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Empire Building Colonials:
The Implications of Size in the Hard Coral

*Plesiastrea versipora*

Karen J. T. Withers

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

Marine Studies Centre/School of Biological Sciences
The University of Sydney

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Statement of Originality

The work embodied in this thesis is the result of my own investigation, and has not previously been submitted for the award of a degree at any institution.

Karen J. T. Withers
Abstract

This is the first comprehensive study of the population biology of a hard coral living in a temperate environment and one of few on the population biology of a coral with a sheet-like morphology. This study was done on *P. versipora* in Sydney Harbour, Australia.

The primary model around which my study was built was that the biology of colonies changes as they grow, such that smaller colonies have faster growth, poorer rates of regeneration and are more likely to die than larger colonies. This is because larger colonies occupy more space and have more total resources than smaller colonies. Consequently, larger colonies are more likely to be injured, have slower growth per unit area, greater fecundity, a greater ability to repair themselves and are unlikely to die. This model was derived from models proposed by Jackson (1979). The second model investigated in this study was that the size-frequency distribution of a population can be used to predict the sizes at which the biology of colonies is likely to change. Both these models were generally upheld by the results of my study.

Colonies ranged in size from smaller than 0.8 mm$^2$ to larger than 1500 cm$^2$; however, the sizes at which the biology of colonies changes are relatively small. The start of reproduction and greatest increase in survivorship of colonies occurs when they are larger than 5 cm$^2$, the greatest amount of damage occurred on colonies that were 20 to 100 cm$^2$, and colonies larger than 120 cm$^2$ were most likely to be fecund. However, contrary to the model, colonies larger than 100 cm$^2$ had less damage than smaller colonies.
Experiments showed that this was not because very large colonies recover faster from injury.

Colonies do not become bigger solely by growth. *P. versipora* colonies often 'cheat' by growing into contact and amalgamating with other nearby colonies. Some of these colonies have complete fusion of their skeleton and tissues, whereas other colonies are not fully integrated. Therefore, I proposed the model that small colonies that join amalgamations of multiple colonies have a similar biology to large colonies that have grown from a single recruit. Experiments to investigate this model showed that the ability to recover from injury was similar between these two types of colonies. Further, the regenerative ability of colonies that have fused was similar to that of colonies that did not join by fusion. Thus, the results of these experiments support the model, and suggest that these two different types of large colonies may have other similarities in their biology. Furthermore, these results suggest that changes in the energetics of colonies that amalgamate, are not wholly (if at all), due to these colonies becoming physiologically integrated.

The reduced damage to very large colonies may be because their size is a 'deterrent' for some disturbances. Alternatively, small colonies may only be able to become large (by growth or by amalgamation) if they occur where disturbance is low. Therefore, the differences shown between colonies of different sizes may not actually be due to their size, but rather due to their history of disturbance. Further experiments are needed to test these models.
If it is the location of colonies that is important in determining their energetics, then the chances of colonies surviving and the maximal size that they can attain is likely to be determined at the time of recruitment. Further, the occurrence of low rates of damage and the consequent regular replacement of polyps on very large colonies, may act to immortalise such colonies and would explain how some colonies can occupy large areas of reef environments for very long periods of time.

Thus, colonial organisms with a sheet-like morphology may only form 'empires' (areas of high cover) where disturbances do not limit their potential to occupy space.
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The species richness and high biological productivity of coral reefs, their economic importance through ecotourism and the fisheries they support, combined with the intrinsic fascination the reefs have for people, have led to there being many studies on the biology of reef corals. Coral reef populations are currently thought to be facing new and increasing stresses, including global warming, increased rates of sedimentation and nutrient enrichment due to agricultural and urban run-off, in addition to pressures from increasing tourism and recreational activities. It is therefore necessary that we improve our understanding of coral populations and the processes that structure them, if these ecosystems are to be successfully managed.

Corals have diverse life-histories, with very different patterns of growth and development between species. Overall, the population biology of corals and other modular marine invertebrates is not well understood. Only a handful of studies have really attempted to identify the processes which control the size of these populations.

Few species of coral live in temperate waters. Corals in temperate habitats are generally exposed to cooler temperatures, lower light intensities, more variable daylength, and higher rates of sedimentation and eutrophication than tropical corals. The constraints of temperate habitats may be reflected in the life-histories of these corals and the structure of their populations. Very few studies have investigated the biology of temperate corals, and even less is known about symbiotic corals in temperate habitats. Learning more
about the biology of temperate corals will provide insight into how the structure of coral populations and the populations of other modular marine invertebrates may change in response to the stresses of different environments.


*P. versipora* is particularly unusual, because it is the only species able to form populations in temperate and tropical habitats around the entire mainland coast of Australia. In Sydney Harbour, colonies of *P. versipora* have a sheet-like morphology and an aggregated distribution. The population biology of this coral has not been previously investigated.

In this chapter, models of the population biology of modular organisms, proposed by Jackson (1979), are described and current literature on the population biology and life-histories of corals and other modular marine invertebrates is reviewed. The main models investigated in my research project are then presented.
1.1 INTRODUCTION

Generally, demographic processes in corals are much more closely linked to the sizes of colonies than to their ages (Hughes & Connell 1987). In other words, the physiology and ecology of colonies change as they grow. This is also true for most unitary organisms except that, in modular organisms, the maximal size individual colonies will attain is indeterminate and potentially many thousand-fold larger than their size at recruitment. Further, unlike unitary organisms, modular organisms are affected by processes such as partial mortality, fission and fusion which generally result in the age and size of colonies being poorly correlated (Hughes & Jackson 1980; Hughes 1984; Hughes & Connell 1987).

Colonies grow by increasing the number of modules they contain; more modules mean a colony has more total resources. Therefore, larger colonies are expected to have faster rates of absolute growth (total increase in area), regeneration and fecundity than smaller colonies.

As colonies grow, the area they occupy increases, meaning that there are ecological implications of size. Jackson (1979) addressed this assertion in his model of disturbance, which proposed that larger colonies are more likely to be affected by a disturbance or occupy heterogeneous habitat than are smaller colonies. Using the same rationale, he also proposed that the likelihood of only part of a colony being affected by a disturbance or occupying less favourable habitat is also increased for larger colonies compared to smaller colonies. Hence, his expectation is that, although larger colonies are more likely to be damaged, smaller colonies are less likely to survive the damage.
Jackson (1979) then extended his model to consider the effects of shape and morphology on the biology of colonies. He recognised that, due to the geometric constraints of circularity, the perimeter to surface area ratio of colonies with a sheet-like morphology decreases as they grow. Most disturbances (competition for space and grazing activities) occur across the surface of the substratum and predominantly at the edges of colonies. This means that the proportion of tissue susceptible to damage at the periphery is less in larger colonies than in smaller colonies. Hence, Jackson (1979) proposed that larger colonies require less energy (per unit area) to maintain the space they occupy, so should have more energy available for growth, repair and reproduction than smaller colonies.

