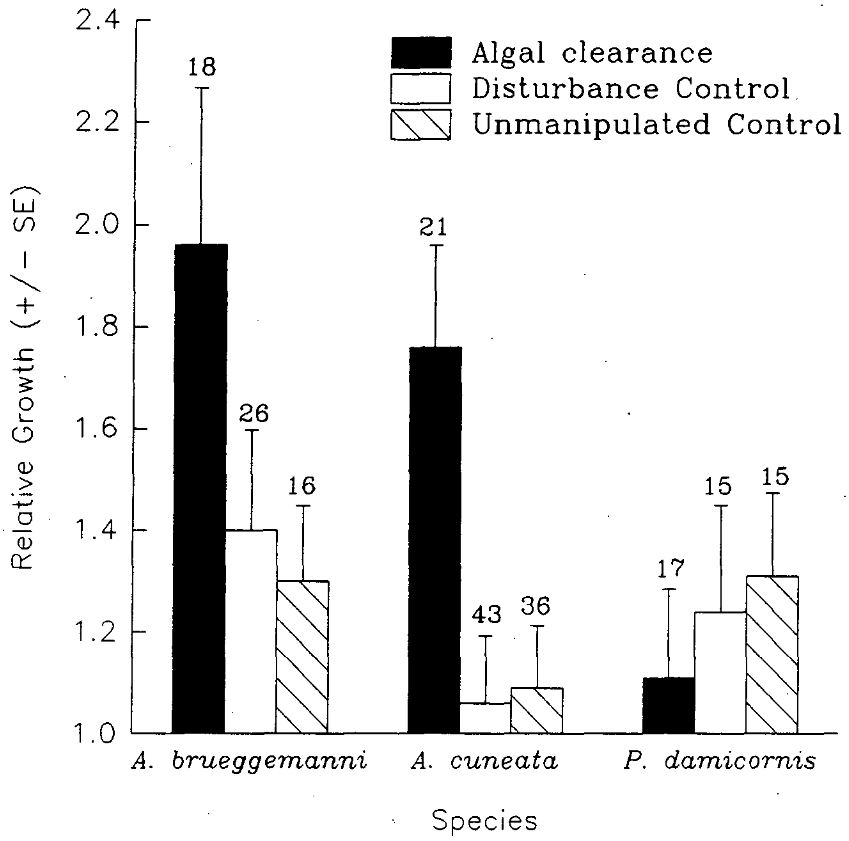

Relative Growth (+/− SE)
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
Algal clearance
Disturbance Control
Unmanipulated Control
18
26
16
21
43
36
17
15
15
*A. brueggemanni*
*A. cuneata*
*P. damicornis*
Species

**Figure 4.5:** Survival rates of coral colonies over two years when competing with macroalgae versus when not competing. Numbers indicate sample sizes. All within species differences are non-significant (Table 4.4).

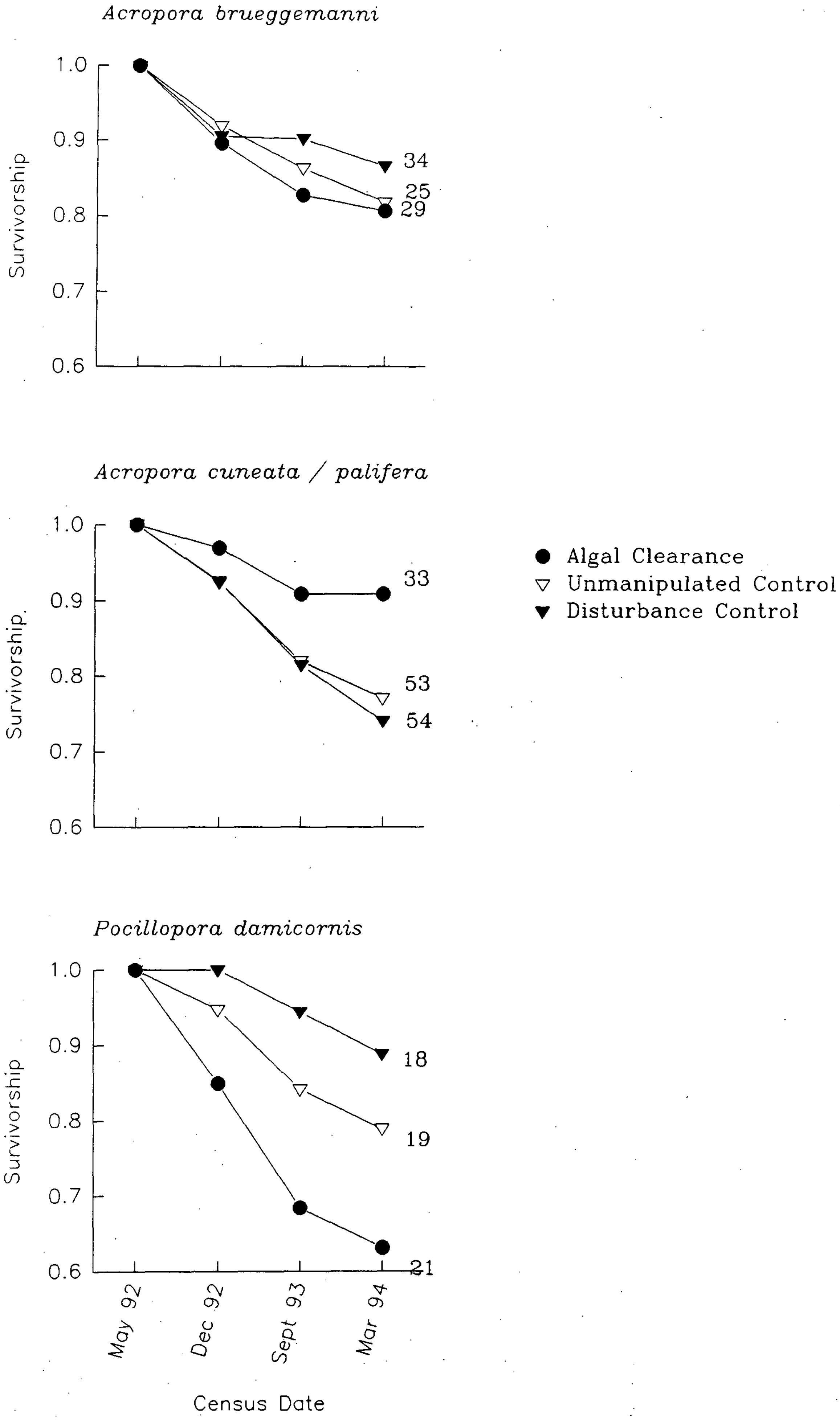

Acropora brueggemanni
Survivorship
1.0
0.9
0.8
0.7
0.6
34
25
29
Acropora cuneata / palifera
Survivorship
1.0
0.9
0.8
0.7
0.6
33
53
54
● Algal Clearance
▽ Unmanipulated Control
▼ Disturbance Control
Pocillopora damicornis
Survivorship
1.0
0.9
0.8
0.7
0.6
18
19
21
May 92
Dec 92
Sept 93
Mar 94
Census Date

**Figure 4.6**: Comparison of the number of colonies of each species in each treatment after two years relative to the number present at the start of the experiment. All differences are non-significant (Table 4.5). Numbers above the columns indicate the number of outcrops used in calculating each mean.

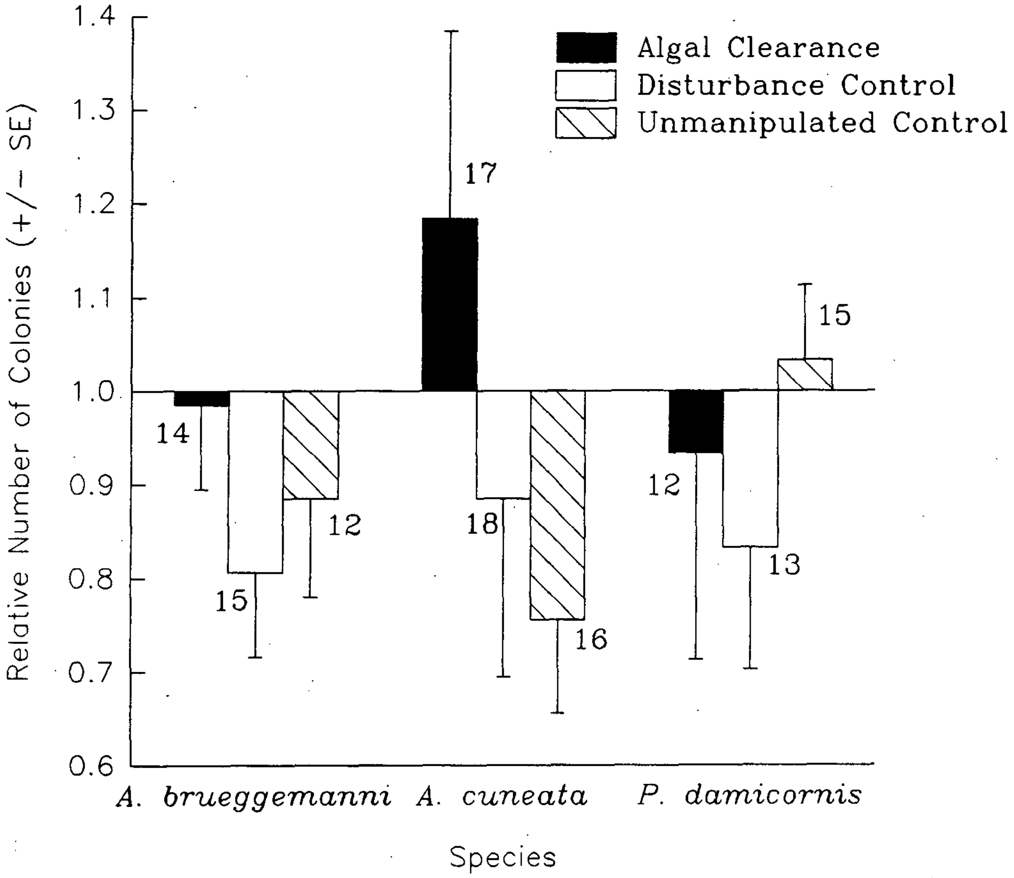
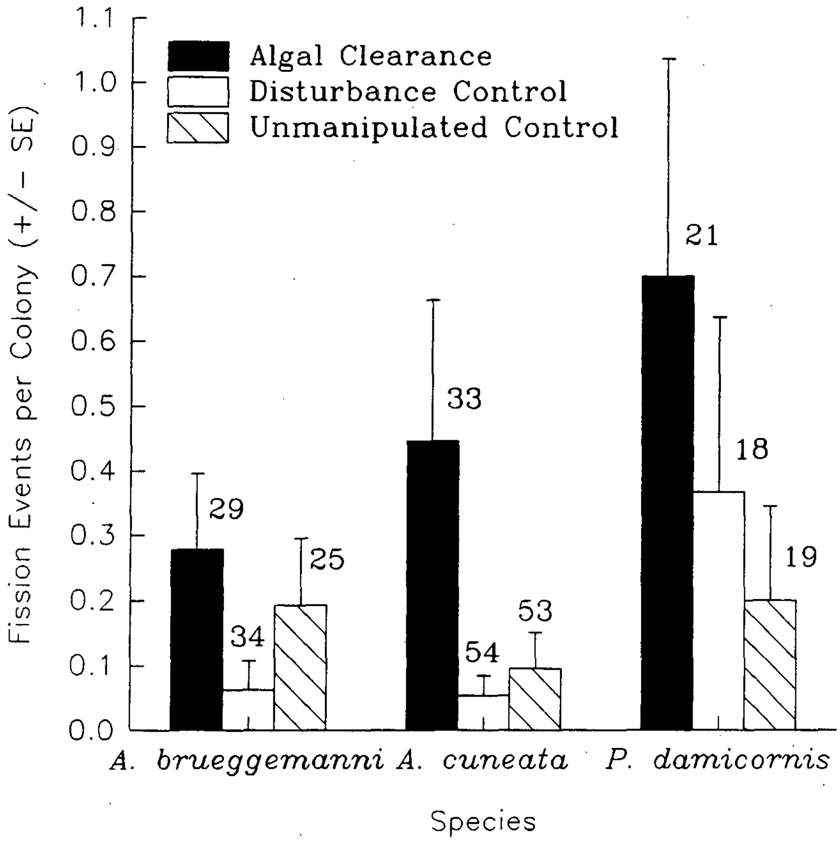

1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
Relative Number of Colonies (+/- SE)
Algal Clearance
Disturbance Control
Unmanipulated Control
14
15
12
17
18
16
12
13
15
A. brueggemanni
A. cuneata
P. damicornis
Species

**Figure 4.7:** Comparison of fission rates over two years as influenced by algal clearance. All within species differences are non-significant (Table 4.6). Numbers above the columns indicate the sample sizes.


Algal Clearance
Disturbance Control
Unmanipulated Control
Fission Events per Colony (+/- SE)
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
29
34
25
33
54
53
21
18
19
A. brueggemanni
A. cuneata
P. damicornis
Species

# Chapter 5

## Species coexistence, keystone species and succession: A sensitivity analysis.

Reference: Tanner, J.E., T.P. Hughes & J.H. Connell. 1994. Species coexistence, keystone species and succession: A sensitivity analysis. Ecology. 75: 2204-2219.

Note on coauthors:
J.H. Connell initiated and conducted the study from which the data for this chapter were obtained. His contribution was to supply photographs of his quadrats, and to comment on several versions of the manuscript. T.P. Hughes drew the maps of the quadrats, and also commented on several versions of the manuscript.

Note on overlap with honours thesis:
Much of the work described in this chapter is an extension of work submitted for the degree of Bachelor of Science with Honours at James Cook University. Data were quantified from the maps as part of my honours, but have been completely reanalysed to obtain results in a more condensed version for publication. Thus approximately 50% of this work was conducted as a part of my honours.

### Abstract:

One of the major questions in ecology is, what controls the structure of communities. We used projection matrix models to examine community dynamics and patterns of succession. The inputs of the model are transition probabilities of species replacements that were measured repeatedly during a long-term (1962-1989) study of diverse coral assemblages on Heron Island, Great Barrier Reef. Transitions varied strikingly among species and sites, reflecting differences in recruitment, growth, longevity (persistence) and the rate of replacement of one species

by another. Species that had a poor ability to persist (e.g. algae and Pocilloporid corals) were generally good colonists. The observed number of transitions expressed as a proportion of the maximum number possible provides an index of the complexity of interactions in an assemblage, analogous to the concept of connectance in food-web analysis. Transitions occurred to and from nearly every species group, indicating that there was no competitive dominant in this system.

We use the models in simulations to track transitory changes in species abundance and community composition following a major disturbance (e.g. due to a cyclone, or outbreak of crown-of-thorns starfish). Some species showed a rapid initial increase followed by a decline to lower equilibrium levels, while others increased smoothly to a generally higher equilibrial abundance. The length of time required to reach a climax assemblage using the same matrix recurrently (approximately 20 years) is far greater than the observed interval between major disturbances, supporting non-equilibrium theories of coral reef communities. Climax assemblages were highly diverse, and varied in composition from site to site. The "intermediate disturbance hypothesis" does not fully predict successional changes in these shallow-water coral assemblages since diversity remained very high at equilibrium (i.e. long after a major disturbance). Competitively inferior species were not eliminated because routine mortality ensured that some space always remained available for colonization.

We also present a novel method for quantifying the relative importance of each species interaction to community composition and the rate of succession, based on a sensitivity analysis of the transition matrix. The analysis shows that the importance of a species to the dynamics of a community may be unrelated to its abundance at equilibrium, with some rare species groups having a greater impact than more common ones. Sensitivity analysis of this type will provide a powerful means of identifying "keystone" species in complex assemblages where experimental manipulation of each species is impossible.

## Introduction:

Community ecologists have focussed much of their attention on the dynamics of assemblages that are recovering from a recent disturbance (e.g. Clements 1928, Drury and Nisbet 1973, Connell and Slatyer 1977, Gray et al., 1986). There is a rich literature describing such successional changes in a wide variety of systems (e.g. terrestrial plants: West et al., 1981; insects: Force 1981; mammals: Fox 1982; fish: Kaufman 1983; birds: Smith 1982; algae: Sousa 1984; and marine invertebrates: Osman 1977, Pearson 1981, Hughes 1985, Colgan 1987, Dean and Connell 1987). However, the use of mathematical modelling to help understand the process of succession has largely been confined to terrestrial plants. Horn (1975, 1976) introduced a matrix model whose elements were transition probabilities between different species, and used these transitions as rules of community dynamics to predict future community structure. The model is similar to the familiar Leslie matrix population model (Leslie 1945). To date, application of Horn's model has been limited to simulation studies of succession in temperate and sub-tropical forests (Horn 1975, Enright & Ogden 1979, Acevedo 1981), alpine vegetation communities (Lough et. al. 1987), and insect assemblages (Usher 1979). While these pioneering studies have provided many insights into successional dynamics, much of the information contained in the matrices remains unexplored. Here, we present a more complete analysis of community models by applying recent advances in matrix theory developed from population studies (Caswell 1989) to a long-term field study of coral assemblages, in order to examine further the mechanisms of succession.

Ecologists have often argued that some species in an assemblage are more important than others, and that some communities are controlled by keystone species (e.g. Paine 1969, 1974). Roughgarden (1983) described a keystone species as "a species whose removal leads to a still further loss of species from the community". Note that this definition includes both keystone predators and keystone competitors (see also Roughgarden 1979, p.546). Thus, for example, coniferous forests, grasslands, kelp beds or coral reefs would cease to exist if the dominant organisms giving them their names were removed. The problem is how to define and quantify "important". To date, the only way the presence of keystone species has been elucidated is by manipulating the densities of individual taxa in a community and observing what happens over a long period of time. We suggest that, for certain assemblages, this can also be done by means of a sensitivity analysis of a matrix of transition probabilities. This approach, described in detail below, allows us to ask how much a small change in each element of the matrix would influence the models outcome. In recent years, sensitivity analysis has been widely employed in population models to examine the relative importance of each demographic transition in determining population structure and growth rate (e.g. Caswell 1989, Lasker 1991, Gotelli 1991). Here we adapt these procedures in order to quantify what species transitions are important in controlling the dynamic behaviour of an assemblage of sessile reef corals.

Coral reefs are generally subject to recurrent major disturbances (such as cyclones, earthquakes, outbreaks of crown-of-thorns starfish, extremely low tides, etc.) which may be so severe as to reduce local coral cover to close to zero (e.g. Connell 1978, Woodley et al. 1981, Glynn 1993, Hughes 1989, 1993). Patterns of recovery are ultimately controlled by differential rates of recruitment, growth and persistence of individual species. Recolonization onto reefs in the Indo-Pacific, Caribbean and Red Sea is known to be far from random, with some species having consistently higher recruitment rates than others (e.g. Connell 1973, Loya 1976, Bak and Engel 1979, Hughes 1985, Hughes and Jackson 1985, Fisk and Harriot 1990). Similarly, coral taxa differ greatly in rates of post-recruitment growth and survival (e.g. review by Hughes et al., 1992). Undisturbed reefs frequently have low diversity, apparently through pre-emption and competitive exclusion, leading numerous authors to conclude that diversity is enhanced at some intermediate frequency of disturbance (e.g. Grigg and Maragos 1974, Connell 1978). Interspecific encounters involving corals occur frequently, and individual colonies may eventually be killed by a variety of competitive mechanisms, including overgrowth, digestion, allelopathy and shading (see review by Lang and Chornesky 1990). This diversity of mechanisms can promote competitive standoffs and reversals, so that competitive rankings may form complex networks rather than strict hierarchies (ibid). Buss and Jackson (1979) suggested that such networks would enhance species coexistence because no single dominant could emerge. However, the trajectory of diversity, and the precise role of recruitment, competition and persistence in coral recovery remains poorly understood. It is also unknown to what extent reefs may approach an equilibrium (climax) assemblage between disturbances.

Experimental approaches to the study of coral dynamics have been hindered by the large size of colonies, their longevity and their susceptibility to caging artifacts. The few existing studies of coral succession involve long-term monitoring, or hindcasting using substrata of known age (e.g. Grigg & Maragos 1974, Pearson 1974, Loya 1976, Connell 1978, Grigg 1983, Hughes 1985, Colgan 1987). Here we develop a matrix model to investigate further the dynamical processes involved in succession. Our goal is not to make precise predictions, but rather to use the model heuristically to examine mechanisms of community dynamics.

**The Model:**

The models we use here are based on a matrix of transition probabilities. These probabilities are arranged so that the columns represent transitions from each species (or group of species) initially present at a specified point, while the rows represent transitions to each species one time interval later. This matrix is then of the form:

$$\mathbf{A} = \begin{pmatrix} p_{11} & p_{12} & p_{13} & \cdots & p_{1n} \\ p_{21} & p_{22} & p_{23} & \cdots & p_{2n} \\ p_{31} & p_{32} & p_{33} & \cdots & p_{3n} \\ . & . & . & & . \\ . & . & . & & . \\ p_{n1} & p_{n2} & p_{n3} & \cdots & p_{nn} \end{pmatrix}$$

where $p_{jk}$ is the probability of transition to species j from k in one time interval. Multiplication of this matrix, **A**, by a column vector $x_{(t)}$ that describes the community composition at time t, gives the community composition at time t+1, according to the equation:

$$\mathbf{A}\, x_{(t)} = x_{(t+1)} \qquad (1)$$

The model analysis is described in detail in a later section.

Much of the mathematical analysis of matrices rests on the use of eigenvalues and eigenvectors of the matrix (see Caswell 1989). Most population studies involving sensitivity analysis of matrices have examined the sensitivity of the first eigenvalue of the matrix, $\lambda_1$, (the population growth rate) to small changes in each transition (e.g. Demetrius 1969, Crouse et. al 1987, Caswell 1989). Less commonly, eigenvector sensitivities have been calculated to quantify how the stable age (or size) distribution ($\mathbf{w}_1$) and the reproductive value schedule ($\mathbf{v}_1$) are influenced by each demographic transition (Caswell 1982, 1989). A sensitivity analysis of the first eigenvalue has little meaning in the context of community models, because this value is always one (Horn 1975, Enright & Ogden 1979). As an alternative, we present a sensitivity analysis of the ratio of the first and second eigenvalues, (i.e. the so-called damping ratio $\lambda_1/\lambda_2$), which in this case specifies how rapidly community equilibrium is regained after a major disturbance. We also subject the eigenvectors of community transition matrices to a sensitivity analysis for the first time, to quantify the importance of each transition in determining species composition at equilibrium (analogous to the equilibrium or stable age-distribution of population models).

A community does not "grow", since the sum of the proportions of its constituent species (plus free space) is by definition unity. Thus, the models we use here are, in mathematical terms, closed. However, biologically, the models mimic an open system with frequent larval recruitment from elsewhere, since they include transitions from bare space to every species.