If the biology of colonies changes as they grow, then the rates at which processes occur in these populations must depend, at least partly, on their size-structure. I investigated this model and found that this is true for *P. versipora*. Further, my results suggest that the size-structure of *P. versipora* populations can provide information which is useful for predicting the rates at which different processes are occurring in these populations and for predicting the sizes at which changes in the biology of colonies are most likely to occur. Such a finding, supported with empirical measures of the rates at which different population processes occur in a population, has not been previously reported for a marine modular invertebrate. If this relationship is shown to be general for *P. versipora* and other modular marine invertebrates, then information about the size-structure of populations could have applications in the management of reef communities, as it could be used to predict the sizes at which the biology of colonies is most likely to change, and could help to identify species- and habitat-specific differences in the biology of different populations and the ways these populations change through time.
The primary objectives of my project were to investigate models about the population biology of modular organisms and the implications of colony size, with emphasis on how colonies occupy space and the way this affects the dynamics of the population.

*Plesiastrea versipora* was the model organism used for these studies. This study provided the opportunity to learn about the population biology of this coral and to investigate some of the processes influencing the structure of the Sydney Harbour population. Reproduction, recruitment, growth, mortality, regeneration and fusion of colonies were investigated. This is the first study on the population biology of a symbiotic hard coral living in a temperate habitat. My findings are likely to be generally applicable to populations of other corals and modular marine invertebrates with sheet-like morphologies.
Colonies can be of different sizes and shapes depending on the number of polyps they contain and the way these polyps are arranged. Size and shape can indicate the stage of development of a colony and directly affect how a colony interacts with its surrounding environment.

Jackson (1979) described a theoretical investigation of the likely implications of morphology for the biology of colonies. He then proposed models, based on the amount of space colonies occupy (their size) and the way the space occupied is distributed (their shape), to predict how the biology of colonies is likely to change, particularly with regard to the rates at which they are affected by different mortality processes.

The parameters Jackson (1979) used to derive his models included: 1) surface area of tissue in a colony, 2) area of substratum encrusted by a colony, 3) circumference of a colony, and 4) maximal linear dimension (length) of colony along the substratum.

Jackson (1979) then proposed what the implications of each of these parameters would be on the biology of colonies. His first model was simple. It was that, as larger colonies have more polyps, they have a greater fecundity, are able to capture more food and have higher rates of photosynthesis, than smaller colonies. Next, he proposed a model of disturbance, in which he proposed that, because larger colonies occupy more space, they are more likely to be disturbed or to occupy heterogeneous habitat, and experience a greater variety of disturbances, than smaller colonies. In this model he also proposed that small colonies are less likely to survive a disturbance than larger colonies. The rate at which colonies are disturbed is not only related
to their size, but was proposed to increase as the area of substratum covered by a colony increases, and/or as the length of circumference of a colony increases, and/or as the length of substratum over which a colony extends increases. Jackson (1979) also proposed that the rate at which a colony is disturbed and the variety of disturbances it encounters are directly proportional to the area of substratum covered by the colony.

These geometric parameters change at different rates depending on the morphology of a colony. Thus, Jackson (1979) presented further models which considered the inter-relationships of the models described above, from which he made predictions about how the biology of colonies will change between colonies of different morphologies. The morphologies he compared were termed runners, sheets, mounds, plates, vines and trees.

In Sydney Harbour, *P. versipora* colonies are flat and encrust on to the sandstone substratum, thus they have a sheet-like morphology. As these colonies are restricted to the substratum surface, they are likely to be at a high risk of damage from substratum associated disturbances. The elliptical shape of sheet-like colonies dictates that the proportion of tissue at the edge of a colony and at most risk of being damaged decreases as sheet-like colonies grow. If colonies are less likely to be damaged, then they are also less likely to use energy for repair. As a result, the overall energetics of colonies are likely to change as they become larger, thereby altering their biology.

Jackson (1979) predicted that sheet-like colonies have indeterminate growth, the ability to grow (increase their area) at an exponential rate and the potential to become fecund early in development (at a young age). He also predicted that the polyps of sheet-like colonies will have different functions depending on where they are located in the colony, with polyps near the
edge of the colony being specialised for defence, whereas polyps near the centre of a colony will be reproductive.

If the rates of damage to colonies increase as their circumferences increase, then colonies that maintain a minimal circumference to area ratio will also minimise their likelihood of experiencing further mortality. Therefore, Jackson (1979) predicted that sheet-like colonies will repair damaged areas quickly and have polyps that are integrated, so that metabolites can be transported to sites of injury.

Therefore, I investigated whether the biology of *P. versipora* colonies changes as Jackson (1979) proposed, by measuring the rates of growth, mortality, fecundity and regeneration for colonies of different sizes (Chapter 3 and 5). I then extended these models in preliminary studies to investigate whether the differences among colonies of different sizes are the same in colonies that grow to become large from a single recruit, as they are in colonies that are large as a result of amalgamating with other colonies (Chapter 5). I also investigated whether the predictions of the disturbance model as it applies to colonies, with regard to the implications of the amount of space they occupy, also apply to patches (aggregations of colonies) (Chapter 3).
1.3 PREVIOUS STUDIES ON THE POPULATION BIOLOGY OF MODULAR MARINE INVERTEBRATES

In corals, the term ‘individual’ can have three meanings: the polyp, the colony, and the genet. The polyps are the building blocks of colonies, each polyp having its own mouth, gastric cavity and gonads. The colony is an interconnected collection of polyps, the biology of which is mostly dependent on the number of polyps the colony contains. The genet is the genetic ‘individual’, and consists of all genetically identical polyps and colonies that have arisen from a single zygote. Thus, corals have a modular construction, as do sponges, ascidians, hydroids and bryozoans and have polyps as their unit of construction (or ‘module’).

Modular organisms can split into many small repeat units or they can amalgamate to form larger, discrete colonies. Each module can exist independently of other modules and has the ability to multiply by somatic growth, to create a colony. On the other hand, the loss of a module from a colony is unlikely to affect the colony greatly, because modules can be regenerated or replaced. Although individual modules have determinate growth and a maximal size, colonies grow indeterminately due to the potentially endless addition or loss of modules. These characteristics apply to populations of modular marine invertebrates and to populations of clonal plants (Chapman 1980); however, in this thesis I consider these processes only in terms of how they apply to modular marine invertebrates.

Generally, the age of a colony is poorly correlated with its size, due to processes of partial mortality, fission, fusion and highly variable rates of growth over time (Hughes & Jackson 1980; Hughes 1984; Hughes & Connell 1987).
Most of the variation between colonies is due to their size (Hughes & Connell 1987; Hughes & Jackson 1985; Babcock 1991). However, some of this variation is due to the ages of colonies. For example, small old colonies generally have slower rates of growth and higher rates of mortality than small young colonies (Hughes & Connell 1987).

Colony size is easy to measure and hence, a simple way to classify the colonies in a population. A number of relationships between colony size and the rates at which different population processes occur are described in the literature. Relative rates of growth (increase in colony area per unit area per unit time) generally decrease with increasing colony size (Connell 1973; Loya 1976; Hughes & Jackson 1985; Hughes & Connell 1987). Similarly, whole-colony mortality declines sharply among larger colonies (Connell 1973; Glynn 1976; Loya 1976; Bak & Engel 1979; Highsmith 1980; Hughes & Jackson 1980; Hughes & Connell 1987; Babcock 1991). In contrast, rates of partial mortality and fission of colonies increase with size (Hughes & Jackson 1980, 1985; Hughes 1984; Stocker 1991), as does colony fecundity (Connell 1973; Rinkevich & Loya 1979; Hughes & Jackson 1985; Babcock 1984, 1991; Szmant-Froelich 1985; Hall & Hughes 1996). The competitive and regenerative abilities of corals, as regard their ability to maintain space, have also been found to increase with size (reviewed in Buss 1982; Hughes 1984). No relationships between rates of fusion and colony size have been reported.