## Methods:

### Fieldwork:

We calculated transition probabilities using data from a long term study of coral communities, initiated in 1962/1963 at Heron Island, Australia (23° 26' S, 151° 55' E). Permanently marked 1m$^2$ quadrats at three sites were relocated by positioning metal stakes at each corner, and photographed on a regular basis for nearly thirty years. The color photographs were traced at half life-size. Each colony was identified in the field, generally to species. Descriptions of the sites and methods are given in Connell (1973), and

Connell et. al. (unpubl. ms.). Two of the sites are intertidal, the Protected Crest and the Exposed Crest, while the Exposed Pools are marginally subtidal. The Exposed Crest and Pools are both vulnerable to cyclones which occur every few years, while the South Crest is sheltered from these by neighbouring Wistari Reef. There have been 6 major cyclones since 1962, each of which caused damage to one or more sites (in 1967, 1972, 1976, 1980, 1992, and 1994)

To quantify rates of transition between species, a square grid of 40 x 40 points, each 2.5 cm apart, was placed over maps of the permanent quadrats, and the taxon present at each grid point was recorded. The species at each point was compared to the species present at the following census, and the number of transitions between each species pair was calculated for each census from 1962/1963 to 1989. Small movements of the quadrat will not influence the results of the model, as they would be random with respect to the species present, and thus losses of a species should balance gains. Such movements only ocurred when stakes were displaced due to cyclone damage. We checked the extensive photographic records carefully to ensure that recorded cases of reversals (transitions from species A to B, and then back to A again) were real, and not due to sampling error. The dynamic nature of these assemblages (with a colony half-life of 3-4 years) also reduced the likelihood of artificially inflating the number of reversals. We pooled transitions for all quadrats at each site (5 at the Exposed Crest, 3 at the Protected Crest, and 2 at the Exposed Pools). The mean time interval between censuses (± S.E.) was 26 ±4 months (n = 12) for the Exposed Pools, 26 ± 5 months (n = 11) at the Exposed Crest, and 19 ± 2 months (n = 16) at the Protected Crest.

A total of 72 coral and 9 algal species were recorded in the quadrats during three decades of study, so in order to reduce the matrices used in the models to a tractable size, we classified benthic species into eight different groups, plus free space (Table 5.1). Species groups were based on taxonomic and morphological considerations, and on sample size. Two of these groups, Tabular *Acropora* (B) and Pocilloporids (H) consist almost entirely of *Acropora hyacinthus* and *Pocillopora damicornis* respectively. *Montipora* have been included in the Encrusting Acroporids (A), and *Porites* in the Massive Corals (G), with all other groups being self-explanatory. A few small unidentified colonies were eliminated from the data set, as were 4 unclassified coral species which were very rare (only 1 or 2 colonies in 27 years). Together these account for less than 0.1% of almost 54,000 transitions that were recorded.

Simulations were initially run using matrices for each time interval at each site, starting with an initial model assemblage consisting of 100% Bare Space. Each matrix defined a distinctive successional sequence, culminating in a unique equilibrium assemblage after 10-30 years. We subjected the equilibrium species compositions to a cluster analysis to identify any outliers, using the average linkage method (SAS 1988). Intervals where cyclones occurred did not cluster, and there was therefore no obvious reason for excluding them (Figure 5.1). To circumvent the problem of short-term (i.e. annual) variation, data for all time intervals were pooled, effectively producing an "average matrix" calculated over a time-scale sufficient for a complete turnover of individuals at these sites (Connell, et al., unpubl. ms.). All subsequent analyses are based on these average matrices.

Testing Model Assumptions:

Before analysing the three sites separately, we tested to see if the transition matrices at each site were statistically different using the procedure derived by Anderson & Goodman (1957). Site differences were determined by testing the null hypothesis $p_{jk}(s) = p_{jk}$; that is, we tested to see if the transition probabilities at all sites s are the same as the probabilities pooled over all sites. This was done by comparing the likelihood ratio $-2\ln\lambda$ to the $\chi^2$ distribution with m(m-1)(S-1) degrees of freedom, where:

$$-2\ln\lambda = 2\sum_{j=1}^{m}\sum_{k=1}^{m}\sum_{s=1}^{S} n_{jk}(s)\ln\left[\frac{p_{jk}(s)}{p_{jk}}\right]$$

$n_{jk}(s)$ = number of transitions to group j from group k at site s.

$p_{jk}(s)$ = transition probabilities for site s.

$p_{jk}$ = transition probabilities pooled over all sites.

S = number of sites (3)

m = order of matrix, (i.e. number of rows, 9)

We also needed to test the assumption that the model is at least a first order Markov chain (i.e. that the present community composition is dependent upon that of one time interval previously). Accordingly, we calculated for each site:

$$-2 \ln \lambda = 2 \sum_{j=1}^{m} \sum_{k=1}^{m} n_{jk} \ln\left( \frac{p_{jk}}{p_j} \right)$$

where:

$$p_j = \sum_{k=1}^{m} \frac{n_{jk}}{\sum_{j=1}^{m} \sum_{k=1}^{m} n_{jk}}$$

$n_{jk}$ = number of transitions to group j from group k.

$p_j$ = sum of all transition probabilities to group j.

and again compared it to the $\chi^2$ distribution, with $(m-1)^2$ degrees of freedom.

In both of these formulae, ln 0 was replaced by 0, following Usher (1979). This situation will only occur if a transition does not take place, and thus either $n_{jk}(s) = 0$, or $n_{jk} = 0$, and has no effect on the final outcome.

Model Analysis:

In order to examine more fully the equilibrium dynamics of the model, the transition probability matrix (**A**) can be subjected to an eigenanalysis. The eigenvalues ($\lambda_j$), and right and left eigenvectors of the transition probability matrix for each site were calculated using the International Mathematics and Statistics Library routine EVCRG (IMSL 1987). These were then used to calculate the damping ratio ($\rho$) and $t_{10}$, the time taken for the contribution to community composition of the first eigenvalue to become ten times as great as the contribution of the second (see Caswell 1989).

A sensitivity analysis of the damping ratio was used to indicate which transitions have the greatest effect on the time taken to reach equilibrium. The formula used for the sensitivities is (Caswell 1989):

$$\frac{\partial \rho}{\partial p_{jk}} = \frac{\lambda}{|\lambda_2|}\left[\frac{\partial \lambda_1}{\partial p_{jk}} - \frac{\rho}{|\lambda_2|}\left(x\,\frac{\partial x}{\partial p_{jk}} + y\,\frac{\partial y}{\partial p_{jk}}\right)\right]$$

where:

$$\frac{\partial \lambda_1}{\partial p_{jk}} = \frac{\bar{v}_j\, w_k}{(\mathbf{w}_1\,,\,\mathbf{v}_1)}$$

and $\frac{\partial x}{\partial p_{jk}}$ and $\frac{\partial y}{\partial p_{jk}}$ are the real and imaginary parts of $\frac{\partial \lambda_2}{\partial p_{jk}}$ respectively. $(\mathbf{w}_1\,,\,\mathbf{v}_1)$ is the inner product of the first right and left eigenvectors.

As well as carrying out a sensitivity analysis on the damping ratio, we repeated this procedure for the first right eigenvector (i.e. the equilibrium community composition). The elements of the eigenvector were first scaled by dividing by the euclidean norm. The formula for sensitivities then becomes (Caswell 1989):

$$\frac{\partial \dfrac{\mathbf{w}_1}{||\mathbf{w}_1||}}{\partial p_{lm}} = \frac{\dfrac{\partial \mathbf{w}_1}{\partial p_{lm}}\,||\mathbf{w}_1|| \;-\; \mathbf{w}_1\,\Sigma_j\,\dfrac{\partial w_j}{\partial p_{lm}}}{||\mathbf{w}_1||^2}$$

where the $\frac{\partial w_j}{\partial p_{lm}}$ are the elements of the vector:

$$\frac{\partial \mathbf{w}_j}{\partial p_{lm}} = w_m^{(j)} \sum_{k \neq j}^{S} \frac{\bar{v}_l^{(k)}}{\lambda_j - \lambda_k}\,\mathbf{w}_k$$

The result of applying this procedure to an n x n matrix is an n x n x n matrix which describes the sensitivity of each element of the eigenvector (i.e. the abundance of each member in the community at equilibrium) to changes in each of the transitions represented by the original matrix. In our case we obtain a three dimensional matrix for each of the three sites containing 729 elements.

**Results:**

Transition Probabilities 1963-1989:

The transition matrices (Table 5.2) are determined by patterns of recruitment, growth and mortality (from competition and other processes), which varied greatly among species and sites. While these processes cannot always be clearly identified in the transition matrices, we can ascribe a restricted group of mechanisms to each transition probability, as follows: (1) Transitions from free space occurred due to recruitment of larvae from elsewhere onto the substrate, or the growth of existing colonies onto previously unoccupied substratum. (Recruitment of fragments into the study area was minimal). (2) Mortality, which may be of the whole colony or only a portion of it (cf. Hughes and Jackson 1980), was represented by transitions to free space. (3) Transitions from a species group to itself were due to either persistence of the original colony, or much less commonly, to its being replaced by another of the same group. Finally, (4) transitions from one species group to another represent species replacements, which could occur directly through competition, or indirectly when a coral was killed and then replaced by a neighbor or a new recruit. It would be a simple extension of the model to subdivide these 4 major mechanisms further, e.g. to distinguish competitive displacement from indirect replacement by representing them as separate elements in the matrix, but this was beyond the scope of this study.

Several interesting patterns emerge from examination of the transition matrices. Firstly, the most remarkable aspect of the matrices is the marked paucity of zeros, i.e. almost every conceivable transition took place, albeit at markedly different rates (Table 5.2). Transitions were therefore almost always reciprocal, although they were not necessarily symmetric. For example, for every 1000 points initially occupied by Encrusting *Acropora* (group A) at the Exposed Crest, an average of 36 were replaced by Bushy *Acropora* (C) after one interval, while at the same time 14/1000 points underwent the reverse transition from C to A. No one dominant group had an unusually high rate of transitions to it from all others, and reversals were ubiquitous. A strictly hierarchical (transitive) outcome would have resulted in many zero rates of transition (e.g. if poor competitors could not displace superior ones), but this is clearly not the case for these coral assemblages. Note however, the reciprocity of transitions does not necessarily mean competitive equivalence, since replacements could occur indirectly (e.g. Bushy *Acropora* to Free Space to Encrusting *Acropora*).

Secondly, the matrix illustrates that rates of survival or persistence varied a great deal among species, reflecting large differences in coral life histories (e.g. Connell 1973, Hughes and Connell 1987, Hughes et al., 1992). The diagonal of the matrix is the probability that a species group will continue to occupy the same point (self-replacement "loops" from A to A, B to B, etc.), while the bottom line is the transition from each taxon to Free Space, category I (Table 5.2). Both of these provide an indication of longevity or turnover. Because these are very diverse assemblages we very rarely observed new recruits occupying the same point as a dead adult of the same species (or species group), which would also result in a loop. For example, at both the Exposed and Protected Crests, the highest transition to Free Space and the lowest loop was for Algae (F) which were much more ephemeral than corals. Free Space (I) had the highest rate of self-replacement at all sites, reflecting generally slow rates of colonization in this system.

Thirdly, the last column (transitions from Free Space) demonstrates greater than an order of magnitude difference among species groups in rates of colonization (Table 5.2). This occurred through larval recruitment of new colonies or by lateral growth of previously established corals, and reflects further a wide range of life histories. For example, Soft Corals (E) were poor colonizers at these sites (transitions to them from free space ranged only from 0.003-0.014 at the three locations) while Bushy *Acropora* (C) occupied free space 6-22 times faster, depending on the site (Table 5.2).

The three sites have significantly different transition matrices ($\chi^2 = 5403$, d.f. = 144, $P << .001$), justifying the decision to analyse each site separately. The persistence of soft corals (0.835) at the Protected Crest was 3-7 times higher than elsewhere, while algae were 4-5 times more persistent at the two Exposed sites (0.137, 0.152) than at the Protected Crest (Table 5.2). Among hard corals (categories A,B,C,D,G, and H), the mean persistence was 0.505 at the Exposed Crest, substantially higher than at the Exposed Pools or Protected Crest, which were very similar (0.356 and 0.358, respectively). The mean rate of colonization of free space (transitions to category I) also varied between sites (ranging from 0.017 to 0.048), with the Exposed Crest being 2-3 times lower than the other sites. The shorter census interval at the Protected Crest might be expected to result in lower transitions to and from each category and higher rates of persistence, but this did not occur; with the exception of soft corals, all persistence probabilities were lower at the Protected Crest (Table 5.2).

The matrices are at least first order as opposed to zero order at each site (Table 5.3), indicating that the species group present at any time t is dependent on the group present at time t-1. Therefore, the null hypothesis of a first-order Markovian process was not rejected. Higher order behavior was also tested for, and found to be largely absent (Tanner, unpubl. data). Consequently, we adopted a first-order Markovian model to explore the dynamics of this assemblage. We first use the matrices in computer simulations, and secondly analytically to predict community composition and to examine mechanisms that are important in maintaining species diversity.

Community Dynamics: Simulations:

Succession, where initially free space is set at 100% and coral cover at zero, is an obvious community process to examine. Simulations were run according to equation 1 to map out the trajectory of coral recovery. The time track of colonization differed markedly among species groups (Figure 5.2). For example, at the exposed pools, 5 of the 9 groups reached an early peak in abundance within 2-6 years and then dropped off, some fairly sharply, before approaching an equilibrium after 10-15 years. This pattern was most striking for Algae and *Pocillopora* (Figure 5.2), both of which are often among the first to invade disturbed reefs and are generally relatively short-lived (e.g. Woodley et al., 1981, Grigg 1983, Harriott 1985, Table 5.2). In contrast, other groups such as Staghorn and Tabular *Acropora* and Soft Corals approached their asymptotic value smoothly and generally more slowly. Free Space dropped off rapidly from 100% at all sites, and also approached its asymptotic value smoothly, indicating that a full recovery would take about 20 years (Figure 5.2).

The abundance of each species group at equilibrium differed greatly, but most significantly, none was eliminated (Figure 5.3). Many were rare however, with 5 out of the 8 living categories reaching less than 1% cover at one or more sites. There were also major differences between sites in the climax community composition (Figure 5.3). The most abundant category at equilibrium at all sites was Free Space, ranging from 74% cover at the Exposed Crest to 50% at the Exposed Pools. Tabular *Acropora* species dominated at the Exposed Pools, occupying approximately 18% of the total area, while the most abundant category at both Crests was Bushy *Acropora* (10-14%). Soft Corals were plentiful only at the Protected Crest (6%), while Algae were most common at the Exposed Pools (4.5% cover; Figure 5.3).

Coral diversity (H') and evenness peaked after a single iteration of the model (Figure 5.4), but then declined to equilibrium values which remained high indefinitely in the absence of a major disturbance. The rapid recovery occured because transitions took place immediately from Free Space to all species groups (Table 5.2). The subsequent decline in diversity and evenness was caused by differences in transition rates among species, which allowed some to achieve higher abundances than others. The surprisingly high equilibrium diversity resulted from the persistence of all species groups due to the absence of a competitive dominant (as illustrated by the reciprocity of transitions (ie. the lack of zeros) in the matrices), and due to the ability of all species to recruit onto Free Space (Table 5.2).

The time taken to reach an equilibrium (using constant, average transitions) varied among sites, ranging from approximately 20-25 years (Figure 5.4), far longer than the observed interval between severe cyclones at Heron Island (Connell et al., unpubl. ms). The Exposed Pools had a lower equilibrium diversity and evenness than elsewhere (Figure 5.4), due to the dominance of Tabular and Staghorn *Acropora* (Figure 5.3) which survive and grow better at this subtidal location (Connell, unpubl. data). In comparison, the Exposed and Protected Crests had similar equilibrial community indices, but for the first 3 - 10 years or so the Protected Crest was less diverse than the other two sites (Figure 5.4).

## Model Analysis:

### Eigenvalue Analysis:

The difference in rate of succession at the 3 sites (Figure 5.4) is indicated further by the damping ratio of each matrix, which was higher at the two exposed sites than at the Protected Crest (Table 5.4). Consequently, the time taken for the contribution of the first eigenvalue to become ten times as great as the second, $t_{10}$, is approximately 9-10 years at the Exposed

Crest and Pools, but about 19 years at the Protected Crest (Table 5.4, see also Figure 5.4).

Sensitivity analysis of the damping ratio indicates substantial differences among taxa and sites in the impact of each transition on the rate of recovery (Table 5.5). The larger the absolute value of the sensitivity, the more sensitive the community's rate of approach to equilibrium is to the corresponding transition. A negative number implies that an increase in this probability will lead to a decrease in the damping ratio (i.e. lower rates of recovery), while a positive number implies the opposite. At the Exposed Crest, numerous transitions to and from Encrusting *Acropora* (A) are more important than those among other groups, as are transitions from Free Space (I). The least important groups at this site were Soft Corals, Massive Corals, and *Pocillopora*. The transition to Encrusting *Acropora* from Free Space (I to A), and persistence of Encrusting *Acropora* (A to A), are particularly influential (Table 5.5), although in opposite directions. Increased colonisation by Encrusting *Acropora* leads to an increase in the damping ratio, or a decrease in the time for recovery, thereby stabilising the community. In contrast, increased persistence of Encrusting *Acropora* decreases the damping ratio, increasing the time taken for recovery to an equilibrium community.

A different suite of transitions had major effects on the rate of succession at the Exposed Pools (Table 5.5). Transitions from Tabular *Acropora* (B) and colonization and persistence of Staghorn *Acropora* (D) were much more important in the Pools than at the other, shallower sites where these two morphologies of corals are restricted in abundance. Particularly low sensitivities occured for transitions from Encrusting *Acropora*, Massive Corals, Soft Corals and Pocilloporids. At the Protected Crest, Soft Corals (E) were important, with high sensitivities for transitions to and from this group. Lowest sensitivities there were for transitions from Tabular *Acropora*, Algae, Massive Corals and *Pocillopora* (Table 5.5).

As might be expected, sensitivities of transitions from Free Space (I) were large and positive at all sites (Table 5.5), since greater rates of colonization intuitively speed up rates of recovery of an assemblage. The three largest sensitivities for colonizing transitions were for Encrusting *Acropora* at the Exposed Crest, Staghorn *Acropora* at the Exposed Pools and Soft Corals at the Protected Crest (Table 5.5).

Sensitivities were not necessarily largest for groups that were the most abundant at equilibrium. For example, at the Exposed Crest, Bushy *Acropora* (C) was twice as abundant as Encrusting *Acropora* (A) at equilibrium (Figure 5.3), but transitions involving the latter were substantially more important (Table 5.5). For instance, the sensitivity of the A to A transition was more than 20 times larger than C to C, while Free Space to A was 3 times greater than to C. Similarly, at the Protected Crest, Soft Corals (E) and Staghorn *Acropora* (D) were equally abundant at equilibrium (Figure 5.3), but sensitivities for the former were generally 3 times larger (Table 5.5).

### Eigenvector Sensitivity Analysis:

The cover of each species group at equilibrium is sensitive to only a small number of transitions, which differ among sites (Table 5.6). Table 5.6 represents a summary of the original 9 x 9 x 9 matrices giving the full eigenvector sensitivity analysis. Positive sensitivities mean that an increase in the associated transition probability will lead to an increase in the representation at equilibrium of the species to which the sensitivity applies. Similarly, negative sensitivities will result in a decrease in representation at equilibrium if the transition probability increases. The vast majority of transitions have very low sensitivities (Table 5.6).

Transitions which were important predominantly involved free space (I), with transitions to and especially from this category having large sensitivities at all three sites (Table 5.6). Transitions involving Bushy *Acropora* (C) were also important at the Exposed Crest. In contrast, those involving Tabular and Staghorn *Acropora* (B and D) were significant at the Exposed Pools, while transitions to and from Bushy *Acropora* and Soft Corals (B and E) were important at the Protected Crest. These groups are all spatial dominants at equilibrium at the sites where they are important (Figure 5.3). Tabular *Acropora* and Soft Corals (B and E) at the Protected Crest were affected by an unusually large number of transitions (the "of" rows), although only the latter group was abundant.

## **Discussion:**

## Community-level Transition Matrices:

Transition matrices like the ones presented here (Table 5.2) have the potential to provide many insights into community ecology. For instance, we suggest that the observed number of transitions expressed as a proportion of the maximum number possible provides an index of the complexity of interactions in an assemblage, analogous to connectance in food-web analysis (e.g. Pimm 1982). Furthermore, the interaction strength is given directly by the transition probabilities. The maximum number of non-zero transitions among n species is $n^2$, or n(n-1) if we exclude self-replacements. However, the number of replacements actually occurring may be much smaller, depending on the assemblage. For example, on Heron Island, we found that 74 of the 81 possible transitions occurred among the 9 groups at the Exposed Crest (Table 5.2), giving a complexity index of 0.91. Published community matrices from other, terrestrial systems range widely from 0.43 to 1.00 (Table 5.7).

Clearly, the number of transitions occurring would be expected to rise in assemblages displaying competitive networks compared to those characterised by linear hierarchies (cf. Buss and Jackson 1979). Similarly, where a low-diversity climax occurs (e.g. coniferous forests, sea grass beds), we would expect high transitions to these dominant species, with very low transitions from them. These predictions appear to hold, with post-glacial and alpine assemblages showing much lower ratios of observed to possible transitions compared to grassland, rainforest and coral reefs (Table 5.7). However, this comparison is clearly preliminary given the paucity of published matrices, and should be interpreted cautiously since the likelihood of obtaining a zero transition also depends on the evenness of the assemblage, on how species are lumped and on sampling intensity, all of which vary among available studies.

Apart from the number of zero transition probabilities, other patterns in the location and magnitude of elements in a projection matrix could be used to compare ecological communities. For example, the mean size of self-replacement transitions along the diagonal of the matrix could be utilized as a measure of persistence (with suitable scaling for matrices with different projection intervals). At Heron Island, the mean persistence for all coral groups combined varied by 42% among sites, with much larger differences among individual taxa (Table 5.2). It would be interesting to be able to make these comparisions with other geographic locations, in deeper water, on polluted or overfished reefs, with terrestrial systems, etc. Similarly, transitions to and from free space could be used to compare colonization and mortality patterns of different assemblages.

Transition rates also have the potential to be used as dependent variables in community-level experiments. Usher (1981) found that the exclusion of rabbits from grassland plots slightly reduced the complexity of interactions (from 1.00 to 0.92, Table 5.7), but this reduction was enough to change the equilibrium species composition significantly. Diversity was enhanced by herbivory because no clear competitive dominant could emerge, as indicated by the complete lack of zero transitions in the control where rabbits were present. A sensitivity analysis (c.f. Tables 5.5 & 5.6) of experimental and control matrices could provide further insights into herbivory and the dynamics of plant communities.

Changes in transition rates could also be used to follow temporal changes in community dynamics and to explore mechanisms of succession, but we are unaware of any such examples in the literature. With one exception (Lough et al., 1987), published community matrix models have measured transitions only once, effectively assuming that transition probabilities are constant over time, i.e. that the Markov process is homogeneous (e.g. Horn 1975, Usher 1979, Table 5.3). Testing this assumption has been done more frequently for population matrices, which have often been found to vary from one time interval to the next (e.g. Bierzychudek 1982, Huenneke and Marks 1987, Hughes 1984). We discuss this and other assumptions of the model below.

Markovian Properties of the Model:

The results in Table 5.3 support the generalisation that ecological succession is at least a first order (Markovian) process, as opposed to a zero order (random) process (Usher 1979). This means that the present community composition is dependent on the community composition one time interval previously. First order behavior could be a real feature of an assemblage in that some species may promote or inhibit settlement and growth of others (cf. the facilitation and inhibition models of Connell & Slatyer 1977), or in some cases it may be due to the time interval of the study being sufficiently short that there is little replacement of individuals. In the latter case, succession may still be a random process. This problem of the length of the time interval can be overcome by employing a semi-Markov model, which explicitly accounts for the persistence time of a species group at any point (e.g. Moore 1990), and will be examined further in a later paper.

The coral assemblage's first order behavior (Table 5.3) occurs because any particular species can replace others (either directly or indirectly) with different degrees of success, i.e. species A may replace species B more frequently than C does (Table 5.2). Alternatively, if replacement rates were the same for all species, transitions would be random, and the system would display zero order behavior. Of course, higher order effects are also extremely likely, due to the history of the assemblage (cf. Hughes 1989). For example, the ability of one species to replace another probably depends on how long the individual being displaced has been present, since competitive outcome is often size- or age-dependent (e.g. Buss 1980). A more refined matrix model could incorporate such effects by distinguishing size-classes within species.

The model presented here also fails to account for temporal variation in transition rates, so that effects of past disturbances, history, or non-linearities such as frequency-dependence have not been considered. Frequency-dependence is very likely. For example, transition probabilities (particularly those due to recruitment or competition) may depend on the amount of free space present, and how coral cover is apportioned between different species. To investigate this possibility, we could extend the models to allow transitions to vary as a function of either total cover, cover of each individual species group, or cover of selected species groups. Acevedo (1981) has investigated the use of a frequency-dependent model of forest dynamics, and this idea has also been utilised in population dynamics models which incorporate density-dependent vital rates (e.g. de Kroon et. al. 1987). The equations involved in these models usually cannot be solved analytically, but they can still be of great use in simulation studies. Temporal variation can also be incorporated by alternating between several different matrices (e.g. Hughes 1984, Gotelli 1991), by using higher order models (e.g. Chatfield & Lemon 1970, Morgan 1976) or semi-markov models (e.g. Moore 1990). However, as more detail is brought into the model its complexity increases, and its analytical tractability decreases.

Thus there is the usual trade off between increased accuracy of the results, the amount of information and time needed to construct the model, and the ease with which it can be analysed and interpreted.

We found very large annual variation in this study, particularly in relation to six cyclones and to patterns of recruitment since 1962 (Connell et al., unpubl. ms, Hughes et al., unpubl. ms.). As might be expected, in years where cyclones occurred, transitions to free space increased at one or more sites, especially among susceptible species. Because it is impossible to capture the dynamics of this system with any single annual matrix, we chose instead to explore here the behaviour of average matrices for each site, calculated over nearly three decades, which was a timespan sufficient for a complete turnover of individuals (Connell et al., unpubl. ms.). Exclusion of years where cyclones occurred from the matrices decreases slightly the amount of free space at equilibrium, as expected, but there are no qualitative differences from the approach we used here. This was highlighted by the cluster analysis of equilibrium community composition (based on the matrices calculated separately for each census), which shows that cyclone years were interspersed among non-cyclone years (Figure 5.1). This presumably occurs because mortality from major physical disturbance at shallow, exposed sites is often non-selective, killing most corals. Our simulations show that if the corals were to behave repeatedly according to the rules of the average matrices (with or without years with cyclones), they would take more than 20 years to reach a climax (Figures 5.2 and 5.3) which is far longer than the interval between major disturbances. We conclude that these shallow-water coral assemblages are nearly always in the process of recovering from the latest cyclone.

As well as recurrent disturbances, temporal fluctuations in larval recruitment may also play a role in determining what species occur at a particular site (e.g. Wallace 1985, Dayton et. al. 1989, Fisk & Harriott 1990, Hughes, Connell and Wallace, unpubl. ms.). Recruitment from outside was included in our model as constant transitions from Bare Space, imitating an open system. It would be a simple extension to allow the recruitment component of the matrix to vary (e.g. Hughes 1990).

Frequency dependence in species transition rates are another form of temporal variation. The models we used have constant transition probabilities, yet some species exhibited a curious trajectory which overshot an equilibrium before being "damped out", a behaviour reminiscent of frequency-dependence (Figure 5.2). This overshoot occurred because the total rate of acquisition (or loss) of space by any one group was dependent on the species composition of the community. The sharp peak, which some species groups displayed (C, F, G, H at the Exposed Pools, and A, G at the Protected Crest) before declining to equilibrium (Figure 5.2), transpired because initially transitions to these groups were mainly from Free Space and gains exceeded losses to other species groups which were slower to colonize. Later, as Free Space declined, transitions from early colonists to later arrivals increased and exceeded new gains, causing the decline to an equilibrium, where eventually colonisation balanced loss of space to other species. These results are in accordance with other empirical studies which indicate that good colonisers are often outcompeted by later arrivals (e.g. Connell & Slatyer 1977). In the model, these early colonists persisted because a large amount of free space was always present (Figures 5.2 and 5.3), onto which they could recruit.

## Sensitivity Analysis and Keystone Species

Sensitivity analysis is a powerful tool in assessing the role of each species in an assemblage. The sensitivity analyses for the coral assemblages we examined show that no one transition is particularly important in controlling the composition of the assemblage. This result was to be expected from inspection of the matrices (Table 5.2) which showed a high degree of reciprocity among transitions. Connell (1976) and Connell & Keough (1985) also found that no one species won or lost consistently in long-term competitive encounters in these coral assemblages. In addition, poor competitors could also replace superior ones indirectly by recruitment onto space recently vacated. The analysis presented here shows that Free Space, however, is an important category, with high sensitivities for transitions *to* this state (but low sensitivities for transitions *from* it). Each of the three sites has different species groups that are the most important in determining both the damping ratio and the equilibrium community composition. These differences reflect spatial patterns in rates of recruitment, growth and persistence of the corals (Connell et al. unpubl. ms).

There are three main reasons why these coral assemblages do not have a keystone species. First, the characteristically high diversity of coral reefs reduces the likelihood of any one species being dominant on purely probabilistic grounds. Secondly, while a species may eventually be able to achieve dominance, it will take a long time for this to occur. Third, the high frequency of disturbance prevents the successional process from running to completion, as indicated by the time-track of our models (Figure 5.3). Alternatively, keystone species may be predators, as in some temperate intertidal communities (e.g. Paine 1974). The form of model presented here does not explicitly include higher trophic levels, although it does include the effects of predation as a component of transitions to Free Space.

In general, the value of damping ratio sensitivities tends to vary more in transitions *from* a species group, rather than transitions *to* a species group (Table 5.5). Thus, for example, at the Exposed Crest, the community is sensitive to most transitions from Encrusting Acroporids (A), but is not sensitive to transitions from Soft Corals (E). This suggests that the community's rate of return to equilibrium is determined more by differential patterns of mortality, than it is by recruitment and growth. The importance of free space provides further evidence for mortality or persistence being the major driving force in determining the community structure, rather than recruitment or growth.

In contrast, the eigenvector sensitivity analysis shows that important transitions occurred to *and* from species groups, with those groups having transitions of consequence in one direction also having significant transitions in the opposite direction (Table 5.6). Thus, both increases in coverage of a species (i.e. recruitment and growth) and decreases (i.e. mortality) were important in determining climax community structure (indicated by the eigenvector sensitivity), whereas patterns of persistence had greater influence on the rate of succession (shown by the damping ratio sensitivity). Note that the eigenvector analysis is an equilibrium sensitivity, while the damping ratio is a transient one. It is not surprising that different species interactions affect the speed of succession versus its eventual outcome. We predict that other systems with species having a wider range of life histories than shallow-water coral assemblages will show a much greater disparity in eigenvector versus damping ratio sensitivities, since proportionally more early succession species will be eliminated during the course of succession.

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**Table 5.1.**

Species Groups Used in the Models of Community Dynamics at Heron Island.

| CODE | GROUP |
|---|---|
| A | Encrusting Acroporid Corals |
| B | Tabular *Acropora* |
| C | Bushy *Acropora* |
| D | Staghorn *Acropora* |
| E | Soft Corals |
| F | Algae |
| G | Massive Corals |
| H | Pocilloporid Corals |
| I | Free Space |

**Table 5.2:**

Transition Probability Matrices. Columns represent the species group at time t, and rows the species group at time t+1. N is the total number of transitions recorded from each group, and gives a measure of average abundance throughout the study. Species group codes are presented in Table 5.1.

Exposed Crest

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| A | 0.623 | 0.005 | 0.014 | 0.013 | 0.000 | 0.049 | 0.036 | 0.037 | 0.022 |
| B | 0.009 | 0.565 | 0.004 | 0.016 | 0.013 | 0.009 | 0.016 | 0.017 | 0.008 |
| C | 0.036 | 0.012 | 0.586 | 0.023 | 0.053 | 0.067 | 0.088 | 0.044 | 0.047 |
| D | 0.019 | 0.005 | 0.011 | 0.475 | 0.040 | 0.076 | 0.024 | 0.044 | 0.026 |
| E | 0.001 | 0.007 | 0.000 | 0.001 | 0.267 | 0.000 | 0.000 | 0.002 | 0.004 |
| F | 0.008 | 0.012 | 0.009 | 0.022 | 0.013 | 0.137 | 0.012 | 0.012 | 0.011 |
| G | 0.001 | 0.000 | 0.004 | 0.002 | 0.000 | 0.012 | 0.424 | 0.005 | 0.006 |
| H | 0.007 | 0.000 | 0.007 | 0.012 | 0.027 | 0.009 | 0.012 | 0.358 | 0.013 |
| I | 0.297 | 0.395 | 0.365 | 0.436 | 0.587 | 0.640 | 0.388 | 0.480 | 0.863 |
| N | 1781 | 595 | 3196 | 1464 | 75 | 328 | 250 | 408 | 1425 |

Table 5.2 (continued)

Exposed Pools

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| A | 0.257 | 0.002 | 0.003 | 0.004 | 0.000 | 0.008 | 0.029 | 0.000 | 0.006 |
| B | 0.053 | 0.575 | 0.062 | 0.079 | 0.077 | 0.104 | 0.052 | 0.115 | 0.104 |
| C | 0.150 | 0.039 | 0.391 | 0.005 | 0.128 | 0.102 | 0.029 | 0.071 | 0.067 |
| D | 0.150 | 0.042 | 0.067 | 0.632 | 0.000 | 0.048 | 0.152 | 0.105 | 0.058 |
| E | 0.000 | 0.002 | 0.000 | 0.000 | 0.128 | 0.005 | 0.000 | 0.003 | 0.003 |
| F | 0.009 | 0.005 | 0.023 | 0.000 | 0.051 | 0.152 | 0.048 | 0.050 | 0.064 |
| G | 0.000 | 0.001 | 0.006 | 0.011 | 0.000 | 0.025 | 0.224 | 0.003 | 0.018 |
| H | 0.027 | 0.008 | 0.012 | 0.011 | 0.077 | 0.031 | 0.019 | 0.178 | 0.036 |
| I | 0.354 | 0.326 | 0.437 | 0.258 | 0.538 | 0.526 | 0.448 | 0.476 | 0.644 |
| N | 113 | 1770 | 1130 | 1006 | 39 | 646 | 210 | 382 | 5937 |

Protected Crest

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| A | 0.354 | 0.046 | 0.032 | 0.032 | 0.000 | 0.071 | 0.025 | 0.039 | 0.059 |
| B | 0.021 | 0.314 | 0.005 | 0.004 | 0.003 | 0.014 | 0.000 | 0.000 | 0.014 |
| C | 0.066 | 0.030 | 0.478 | 0.082 | 0.016 | 0.090 | 0.076 | 0.105 | 0.091 |
| D | 0.049 | 0.016 | 0.038 | 0.439 | 0.009 | 0.057 | 0.031 | 0.053 | 0.039 |
| E | 0.001 | 0.005 | 0.005 | 0.004 | 0.835 | 0.005 | 0.011 | 0.000 | 0.014 |
| F | 0.009 | 0.036 | 0.007 | 0.004 | 0.000 | 0.033 | 0.015 | 0.000 | 0.007 |
| G | 0.015 | 0.003 | 0.013 | 0.014 | 0.006 | 0.052 | 0.340 | 0.000 | 0.032 |
| H | 0.002 | 0.005 | 0.001 | 0.001 | 0.000 | 0.000 | 0.000 | 0.224 | 0.004 |
| I | 0.482 | 0.544 | 0.421 | 0.421 | 0.131 | 0.678 | 0.501 | 0.579 | 0.741 |
| N | 1598 | 366 | 3325 | 1478 | 321 | 211 | 720 | 76 | 12150 |

**Table 5.3.**

Test to see if community dynamics are best described as a zero order or a first order process. ($H_0$: The system is zero order as opposed to higher order.)

| Site | $\chi^2$ | d.f. | Probability |
|---|---|---|---|
| Exposed Crest | 15965 | 64 | $<<.001$ |
| Protected Crest | 8976 | 64 | $<<.001$ |
| Exposed Pools | 5359 | 64 | $<<.001$ |

**Table 5.4:** Recovery Rates of Simulated Communities.

| Site | $\lambda_1$ | $\lambda_2$ | $\rho$ | $t_{10}$ (years) |
|---|---|---|---|---|
| Exposed Crest | 1 | 0.602 | 1.661 | 9.8 |
| Exposed Pools | 1 | 0.573 | 1.745 | 9.0 |
| Protected Crest | 1 | 0.825 | 1.212 | 19.0 |

$\lambda_i$ - ith eigenvalue of the transition probability matrix P.

$\rho$ - damping ratio ($=\lambda_1/\lambda_2$).

$t_{10}$ - time taken for $\lambda_1$ to outweigh $\lambda_2$ by a factor of ten in determining community composition.

**Table 5.5:**

Damping Ratio Sensitivity Analysis.
(See text for explanation).

Exposed Crest

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| A | -2.538 | -0.032 | 0.676 | 0.167 | 0.023 | 0.037 | 0.080 | 0.082 | 3.175 |
| B | 1.011 | 0.053 | -0.016 | 0.043 | 0.002 | 0.015 | -0.008 | 0.011 | 0.553 |
| C | 0.454 | 0.040 | 0.092 | 0.062 | 0.005 | 0.019 | 0.006 | 0.022 | 0.960 |
| D | 0.341 | 0.037 | 0.114 | 0.066 | 0.006 | 0.019 | 0.008 | 0.024 | 1.044 |
| E | 0.385 | 0.038 | 0.106 | 0.065 | 0.006 | 0.019 | 0.007 | 0.024 | 1.011 |
| F | 0.060 | 0.030 | 0.169 | 0.076 | 0.008 | 0.021 | 0.015 | 0.030 | 1.250 |
| G | 0.070 | 0.030 | 0.167 | 0.076 | 0.007 | 0.021 | 0.015 | 0.030 | 1.245 |
| H | 0.065 | 0.030 | 0.168 | 0.076 | 0.008 | 0.021 | 0.015 | 0.030 | 1.246 |
| I | 0.188 | 0.033 | 0.144 | 0.072 | 0.007 | 0.020 | 0.012 | 0.028 | 1.156 |

Table 5.5: (continued.)

Exposed Pools

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| A | 0.017 | 0.537 | 0.359 | -0.299 | 0.009 | 0.167 | 0.042 | 0.093 | 1.534 |
| B | 0.014 | 0.300 | -0.059 | 1.384 | 0.001 | 0.012 | 0.035 | 0.036 | 0.738 |
| C | 0.016 | 0.427 | 0.164 | 0.489 | 0.005 | 0.095 | 0.039 | 0.066 | 1.163 |
| D | 0.021 | 0.817 | 0.852 | -2.288 | 0.019 | 0.350 | 0.050 | 0.161 | 2.471 |
| E | 0.015 | 0.356 | 0.040 | 0.985 | 0.003 | 0.049 | 0.037 | 0.049 | 0.926 |
| F | 0.015 | 0.399 | 0.115 | 0.686 | 0.004 | 0.077 | 0.038 | 0.060 | 1.070 |
| G | 0.017 | 0.530 | 0.345 | -0.241 | 0.009 | 0.162 | 0.042 | 0.091 | 1.508 |
| H | 0.016 | 0.441 | 0.189 | 0.389 | 0.006 | 0.104 | 0.039 | 0.070 | 1.210 |
| I | 0.015 | 0.404 | 0.124 | 0.649 | 0.005 | 0.080 | 0.038 | 0.061 | 1.086 |

Protected Crest

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| A | 0.118 | 0.030 | 0.237 | 0.110 | 0.341 | 0.024 | 0.066 | 0.006 | 1.099 |
| B | 0.121 | 0.030 | 0.241 | 0.112 | 0.315 | 0.024 | 0.067 | 0.006 | 1.115 |
| C | 0.120 | 0.030 | 0.240 | 0.111 | 0.325 | 0.024 | 0.066 | 0.006 | 1.110 |
| D | 0.119 | 0.030 | 0.239 | 0.111 | 0.334 | 0.024 | 0.066 | 0.006 | 1.108 |
| E | 0.391 | 0.078 | 0.692 | 0.312 | -2.504 | 0.052 | 0.174 | 0.021 | 2.805 |
| F | 0.121 | 0.030 | 0.243 | 0.112 | 0.310 | 0.024 | 0.067 | 0.006 | 1.121 |
| G | 0.124 | 0.030 | 0.246 | 0.114 | 0.283 | 0.024 | 0.068 | 0.007 | 1.134 |
| H | 0.119 | 0.030 | 0.238 | 0.110 | 0.339 | 0.024 | 0.066 | 0.006 | 1.103 |
| I | 0.125 | 0.031 | 0.248 | 0.115 | 0.276 | 0.024 | 0.068 | 0.007 | 1.143 |

**Table 5.6:**

Eigenvector Sensitivity Analysis Summary. Numbers in the table indicate the frequency of each range of sensitivities. Those rows labelled 'Of', give the number of transitions out of 81 to which equilibrium cover of each species group displays a given level of sensitivity. Similarly, rows labelled 'From' summarise the importance of transitions from each species group, and those labelled 'To' summarise the importance of transitions to each group. (See text for explanation.)

Table 5.6 (continued)

Exposed Pools

| | | Sensitivity Range | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | < -1 | -1 to -0.5 | -0.5 to -0.1 | -0.1 to 0.1 | 0.1 to 0.5 | 0.5 to 1 | > = 1 |
| Of | A | | | 3 | 74 | 3 | 1 | |
| | B | | | 4 | 73 | 3 | 1 | |
| | C | | | 3 | 74 | 3 | 1 | |
| | D | | 1 | 4 | 72 | 3 | | 1 |
| | E | | | 3 | 75 | 2 | 1 | |
| | F | | | 3 | 75 | 2 | 1 | |
| | G | | | 3 | 75 | 3 | 1 | |
| | H | | | 2 | 76 | 2 | 1 | |
| | I | | | 2 | 76 | 3 | | |
| From | A | | | | 81 | | | |
| | B | | | 5 | 69 | 9 | | |
| | C | | | | 76 | 5 | | |
| | D | | | 2 | 70 | 9 | | |
| | E | | | | 81 | | | |
| | F | | | | 81 | | | |
| | G | | | | 81 | | | |
| | H | | | | 81 | | | |
| | I | | 1 | 20 | 51 | 1 | 7 | 1 |
| To | A | | | | 77 | 3 | 1 | |
| | B | | | 8 | 69 | 3 | 1 | |
| | C | | | 1 | 76 | 3 | 1 | |
| | D | | | 5 | 72 | 3 | | 1 |
| | E | | | | 78 | 2 | 1 | |
| | F | | | | 78 | 2 | 1 | |
| | G | | | | 77 | 3 | 1 | |
| | H | | | | 78 | 2 | 1 | |
| | I | | 1 | 13 | 64 | 3 | | |

**Table 56:** continued.

Exposed Crest

| | | Sensitivity Range | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | < -1 | -1 to -0.5 | -0.5 to -0.1 | -0.1 to 0.1 | 0.1 to 0.5 | 0.5 to 1 | > = 1 |
| Of | A | 1 | | 2 | 75 | 3 | | 1 |
| | B | 1 | | 4 | 73 | 2 | | 1 |
| | C | 1 | | 2 | 75 | 2 | | 1 |
| | D | | 1 | 3 | 75 | 1 | | 1 |
| | E | | 1 | 2 | 76 | 1 | | 1 |
| | F | | 1 | 1 | 77 | 1 | 1 | |
| | G | 1 | | 1 | 77 | 1 | | 1 |
| | H | | 1 | 2 | 76 | 1 | | 1 |
| | I | | | 1 | 79 | 1 | | |
| From | A | | | | 78 | 3 | | |
| | B | | | | 81 | | | |
| | C | | | 6 | 67 | 8 | | |
| | D | | | | 80 | 1 | | |
| | E | | | | 81 | | | |
| | F | | | | 81 | | | |
| | G | | | | 81 | | | |
| | H | | | | 81 | | | |
| | I | 4 | 4 | 12 | 52 | 1 | 1 | 7 |
| To | A | | | 4 | 73 | 3 | | 1 |
| | B | | | | 78 | 2 | | 1 |
| | C | | | 7 | 71 | 2 | | 1 |
| | D | | | 1 | 78 | 1 | | 1 |
| | E | | | | 79 | 1 | | 1 |
| | F | | | | 79 | 1 | 1 | |
| | G | | | | 79 | 1 | | 1 |
| | H | | | | 79 | 1 | | 1 |
| | I | 4 | 4 | 6 | 66 | 1 | | |

**Table 5.6:** continued.

Protected Crest

| | | Sensitivity Range | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | < -1 | -1 to -0.5 | -0.5 to -0.1 | -0.1 to 0.1 | 0.1 to 0.5 | 0.5 to 1 | >= 1 |
| Of | A | | 1 | 4 | 72 | 2 | 2 | |
| | B | 1 | | 6 | 68 | 4 | 1 | 1 |
| | C | | 2 | 3 | 71 | 4 | 1 | |
| | D | | | 4 | 74 | 2 | 1 | |
| | E | 1 | 1 | 9 | 64 | 4 | 1 | 1 |
| | F | | | 2 | 77 | 2 | | |
| | G | | | 4 | 75 | 2 | 1 | |
| | H | | | 3 | 76 | 1 | 1 | |
| | I | | | 1 | 78 | 2 | | |
| From | A | | | 3 | 76 | 2 | | |
| | B | | | | 81 | | | |
| | C | | | 8 | 63 | 9 | 1 | |
| | D | | | 2 | 76 | 2 | | |
| | E | | | 1 | 78 | 2 | | |
| | F | | | | 81 | | | |
| | G | | | 1 | 79 | 1 | | |
| | H | | | | 81 | | | |
| | I | 2 | 4 | 21 | 39 | 7 | 7 | 2 |
| To | A | | | 3 | 75 | 2 | 1 | |
| | B | | | | 78 | 2 | 1 | |
| | C | | 2 | 4 | 67 | 6 | 1 | 1 |
| | D | | 1 | 2 | 74 | 3 | 1 | |
| | E | | | 8 | 67 | 4 | 1 | 1 |
| | F | | | | 80 | 1 | | |
| | G | | | 3 | 75 | 2 | 1 | |
| | H | | | | 79 | 1 | 1 | |
| | I | 2 | 1 | 16 | 59 | 2 | 1 | |

**Table 5.7.**

Summary of complexity ratios, (defined as the number of observed transitions divided by the maximum number possible), from published transition matrices.

| Community Type | Complexity Ratio | Matrix Size | Author |
|---|---|---|---|
| Temperate grasses grazed by rabbits. | 1.00 | 8 x 8 | Usher (1981) |
| Tropical rainforest trees. | 0.93 | 13 x 13 | Enright & Ogden (1979) |
| Temperate grasses protected from grazing. | 0.92 | 8 x 8 | Usher (1981) |
| Sub-tropical shallow water corals | | | This paper |
| (a) Exposed Crest | 0.91 | 9 x 9 | |
| (b) Protected Crest | 0.88 | 9 x 9 | |
| (c) Exposed Pools | 0.88 | 9 x 9 | |
| Temperate deciduous forest trees. | 0.81 | 11 x 11 | Horn (1975) |
| Woody alpine vegetation. | 0.59 | 8 x 8 | Lough et al. (1987) |
| Post-glacial plant assemblages. | 0.43 | 12 x 12 | Van Hulst (1981) |

**Figure 5.1.** Cluster analysis of equilibrium community composition predicted by matrices for each interval. Censuses in which a cyclone occurred are indicated in bold.