The slower rates of relative growth of larger colonies compared to smaller colonies may be because, if an expanding colony is to maintain a constant rate of relative growth, new periphery has to be added at an ever-increasing pace (i.e. the linear growth rates of colonies will have to increase exponentially as they grow) (Connell 1973).
Most of the variation among colonies in their rates of growth and mortality is due to the rates these processes occur at in very small corals (recruits) compared to larger colonies. This is likely to represent changes in the energetics of colonies as they grow. In many species of coral, colonies delay the onset of reproduction until after they attain a threshold size. Consequently, the change in growth rate between small and large colonies could simply be due to the onset of sexual reproduction (Jackson 1979). Generally, non-reproductive colonies are faster growing with higher rates of mortality than reproductive colonies (Johnson 1992). Delaying the onset of reproduction until colonies are larger is thought to enable juvenile colonies to grow quickly to a size which has much greater survivorship.

The age and size of colonies at first reproduction is not known for most corals (Fitzhardinge 1988), but has been shown to vary greatly among species. Some species can become reproductively mature when they are only a few polyps in size, while other species delay the onset of reproduction until they are more than 10 years old or larger than 59 cm$^2$ (Kojis & Quinn 1985; Szmant-Froelich et al. 1985; Wallace 1985; Szmant 1991; Hall & Hughes 1996).

Generally, the fecundity of colonies depends on the size of the colony, the age of the colony and the age of individual polyps within the colony (Connell 1973; Kojis & Quinn 1985; Szmant-Froelich 1985; Hall & Hughes 1996). Larger colonies not only have greater reproductive output in total, but often also have greater fecundity per unit area than smaller colonies (Connell 1973; Jackson 1979; Babcock 1984, 1991; Hall & Hughes 1996). Often, the polyps in a fecund colony do not all contain gonad. Marginal polyps are often non-reproductive and function for colony defence and repair (Hidaka 1985b; Szmant 1991; Hall & Hughes 1996). Marginal polyps are usually also younger
than other polyps, as the edge of the colony is where most growth occurs (Soong 1992; Hall & Hughes 1996).

The sizes at which the biology of colonies change are likely to vary among colonies exposed to different environmental conditions. In *Goniastrea* sp., the maximal rates of fecundity (mean number of eggs per mesentery) occurred for colonies of a smaller size and younger age at Orpheus Island than at Magnetic Island (Babcock 1991), showing that the energetics of colonies differed between these islands. Colonies of *Manicina areolata* become reproductively mature in the same size-class colonies also have a marked increase in survivorship (Johnson 1992). This suggests that the onset of reproduction and rates of survivorship of colonies are interrelated and hence, that the size at which whole colony mortality is greatest may also vary among locations. These results are interesting because they suggest that the energetics of colonies are not purely related to their geometric size, but are perhaps more a consequence of the regimes of disturbance to which they are exposed.

The mechanisms controlling sex determination in scleractinians have yet to be identified (Fadlallah 1983). Colony size influences sexuality in some corals which have small colonies that are male and larger colonies that are hermaphroditic (protandrous hermaphroditism). However, true sex change (male to female) of colonies with size has not been found in scleractinian corals (Fadlallah 1983).

The amalgamation of multiple colonies to form a single discrete colony enables colonies to increase their size much more quickly than is possible through growth alone. These amalgamations may or may not consist of colonies that have fused together. The historecognition reactions that occur
between colonies that touch each other are controlled by genetic and environmental processes.

In corals, colonies from the same genet (clones) almost always fuse, while genetically distinct colonies are rarely able to fuse (Frank & Rinkevich 1994; Frank et al. 1996). In some species, genetically distinct metamorphosing settlers and juvenile corals are able to fuse, while genetically distinct adult colonies cannot (Duerden 1902; Hidaka 1985a, 1997; Jackson 1986; Hidaka et al. 1997). This is thought to be because these young corals have histocompatibility systems that have not yet fully developed (Hidaka 1985a). In the corals for which fusion between genetically distinct colonies has been described (Heyward & Stoddart 1985; Willis & Ayre 1985; Resing & Ayre 1985; Chornesky 1991; Frank & Rinkevich 1994), the stability and consequences of these fusion reactions have not been investigated (reviewed by Hidaka et al. 1977).

Early studies described historecognition in corals as a simple dichotomy of fusion and rejection (Hildemann et al. 1977; Jokiel et al. 1983; Neigel & Avise 1983; Resing & Ayre 1985); however, more recent studies have shown that it is more complex. Some corals have delayed historecognition in which colonies initially fuse, but later reject each other (Potts 1976; Chadwick-Furman & Rinkevich 1994; Hidaka et al. 1997). As a consequence of these studies, it is now known that histocompatibility responses need to be observed repeatedly, over long periods of time, if the long-term outcome of colonies growing into contact is to be established.

In corals, historecognition is thought to be primarily genetically controlled (Rinkevich & Loya 1983a; Hunter 1985; Willis & Ayre 1985); however, the basis of histocompatibility, in terms of the number of alleles, number of loci,
and the extent to which histocompatibility reactions are affected by the environment, are not known (Neigel & Avise 1983; Grosberg 1988).

There are two models for the genetic basis of historecognition in marine invertebrates (Stoddart 1988). The first is clonal recognition, in which only identical genotypes can fuse. This occurs in sponges, anemones and corals (Hildemann et al. 1977; Neigel & Avise 1983). The second model proposes that the historecognition response is less specific, requiring colonies to share only a single gene at the historecognition locus if they are to fuse. This mechanism of historecognition was identified in the ascidian Botryllus schlosseri (Schofield et al. 1982), which has a locus for recognition that is highly polymorphic (Sabbadin 1962; Schofield et al. 1982), suggesting that only related colonies are likely to share a histocompatibility allele (Grosberg & Quinn 1986). Studies on other invertebrate species also show that fusion is controlled by the gene products of one, or at most a few, loci (Oka & Watanabe 1960; Sabbadin 1962; Schofield et al. 1982; Kingsley et al. 1989; Raftos & Briscoe 1990).

However, historecognition reactions are not solely controlled by genetics. Repeated contacts between conspecific anemones can result in enhanced (faster) aggressive responses or highly specific habituation (Sebens 1984; Ayre & Grosberg 1995). Therefore, increased rates of fusion between colonies sampled from near each other may have ‘habituation’ as a major confounding effect. The outcome of allogenetic reactions may be affected by other factors, including the size of colonies (Brace et al. 1979; Rinkevich & Loya 1985; Sebens 1986; Francis 1988), differences in growth form (Buss et al. 1984; Willis & Ayre 1985; Buss & Grosberg 1990; Yund 1991), differences in colour morph (Rinkevich & Loya 1985; Gleason 1993) and the numbers of stinging tentacles (Ayre & Grosberg 1995).
Little is known about the consequences of colonies forming amalgamations and fusing with each other; however, Buss (1982) and Grosberg & Quinn (1986) proposed some possible advantages of fusion, related to how the physiology of these colonies may change and how the way they occupy space changes.