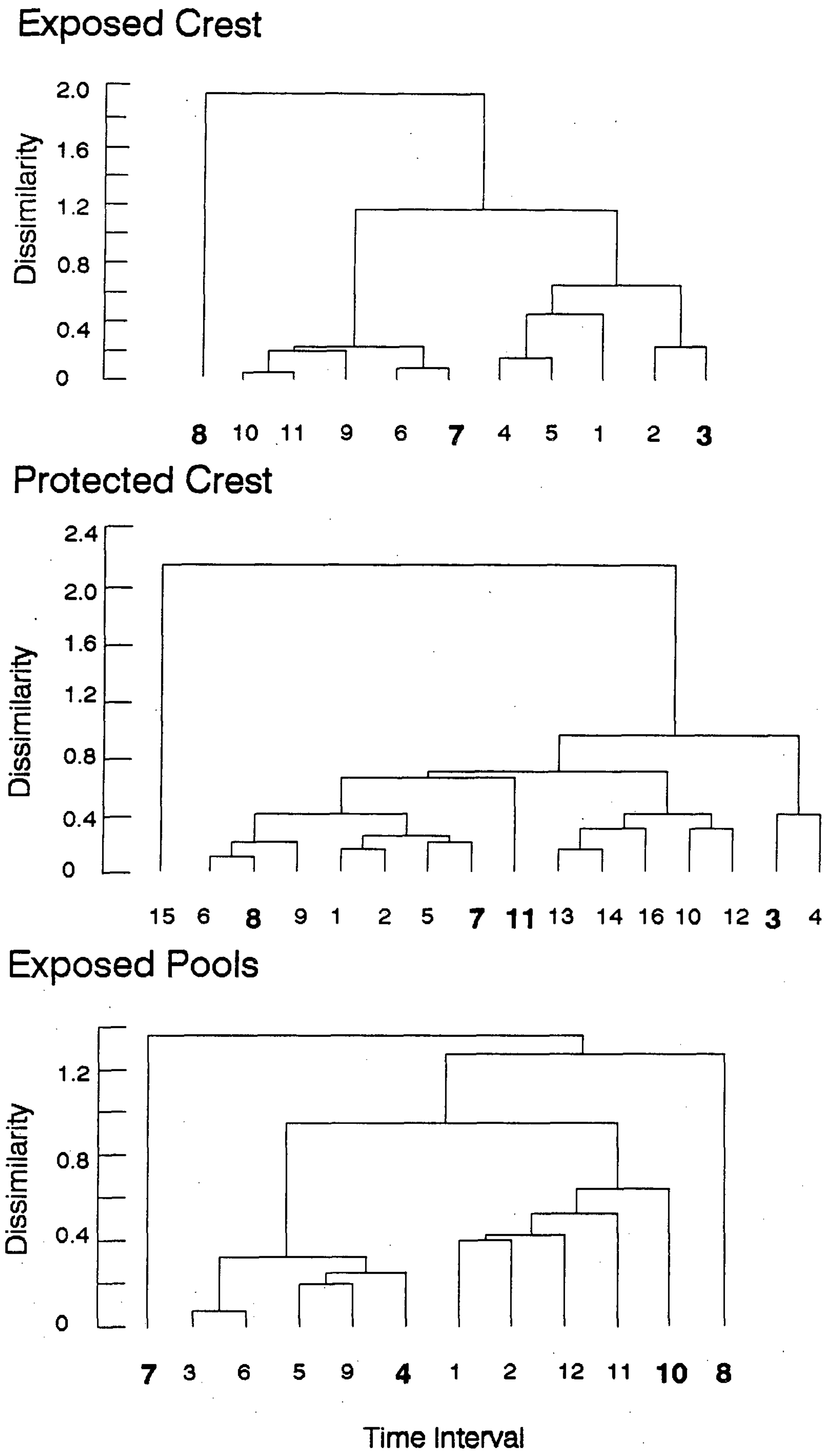

Exposed Crest
Dissimilarity
2.0
1.6
1.2
0.8
0.4
0
8 10 11 9 6 7 4 5 1 2 3
Protected Crest
Dissimilarity
2.4
2.0
1.6
1.2
0.8
0.4
0
15 6 8 9 1 2 5 7 11 13 14 16 10 12 3 4
Exposed Pools
Dissimilarity
1.2
0.8
0.4
0
7 3 6 5 9 4 1 2 12 11 10 8
Time Interval

**Figure 5.2.** Simulated species group abundances over fifty years, starting from total destruction of the existing community. Note the different scales on the Y-axis.

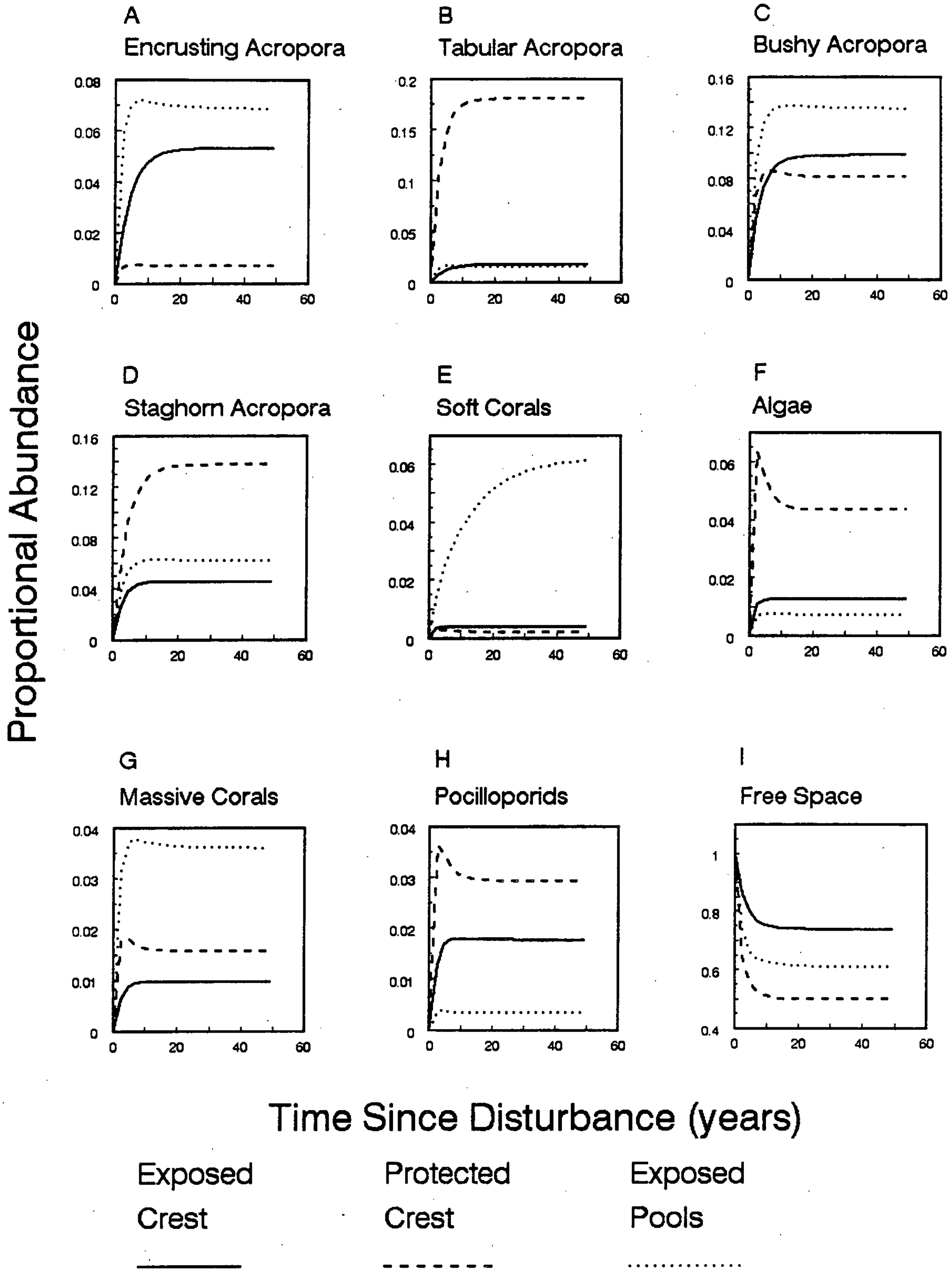

A
Encrusting Acropora
0.08
0.06
0.04
0.02
0
0
20
40
60
B
Tabular Acropora
0.2
0.15
0.1
0.05
0
0
20
40
60
C
Bushy Acropora
0.16
0.12
0.08
0.04
0
0
20
40
60
D
Staghorn Acropora
0.16
0.12
0.08
0.04
0
0
20
40
60
E
Soft Corals
0.06
0.04
0.02
0
0
20
40
60
F
Algae
0.06
0.04
0.02
0
0
20
40
60
G
Massive Corals
0.04
0.03
0.02
0.01
0
0
20
40
60
H
Pocilloporids
0.04
0.03
0.02
0.01
0
0
20
40
60
I
Free Space
1
0.8
0.6
0.4
0
20
40
60
Proportional Abundance
Time Since Disturbance (years)
Exposed Crest
Protected Crest
Exposed Pools

**Figure 5.3.** Simulated equilibrium abundance of nine species groups at three sites at Heron Island.

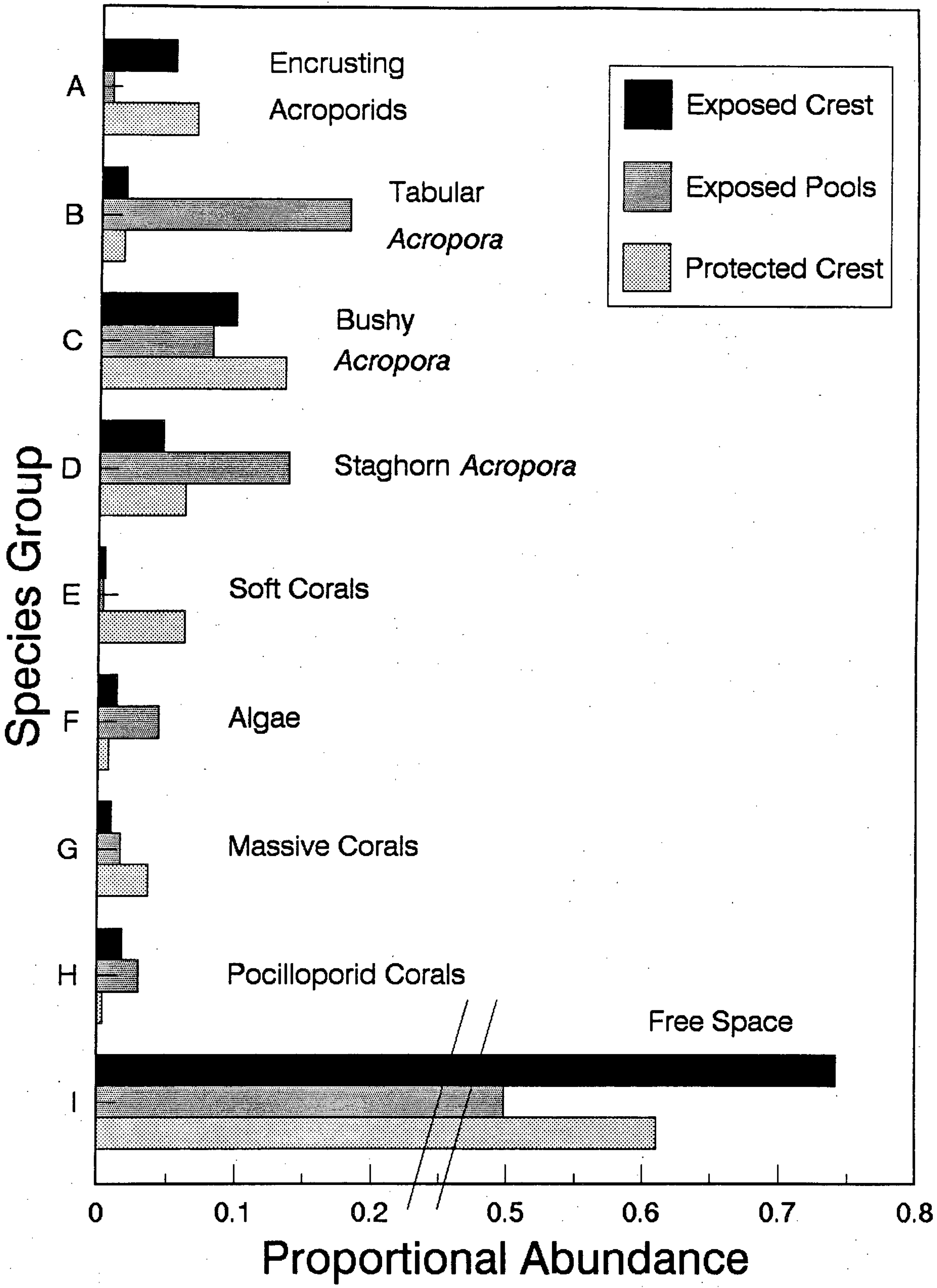
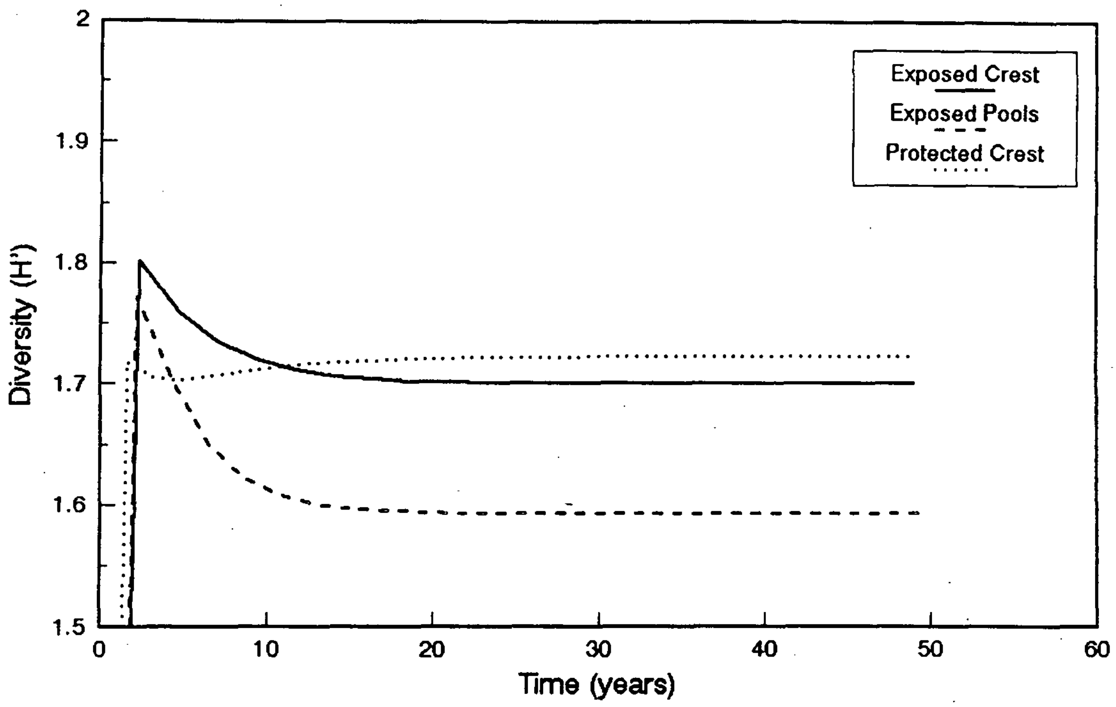
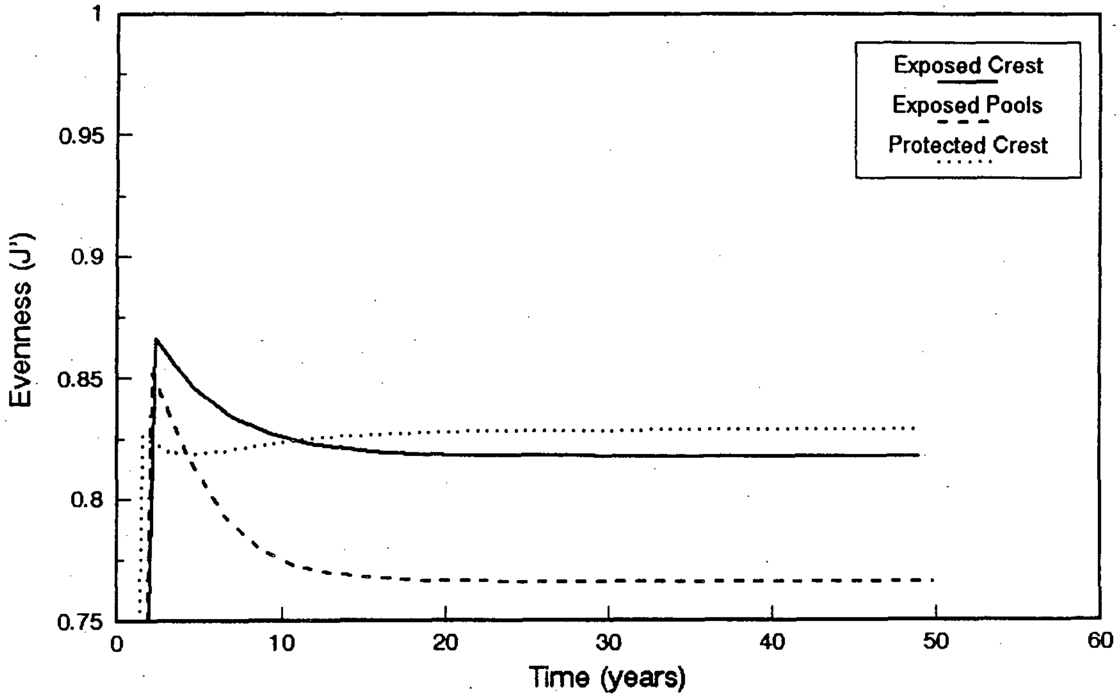

Species Group
A
Encrusting Acroporids
B
Tabular *Acropora*
C
Bushy *Acropora*
D
Staghorn *Acropora*
E
Soft Corals
F
Algae
G
Massive Corals
H
Pocilloporid Corals
I
Free Space
Exposed Crest
Exposed Pools
Protected Crest
0
0.1
0.2
0.5
0.6
0.7
0.8
Proportional Abundance

**Figure 5.4.** Simulated diversity and evenness of coral assemblages over time, starting from an initial cover of zero.


Diversity (H')
2
1.9
1.8
1.7
1.6
1.5
0
10
20
30
40
50
60
Time (years)
Exposed Crest
Exposed Pools
Protected Crest


Evenness (J')
1
0.95
0.9
0.85
0.8
0.75
0
10
20
30
40
50
60
Time (years)
Exposed Crest
Exposed Pools
Protected Crest

# Chapter 6

## The role of history in community dynamics: A modelling approach.

Reference: Tanner, J.E., T.P. Hughes & J.H. Connell. 1995. The role of history in community dynamics: A modelling approach. Ecology. In Press.

Note on coauthors:
J.H. Connell initiated and conducted the study from which the data for this chapter were obtained. His contribution was to supply photographs of his quadrats, and to comment on several versions of the manuscript. T.P. Hughes drew the maps of the quadrats, and also commented on several versions of the manuscript.

**Abstract:**

Recent history plays an important role in the physiology, behaviour and ecology of individuals, and in the dynamics of populations and assemblages of species. In this paper, we examine the impact of history on the species composition of intertidal reef corals, by comparing simulation models that incorporate four different levels of knowledge about the recent past (over a time-scale of 1-27 years). The models are markov or semi-markov transition probability matrix models, based on rates of colonisation, persistence and species replacement measured from a long-term study spanning 3 decades at Heron Island, Great Barrier Reef.

Rates of colonisation (transitions from free space) varied 20-fold for different species groups, while mortality (transitions to free space) ranged 5-fold, reflecting a wide range of life-histories among the coral assemblage. Virtually all species groups could undergo reciprocal transitions (e.g. from A to B, and B to A) in a single time interval, indicating the lack of a single competitive dominant that was capable of outcompeting all or most other species.

Transition probabilities changed markedly as a function of history. For most species groups, the probability of persisting (i.e. "transitions" from A to A) increased with time. Thus, a colony which had occupied space for some time was generally more likely to continue to do so than a new arrival. This result is consistent with an escape in size for older colonies from mortality agents such as competition and predation. However, three species groups showed the opposite pattern. Algae, Pocilloporid corals and fragile tabular *Acropora* showed marked increases in transitions to free space after 3-5 years, reflecting a more ephemeral suite of life history traits. Similarly, free space which had recently been generated had a higher rate of colonisation than substratum that had been unoccupied for some time. These results falsify a major assumption of standard first order models, i.e that transition probabilities are constant, and that history is irrelevant.

Although the changes in transition probabilities as a function of history were often striking, the four different models we employed show only minor variation in community composition in both transitory and climax (equilibrium) phases. Thus, while recent history was important in determining transition probabilities, it had little effect on community dynamics and structure in this system. This discrepancy is due to the rapid turnover of corals and algae on shallow reef crests, where only a small proportion of colonies survive long enough to display effects of history. All models agreed that the length of time required for this system to reach an equilibrium community structure is far longer than the observed interval between recurrent disturbances from tropical cyclones.

## Introduction:

The ecological consequences of history are often ignored. For example, almost all mathematical models of the dynamics of populations or communities assume that a system's future depends solely on its present state, and that even its immediate past is irrelevant. However, there have been numerous demonstrations that events occurring earlier in an individuals life may significantly alter its current rates of growth, fecundity and survivorship (cf. Hughes 1984, Hughes and Jackson 1985, Wilbur and Alford 1985, Peterson and Black 1988, Briske and Anderson 1992). For instance, corals which have been recently injured have different probabilities of growth and mortality compared to uninjured colonies (Hughes 1984, Hughes & Jackson 1985, Babcock 1991). Similarly, the level of mortality of bivalves on sand-flats depends on the history of crowding that each individual has experienced (Peterson and Black 1988).

Life history trade-offs may also have a historic component. For example, high rates of reproduction early in the life of an animal or plant can result in reduced fecundity and increased rates of mortality in older stages (e.g. Law 1979, Nur 1988, Gustafsson and Part 1990). Ignoring historical effects such as these may seriously compromise our ability to understand and predict the present or future dynamics of individuals, populations or communities.

Studies of the effects of history at the community level have generally focussed on the role of chance events in structuring assemblages (e.g. Sutherland 1974, May 1977, Lubchenco 1978, Hubbell & Foster 1986, Dublin et al. 1990). For instance, the order of arrival (or subsequent establishment) of species can strongly influence community structure (e.g. Sale 1977, Chesson & Case 1986, Wilbur and Alford 1985, Robinson & Dickerson 1987, Butler & Chesson 1990). Some mechanistic models of succession implicitly address the importance of sequences of interactions (e.g. facilitation and inhibition *sensu* Connell and Slatyer 1977). Similarly, the history of unpredictable disturbances may also play a role in changing the trajectory of an assemblage (e.g. Lewontin 1969, Dublin et al. 1990, Law & Morton 1993). If a community has a single stable point which exhibits global attraction, then history is important only in that it determines where on the road to recovery the community is. However, if multiple stable points exist, the community may be perturbed into a new domain of attraction (e.g. Lewontin 1969, Holling 1973, Peterman et al. 1979). In this case, the community's history must be known in order to explain both its current configuration and trajectory (e.g. Hughes 1989, 1994, Dublin et al. 1990, Law & Morton 1993).

The aim of this study is to examine the role that history plays in determining community dynamics, using data from a longterm monitoring study of coral assemblages at Heron Island, on the Great Barrier Reef, Australia (see Connell 1973, 1978, Hughes and Connell 1987, Tanner et al., 1994).

Specifically, we test the hypothesis that incorporating knowledge about the recent past (1-27 years) in simulation models may influence the models outcomes. The types of models we use are described briefly below.

## First Order Models:

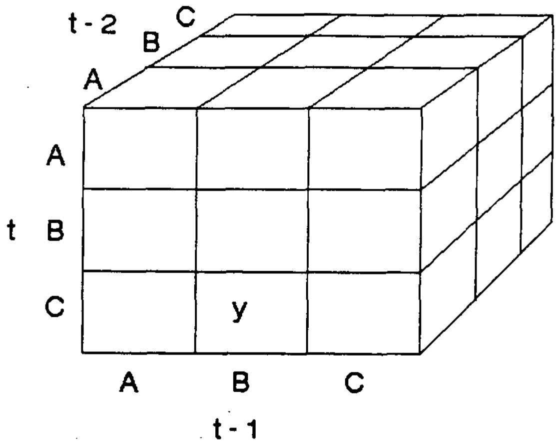
Conventional matrix models are first order models, i.e. they assume that the community's future is dependent solely on its present state, and that history is immaterial. Thus, the state distribution at time t + 1 depends solely on the state distribution at time t. This model is based on a matrix (**A**) of transition probabilities that describes the probability of any unit in state i at time t moving into state j at time t + 1. When the matrix is post-multiplied by a vector x(t) representing the assemblage's composition at time t, according to the equation:

$$x(t+1) = \mathbf{A}\, x(t)$$

the resultant vector x(t + 1) describes the composition of the assemblage at time t + 1. The equation can be used iteratively to simulate the composition of the system over time, and the matrix **A** can also be treated analytically to calculate the equilibrium community composition, and the sensitivity of the model's predictions to each matrix element (Caswell 1989). Previous applications of this model have been used to study the dynamics of succession in forests (Horn 1975, Enright & Ogden 1979, Acevedo 1981, Alvarez-Buylla & Garcia-Barrios 1993), alpine assemblages (Lough et al., 1987), and coral reefs (Tanner et al. 1994).

## Second Order Models:

When the markovian process is extended to be second order, the state distribution at time t becomes dependent upon the distribution at time t-2, as well as that at time t-1. This allows a limited influence of the system's history, extending over a period of three censuses. The matrix of transition probabilities in a second order model is no longer two dimensional, but instead becomes three dimensional, with $n^3$ elements compared to $n^2$ for the conventional model, and has the form:



Here, y represents the probability that a point which was in state A at time t-2 and state B at time t-1, will be in state C at time t. The equation used for simulating the system is:

$$x(t, t-1) = \mathbf{A}\, x(t-1,t-2)$$

where **A** is the transition probability matrix (now three dimensional), and x(t, t-1) is a two dimensional matrix describing the joint state distributions at times t and t - 1, and having the form:

| | | | | |
|---|---|---|---|---|
| | A | j | k | l |
| t | B | | | |
| | C | | | |
| | | A | B | C |
| | | | t-1 | |

In this case, k represents the proportion of the system in state A at time t, and in state B at time t-1. While it is entirely feasible to multiply 3-dimensional matrices, for ease of computation the matrix can be converted to two-dimensional form (e.g. Harbaugh & Bonham-Carter 1970), which allows the suite of analytical procedures developed for first order models to be employed.

Second order transition processes have received some attention in behavioural studies (eg Chatfield & Lemon 1970, Morgan 1976) and geology (Harbaugh & Bonham-Carter 1970), but have not yet been applied in detail to ecological problems. Chatfield & Lemon (1970) and Morgan (1976) modelled bird-song as a markovian process, and examined several song sequences to determine their order of dependency. Chatfield & Lemon (1970) concluded that wood peewee songs showed second order dependence, i.e. the identity of each element of the song was determined by the identities of the previous two elements. In contrast, Morgan (1976) found that the songs of blackbirds were strictly first order, i.e. the identity of each element was determined only by the identity of the previous element. Usher (1987) gives a brief example of a second order model in an ecological context. He constructed both first and second order community models of a grassland, and found differences between the equilibrium community compositions of the two models. Based on this result, he concluded that successional processes are generally greater than first order.

## Semi-Markov Models:

Historical effects can also be incorporated into matrix models by using a semi-markov process (Moore 1990, Howard 1971), which takes into account how long a unit of space has been occupied. The rate of replacement is accounted for by randomly assigning each unit a waiting time when it first enters a new state, based on the observed frequency-distribution of waiting times in the field. At the end of this waiting time, the unit may undergo any of the possible transitions to other states with probabilities that are an empirically derived function of the waiting time. A semi-markov model is likely to be more realistic than markov models because persistence ability is a function of age or size in many organisms (e.g. Buss 1980, Hughes 1984, Osenberg & Mittelbach 1989). Here, we use two versions of a semi-markov matrix model which differ in waiting times (i.e. in the amount of history of the dynamics of the assemblage). Semi-markov type models have received little attention in ecology. Henderson & Wilkins (1975) use such a model to mimic variable periods between fires in an analysis of forest communities in Tasmania.

In this paper, we construct four different types of model based on matrices of transition probabilities among species groups. The first is a standard first order matrix model (e.g. Horn 1975, Usher 1981, Tanner et al. 1994), which assumes that there is no effect of history. It gives us a base with which to compare a second order model and two variants of a semi-markov model, that incorporate historical effects in different ways, and to different extents (see below for further details). We also searched for the presence of historical effects by examining the ergodic nature of each of the four models. Ergodicity is the tendency of a model to forget its past, so that simulations run with different initial conditions eventually converge to the same result (e.g. Cohen 1976, Caswell 1989).

## Methods:

To examine the importance of history in the dynamics of a community, we constructed simulation models of the types described above using data from a long-term monitoring study of a coral reef at Heron Island, Great Barrier Reef, Australia (23° 26' S, 151° 55' E). Transition probabilities among species were calculated from half life-size maps traced from photographs of coral colonies (5,156 records) contained within three permanently marked 1 $m^2$ quadrats, which were placed on the southern, relative protected reef crest. A total of 17 censuses of the quadrats were taken in the period 1962 - 1989, with a mean interval (± SE) of 19 ± 2 months. Rates of transition between consecutive censuses were quantified by comparing the species present under each point on a 20 x 20 square grid placed repeatedly over each map (a total of 19,200 transitions). Each quadrat was permanently positioned by steel stakes at each corner, so that the same points could be identified at each census. Any occasional small movements of the quadrat would be random with respect to the species present, and thus losses and gains will balance out for each species group.

To reduce the complexity of the models, we grouped the 72 coral and 9 algae species that occurred in the quadrats into eight different categories, based on taxonomic and morphological considerations (Table 6.1). We chose 6 categories of hard corals, and one each of algae and soft corals. Free space (space without corals and macroalgae, but usually containing crustose coralline algae) has also been included as a category so that all possible states occur in the model. Colonization by recruitment or growth was recorded as a transition from Free Space. For more detailed descriptions of the site and methods see Connell (1973), Hughes and Connell (1987), and Tanner et al. (1994).

We calculated transition probabilities for a second order markov model by comparing the species present under each point over three consecutive censuses. Accordingly, the 17 censuses allowed a total of 15 sets of second order transition probabilities to be estimated. Transition probabilities were also calculated for two semi-markov models (Semi-Markov 1 and 2). The first model has a complete range of waiting times of one to eleven iterations. (A maximum of eleven was chosen because no single point at this site was occupied by the same species group for more than twelve censuses). To avoid bias in the calculation of these probabilities, a point was not scored until it had undergone a transition from the state that it occupied at the initial census, i.e. we used only those transitions where it was known how long the point had been in its present state. In the Semi-Markov 2 model, we used only two different sets of transition probabilities, for waiting times of 1 and 2 census intervals combined, and for waiting times of greater than two census intervals. Thus, the Semi-Markov Model 2 incorporates less history than Model 1.

For all models, we pooled the transition probabilities over time to overcome short-term fluctuations and to increase sample size. Thus, we essentially calculated average matrices for the 27 year duration of the study. Cyclones affect Heron Island every 5-10 years, although damage from each of 4 cyclones during the period from 1962-1989 at the southern, relatively protected reef crest was relatively minor, ranging from a 2-40% reduction in cover (J.H. Connell, T.P. Hughes, and C.C. Wallace, unpubl. ms.). A cluster analysis of the equilibrium community composition predicted by the first order matrix for every census did not isolate years with cyclones (Tanner et al., 1994), so they were not excluded.

To determine whether the differing levels of history incorporated into the different models have any effect on community development, simulations were run for all four models, starting with a "community" consisting entirely of free space. This simulates the recovery of the coral assemblages following a severe disturbance, such as a cyclone, which can completely denude the substrate of shallow reef areas. Simulations were also run with different starting vectors, to examine the ergodic properties of the models.

**Results:**

Transition probabilities:

The transition probability matrices for all four models are determined by the demographic features (recruitment, growth and mortality) of the different species groups within the coral and algal assemblage, as well as by the way that they interact with each other. The matrix for the first order model (Table 6.2), shows clearly that these processes differ markedly for the different species groups. For example, transitions from Free Space to each category (i.e. recruitment and growth), varied 20-fold from 0.004 to 0.090, reflecting differences in their abilities to colonise new substratum by recruitment from the plankton or by growth of existing colonies. Similarly, transitions to Free Space (i.e. mortality), ranged 5-fold, from 0.131 for long-lived Soft Corals to 0.678 for ephemeral Algae. Self-replacements (e.g. "transitions" from category A to A) varied 25-fold, indicative of a wide range of abilities among species groups to persist and retain space (e.g. Connell 1973, Bak and Engel 1979, Hughes and Jackson 1985, Hughes et al., 1992).

There was no overwhelming competitive dominant in this study, as indicated by the paucity of zeros in the first order model (Table 6.2). A highly competitive species would have low or zero transitions from it to other species, and high transitions to it. Instead, we found that transitions occurred both to and from most species groups. Only 10 of the 81 possible transitions (14%) did not take place during the 27 year study, reflecting a high degree of reciprocity in replacement patterns. Furthermore, transitions which did not occur directly (in one time interval), could all take place indirectly in two (or more) steps.

Higher order matrices reveal that persistence times vary among taxa, and that rates of transition depend critically on history. For brevity, we present here the matrices for zero, 1-2 and >2 waiting intervals (Table 6.2, 6.3a and 6.3b, respectively). The zero waiting time matrix is that used in the first order model, while the other two matrices come from the second semi-markov model. The role of history is revealed by comparing transitions with different waiting times. There are 2 distinct patterns, determined by the relative persistence of taxa (Figure 6.1). Three species groups, Algae, Pocilloporids and Tabular *Acropora* showed marked declines in persistence probabilities with time. Algae (F) did not hold onto a unit of space for more than two consecutive censuses (i.e. there are no transitions from this group in Table 6.3b), while Pocilloporids (H) persisted for three censuses at most (indicated by the transition to Free Space for waiting times of >2, Table 6.3b). Similarly, Tabular *Acropora* (B), had a probability of 0.305 of retaining space (the B to B transition, Table 6.3a) for the first two time intervals, that subsequently dropped off markedly to 0.063 due mainly to a high mortality rate (the transition from B to Free Space, Table 6.3b) of these older colonies. In contrast, the other 5 groups (A, C, D, E, G), all showed small increases in persistence probabilities with time, i.e the longer a colony held onto space the more likely it was to continue to do so. Free Space showed a similar pattern; the longer a patch of substratum remained bare, the more likely it was to remain uncolonised. The standard first order model assumes that transition probabilities are constants. Clearly, this assumption is incorrect.

### Simulations:

In most respects, simulations from the four different models show remarkable conformity. The equilibrium compositions of the four model assemblages are almost identical, with the exception of Soft Corals (E) which are more abundant in the second order model (Figure 6.2, 6.3). The increase in Soft Corals in the second order model comes mainly at the expense of Free Space, although all other groups show slight decreases in abundance compared to the first order model. All four models predict a high proportion of Free Space (I) at equilibrium (close to 60%). Similarly, Tabular *Acropora* (B), Algae (F), and Pocilloporid Corals (H) are relatively rare at equilibrium (<2% cover) in every case (Figures 6.2, 6.3). Each of the models converged to the same equilibrium composition when simulations were run with different starting conditions (J.E. Tanner and T.P. Hughes, unpubl. data).

The length of time required to reach equilibrium from an initial condition of 100% Free Space was at least 20 years, and up to 100 years for the second-order model (Figure 6.2). The actual time to reach equilibrium is probably longer, because some instances of colonization in the models were due to transitions from Free Space by previously settled corals (in addition to larval recruitment, which would predominate after a major disturbance). Significantly, the frequency of major cyclones at Heron Island is every 5-10 years. Since this study began in 1962, six destructive cyclones have caused varying amounts of damage to corals on Heron Island (in 1967, 1972, 1976, 1980, 1992, and 1994). Thus, shallow reef-crest assemblages (even at the relatively sheltered south crest) are continually recovering from the most recent disturbance(s), and are rarely close to equilibrium (Connell 1978, Tanner et al., 1994). It is crucial therefore to compare the transitory (non-equilibrium) phase of the models, since the equilibrial phase is an academic construct that is unlikely to exist in the real world at this spatial scale.

However, the trajectory of the transitory phase (i.e. before equilibrium was reached) was also similar for all 4 models. The only notable differences were the higher abundance of Soft Corals in the second order model, and the erratic trajectories of some taxa (Tabular *Acropora*, Algae and Pocilloporid Corals) in the first semi-markov model. Both of these differences are likely to be artefacts of relatively small sample sizes. In the second order model, there were only a few transitions to Soft Corals from t-2 to t-1, and many of them persisted to time t. Similarly, stochasticity in transitions for Tabular *Acropora*, Algae and Pocilloporid Corals probably relates to their rarity in the field.

## Discussion:

### Effects of history:

The assumption of first order models that history is irrelevant (and that transitions are constant) is clearly incorrect. For example, our data demonstrate that rates of persistence change as a function of past events (Table 6.2, 6.3). The poor survival of Algae and Pocilloporid Corals after 2-3 intervals (3-5 years) is supported by numerous empirical studies, which demonstrate that these two groups have ephemeral life histories (e.g. Grigg 1983, Harriott 1985, Martin-Smith 1994, Tanner et al. 1994). Similarly, Tabular *Acropora* on shallow reef crests are likely to become increasingly vulnerable to physical disturbance as they grow larger, because of their characteristic morphology. Colonies consist of a small attachment trunk, which supports a rapidly-growing horizontal table that is susceptible to wave damage, particularly for large individuals (J.H. Connell, T.P. Hughes & C.C. Wallace, unpubl. data). In contrast, all other categories of corals showed an increase in their ability to retain space with time (Figure 6.1, Table 6.2, 6.3). This effect was largest for Encrusting *Acropora* (A) and Soft Corals, which showed about a 20% increase in persistence probabilities for waiting times of >2 compared to <2 censuses. This observation is consistent with numerous demographic studies which show a general decline in mortality rates for older, larger colonies (e.g. Connell 1973, Hughes and Connell 1987, Hughes et al., 1992, Babcock 1991).

Rates of persistence of Free Space also increased with time (Table 6.2, 6.3), probably due to spatial differences of habitat quality or patterns of habitat selection by new recruits. Presumably, microhabitats that are unsuitable for colonisation (or early survival) will remain bare for longer than more favourable sites. Plant biologists have developed the concept of "safe sites", a subset of the substratum which provides physical and biological conditions necessary for establishment (Harper 1977). Similarly, for coral larvae or algal spores, settlement cues and habitat heterogeneity at the scale of a single propagule (e.g. grooves of a parrot-fish bite, tentacles of a filter-feeder, or shade from a coral branch) may profoundly influence rates of recruitment (e.g. Brock 1979, Birkeland and Randall 1981, Morse et al. 1988).

We found a very high degree of reciprocity of transitions between taxa (Table 6.2), i.e. virtually all species groups could replace each other. Field observations and experiments indicate that many of these species are competitively equivalent at this site, (probably because the shallow depth prevents vertical overtopping and shading) and they frequently exhibit competitive reversals and standoffs (Connell 1976, Connell and Keough 1985, Tanner 1992). Indirect replacements also occasionally took place during the study, where a colony died leaving bare substratum which was colonised before the next census. Whatever the mechanism, reciprocal transition probabilities point to a limited role of history in determining equilibrial community composition, because competitive exclusion or preemption by a subset of species (e.g. by corals that were first to colonise an area after a disturbance) is unlikely. Instead, we found that any initial arrangement of species (behaving by the rules of community dynamics encapsulated in the matrices) eventually converged to the same species configuration. This result indicates that the four models we used all display strong ergodicity (Cohen 1976, 1977 a, b, 1979), i.e. each model "forgets its past" so that community dynamics become independent of initial abundances. A summary of the conditions needed for a first order markov model to be ergodic is given in Caswell (1989). However, to our knowledge, this important property has not been examined before for second order and semi-markov models.

The effects of history on changes in persistence of individual colonies (Table 6.2, 6.3) were not reflected at the community level (Figures 6.2, 6.3). Despite differences in transition probabilities for different persistence times (Figure 6.1, Table 6.2, 6.3), the four models we used were in close accordance, suggesting that history does not play a significant role in determining the dynamics of this coral assemblage. The equilibrium community composition is almost identical for all models (Figure 6.3), although there are some differences in the transient dynamics shown by the first semi-markov model (Figure 6.2). Even here, the small differences we observed are probably due only to sampling error for the 3 rarest taxa (Algae, Pocilloporid corals, and Tabular *Acropora*). In contrast, the three most abundant groups, Free Space, Bushy *Acropora* and Soft Corals, all show very limited fluctuations. Additionally, when the waiting times are condensed into two groups (semi-markov model 2), rather than eleven (semi-markov model 1), these fluctuations are eliminated (Figure 6.2), as would be expected if they were solely due to stochastic differences from one waiting period to the next. It is likely that these short-term differences occurred in colony growth and/or recruitment, as the semi-markov 1 model shows large peaks in species abundances above those of the first order model, with much smaller troughs below it.

The most probable reasons for the minimal effect of history on the system studied here is the high rate of turnover of individuals. For example, although we found a sharp drop in the persistence probability of Pocilloporid

Corals (H) from 0.229 to zero for waiting times of 1-2 versus >2 intervals, only $0.2292^2$ or 5.2% of colonies would survive to the third census, so even their entire loss after 3 censuses would be trivial. Similarly, the rise in persistence probabilities for Encrusting *Acropora* (A) from 0.341 to 0.410 would only affect $0.341^2$ or 11.6% of colonies in the third interval, and 4.0% in the fourth. Although survivorship data from elsewhere are scarce, the turnover of corals on the reef crest at Heron Island is probably close to the upper limit for corals, especially at sites exposed to damage from cyclones. Even at the Protected South Crest, only 12% of colonies initially present in 1962 were alive ten years later (J.H. Connell and T.P. Hughes, unpubl. data). In comparison, Hughes (1988) found 61% survival after a decade for the plate coral *Montastrea annularis,* on deep-water reefs (35m depth) off Jamaica. The high turnover of corals at Heron Island is reflected in the large amount of Free Space at equilibrium in the model communities, which results from the inclusion in the matrices of transitions due to both small- and large-scale disturbances. We also ran a first order model using a matrix which excluded transitions from years with cyclones, but the amounts of Free Space at equilibrium was only slightly less than the trajectories presented here (Figure 6.2), because of routine, small-scale disturbances which are a constant feature of reef crest environments (e.g. Connell 1978).

One important consideration in constructing and interpreting these models is the time scale of the observations. It is important that the data come from censuses which are sufficiently close together that past events are not already forgotten, but not so close that there is effectively no past. The census interval should also be less than the interval between major disturbances such as cyclones, or any other events that have a substantial impact on the community. The census interval of 19 ± 2 (SE) months used here corresponded to levels of turnover of colonies between censuses in the range of of 25 - 50 %, which meets these requirements.

Future studies of historical effects:

If we had found significant differences between the first and second order models, it would of course be possible to extend the modelling effort to still higher orders, thus further extending the influence of history in the model.

An obvious problem with higher order models however, is that the state space becomes excessively large. Thus, for a model of order a, there are $n^{a+1}$ transition probabilities which need to be estimated. Even if only a few state categories are employed, a very large amount of data would be needed to construct models of order three or greater. Of course, if sufficient data are available, and the second order model differs significantly from the first order model, it may well be worthwhile searching for even higher order effects. However, if there are no second order effects, there will also be no impacts of any higher order (Usher 1987).

Another way in which the modelling process can be extended is to make transition probabilities conditional on the abundance of all or some of the species groups. Such models will be analogous to density dependent populations models (e.g. De Kroon et al. 1987, Desharnais & Liu 1987, Allen 1989). This is likely to be especially fruitful if some species inhibit or promote the establishment of others, i.e. if inhibition or facilitation mechanisms are occurring (Connell & Slatyer 1977). The transition probabilities for the affected species could then be allowed to vary as a function of the density of the species that either inhibits or promotes it (see Caswell & Cohen 1991 for an example). However, if inhibition is simply by preemption of space, or promotion is via direct acquisition of space from the facilitating species, then the transition probabilities in a standard model already take these processes into account.