The physiological advantages they proposed were: 1) that amalgamations contain more than one genotype, so will be able to tolerate a greater range of environmental conditions, and 2) that due to their larger size, colonies that fuse with a neighbouring colony will have more resources for growth, repair and reproduction. Further, small colonies that fuse with a larger colony may be able to become reproductively mature sooner than small colonies that remain independent of other colonies.

The ability of colonies to form amalgamations affects the way these colonies occupy space with regard to their geometry and their locations relative to other colonies. Therefore, Buss (1982) and Grosberg & Quinn (1986) proposed 3) because colonies that form amalgamations become larger, they potentially increase their rates of survivorship; 4) species that form amalgamations can potentially maximise their occupation of space and thus reduce their likelihood of interspecific competition; in addition they reduce the likelihood of colonies being involved in aggressive intraspecific competition for space; and 5) colonies that occur very near to each other will have higher rates of fertilisation.

However, Buss (1982) also identified some potential disadvantages of colonies fusing. For example, the different genotypes in these amalgamations may have to compete for resources and positions in the germ line and there may be increased potential for the transfer of disease and parasites between
colonies. Buss (1982) concluded that the benefits of fusion were probably limited to closely related individuals, as this minimises the effects of competition between the cell lines.

Of course, the biology of colonies that form amalgamations may change without the colonies actually needing to fuse. For example, colonies that grow together, completely filling all space between them, greatly reduce the length of periphery each colony in the amalgamation has exposed to the risk of damage from bottom-dwelling grazers and aggressive neighbours. This, in turn, could potentially change the energetics of these colonies.

In some corals, growth eventually causes the skeletons of colonies to become cemented together. This can increase the mechanical rigidity of each of the cemented partners, making them less prone to breakage and being detached than independent colonies (Bak & Criens 1982; Chornesky 1991). Cementation between colonies that fuse is even more mechanically stable than colonies that do not become physiologically integrated (Chornesky 1991).

Overall, the ability of colonies to fuse varies greatly between species. The frequency of fusion between colonies in the field is unknown for any coral (Hughes et al. 1992), and the ecological implications for populations, of high levels of fusion between genetically distinct colonies, are also unknown.
The models investigated in these studies were derived from the literature on the population biology of modular marine invertebrates and observations of *P. versipora* populations at local sites. These models are predominantly related to how colonies occupy space and the way this affects how they interact with their surrounding environment and consequently, affects their biology. If the biology of colonies depends on their size and shape, then the size-frequency distribution of colonies in a population is likely to contain information that can be used to make predictions about the dynamics of colonies in the population. Hypotheses to investigate this model were also identified. Finally, I investigated models proposing that colonies that grow into contact and fuse with a neighbouring colony to become large, have a similar biology to colonies that grow to become large from a single recruit.

a) The implications of colony size in *P. versipora*

Jackson (1979) derived models related to the geometry of colonies and how colonies interact with their environment, to predict how mortality processes (whole colony mortality and partial colony mortality) affect colonies of different sizes and different morphologies. Amongst these models Jackson (1979) proposed his model of disturbance (Chapter 1.2). Therefore, the first model in this research project is:

*General Model 1:* That the physiology and ecology of colonies change as they grow.
This model was broken into a series of more specific models that addressed how different aspects of the life-history of colonies may change as they grow. The hypotheses for each of these models are presented in the chapters where they were tested as indicated by the references given in brackets.

Models derived from the literature to investigate the dynamics of sheet-like colonies of different sizes:

- Small colonies have faster rates of relative growth than larger colonies (Chapter 3 - Model C1)
- Small colonies have higher rates of whole colony mortality than larger colonies (Chapter 3 - Model C2)
- Larger colonies have higher rates of partial mortality than smaller colonies (Chapter 3 - Model C3; Chapter 5 - Model E)
- Start of reproduction is delayed in small colonies until they reach a larger size (Chapter 3 - Model E)
- Fecundity increases with increasing colony size (Chapter 3 - Model E)
- Rates of colony fission increase with colony size (Chapter 3 - Model C4)
- The regenerative abilities of colonies increase with colony size (Chapter 5 - Model F)
- Most of the variation between colonies in their rates of growth and mortality are due to the rates at which these processes occur in recruits compared to larger colonies (Chapter 3 - Model G)

b) Predictions based on the size-structure of the population

The dynamics of populations are determined by the dynamics of individual colonies in the population, and the dynamics of colonies should be strongly related to their size. Therefore, the size-structure of the population is likely
to be useful for predicting the sizes at which the biology of colonies is most likely to change. The size-structure is also likely to vary spatially and temporally as the environmental conditions under which colonies exist change.

**General Model 2a:** That the population size-frequency distributions provide some insight into the dynamics of a population and can be used to predict the sizes at which the biology of colonies is most likely to change.

**General Model 2b:** That the size-frequency distributions of colonies vary between sites, because the rates of transition of colonies in the same size-class vary between sites.

**General Model 2c:** That the size-frequency distributions of populations fluctuate over time.

**General Model 2d:** That differences between the size-frequency distributions of populations at each site represent differences in the rates at which growth, mortality and recruitment occur at these sites.

The hypotheses to test these models are given in Chapter 3.1.1 and were derived based on the following observations.

The size-frequency distributions of colonies of *P. versipora* (Figure 2.2) suggest that colonies smaller than 20 cm$^2$ are much more likely to change size intervals than larger colonies, as these smaller size intervals contain
many more colonies and have greater variation in the number of colonies they contain than size intervals of colonies larger than 20 cm².

In contrast, there are many fewer colonies in the larger size intervals (> 20 cm²), and these size intervals are more consistent in the numbers of colonies they contain than the smaller size intervals. This suggests that larger colonies (> 20 cm²) have good survivorship and lower rates of growth, with either few transitions between the upper size intervals, or rates of transition between size intervals that cancel out over the population, due to as many colonies increasing their size interval as decreasing their size interval.

The size-structure of the population differed between sites. There were significantly more colonies in the 1 < 5 cm² size-class at Fairlight than at Green Point (Figure 2.2). This could be due to differences in the rates of recruitment between sites in some years, and/or differences in the rates of transition of colonies between different size-classes due to the rates of growth, mortality, fission and fusion at the two sites.

Based on these observations of the size-frequency distributions, the following size-classes were chosen to test the effects of colony size: < 1 cm² (I), as this size-class has been used in studies on tropical corals and is assumed to represent corals that have recently recruited to the population and are less than a year old; 1 < 5 cm² (II), as this size interval had the greatest number of colonies in it at each site, and appeared to represent some sort of 'turning-point' in the population; 5 < 10 cm² (III) and 10 < 20 cm² (IV), as these size-classes appear to have a sudden decline in the number of colonies they contain compared to size-class II, but still have a large number of colonies; > 20 cm² (V), each of the size intervals within this range (Figure 2.2) had many fewer colonies than the smaller size intervals, and there was
less variation in the number of colonies that these larger size intervals contained. The derivation of these size-classes is explained further in Chapter 2.6.

c) Cheating the system to get big quick: frequency and consequences of growing into contact with a neighbouring colony

In corals it is unusual for genetically distinct colonies to fuse, and generally fusion occurs only between larvae or recent settlers. In *P. versipora*, however, many discrete colonies are made up of multiple colonies that have amalgamated, and in some of these amalgamations the colonies fuse (Plates 2.1, 5.1 and 5.2).

My studies on *P. versipora* (Chapter 3) and the findings of similar studies on other modular marine invertebrates, show that the biology of colonies does change as they grow. These changes are mostly related to the effects of mortality processes, in that small colonies have higher rates of whole colony mortality, whereas large colonies, which are much less likely to die, have higher rates of partial mortality. Interestingly, however, in *P. versipora* colonies that are very large (> 100 cm²) have rates of partial mortality that are less (per unit area) than smaller colonies (Chapter 5).

Therefore, the ability of *P. versipora* colonies to form amalgamations with other colonies may increase the rate at which the population can grow, if it enables colonies to quickly attain a size that has greater rates of survivorship and that may also have lower rates of partial mortality (per unit area). In addition to this, the fact that some colonies that grow into contact fuse, may mean that these colonies not only have reduced rates of mortality due to their
increased size, but that they may also have access to more metabolites (in total) which could be used to aid colony repair.

**General Model 3a:** That colonies that become large as a result of amalgamating with other colonies have a similar change in their biology as colonies that grow to become large from a single recruit.

**General Model 3b:** That the amalgamation of colonies is important in structuring the population.

**General Model 3c:** In corals, only highly related colonies are able to fuse.

Therefore, the following models were proposed to investigate how important fusion and the amalgamation of colonies are in structuring the population:

- Colonies frequently grow into contact with neighbouring colonies, and often colonies that grow into contact fuse (Chapter 4 - Model A)
- The histocompatibility reactions between colonies that grow into contact are stable (do not change over time) (Chapter 4 - Model B)
- Colonies that join amalgamations become larger (in total) and are not resorbed (Chapter 4 - Model C).
- Colonies that have amalgamated with other colonies to become large, have rates of regeneration that are similar to the rates of regeneration of large colonies that have grown from a single recruit (Chapter 5 - Model H)
- Colonies that form amalgamations and fuse with other colonies may have more resources available for repair, and therefore recover from injury more quickly than colonies that form amalgamations in which the colonies do not fuse (Chapter 5 - Model I)
In the following chapters, I describe observations made from preliminary surveys of the population and provide definitions of terms used in this research project (Chapter 2); present the results from studies on the rates of growth, mortality and reproduction of colonies, and provide a summary of the rates at which different population processes occur for colonies of different sizes (Chapter 3); investigate histocompatibility and the processes affecting the rates of fusion between colonies (Chapter 4); measure the rates colonies are injured at, and compare the rates colonies of different sizes recover from injury (Chapter 5). The results of these studies are then summarised and discussed with reference to the models described above (Chapter 6).
In Sydney Harbour, *Plesiastrea versipora* has elliptical colonies, that grow by encrusting over the sandstone substratum. Colonies have a patchy distribution, mostly occurring in aggregations surrounded by encrusting corallines or other turfing algae (Plate 2.1). The relatively high local abundance of this temperate coral, make it a good organism for investigating models about the population biology of long-living, modular marine invertebrates.

Preliminary surveys determined the sizes of colonies and their distribution at local sites. Observations from these surveys, combined with findings from the literature on modular marine invertebrates, were then used to derive models and testable hypotheses, to investigate how different processes act to affect the structure of these populations (Chapter 1.3).

### 2.1 *Plesiastrea versipora*: Species Description

*Plesiastrea versipora* is the only reef building coral whose geographic range extends around the entire mainland coast of Australia. It is one of only two colony-forming, scleractinian species on rocky reefs around Sydney. The polyps are generally 2 to 3 mm in diameter (Appendix I), and colonies can be up to 3 m in diameter (Howchin 1909).
Plate 2.1: A ‘patch’ of *Plesiastrea versipora* colonies growing on a sandstone outcrop at Fairlight. Corals of the green (g) and blue (b) morphs are present.
Within Sydney Harbour, *P. versipora* occurs most abundantly on the northern side of the Harbour, around North, South and Middle Heads (Figure 2.1) (Farrant 1979; my pers. obs.), at depths between 2 and 20 metres.

The tissues of *P. versipora* contain symbiotic algae or zooxanthellae (*Symbiodinium* sp. (Udy et al. 1993)) which photosynthesise, providing nutrients to the coral animal and enhancing the growth of colonies (Goreau & Goreau 1959; Kevin & Hudson 1979).

Colonies of *P. versipora* are different colours, including bright green, grey-blue and brown. The brown colouration is that of the photosynthetic pigments in the zooxanthellae; the blue and green colours appear to be pigments produced by the animal. Colonies are usually pale-coloured or brown in the tropics and brightly coloured in high latitudes, where pigments in the tissue mask the colour of the zooxanthellae (Plate 2.1).

Although *P. versipora* has been the subject of a number of physiological and biochemical studies (Kevin & Hudson 1979; Sutton & Hoegh-Guldberg 1990; Stafford-Smith 1993; Ritchie *et al.* 1993; Grant *et al.* 1997 & 1998; Withers *et al.* 1998), the population biology and ecology of this coral have not previously been investigated.

### 2.2 STUDY SITES

This study was done in Port Jackson (33° 48' S; 151° 15' E), New South Wales, Australia, where average monthly seawater temperature ranges from 12 to 24 °C. The sites used were Fairlight Bay and Green Point (Figure 2.1). These study
Figure 2.1: Location of Study Sites

a) Map of Australia showing areas along the coast where coral reefs form.

b) Heads of Sydney Harbour showing Fairlight and Green Point, the two sites used in these studies on *P. versipora*.
sites were chosen as they have a greater abundance of *P. versipora* and are more readily accessible from the shore than other Harbour sites.

At Fairlight, colonies of *P. versipora* occur at 5 to 9 m depth, encrusting rocky surfaces along the base of the rock wall where the reef drops from 3 to 5 m and on rocky outcrops near the mouth of the bay. The assemblage of organisms surrounding colonies is either that of 'barrens', with coralline algae, urchins (*Centrostephanus rodgersii*), sporadic large barnacles, tent shells (*Australium tentoriforme*) and tube worms (Jones & Andrew 1990); or that of turf algae, with occasional, isolated sponges and colonies of soft corals (*Capnella gaboensis, Erythropodium hicksoni*) and ascidians.

At Green Point, colonies of *P. versipora* occur at depths between 1.5 and 4 m. They form 'patches' in channels and amongst boulders, below the overhanging stand of the kelp *Ecklonia radiata*. The surrounding substratum is covered by coralline algae, barnacles, tube-worms and grazing urchins (*Centrostephanus rodgersii*).

2.3 DEFINITIONS OF TERMS USED IN THIS STUDY

In this study of *P. versipora* (except where otherwise specified), the word ‘colony’ describes a collection of polyps that are in contact with each other and form a discrete entity. Therefore, ‘colony’ applies to colonies that have grown from a single recruit and to colonies composed of multiple corals that have grown into contact and amalgamated (without necessarily fusing) to create a single, discrete colony. This second type of colony is not an individual in a genetic sense, if it consists of more than one genome. Studies
investigating the consequences of colonies forming multi-genetic amalgamations, are presented in Chapters 4 and 5.

Five types of historecognition responses were found to occur between colonies of *P. versipora* that grow into contact with each other. These were termed: blend (or fusion), distinct, ridge, alternate and mix. Full descriptions of these different reactions are given in Chapter 4.2.