In conclusion, the approach presented here, using a family of models with increasing levels of complexity, may hold a great deal of potential for identifying the role of recent history, both in community dynamics and in population dynamics. The models we use have application not only for sessile marine benthos, but can be used for a wide range of both terrestrial and aquatic organisms, especially at the population level (e.g. Usher 1987, Caswell 1989, Tanner et al. 1994). While we have found that history plays only a minor role in structuring the community we studied, this is probably due to the physically harsh environment of the reef crest, where the short life-span of most corals does not allow sufficient time for history to become important. However, elsewhere (e.g. where organisms are longer lived or where priority effects occur, see Wilbur & Alford 1985, Robinson & Dickerson 1987, Robinson & Edgemann 1988, Drake 1991), history is much more likely to play an important role in determining both population and community dynamics.

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**Table 6.1.**

Species groups used in the community models. Seventy-two coral and 9 algal species were categorized into 8 groups to reduce the complexity of the models.

| CODE | Group |
|---|---|
| A | Encrusting Acroporid Corals |
| B | Tabular *Acropora* |
| C | Bushy *Acropora* |
| D | Staghorn *Acropora* |
| E | Soft Corals |
| F | Algae |
| G | Massive Corals |
| H | Pocilloporid Corals |
| I | Free Space |

**Table 6.2.**

Transition probability matrix for the first order model. Columns represent the species group present at time t, and rows the species group present at time t+1. The diagonal, in bold, is the probability of self-replacement. N is the total number of transitions recorded from each group. Species group codes are presented in Table 6.1. (From Tanner et al. 1994).

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| | **0.354** | 0.046 | 0.032 | 0.032 | 0.000 | 0.071 | 0.025 | 0.039 | 0.059 |
| A | 0.021 | **0.314** | 0.005 | 0.004 | 0.003 | 0.014 | 0.000 | 0.000 | 0.014 |
| B | 0.066 | 0.030 | **0.478** | 0.082 | 0.016 | 0.090 | 0.076 | 0.105 | 0.091 |
| C | 0.049 | 0.016 | 0.038 | **0.439** | 0.009 | 0.057 | 0.031 | 0.053 | 0.039 |
| D | 0.001 | 0.005 | 0.005 | 0.004 | **0.835** | 0.005 | 0.011 | 0.000 | 0.014 |
| E | 0.009 | 0.036 | 0.007 | 0.004 | 0.000 | **0.033** | 0.015 | 0.000 | 0.007 |
| F | 0.015 | 0.003 | 0.013 | 0.014 | 0.006 | 0.052 | **0.340** | 0.000 | 0.032 |
| G | 0.002 | 0.005 | 0.001 | 0.001 | 0.000 | 0.000 | 0.000 | **0.224** | 0.004 |
| H | 0.482 | 0.544 | 0.421 | 0.421 | 0.131 | 0.678 | 0.501 | 0.579 | **0.741** |
| I | | | | | | | | | |
| N | 1598 | 366 | 3325 | 1478 | 321 | 211 | 720 | 76 | 12150 |

**Table 6.3.**

Transition probabilities for the semi-markov 2 model. Columns represent the species group present at time t, and rows the species group present at time t+1. The diagonal, in bold, is the probability of self-replacement. N is the total number of transitions recorded from each group. Species group codes are presented in Table 6.1.

a). Transition probabilities for a waiting time of 1 - 2 census intervals.

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| A | **0.341** | 0.052 | 0.037 | 0.035 | 0.000 | 0.068 | 0.026 | 0.043 | 0.067 |
| B | 0.016 | **0.305** | 0.008 | 0.007 | 0.004 | 0.014 | 0.000 | 0.000 | 0.014 |
| C | 0.069 | 0.047 | **0.468** | 0.098 | 0.019 | 0.073 | 0.083 | 0.114 | 0.109 |
| D | 0.046 | 0.022 | 0.043 | **0.424** | 0.012 | 0.068 | 0.036 | 0.057 | 0.051 |
| E | 0.001 | 0.005 | 0.005 | 0.005 | **0.805** | 0.005 | 0.013 | 0.000 | 0.013 |
| F | 0.008 | 0.025 | 0.007 | 0.005 | 0.000 | **0.037** | 0.016 | 0.000 | 0.008 |
| G | 0.016 | 0.005 | 0.016 | 0.016 | 0.008 | 0.050 | **0.324** | 0.000 | 0.031 |
| H | 0.002 | 0.005 | 0.001 | 0.001 | 0.000 | 0.000 | 0.000 | **0.229** | 0.005 |
| I | 0.500 | 0.533 | 0.414 | 0.410 | 0.152 | 0.685 | 0.503 | 0.557 | **0.703** |

Table 6.3 (continued)

b). Transition probabilities for waiting times of greater than 2 census intervals.

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| A | **0.410** | 0.031 | 0.028 | 0.020 | 0.000 | 0.000 | 0.033 | 0.000 | 0.053 |
| B | 0.060 | **0.063** | 0.017 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.017 |
| C | 0.045 | 0.031 | **0.501** | 0.020 | 0.000 | 0.000 | 0.044 | 0.000 | 0.080 |
| D | 0.075 | 0.000 | 0.024 | **0.477** | 0.000 | 0.000 | 0.000 | 0.000 | 0.027 |
| E | 0.000 | 0.000 | 0.004 | 0.000 | **0.905** | 0.000 | 0.000 | 0.000 | 0.018 |
| F | 0.015 | 0.125 | 0.004 | 0.000 | 0.000 | **0.000** | 0.011 | 0.000 | 0.006 |
| G | 0.005 | 0.000 | 0.004 | 0.007 | 0.000 | 0.000 | **0.363** | 0.000 | 0.036 |
| H | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | **0.000** | 0.003 |
| I | 0.390 | 0.750 | 0.419 | 0.477 | 0.095 | 0.000 | 0.549 | 1.000 | **0.759** |

**Figure 6.1.** Effects of history on persistence probabilities. A waiting time of zero corresponds to the first order model (Table 6.2), and waiting times of 1-2 and >2 are from the second semi-markov model (Table 6.3). (A). Taxa which show reductions in survivorship with waiting time. (B). Examples of taxa which show slight increases in survivorship with waiting time.

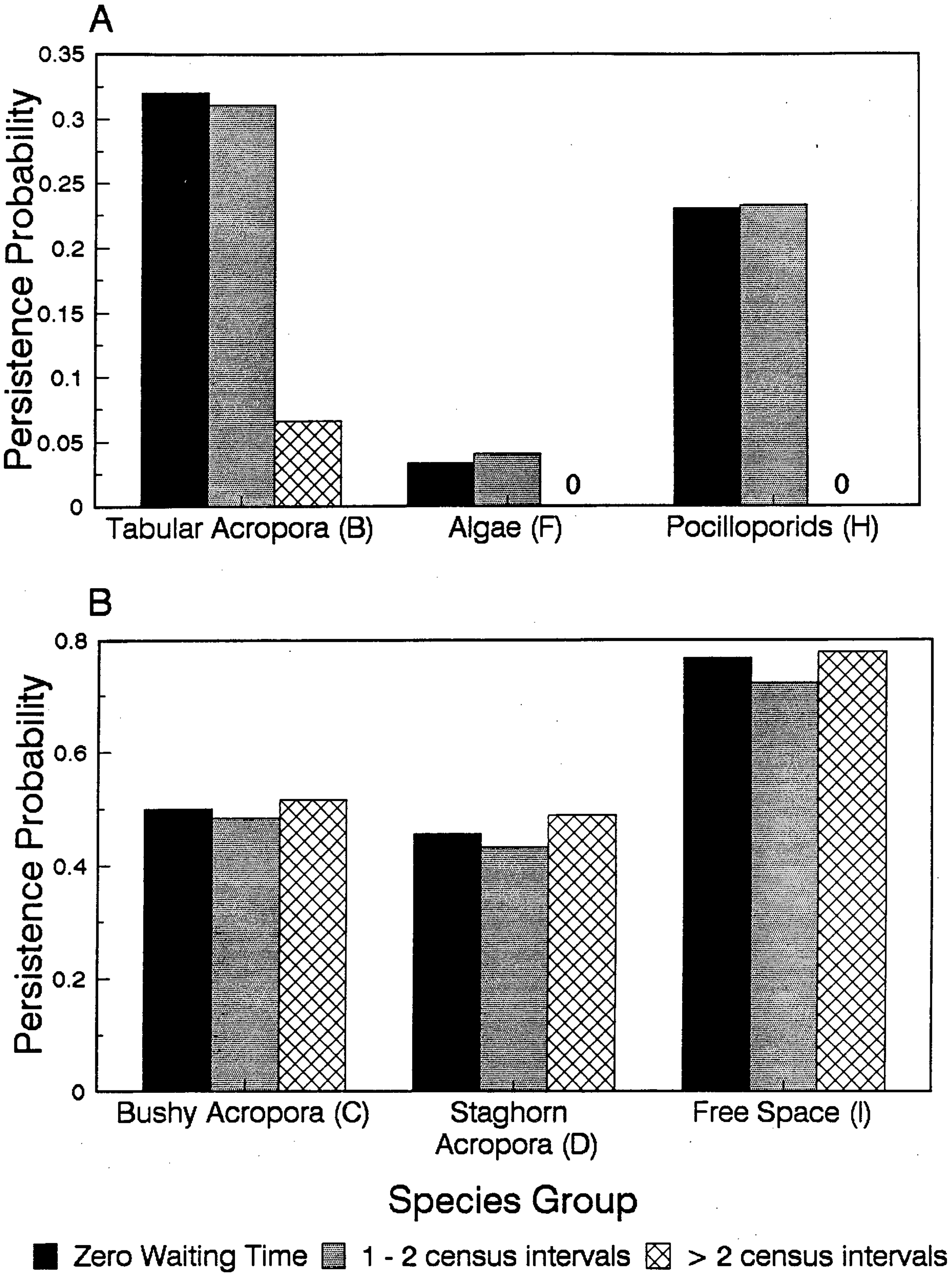

A
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Persistence Probability
0
0
Tabular Acropora (B)
Algae (F)
Pocilloporids (H)
B
0.8
0.6
0.4
0.2
0
Persistence Probability
Bushy Acropora (C)
Staghorn Acropora (D)
Free Space (I)
Species Group
Zero Waiting Time
1 - 2 census intervals
> 2 census intervals

**Figure 6.2.** Simulated abundance of species groups for the first 80 years after a disturbance that totally destroyed the community, using four models incorporating different amounts of history (first order, second order and two types of semi-markov models).

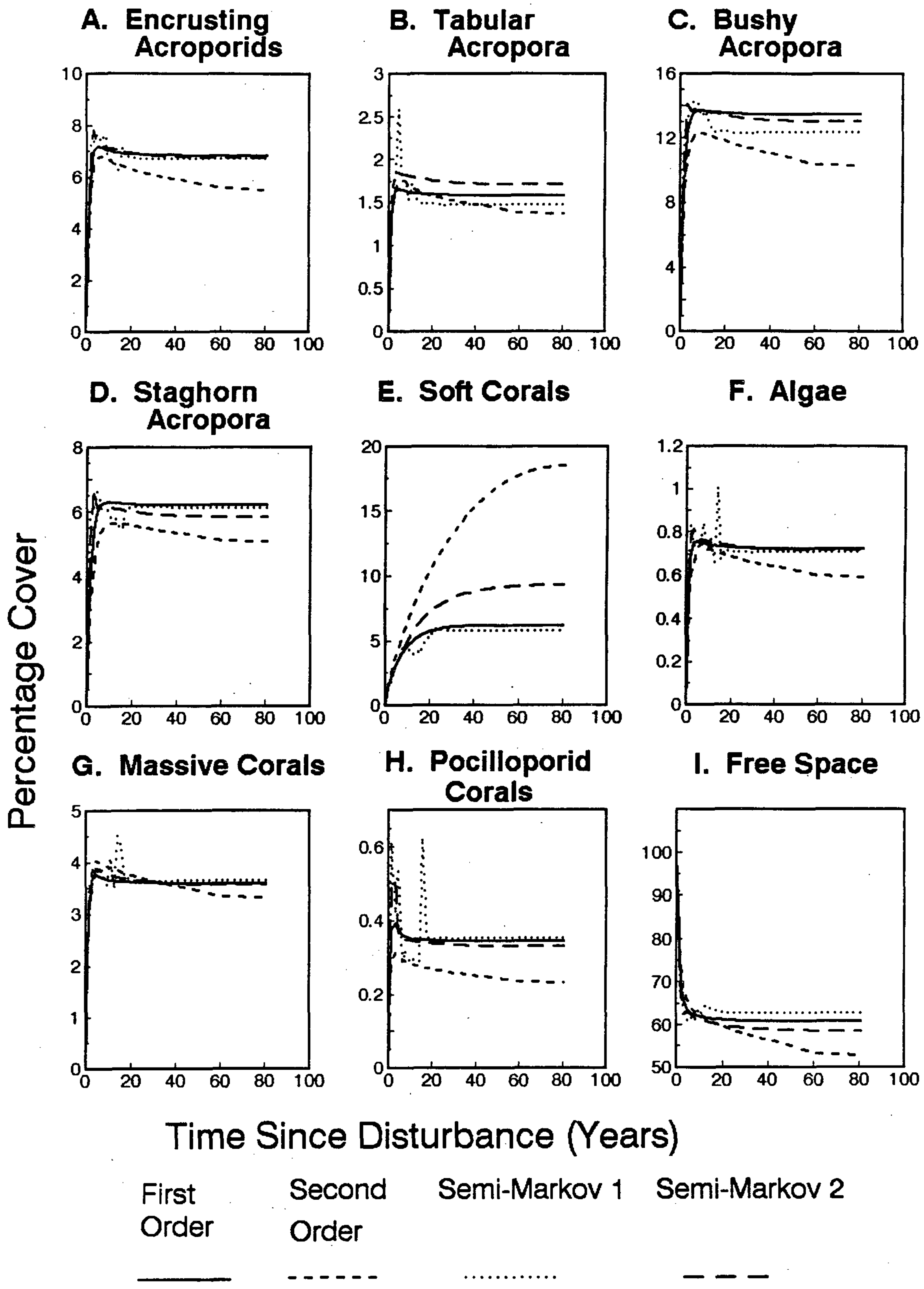
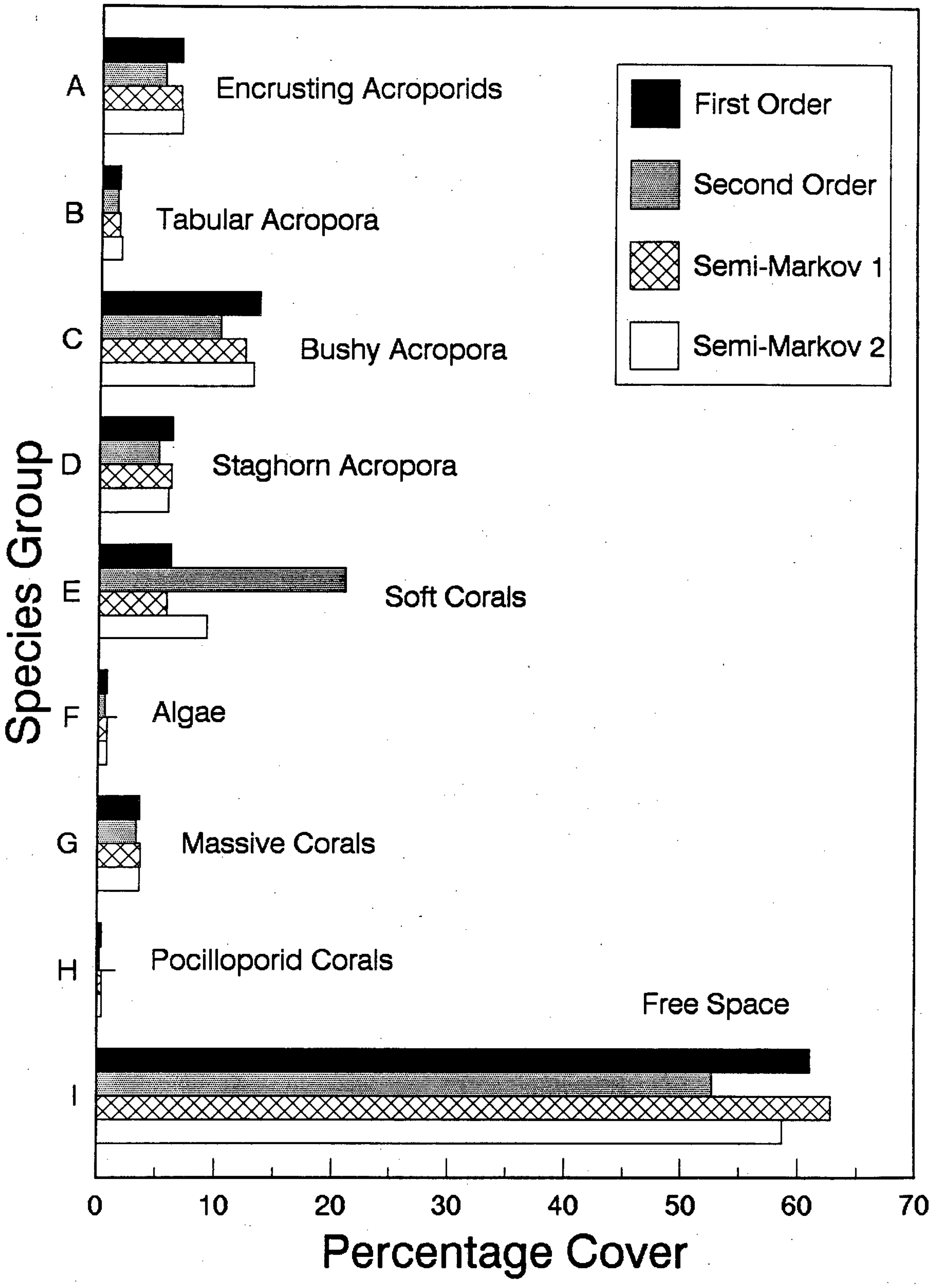

A. Encrusting Acroporids
B. Tabular Acropora
C. Bushy Acropora
D. Staghorn Acropora
E. Soft Corals
F. Algae
G. Massive Corals
H. Pocilloporid Corals
I. Free Space
Percentage Cover
Time Since Disturbance (Years)
0
20
40
60
80
100
First Order
Second Order
Semi-Markov 1
Semi-Markov 2

**Figure 6.3.** Comparison of simulated equilibrium abundances of species groups between model types.


A
Encrusting Acroporids
B
Tabular Acropora
C
Bushy Acropora
D
Staghorn Acropora
E
Soft Corals
F
Algae
G
Massive Corals
H
Pocilloporid Corals
Free Space
I
First Order
Second Order
Semi-Markov 1
Semi-Markov 2
Species Group
0
10
20
30
40
50
60
70
Percentage Cover

# Chapter 7

## General Discussion.

The dynamics of coral assemblages are controlled by a complex interplay of many different factors. In this thesis I have examined just a few of these factors, concentrating on the role of interactions between the biological elements of coral reef benthic communities. This is not to deny the importance of many other processes which I have not discussed, such as the obvious roles that predation (e.g. Cox 1986, Colgan 1987, Turner 1994), herbivory (e.g. Lewis 1986, Hughes et al. 1987, Steneck 1988), depth and light regime (e.g. Wethey & Porter 1976, Burns 1985, Stromgren 1987), water quality (e.g. Smith et al. 1981, Tomascik & Sander 1987, Wittenberg & Hunte 1992), and physical disturbance (e.g. Woodley et al. 1981, Done & Potts 1992, Hughes 1993), to name but a few, play in structuring coral communities.

Competition obviously plays a significant role in determining how both low and high diversity coral assemblages are structured at Heron Island, and is probably important throughout the geographic range of coral reefs. In fact, one of the major hypotheses as to why coral reefs are restricted to tropical and near tropical waters is because of the inability of corals to compete successfully with macroalgae (e.g. Veron 1986). In the tropics, macroalgae tend to be a minor component of benthic ecosystems biomass wise because of the high density of herbivorous fish, which keep algal standing crop low (Hay et al. 1983, 1991, Lewis 1986, Berner 1990). In contrast, herbivorous fish are much less common in temperate waters, allowing macroalgae to maintain much higher standing crops, and to outcompete corals. It has also been demonstrated fairly conclusively that when herbivores are removed from coral reefs, macroalgae proliferate, smothering corals and virtually eliminating them (Lewis 1986, Hughes 1994). In chapter 4, I showed that macroalgae can have a substantial negative impact on scleractinian corals even at natural levels of abundance on a tropical reef. This study was conducted on an intertidal reef flat with algal cover of approximately 50%, which is probably at the higher end of the range for undisturbed tropical coral reefs, but it does show the important consequences that competition with macroalgae can have on many reefs, especially inshore, which do have naturally high levels of macroalgal cover (e.g. Morrissey 1980).

While algal clearance had a significant effect on changes in coral cover (chapter 4), this effect was not consistent across species, with *Acropora* spp. benefiting from the removal of algae, while *Pocillopora damicornis* showed no response. Presumably *P. damicornis* has some means of protecting itself from competition with algae, possibly related to its morphology. This indicates that competition with algae does not impact equally on all members of the community, and that it thus has an important role to play in determining community structure. Even though macroalgae of itself does not directly benefit *P. damicornis,* it does cause a decrease in the cover of *Acropora* spp., which tend to dominate in competitive encounters with *P. damicornis* (e.g. Tanner 1993). Thus, by decreasing the cover of a superior competitor, macroalgae is indirectly benefiting *P. damicornis,* allowing it to maintain a more prominent position in the coral assemblage than might otherwise be possible.

Algae are not the only competitors that can influence coral community structure. The results obtained in chapters 2 and 3 imply that coral-coral competition can also have a significant impact on community structure. In chapter 2, I showed that once coral cover reached about 35%, every coral competed with an average of one other colony. As would be intuitively expected, the mean number of competitors per colony increased with coral cover. It was also found that very few colonies avoided competition totally. This then sets the scene for competition among corals to be an important determinant of community dynamics, as well as for it to have important consequences for every individual colony. The high frequency of competitive encounters, combined with the knowledge that an encounter does have a significant effect on the fitness of the colonies involved, as found in chapter 3, points very strongly to coral-coral competition being an important determinant of coral community structure. This interpretation is further supported by the results of an ongoing experiment at Lizard Island by T.P. Hughes, which has shown that the removal of the scleractinian coral *Acropora hyacinthus* has substantially altered the composition of the shallow reef slope community (T.P. Hughes pers. com.).

The next step in determining the fitness costs of competition for corals is to quantify the reduction in fitness caused by competition. As current technology does not allow individual larvae of most species to be tracked until settlement, fitness cannot be measured directly. However, it is possible to examine the fitness of corals, and similar organisms with open populations, using mathematical models of population dynamics. Once growth rates, mortality rates and reproductive output are known, size-classified matrix models can be constructed which will give population growth rate (reviewed in Caswell 1989). Unfortunately, to get a true estimate of population growth rate, an estimate of larval survival is also needed. If, on the other hand, the aim is simply to compare two different populations, in this case competing and non-competing, an estimate of relative population growth rate may be obtainable without a knowledge of larval survival. This estimate will be based on the assumption that larval survival is the same for both populations, or that the difference in larval survival rates can be estimated from other factors. In the case of marine invertebrates such as corals, an estimate of relative larval survival rates can probably be obtained from a comparison of the mean size of eggs in each population. For the *Acropora hyacinthus* studied in chapter 3, the mean egg size did not vary between competing and non-competing colonies, thus it is likely that larval survival is the same in both groups.