Almost all the colonies at my study sites were green or blue. Discrete colonies formed by the amalgamation of multiple corals could consist of blue and green colonies and sometimes colonies of different colour morphs were observed to have fused (Plates 2.1 and 4.2).

‘Recruits’ (except where otherwise stated), is used for corals that had only one polyp. In photographic surveys of fixed quadrats, all corals smaller than 50 mm$^2$ were considered to be ‘recruits’ (Chapter 3.7 and Appendix II). Recruits could be the product of sexual or asexual reproduction. No distinction between these two types of recruit has been made in these studies.

In the text of this thesis, the colony sizes were generally abbreviated using mathematical notation. For example, the size-class $1 < 5$ cm$^2$ refers to colonies that were at least 1 cm$^2$ and were smaller than 5 cm$^2$.

A patch is defined as any area where corals occur. Generally, a patch contains an aggregation of colonies; a few patches however, have only one colony. Determining the size (area) of a patch is subjective, due to the subjective nature of deciding where one patch ends and the next begins. Aggregations of colonies are partly isolated from other aggregations due to the complex structure of the reef substratum. However, colonies also form discrete
aggregations over large, even areas of sandstone. Therefore, the bounds of a patch are defined by a combination of physical constraints (where corals occurred in a hollow, on top of a boulder, or in the recess of a channel) and biological constraints (where one aggregation of colonies was distinct from the next aggregation over an even surface).

2.4 OUTLINE OF PRELIMINARY OBSERVATIONS

Preliminary surveys of the population were done in March 1994. Measurements were recorded for colonies in patches at Fairlight (n = 340) and Green Point (n = 219). The population of *P. versipora* in Sydney Harbour is dominated, in number, by small colonies. At Fairlight, most colonies (> 50%) were smaller than 5 cm². At Green Point most colonies (> 50%) were smaller than 10 cm² (Figure 2.2). Colonies ranged in size from < 0.01 cm² to > 1600 cm². Generally, colonies smaller than 5 cm² had fewer than 35 polyps and colonies smaller than 10 cm² had fewer than 70 polyps (Figure 2.3).

In these surveys, the area (A) of colonies was estimated using the equation for the area of an ellipse:

\[ A = \pi \frac{ab}{4} \]

where \( a \) is the longest diameter (cm) and \( b \) is the maximal diameter perpendicular to \( a \) (cm). This measure was chosen because it provides an accurate estimate of the number of polyps in a colony (Figure 2.3 and Appendix I) and is therefore a relevant and important variable.

The frequency distributions of colony sizes were significantly different.
Figure 2.2: Size frequency distributions of discrete colonies at a) Fairlight (n = 340), and b) Green Point (n = 219).

Where, □ indicates discrete colonies composed of multiple corals that have grown into contact and amalgamated, and ■ indicates discrete colonies that have grown from a single recruit. Data collected in March 1994.
Figure 2.3: Number of polyps in colonies of different size, a) area of a colony plotted against number of polyps in the colony; and b) longest diameter of a colony plotted against number of polyps in the colony. Data collected in September 1994 (n = 12 colonies).
a) 

No. Polyps in a Colony vs. Estimated Colony Area (cm$^2$)

$y = 7.18x$

$r^2 = 0.92$

b) 

No. Polyps in a Colony vs. Longest Diameter of Colony (cm)

$y = 14.98x$

$r^2 = 0.67$
between Fairlight and Green Point (Kolmogorov-Smirnov Test, \( P < 0.001 \)). The greatest difference between the two sites occurred for colonies in the \( 1 < 5 \) \( \text{cm}^2 \) size-class. Fairlight had a larger proportion of small colonies (\(< 5 \text{ cm}^2\)), but there was no significant difference between the two sites in the proportion of recruits (\(< 1 \text{ cm}^2\)) (Figure 2.2). This suggests that some population processes may be occurring at different rates at these sites.

A large proportion of the discrete colonies surveyed consisted of multiple corals that had amalgamated. More colonies were composed of multiple corals at Green Point (20.6%) than at Fairlight (14.5%); however, the proportion of colonies incorporated into these chimeric individuals was very similar at each site (48.2% at Fairlight and 48.5% at Green Point). Some amalgamated colonies appear to have fused, as their tissues and skeletons were continuous across the area of contact and pigments from each colony of a fused pair occurred within single polyps where the colonies were joined. Results from the surveys show that discrete colonies at Fairlight incorporate more corals into them than discrete colonies at Green Point. Consequently, colonies are larger at Fairlight than at Green Point. Consistent with this observation, the size-frequency distributions of colonies formed by the amalgamation of multiple corals differed between sites (Figure 2.2). Overall, there were more, much larger colonies (> 200 \( \text{cm}^2 \)) at Fairlight (6%) than at Green Point (0.05%). Most of these larger colonies were mosaics of multiple corals that had grown together. One colony at Fairlight was estimated to have at least 52 colonies incorporated into it and had a total area of 1 590 \( \text{cm}^2 \).

Intraspecific fusion does not commonly occur in corals. However, populations of colonies that do fuse are likely to have a significantly different size-structure, as fusion enables these populations to gain more
large colonies, more quickly, than is possible if colonies must grow to become large. Difference in size-structure will be further accentuated if the large colonies that form after fusion have higher rates of survivorship, fecundity and regeneration than smaller colonies (reviewed in Chapter 1).

Most of the area of coral in the population is due to larger colonies, even though these colonies are fewer in number than small colonies (Figure 2.4). At Fairlight, colonies larger than 100 cm$^2$ make the greatest contribution to area cover. At Green Point, the greatest cover (approximately 50%) is from colonies in the 100 < 1 000 cm$^2$ size-class, and colonies in the 10 < 100 cm$^2$ size-class contribute a further 42% of the total cover of coral. Therefore, changes in the coral area of the population will mostly be due to changes in the area cover of large colonies. The condition of reef populations is often assessed by measuring changes in coral cover. If the processes acting on large colonies are different from the processes acting on small colonies, cover will provide a very limited measure of the vitality of a population. For example, changes in cover will not detect sudden changes in the number of small colonies in the population, which (in the longer term) is likely to be much more detrimental to the population than is the loss of area due to the partial mortality of a few large colonies.

Some colonies had injuries on their surfaces. In this study, areas where the tissue had been removed, or had died, and the skeleton had been exposed on a colony were called lesions. Lesions were estimated to cover 1.4% of the total area of coral at Fairlight and were more common on larger colonies than on smaller colonies. Proportionally, lesions represent more mortality (on an area cover basis) than if half the colonies less than 5 cm$^2$ at Fairlight were to die, which (on a number of colonies basis) is equivalent to the death of more than a quarter of the colonies in the population.
Figure 2.4: Frequency distributions of colonies in log size intervals, a) and c) size frequency distributions of colonies in each size interval at each site; b) and d) total area of coral in each size interval at each site. Data collected at Fairlight (n = 340) and Green Point (n = 219), in March 1994.
The aggregated distribution of colonies at local sites could be due to *P. versipora* larvae having gregarious settlement, preferences for particular microhabitats or limited dispersal. Alternatively, these patterns of distribution may occur because larvae that settle in patches have greater survivorship than larvae that settle outside patches (Carlon & Olson 1993). The aggregated distribution of colonies increases the likelihood of corals growing into contact and therefore also increases the potential of colonies to fuse.

Unlike corals on tropical reefs, *P. versipora* in Sydney Harbour is rarely observed to be in competition for space with other sessile invertebrates (Plate 2.1). Hence, colonies appear to have the potential to occupy almost 100% of the area inside patches. Cover of coral in patches ranged from 1.7% to 76%; however, most patches had less than 30% cover (Figure 2.5). Patches at Green Point had a lower percentage cover than patches at Fairlight. Therefore, processes such as grazing by the locally abundant urchin *Centrostephanus rodgersii* may limit the growth of colonies, with grazing being more intense at Green Point than at Fairlight.

Environmental conditions can affect coral growth and consequently, affect the sizes of colonies and the percentage cover of coral in patches. Therefore, patch data were also considered in terms of the type of patch (for example: hollows, platforms and shelves) and the depth at which patches occurred (3, 6 and 7 m) to investigate this model to find out whether there are any relationships between the type of patch and the sizes of colonies or percentage cover of coral in a patch. No relationships between patch type and mean colony area or percentage cover of coral in a patch were identified (Figure 2.5). Similarly, there were no significant differences between the depth at which a patch occurred and the percentage cover of coral or
Figure 2.5: Abundance of corals in patches of different types, a) mean areas of discrete colonies in a patch plotted against patch type; and b) mean percentage coral cover in a patch plotted against patch type. Graphs include pooled data from Fairlight and Green Point; error bars represent standard deviations and ‘n’ is the number of patches. Data collected in March 1994.

The substratum *P. versipora* colonies grow on has a complex structure, and ‘patch type’ has been defined according to the structure of the sandstone around a patch. ‘Channels’ is the term given to the gullies, up to 1.5 m below the rock, that run between large sandstone outcrops. Patches in the base of channels are called ‘channel hollows’, unless the corals are on a boulder in the base of the channel when they are called ‘channel rocks’. Colonies can also grow on the sides of channels, on ‘channel shelves’. ‘Deep hollows’ can be up to 2 m below the upper surfaces of rocks, occurring in gaps between sandstone outcrops. ‘Exposed rock’ is the term for small sandstone outcrops with corals growing on top of them. A ‘platform’ is a level area of sandstone above channels and deep hollows, and ‘platform hollows’ are small depressions in platforms. A large area of sandstone that has a vertical surface is called a rock wall; these occur on the sides of large platforms. ‘Rockwall base’ is the term given to coral patches at the base of a rock wall.
a) Mean Colony Area in Patch (cm²)

- CHANNEL HOLLOW: n=3
- CHANNEL ROCK: n=5
- DEEP HOLLOW: n=4
- EXPOSED ROCK: n=2
- PLATFORM: n=2
- PLATFORM HOLLOW: n=5
- ROCKWALL BASE: n=5
- SHELF IN CHANNEL: n=7

b) Mean % Coral Cover in Patch

- CHANNEL HOLLOW: n=3
- CHANNEL ROCK: n=5
- DEEP HOLLOW: n=4
- EXPOSED ROCK: n=2
- PLATFORM: n=5
- PLATFORM HOLLOW: n=4
- ROCKWALL BASE: n=7
- SHELF IN CHANNEL: n=7
average size of colonies (ANOVA, p < 0.05), (Figure 2.6).

2.5 SUMMARY OF OBSERVATIONS OF P. VERSIPORA IN SYDNEY HARBOUR

i Colonies have an aggregated distribution, occurring in 'patches'.

ii Colonies are a wide range of different sizes (< 0.8 mm$^2$ to > 1 600 cm$^2$).

iii Most colonies are small (< 10 cm$^2$).

iv The size-frequency distributions of discrete colonies were significantly different between Fairlight and Green Point. Fairlight had a significantly greater proportion of colonies in the 1 < 5 cm$^2$ size-class than Green Point.

v Some discrete colonies are composed of multiple corals that have grown together and amalgamated. Some of these colonies have fused.

vi The size-frequency distributions of discrete colonies formed as a result of multiple corals amalgamating are also different between sites.

vii The area of coral in the population is mostly contributed by colonies in the larger size-classes.

viii Colonies at each site have lesions (areas of partial mortality). Lesions were estimated to represent damage to 1.4% of the total area of coral in the population.
Figure 2.6: Relationship between coral abundance in patches and depth, a) mean area of discrete colonies in patches at 3, 6 and 7 m depth; and b) mean percentage coral cover in patches at 3, 6 and 7 m depth. Data collected in March 1994. Error bars represent standard deviations. Patches at 3 m were at Green Point, and patches at 6 m and 7 m were at Fairlight.
a)

Mean Colony Area (cm²)

<table>
<thead>
<tr>
<th>Patch Depth (m)</th>
<th>n = 12</th>
<th>n = 15</th>
<th>n = 6</th>
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<td>3</td>
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b)

% Coral Cover in Patches

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<tr>
<th>Patch Depth (m)</th>
<th>n = 12</th>
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2.6 DETERMINATION AND CLASSIFICATION OF SIZE-CLASSES

The fact that the population has more smaller colonies than larger colonies (Figure 2.2), combined with findings from the literature on modular organisms (Chapter 1), suggests that, in *P. versipora*, the demography of colonies smaller than 5 cm$^2$ is likely to be different from the demography of larger colonies.

Further, the fact that there are fewer colonies in the $< 1$ cm$^2$ size interval than in the $1 < 5$ cm$^2$ size interval suggests that these colonies are demographically different. Colonies in the $1 < 5$ cm$^2$ size interval are also likely to be different from colonies in the $5 < 10$ cm$^2$ size interval, as these size intervals appear to represent some sort of "turning point" in the population after which the larger size intervals contain fewer colonies. These differences between size intervals could be due to differences between recruitment events, differences in the rates of transition of colonies between size intervals, differences in the rates of survivorship between size intervals, and/or differences between size intervals in their rates of colony fission and fusion.

Larger colonies ($> 20$ cm$^2$) are likely to have a different demography again, as they are much fewer in number than smaller colonies, and the number of colonies in each of the larger size intervals varies less than between the smaller size intervals. This could be due to larger colonies having good survivorship between size-classes, and/or greatly reduced rates of growth with few transitions between size-classes, and/or similar numbers of larger colonies increasing their size-class as decreasing their size-class.

If, as these observations suggest, colonies of different sizes have different life-histories, then these differences are likely to affect the size-structure of the population. Therefore, the following size-classes were chosen as the most
relevant for studying the size-structure of the *P. versipora* population in Sydney Harbour:

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<tr>
<td>I</td>
<td></td>
<td>&lt; 1 cm$^2$</td>
</tr>
<tr>
<td>II</td>
<td></td>
<td>1 &lt; 5 cm$^2$</td>
</tr>
<tr>
<td>III</td>
<td></td>
<td>5 &lt; 10 cm$^2$</td>
</tr>
<tr>
<td>IV</td>
<td></td>
<td>10 &lt; 20 cm$^2$</td>
</tr>
<tr>
<td>V</td>
<td></td>
<td>$\geq$ 20 cm$^2$</td>
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</tbody>
</table>

And, except where specified:

- **small** colonies were < 5 cm$^2$
- **medium** colonies were 5 < 20 cm$^2$
- and, **large** colonies were $\geq$ 20 cm$^2$. 
CHAPTER 3: GROWTH AND SURVIVORSHIP OF PLESIASTREA VERSIPORA IN SYDNEY HARBOUR

3.1 INTRODUCTION

Polyp budding is the primary means by which coral colonies increase in size. Growth of polyps is considered determinate and the maximal size of polyps is thought to be genetically controlled. Colonies and genets can, however, grow indeterminately through the potentially endless addition of new polyps. Colonies can increase their polyp number either through somatic growth, or by amalgamating with neighbouring colonies to form a single, larger, discrete colony.