Before any general conclusions can be made, the results found here need to be extended to other species. In particular, the effect that competition has on reproduction in *Pocillopora damicornis*, or some other brooding coral, needs to be investigated. This work is currently underway, although the tendency of *P. damicornis* to exhibit different reproductive patterns at different geographic locations complicates the study of reproduction in this species. Before a comparison of reproduction in competing and non-competing colonies can be made, it is first necessary to determine in what seasons and on what lunar phase *P. damicornis* is releasing larvae at Heron Island. This has been completed as a part of the work described here (Appendix 1), but not in time to sample competing colonies to determine their reproductive output, which will now be done at a later date.

As only two species have been studied here, the response to competition found may not generalise across the whole of the Scleractinia. There is, however, some evidence available that other species do react similarly. In a study of competition between *Pocillopora damicornis* and *Cyphastrea ocellina* in Hawaii, Romano (1990) found that *C. ocellina* halted growth, while *P. damicornis* slowed growth. Similarly, Rinkevich & Loya (1985) have found that intraspecific competition in *Stylophora pistillata* slows growth and reduces reproductive output. It would be interesting also to see how competition influences the biochemistry of corals. Even though growth, and to a certain extent reproduction, are decreased in the short term (i.e. 2 - 3 years), if a corals' energy reserves are being depleted to maintain at least some growth and reproduction, or even just to survive, then the longer term consequences may be even more substantial. Different mechanisms of competition also need to be examined. The interactions studied here consisted of a mix of extracoelenteric digestion, sweeper tentacles, overgrowth and histoincompatability, i.e. the main mechanisms that are employed when two coral come into direct contact with one-another. While it would be nice to know what happens when each mechanism of competition is employed by itself, it is impossible to control the way corals react once they have been brought into contact with one another, thus the mechanisms cannot be kept distinct. It would, however, be possible to study the effects of overtopping without other processes confounding the results, simply by transplanting corals underneath for example table *Acropora*, and comparing their reaction to that of corals transplanted to open habitats, as has been done by Stimson (1985).

Romano (1990) has suggested that *Pocillopora damicornis* can escape from competition by reorienting its growth whenever it comes into contact with another coral. It would be interesting to find out if corals can also escape from competition early in their life by choosing settlement sites that are free from immediate neighbours. This would then allow them a few years of growth early in life, when they would be most susceptible to being totally killed by competitors (e.g. Hughes & Jackson 1985), without having to divert resources to competition. It would, however, be difficult to distinguish between avoidance of existing colonies by larvae, and the inhibition of larval settlement or destruction of new recruits by the existing colony. Either case would result in successful recruits tending to settle in areas free of immediate competitors, but the overall effects on the community could be strikingly different. It is known that recruitment to settlement plates underneath table and staghorn *Acropora* is lower than to settlement plates placed in the open (Fisk & Harriott 1993, Baird 1994), but the reasons for this are not yet clear. In this case, as well as active avoidance by larvae and inhibition by the *Acropora*, settlement could be low simply because reduced waterflow reduces larval supply.

No clear evidence of a successional sequence was found in the shallow reef crest communities studied in chapter 5. Rather, all species recruited early, with most rapidly reaching their peak abundance. There is, however, some suggestion that algae and pocilloporid corals may be regarded as early successional species, as they peak in abundance very early and then decline (Figure 5.2). At the same time, the *Acropora* and soft corals follow the pattern of climax species, with more gradual recruitment and a steady increase to equilibrium abundance. These patterns would tend to fit the tolerance model of succession (Connell & Slatyer 1977), rather than the facilitation or inhibition models. If facilitation were occurring, the climax species would not recruit until after the pioneer species had become established, whereas here they are recruiting at the same time. The inhibition model, on the other hand, states that the pioneer species will inhibit the climax species from recruiting, which again is obviously not what is occurring. While the other species groups follow the expected pattern in their classification as either pioneering or climax species, the massive corals present an anomaly. This group is composed of slow growing species that resist disturbance, and would thus be expected to show a very slow steady increase to equilibrium abundance. Instead, the massive corals show a rapid peak in abundance, after which they decline to their equilibrium, the same pattern as is found for the pioneer species.

The pattern of succession in the models may be blurred somewhat by the pooling of transitions over time, and the disregard paid to any spatial effects. The first is unlikely, as the second order and semi-markov models presented in chapter 6 display much the same patterns as does the first order model in chapter 5. Although these later models do not account fully for temporal variation, they do start to incorporate time effects. The importance of spatial effects is still to be examined, however. This can be done most easily by the use of either cellular automata models (e.g. Molofsky 1994, Sole & Manrubia 1995), or interacting particle system models (e.g. Durrett & Levin 1994 a, b), both of which operate in a spatially explicit framework.

It is not really surprising that no keystone species was found in any of the three coral assemblages studied in chapter 5. Even though keystone species have been found in plant assemblages (e.g. Bazzaz 1984), the high diversity of coral assemblages, and the many ways by which corals interact both directly and indirectly, mean that any keystone species in a coral reef community is unlikely to be a coral itself. Suggested keystone species on coral reefs include crustaceans which inhabit certain species of coral and protect them from predation by *Acanthaster* (Glynn 1990), and herbivorous damselfish which alter the benthic community by encouraging algal growth and thus eliminating corals (Williams 1980, Hixon & Brostoff 1983). The long life span of most scleractinian corals in combination with the frequent occurrence of cyclones, also means that any coral that does act as a keystone species in some areas, is unlikely to do so on the shallow reef crest at Heron Island. However, in more sheltered locations or habitats, such as at the base of the reef slope, or in the lee of continental islands, it is more likely that a keystone species will occur, especially if coral diversity is low.

Although in chapter 6 I find no effect of history on community dynamics, this does not totally rule out history as being important in the community studied. History may still be important for each species population, or even more likely for each colony, without this importance being reflected in community dynamics. Thus it is important that the study of history be extended to both of these levels. The particular habitat chosen for study, the wave-swept, cyclone battered reef crest, is likely to play a large role in my failure to detect any historical effects, as well as being important in preventing any species attaining the status of a keystone, and potentially reducing the importance of succession. Again, studies of less severely disturbed habitats on coral reefs may show that history can be important.

In this thesis, I have shown that interactions between members of coral reef benthic assemblages play an important role in determining community structure. Competition in particular is highly important, probably in most coral communities. Although no keystone species was found at any of the three sites studied, and history was not found to be important at these sites, it remains to be determined how general these results are. There is still much work to do if we are to gain a full understanding of the role of interaction between sessile invertebrates in structuring coral reef communities, although we are starting to plug some of the gaps in our knowledge.

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# Appendix 1

## Lunar periodicity and seasonality in the reproduction of pocilloporid corals.

The research presented in this paper was conducted during my PhD. The purpose was to pinpoint the timing of larval release in *Pocillopora damicornis* so as to be able to determine the effect of competition on reproduction. Unfortunately the work was not completed in time to be able to do this, so it is presented as an appendix rather than a chapter.

Reference: Tanner, J.E. 1996. Lunar periodicity and seasonality in the reproduction of pocilloporid corals. Coral Reefs. In Press.

**Abstract:**

Reproductive seasonality and lunar periodicity of planula release were investigated for the three brooding corals *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata* at Heron Island in the southern Great Barrier Reef. Branch fragments collected from undisturbed colonies in the field were used to determine when planulae were present for all three species, and direct observations of planula release were made on colonies of *Pocillopora* kept in aquaria. All three species displayed marked seasonal variation in reproductive output, with nearly all reproductive activity occurring over the summer months. *Pocillopora* exhibited distinct lunar periodicity in planulation, with planula release occurring around three quarter moon, and no planulae being present in samples collected between new and full moons. *Seriatopora* also displayed lunar periodicity of planula release, although it was not as distinct as for *Pocillopora*, while *Stylophora* did not show any lunar periodicity.

## Introduction:

The timing of reproduction in scleractinian corals has received considerable attention in recent years, especially since the discovery of the mass spawning phenomenon on the Great Barrier Reef in the early 1980's (e.g. Babcock et al. 1994, Harrison & Wallace 1990), and subsequently in the Caribbean (e.g. Wyers et al. 1991, Gittings et al. 1992). With these discoveries, the primary focus of reproductive studies in the Scleractinia switched from brooding species to broadcast spawners. Both broadcast spawning and brooding species tend to exhibit seasonal and lunar patterns in the timing of reproduction (reviewed in Harrison and Wallace 1990). These temporal patterns in reproduction probably have major consequences for many aspects of the life-histories of the participating species, including fertilisation success, juvenile survival, and adult growth and mortality patterns (e.g. see Pennington 1985, Oliver et al. 1988, Pearse & Cameron 1991). For instance, if the energetically costly stages of reproduction take place when energy intake is high, growth may continue unaffected, whereas it may slow down or even stop if energy is required for reproduction when little is available. Determining why these temporal patterns in reproduction have developed is therefore important for the understanding of the ecology and evolution of this group of animals.

It is thought that the mass spawning of corals occurs due to environmental constraints, such as temperature and tidal patterns, which limit the participating species to a couple of days a year for spawning if they are to maximise their reproductive success (Oliver et al. 1988). Other postulated advantages include increased fertilisation success, predator satiation, and increased larval dispersal or retention (Babcock et al. 1986, Oliver et al. 1988, Pearse 1991). Recently, it has also been suggested that an additional advantage of mass spawning is hybridisation between species (Willis et al. unpubl.). Less attention has been paid to the reasons for synchronised larval release in brooding corals.

To examine seasonal and lunar patterns of reproduction in brooding corals, I document patterns of planulation in three species of the family Pocilloporidae at Heron Island in the southern Great Barrier Reef. The three species chosen for study are *Pocillopora damicornis*, *Stylophora pistillata*, and *Seriatopora hystrix*. All three species brood their planulae, and planulate according to lunar phase in at least one location (e.g. Marshall & Stephenson 1933, Atoda 1947a, 1951, Rinkevich & Loya 1979a, b, Stoddart & Black 1985). They also reproduce repeatedly throughout at least part of the year, unlike most broadcast spawning corals, which generally only spawn once a year (e.g. Harrison et al. 1984, Babcock et al. 1986, Harrison & Wallace 1990). These species are also simultaneous hermaphrodites, although small colonies of *S. pistillata* at least may only produce male gametes (Rinkevich & Loya 1979a). At both Heron Island and nearby One Tree Island, *P. damicornis* is known to reproduce sexually (T.P. Hughes pers. com., Benzie et al. 1995).

Lunar periodicity of planula release in scleractinian corals of the family Pocilloporidae, especially *P. damicornis*, has been widely studied throughout the Indo-Pacific (northern Great Barrier Reef: Marshall & Stephenson 1933, Harriott 1983; Palau: Atoda 1947a, b, 1951; Hawaii: Harrigan 1972, Jokiel 1985, Jokiel et al. 1985; the Red Sea: Rinkevich & Loya 1979a, b; Enewetak: Richmond & Jokiel 1984; central GBR: Muir 1984; Western Australia: Stoddart & Black 1985). While most of the studies on *P. damicornis* have documented lunar periodicity in planula release, the patterns are not consistent between locations, and may even differ between different morphs within the same location. For example, in Hawaii, one morph of *P. damicornis* displays peak planula release between first quarter and full moon, while another peaks around three quarter moon (Richmond & Jokiel 1984). These phase differences occurred in corals collected from the same site, and so are probably genetic not environmental. Similar differences occur between different morphologies of *P. damicornis* in the central GBR (Muir 1984). Such sympatric differences in reproduction may indicate that cryptic speciation has occurred, or is in the process of occurring (e.g. Richmond & Hunter 1990), although this has yet to be thoroughly examined.

Seasonal patterns of planula release in *P. damicornis* also vary between locations. At Lizard Island and Low Isles, in the northern Great Barrier Reef, *P. damicornis* planulates heavily on the full moon over winter, and sparsely on the new moon over summer (Marshall & Stephenson 1933, Harriott 1983). This seasonal pattern is reversed in Western Australia, where planulation only occurs over summer, predominantly just before new moon (Stoddart & Black 1985). In Hawaii, Enewetak, and Palau, however, planulation occurs year round, with no seasonal phase shifts in lunar period as described above for Lizard Island (e.g. Atoda 1947a, Harrigan 1972, Richmond & Jokiel 1984). In the eastern Pacific, there is no evidence that *P. damicornis* planulates at all (Richmond 1985, 1987, Glynn et al. 1991), and reproduction is by hermaphroditic broadcast spawning (Glynn et al. 1991), and asexual fragmentation (Glynn 1976, Richmond 1987). *P. damicornis* has also been inferred to broadcast spawn in Western Australia (Ward 1992), where there is evidence that brooded planulae are also produced asexually (Stoddart 1983).

The pocilloporid coral, *S. pistillata*, also shows different patterns of reproduction at different locations, although it has not been as well studied as *P. damicornis*. In Palau, *S. pistillata* shows lunar periodicity in planula release, with reproduction occurring year round (Atoda 1947b). In contrast, in the Red Sea there is no lunar periodicity in planula release, and reproduction only occurs during summer (Rinkevich & Loya 1979b). At Lizard Island in the northern GBR, *S. pistillata* also only reproduces over summer (Loya 1983), but its lunar periodicity has not been documented.

## Methods:

This study was conducted at Heron Island, a coral cay at the southern end of the Great Barrier Reef, Australia (23° 26' S, 151° 55' E). To determine seasonal trends and lunar periodicity in planula presence in pocilloporid corals, single branch fragments from approximately five colonies of each of *P. damicornis*, *S. pistillata* and *S. hystrix* were collected daily during early to mid-afternoon, from the reef slope on the southern side of Heron Island reef in 5-10 metres of water. All colonies sampled were greater than 15 centimetres in diameter. Within each sampling period (Table A1), fragments were collected from different colonies to minimise the possibility of colonies being sampled after ejecting larvae due to stress from collecting damage to the colony. All fragments were collected from colonies of similar morphology, and only the section approximately 3 to 5 centimetres below the branch tip was kept, to avoid sterile areas and areas of low fecundity at the tips of the branches (Harrigan 1972, Stimson 1978). Fragments were immediately placed in sealed containers, and transported back to the laboratory, where they were placed in 10% formalin seawater for 24 to 48 hours. They were then transferred to a solution of 10% hydrochloric acid and 5% formalin for decalcification. After two to three days, when decalcification was complete, all samples were preserved in 75% alcohol. Each sample was examined under a dissecting microscope for the presence of mature planulae, which could easily be seen without the need for dissecting or histological examination. To compare the sizes of mature planulae between species, five polyps from each of nine randomly chosen samples containing mature planulae were dissected and their planulae counted and measured. Mature planulae were defined as those having developed mesenteries. Sampling commenced in February 1992, and continued intermittently until March 1994 (see Table A1 for sampling periods). In total, 1973 fragments of *P. damicornis*, 1420 of *S. hystrix*, and 1430 of *S. pistillata* were collected and examined for the presence of planulae.

To examine the timing of planula release directly, ten colonies of *P. damicornis* 15 to 20 cm in diameter were maintained in separate flow-through aquaria between 17 March and 27 September 1993, 28 October and 10 December 1993, and 17 February and 26 March 1994. The outflow of each aquarium passed through a sieve of terylene cloth, mesh size approximately 300 µm, which retained any larvae that were released. These colonies were replaced every two to six weeks so that only healthy colonies were being examined. The number of larvae released by each colony was counted every morning, as planulation only occurred during the night.

To determine the lunar periodicity of planula presence and release, data for the entire study period were pooled according to lunar day for both the fragment collections and live colony observations. Rayleigh's test (Zar 1984) was then used to test the null hypotheses that planula presence and release were uniformly distributed throughout the lunar cycle. If the null hypothesis was rejected, the mean lunar day of planula presence or release was then calculated using circular statistics (Zar 1984), to determine in what phase of the moon reproduction was predominant.

## Results:

Planula presence in fragments:

All three species showed marked seasonality in reproduction, with the presence of planulae being common over the summer months, and rare or nonexistent over winter (Figure A1). On average, *S. pistillata* and *S. hystrix* had considerably higher incidence of planula presence than did *P. damicornis*, with peaks in planula abundance for the former two species being both higher and lasting longer than the latter. While a few samples of all three species collected over winter did contain planulae, these were isolated occurrences, with all other samples collected that day, and several days before and after, totally lacking planulae.

*Pocillopora damicornis* generally contained planulae during the third lunar quarter, and planula release occurred predominantly around lunar days 23 and 24 (Figure A2), where lunar day one is new moon. The mean lunar day of planula presence for this species was 20.5 with an angular deviation of 4.4, and the clustering of planulae around this day was highly significant (Table A3). Of the 1973 samples of *P. damicornis* collected, only 84 (4.3%) contained larvae. Throughout the two years of the study 48 samples were collected on lunar day 22, the day with the most samples containing larvae, and only ten (21%) of these contained planulae. For each of lunar days 2 to 14 and 27 to 29 (approximately between new moon and full moon), only one or two samples in total contained larvae. The outlying peak on day 1 (full moon) was a result of 5 out of 50 samples containing larvae, with these samples all being collected in different months. All planulae detected were fairly large (mean diameter ± SE = 879 ± 21 μm). At most, only two planulae were ever found per polyp, with greater than 99% of fecund polyps containing only one planula. Even in the most fecund samples, fewer than 20% of polyps contained planulae.

*Seriatopora hystrix* showed less variation in planula presence within the lunar cycle than did *P. damicornis*. There were, however, more planulae present around full moon than at other times of the month, with the mean lunar day of planula presence being 15.0 ± 6.1 (Figure A2, Table A3). Of the 1420 samples collected, 261 (18.4%) contained planulae, substantially more than the 4.3% for *P. damicornis*. Greatest planula presence occurred on lunar day 9, when 10 out of 20 samples contained planulae, with another peak occurring on day 15 (full moon) with 15 out of 34 (44%) samples having planulae. These two peaks are separated by an unexplained dip, with only 3 of 28 samples having larvae on day 12. This dip makes it difficult to determine when planula release occurs, although the most likely times are just after quarter moon and just after full moon. The presence of larvae between days 21 and 6 (i.e. approximately one week either side of new moon), is variable but relatively low, although at least 10% of samples contained planulae on any lunar day. Planulae were only 72% of the size of those of *P. damicornis*, having a mean diameter of 633 ± 15 μm, but showed a much greater variation in development state. In contrast to *P. damicornis*, many *S. hystrix* polyps contained two planulae, with the maximum recorded in a single polyp being 4, and approximately 90% of polyps in the most fecund samples contained planulae.

Unlike the other two species, *S. pistillata* failed to show any lunar periodicity in planula presence within the polyps, with the null hypothesis of planulae being uniformly present throughout the month not being rejected at $\alpha = 0.05$ (Table A2). However, planula presence in the lunar fourth quarter did tend to be lower than for the rest of the month (Figure A2). A total of 289 out of 1430 samples (20.2%) collected over two years contained larvae. The greatest proportion of samples of *S. pistillata* with planulae were collected on lunar day 6 (58 %), and again, more than 10% of samples collected on any lunar day had planulae. The overall pattern for *S. pistillata* is closer to that of *S. hystrix* than it is to *P. damicornis*. The number of planulae per polyp ranged between one and eight, although most polyps only contained two. *S. pistillata* had the smallest planulae of the three species, with a mean diameter of 556 ± 11 μm, this being 63% of the size of *P. damicornis* larvae and 88% of those of *S. hystrix*. In the most fecund samples, 80 - 90 % of polyps contained planulae.

Direct observations of planula release:

Planula release by *P. damicornis* kept in aquaria showed very similar patterns to the material collected in the field. Again, planulae were released predominantly over the summer months (Figure A3), with only three planulae released from mid April to mid September, while 12755 were released over the summer. Even at times of peak planula release, there were between two and nine colonies (out of ten), which did not planulate during the entire period of planulation, which usually lasted about 7 to 10 days. Those colonies which did planulate during a given episode tended to release a small number of larvae several days before and after the peak in release, with all corals peaking over the same one or two nights. This pattern is shown by the peak on the 21st September 1993 (Figure A3), which was produced by a single colony which planulated over 12 nights. On peak nights, a mean of about 200 larvae were released per colony, although most were contributed by only one or two colonies. The maximum number of larvae released by a single colony on any one night was 765, with this colony releasing a total of 1374 larvae over eleven nights. The largest release of larvae by a single colony over consecutive nights was 2172 over nine nights.

The lunar distributions of both number of planulating colonies and number of planulae released are highly non-uniform (Table A3, Figure A4), with both means lying around lunar day 23 (three quarter moon). Peak larval release occurred on lunar day 25, when 2310 larvae out of a total 12758 (18.1%) were released. In total, 46% of planulae were released between days 22 and 24. Fewer than ten larvae were released on each of lunar days 2 to 16 (between new and full moons), over the entire year of sampling, except for one colony which peaked at 576 larvae released on the 21st September 1993 (lunar day 7). The number of colonies planulating on each lunar day is more spread out than the number of larvae released, although hardly any colonies released planulae between new and full moons (Figure A4). The greatest number of colonies releasing planulae was recorded on lunar day 22, when 23 out of a total of 90 colonies (26%), released at least 1 planula. Mean larval release reached a maximum on lunar days 25 and 26, with a mean ± SE of 122 ± 50 and 123 ± 36 larvae released respectively.

## Discussion:

### Temporal variation in planulation:

Planulation in *P. damicornis* is clearly related to lunar phase, with both fragment collections, and planula release from colonies held in aquaria, showing that planulation peaks between three quarter and new moon. The sudden decrease in planula presence just before new moon is due to the release of planulae, but the sudden increase on full moon is more difficult to explain. Samples collected prior to the full moon almost invariably lacked planulae, although those under 100 - 200 µm in diameter would not have been detected. Those samples collected after full moon, however, did sometimes contain planulae, and these planulae were almost fully developed (at least 500 µm in diameter). This leaves the question of why no intermediate stages of development (which were seen in *S. pistillata* and *S. hystrix*) were found, a situation in common with other studies which have looked for planulae within individual *P. damicornis* polyps (e.g. Harriott 1983, Muir 1984). Muir (1984), has suggested that planulae differentiate rapidly from pharyngeal bodies, based on a correlation between the presence of planulae and the presence of pharyngeal bodies several days previously. In the present study, however, the presence of pharyngeal bodies showed no lunar periodicity or seasonality, and there was thus no correlation between their presence and the presence of planulae several days latter (unpublished data).

Both *S. hystrix* and *S. pistillata* showed sudden decreases in planula presence between quarter and full moons, with subsequent rapid increases around full moon. This dip may indicate that they were releasing planulae just prior to full moon, with some colonies then rapidly maturing a new batch, with the difference between these two species and *P. damicornis* being that the former retain their planulae longer after the initial period of rapid development than does the latter. The subsequent decline from the full moon peak would then be due to some colonies which completed planula release a few days later than most of the population. Such desynchronisation has been found to occur in colonies which have been injured, or are severely affected by competition (Rinkevich & Loya 1985, 1989). Alternatively, these two species may each have two distinct populations in the study area, with no obvious morphological differences between each population, and one population planulating approximately one week after the other.

In addition to temporal variation at the scale of lunar months, there is also an obvious seasonal component to reproduction in all three species, with planula release occurring almost exclusively over summer. This trend is very similar for all three species, with the reproductive season extending from September / October to April, and only isolated colonies containing planulae during the winter.

Spatial variation in planulation: comparisons with previous studies:

The lunar and seasonal patterns of reproduction in *P. damicornis* at Heron Island are similar to those in southern Western Australia (Stoddart & Black 1985), where planula production peaks on lunar day 27, compared to day 25 at Heron Island, and only one of approximately 200 colonies sampled planulated during the winter. The reproductive season in Western Australia was several months shorter than for Heron Island (Stoddart & Black 1985), with March being the only month with high levels of planula release (Ward 1992). Seasonality in planulation at Heron Island and Western Australia (both southern locations), is in contrast to Lizard Island in the northern Great Barrier Reef, where *P. damicornis* planulates predominantly during the winter months on the full moon, with summer activity being restricted to small numbers of planulae released on the new moon. This phase shift has also been found at nearby Low Isles (Marshall & Stephenson 1933). In the central Great Barrier Reef, Muir (1984) found planula release in two different morphs at Magnetic Island to occur during the lunar first and third quarters, which is distinct from other records in Australia, but shows similar periodicity to corals in Enewetak and Hawaii (Richmond & Jokiel 1984). The lunar pattern of planulation at Heron Island is also approximately the same as that for Palau (Atoda 1947 a) and Hawaii type Y (Richmond & Jokiel 1984), however, planulation occurs year round at these later locations.

*Stylophora pistillata* at Heron Island lacks lunar periodicity in planula presence, as it does in the Gulf of Eilat, Red Sea (Rinkevich & Loya 1979 b). In contrast, in Palau planulation occurs between full and new moons (Atoda 1947 b). Seasonal planulation in *S. pistillata* at Heron Island is also similar to the Gulf of Eilat (Rinkevich & Loya 1979b), and Lizard Island in the northern Great Barrier Reef (Loya 1983). Again, however, the pattern of seasonality observed in the current study differs from Atoda's study (1947b) in Palau, where *S. pistillata* reproduced year round.

*Seriatopora hystrix* shows the same lunar pattern of planula presence at Heron Island as it does in Palau (Atoda 1951), the only other location where its lunar periodicity has been studied. *S. hystrix* is only reproductively active during the summer months at Heron Island, whereas in Palau it planulates year round (Atoda 1951). Sammarco (1982), found peak planulation in this species to occur in November in the central Great Barrier Reef (18° - 19° S), with only 0 - 3 larvae released per colony at other times of the year. Peak planulation at Heron Island may also occur during November, but there are at least moderate numbers of planulae present in the polyps during February / March. Whether the planulae present in February / March are released or resorbed is unknown, however, some of these planulae appeared to be highly developed and ready for release, making their resorption improbable.

## Causes of temporal and spatial variation in reproduction:

Seasonal variation in reproductive output is most probably related to changes in water temperature, with differences in seasonality between locations being due to latitudinal variation in water temperature. The optimum temperature for reproduction in *P. damicornis* at Hawaii was 26 - 27 °C, and fecundity dropped rapidly once this temperature was exceeded by even 1 °C (Jokiel & Guinther 1978). While populations in other locations are likely to have developed different temperature optima for reproduction, this result from Hawaii does suggest that it is possible for water temperature to become too high for reproduction. At Heron Island, and in southern Western Australia, winter water temperatures fall substantially below 20°C, thus accounting for the lack of winter reproduction, while the summer peaks are 29°C and 26°C respectively (Stoddart & Black 1985, Lough 1994, M. Preker pers. com.). At Lizard Island, however, summer temperatures exceed 30°C, while water temperature in winter is around 24 - 25°C (Wolanski & Pickard 1985, Lough 1994). Thus, summer temperatures are probably near optimal for reproduction at higher latitudes such as Heron Island and southern Western Australia, but too warm at Lizard Island, while winter temperatures in southern locations are too cold, but may be near optimal in more equatorial areas. Reproduction in all three species at Palau is year round, as would be expected from Palau's location near the equator (7.5° N), which probably results in minimal seasonal variation in water temperature (e.g. Gross 1987). Similar patterns, with shorter breeding seasons as latitude increases, are also displayed by many other scleractinian species (Harrison & Wallace 1990). Studies on echinoderms have also shown latitudinal gradients in reproductive seasonality, with the patterns for some species being similar to those described here for *P. damicornis*, with both minimum and maximum temperatures for reproduction (reviewed in Pearse & Cameron 1991). Low temperatures may inhibit reproduction by increasing development time (e.g. Pearse et al. 1991), which would result in larvae spending more time in the plankton where mortality is generally considered to be high, thus decreasing reproductive success. At high temperatures on the other hand, gametes may not be viable. Light levels and food availability have also been shown to determine reproductive seasonality in some echinoderms (Pearse & Cameron 1991). Irradiance may be particularly significant in determining the reproductive season of zooxanthellate scleractinian corals, with lower levels over winter being insufficient to meet the corals energy requirements if it is to reproduce.

The reasons for lunar periodicity in planula release are less obvious than for seasonality. Lunar cycles in spawning for broadcast spawning corals may allow them to cue into neap tides (e.g. Oliver et al. 1988, Babcock et al. 1994), but this does not appear to be the case for *P. damicornis*. At Lizard Island, spawning occurs on the spring tides in both summer and winter, despite the change in lunar periodicity between seasons (Harriott 1983). In the central GBR however, spawning occurs at either quarter or three quarter moon (Muir 1984), which corresponds to the neap tides, as does planulation at Heron Island. The main hypothesised benefit of spawning on neap tides is that gametes are kept together for an extended time, increasing fertilisation rates (e.g. Babcock et al. 1986), a factor that is obviously of little importance to the release of already fertilised planulae. It is more likely that the periodicity in release of larvae is a result of earlier periodicity in spawning of male gametes, and a fixed maturation time for larvae, as occurs in the Caribbean *Favia fragum* (Szmant-Froelich et al. 1985). Male gamete release may be cued to lunar phase to take advantage of tides either for increased or decreased dispersal, or it may simply be a convenient way to ensure male gametes are only released when female gametes are mature and ready to be fertilised. Studies on echinoderms have shown that increasing the number of males releasing sperm at any one time more than proportionally increases fertilisation rates (e.g. Pennington 1985), and this may be of even greater importance to corals which cannot move in order to spawn near a potential mate.

Interspecific Comparisons:

One of the most interesting differences between the three species studied here is the low percentage of *P. damicornis* colonies with planulae present. While this might initially suggest that *P. damicornis* is much less fecund than the other two species (especially as it also contains fewer planulae per polyp and has a lower proportion of fertile polyps), the rapid development rate of *P. damicornis* planulae may reduce this difference. The tight synchronisation of the presence of mature planulae, and their rapid appearance, indicate that in *P. damicornis* planulae are only present for a few days. *S. pistillata* and *S. hystrix* on the other hand, do not display such tight synchronicity, and this may be due to mature planulae residing in the polyps for longer, thus inflating the number of colonies found with planulae.

The peaks in planulation of *P. damicornis* on the 8th November 1993 and 2nd December 1993, and the peaks in planula presence in samples, coincided with the coral mass spawning event at Heron Island. In 1993, the mass spawning was split over two months, with some corals releasing gametes around the 7th November, but most spawning between the 4th and 6th of December (pers. obs.), these being lunar days 24 and 20 to 22 respectively. *S. hystrix* on the other hand, failed to show much activity around the time of the November spawning, but showed a broad peak in planula presence just prior to the December spawning episode. *S. pistillata* was similar to *S. hystrix*, with no reproductive activity in early November, and a broad peak from mid-November to mid-December, which encompassed the December mass spawning. Thus *P. damicornis* especially would presumably gain the benefit of predator satiation (e.g. Harrison et al. 1984) associated with releasing planulae during the mass spawning. It is doubtful that this plays a major role in determining the lunar periodicity of planulation however, as this benefit will only occur once, or occasionally twice, a year, whereas *P. damicornis* planulates monthly between September and April at Heron Island, and for even longer periods elsewhere.

## Conclusions:

The results of this study are in agreement with previous studies (e.g. Stoddart & Black 1985), which suggest that latitude, and thus probably water temperature, are major factors determining seasonal variation in reproduction of brooding corals, especially *P. damicornis*. The reasons for lunar periodicity in planulation, however, are still unclear, although the most probable explanation is that it is a function of lunar periodicity in male gamete release to ensure maximum fertilisation. Although *P. damicornis* participates in the mass spawning at Heron Island, its brooding mode of reproduction means that it is unlikely to do so for the same reasons as proposed for broadcast spawning species. Further work to confirm the timing of planula release in *S. hystrix* and *S. pistillata*, and other closely related species, would help in determining the reasons for lunar periodicity in planulation. For instance, if all species planulate at different times at the same site, it would suggest that environmental factors affecting larval survival are not the ultimate cause of lunar periodicity, but rather that synchronicity is aimed at increasing fertilisation success. If all species planulate at the same time, then environmental parameters, such as tidal movements and predation, are much more likely to be important, as differences between locations within a single species all but rule out phylogenetic constraints on the timing of reproduction.

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**Table A1:** Sampling periods for collection of Pocilloporid fragments.

| *Pocillopora damicornis* | *Stylophora pistillata* / *Seriatopora hystrix* |
|---|---|
| 10.2.92 - 7.3.92 | 10.2.92 - 7.3.92 |
| 30.4.92 - 31.7.92 | 30.4.92 - 5.6.92 |
| 16.8.92 - 29.9.92 | 16.8.92 - 29.9.92 |
| 6.11.92 - 24.12.92 | 6.11.92 - 24.12.92 |
| 21.3.93 - 15.4.93 | 21.3.93 - 15.4.93 |
| 9.6.93 - 1.9.93 | 9.6.93 - 16.7.93 |
| 29.10.93 - 8.12.93 | 29.10.93 - 8.12.93 |
| 17.2.94 - 18.3.94 | 17.2.94 - 18.3.94 |

**Table A2:** Test for uniformity of lunar distribution of Pocilloporid fragments containing planulae. z is the test statistic (Rayleigh's Test, Zar 1984), and n is the number of fragments containing planulae.

| | *Pocillopora damicornis* | *Stylophora pistillata* | *Seriatopora hystrix* |
|---|---|---|---|
| Mean lunar day | 20.5 | 19.7 | 16.0 |
| Angular deviation | 4.4 | 6.2 | 6.1 |
| z | 25.59 | 2.644 | 4.722 |
| n | 84 | 289 | 261 |
| Probability of a uniform distribution | $P << 0.001$ | $0.05 < P < 0.1$ | $0.005 < P < 0.01$ |

**Table A3:** Test for uniformity of lunar distribution of planulating colonies and number of planulae released by *Pocillopora damicornis* in flow through aquaria. z is the test statistic (Rayleigh's Test, Zar 1984), and n is the number of planulating colonies or number of planulae released.

| | Number of Planulating Colonies | Number of Planulae Released |
|---|---|---|
| Mean lunar day | 22.9 | 23.6 |
| Angular deviation | 4.0 | 4.0 |
| z | 87.20 | 4972 |
| n | 217 | 12758 |
| Probability of a uniform distribution | $P << 0.001$ | $P << 0.001$ |

**Figure A1:** Planula presence in fragments of three species of pocilloporid coral during the period 10th February 1992 to 18th March 1993. Data has been pooled within calender months and across years.

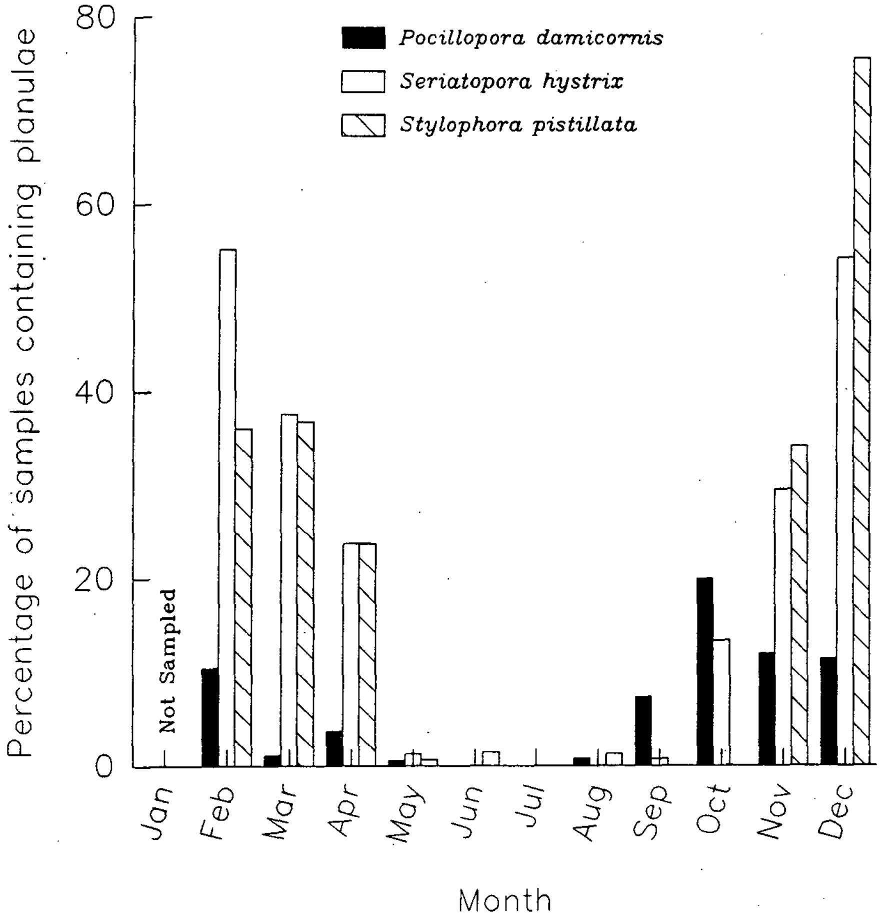
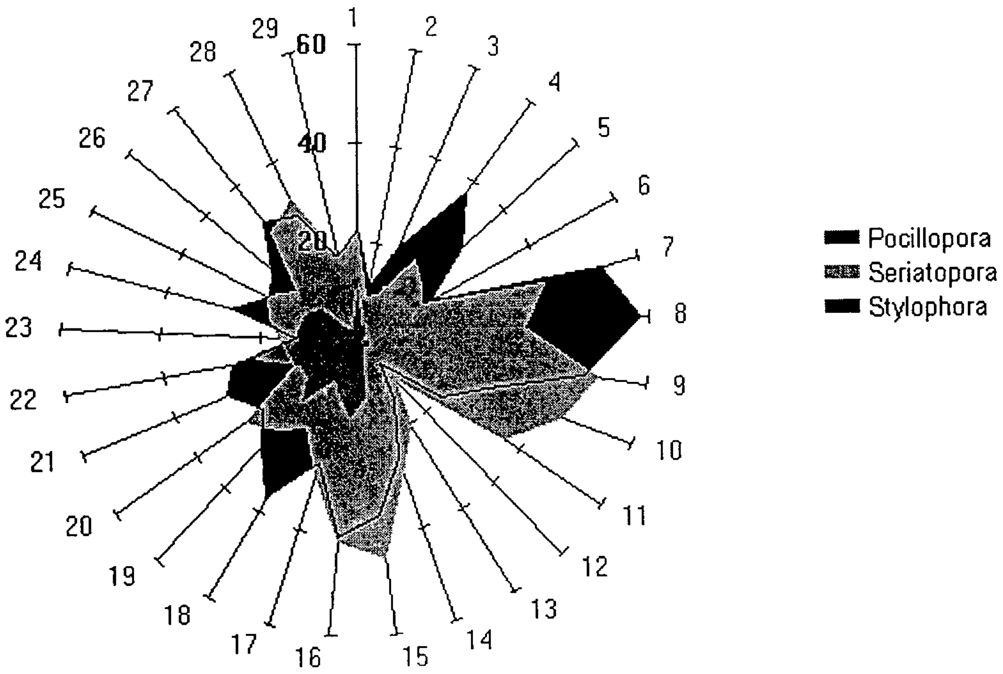

Pocillopora damicornis
Seriatopora hystrix
Stylophora pistillata
Percentage of samples containing planulae
0
20
40
60
80
Not Sampled
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

**Figure A2:** Lunar periodicity of planula presence in three pocilloporid species, expressed as percentage of fragments collected on each day which contain planulae. Data for each lunar month in the period 10th February 1992 to 18th March 1993 are pooled. Numbers in bold are axis labels (i.e. the percentage of fragments with planulae). Numbers around the circumference indicate lunar day (day 1 = new moon).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Pocillopora
Seriatopora
Stylophora

**Figure A3:** Planula release from colonies of *Pocillopora damicornis* kept in aquaria during the period 8th March 1993 to 26th March 1994. Horizontal lines at the base of each graph indicate periods in which planulation was monitored.

**A.** Number of colonies (out of ten), planulating on any day.

**B.** Total number of planulae released on each day.

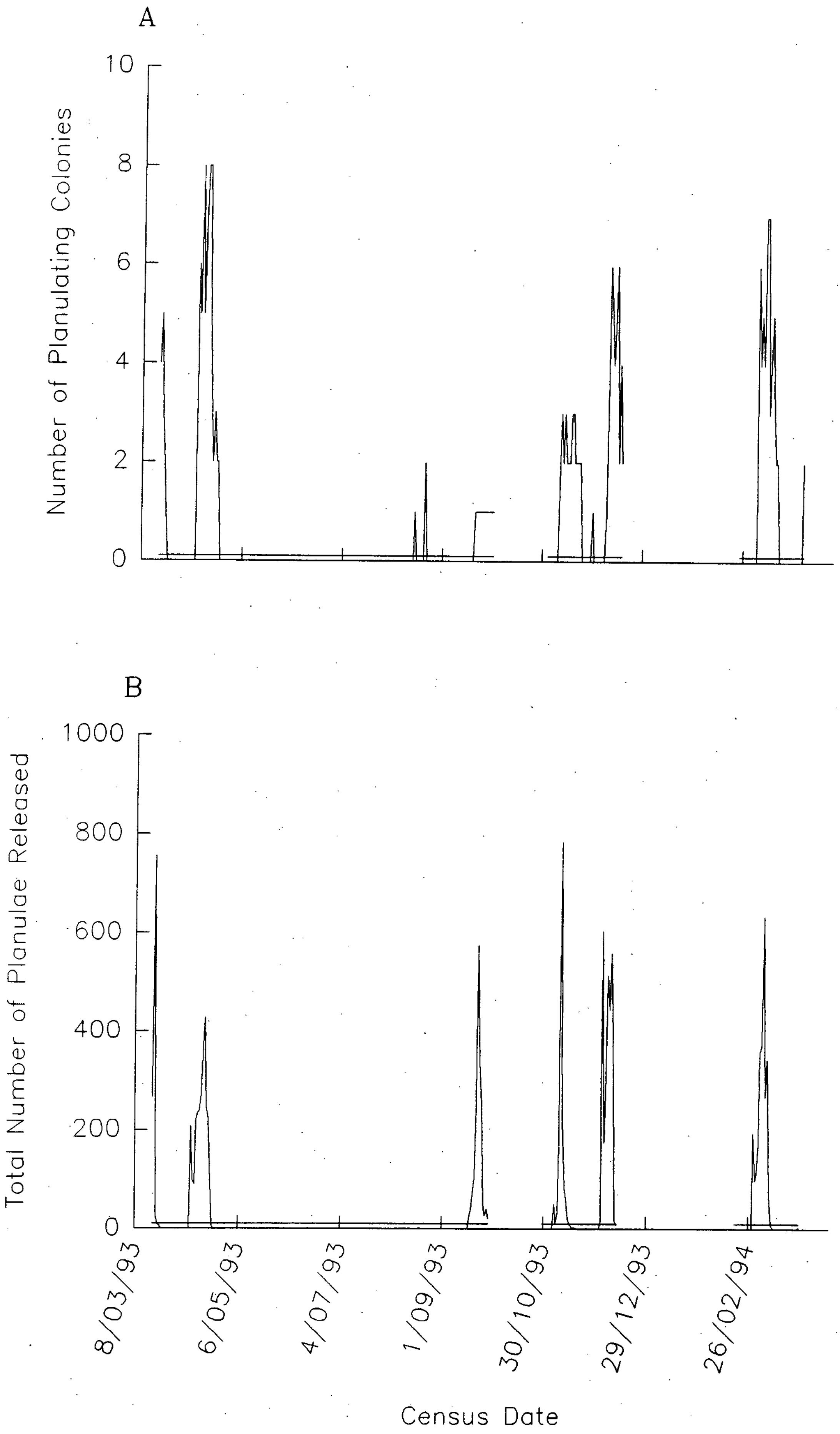
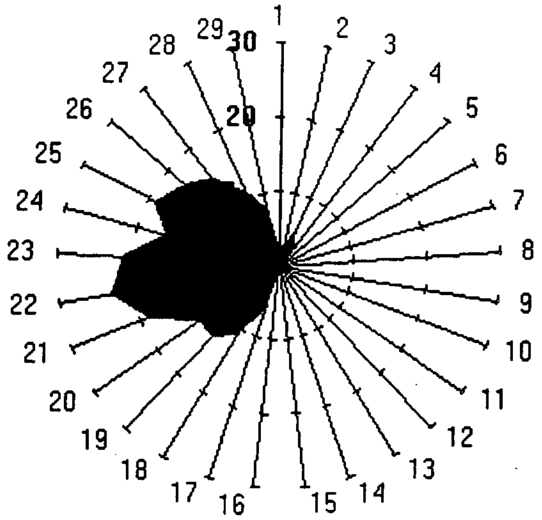

A
Number of Planulating Colonies
10
8
6
4
2
0
B
Total Number of Planulae Released
1000
800
600
400
200
0
8/03/93
6/05/93
4/07/93
1/09/93
30/10/93
29/12/93
26/02/94
Census Date

**Figure A4:** Lunar periodicity in planula release of *Pocillopora damicornis* kept in aquaria. Data for each lunar month are pooled. Numbers in bold are axis labels (i.e. the number of colonies planulating or the number of planulae released). Numbers around the circumference indicate lunar day (day 1 = new moon).

**A.** Number of colonies planulating on any one lunar day.

**B.** Total number of planula released on each lunar day.

A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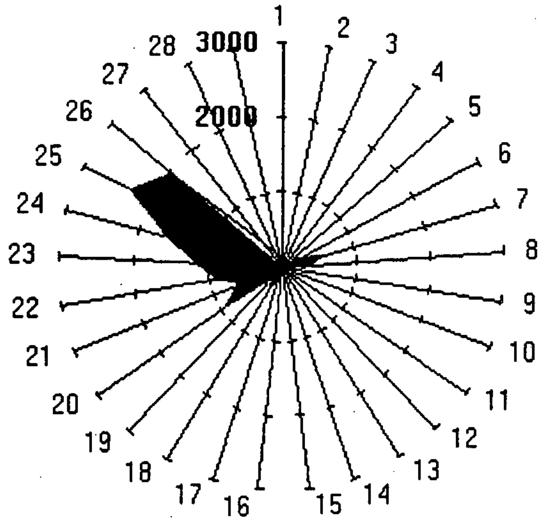
B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