Corals have two types of mortality, whole colony mortality and partial colony mortality (the death of some polyps in a colony). Extensive partial mortality can result in parts of a colony separating from each other. This process is called colony fission.

Colonies vary a lot in their rates of growth, mortality and fecundity. Much of this variability can be attributed to the ages and sizes of colonies, with the effects of size being greater than the effects of age (Hughes & Connell 1987).

Colony size affects the growth and mortality rates of corals. Generally, the relative growth rate (increase in area per unit area) of a colony is related to the size of the colony, in that small colonies often grow more quickly than larger colonies (Connell 1973; Loya 1976; Hughes & Jackson 1985; Hughes & Connell 1987). Similarly, the probability of whole colony mortality is much higher for smaller colonies than for larger colonies (Connell 1973; Pearson

In the experiments described in this chapter, I measured the rates of coral growth and mortality at both the population and colony levels and investigated models proposed to explain the size-structure of the *P. versipora* population(s) in Sydney Harbour (Chapter 1.4). The effect of size on the reproductive biology of *P. versipora* was also investigated.

In these studies, growth of colonies has been measured as the change in area and as the increase in linear extension. In this chapter, partial mortality is only considered in terms of colonies shrinking (having a net loss of area over a year). This type of mortality occurs at the edge of colonies and around large, seemingly permanent, areas of colony dieback. Partial mortality in terms of injuries on the surfaces of colonies was investigated in separate studies described in Chapter 5.

This chapter consists of four main parts: in the first part the rates of growth and mortality at the level of the population are measured at each site in each year; in the second part the rates of growth, mortality and reproduction at the level of colonies are compared between colonies of different sizes and at different sites; in the third part, the different population parameters measured at Fairlight and Green Point are summarised in a table to show the
effects of different colony level processes on the size-structure of the population; finally, the results of these studies are discussed with reference to the models proposed below.

3.1.1 Models and Hypotheses for Studies on Growth, Mortality and Reproduction in *P. versipora*

Population growth was measured to find out whether the local population is growing, at equilibrium, or declining, and whether the rates of population growth are similar at Fairlight and Green Point.

MODEL A: That the *P. versipora* population in Sydney Harbour is growing.

Ha1) That the area cover of the population increases at each site, in each year.

Ha2) That the number of colonies in the population increases at each site, in each year.

The cover of coral in patches ranges from 1.7% to 76%, but most patches have less than 30% cover (Chapter 2.4). This suggests that the growth of colonies in patches is limited when coral cover is high. One explanation for this observation could be that the net growth of colonies is density dependent, in that where coral cover is high, colonies occupy a lot of space and therefore, have a greater probability of being damaged than do colonies in patches that have less coral cover. This reasoning is consistent with Jackson’s (1979) model of disturbance, in which he proposed that the rates at which colonies are damaged are directly proportional to the area of substratum they cover, except that in this case the model has been extended from the effects of colony level processes to the level of patches. Thus, the following model was investigated:
MODEL B: That the cover of coral in patches is limited due to the net growth of corals within patches decreasing as the percentage cover of coral increases.

Hb1) That patches with more than 30% coral cover increase their coral area less each year (on average) than patches with less than 30% coral cover.

Hb2) That quadrats with more than 30% cover are more likely to lose some of their coral cover than quadrats with less than 30% cover.

The surveys of fixed quadrats provided measures of the rates at which growth, mortality, recruitment, fission and fusion occur in the population, and the effect these processes have on the size-structure of the population at each site.

As expected, growth rates were highly variable between colonies. Therefore, the population growth data were broken down to investigate colony level processes, so that the effects of colony size and the implications of how colonies occupy space could be investigated. The models to investigate colony level processes were chiefly derived from Jackson (1979) (reviewed in Chapter 1) and General Model 1 (Chapter 1.4), that the physiology and ecology of colonies change as they grow.

The size-frequency distributions (Figure 2.2) showed that there were different numbers of colonies in each of the size intervals chosen, and that most colonies were less than 20 cm², yet some colonies were more than 1500 cm². This distribution of colony sizes is likely to reflect the way the biology of colonies changes as they grow and the annual rates of recruitment to the population. Therefore, with reference to observations of the size-frequency data given in Figure 2.2 the following hypotheses were derived to investigate models proposed in Chapter 1.4 (General Models 1 and 2a) and here:
MODEL C1: Small colonies have faster rates of relative growth (increase in polyp number per polyp) than larger colonies.

MODEL C2: Small colonies have higher rates of whole colony mortality than larger colonies.

MODEL C3: Small colonies have lower rates of partial colony mortality than larger colonies.

MODEL C4: Small colonies have lower rates of fission than larger colonies.

MODEL C5: The rates of recruitment to the population vary from year to year.

Hc1) Colonies grow out of size-class I (visible < 1 cm²) more quickly than colonies grow out of size-class II (1 < 5 cm²).

Hc2) Small colonies (< 5 cm²) are more likely to die than larger colonies.

Hc3) Small colonies (< 5 cm²) are less likely to shrink than larger colonies.

Hc4) Small colonies (< 5 cm²) are less likely to have colony fission than larger colonies.

Hc5) That the rates of recruitment to the population vary each year.

The colony size distributions (Figure 2.2) were significantly different between Fairlight and Green Point, with the greatest difference being that there were more colonies in the 1 < 5 cm² size-class at Fairlight than at Green Point. These differences could be due to the size-frequency distributions varying through time or they could be due to the rates of growth, mortality and recruitment being significantly different between sites. Therefore, the following hypotheses were derived to investigate General Models 2b, 2c and 2d (Chapter 1.4) and explain this difference between sites:

Hd1) That the size-frequency distributions of colonies vary within sites, over time.

Hd2) That the rates of growth, mortality and recruitment vary among sites.
Hd3) That small colonies (< 5 cm²) grow more rapidly at Green Point than at Fairlight and therefore, transitions out of the smaller size-classes are faster at Green Point than at Fairlight.

Hd4) That the mortality of small colonies (< 5 cm²) is higher at Fairlight than at Green Point.

Hd5) That the rates of recruitment are higher at Fairlight than at Green Point.

Many colony forming invertebrates do not become reproductively active until they reach a certain size. Colonies of *Manicina areolata* first become reproductive in the same size-class colonies have a dramatic increase in their rates of survivorship (Johnson 1992). Once colonies become reproductive their fecundity (per unit area) generally continues to increase as they grow (Hall & Hughes 1996). Some corals have a type of ‘sex change’ in which small colonies are male and large colonies are hermaphrodites. This delay in the start of reproduction between the sexes is thought to be due to colonies requiring more energy to develop lipid-filled oocytes than to develop spermaries (Harrison & Wallace 1990). Therefore, I wanted to investigate whether there were similar relationships between colony size and the reproductive biology of *P. versipora*, and determine the sizes (if any) at which the reproductive biology of colonies changes.

One model commonly proposed in biology is that the growth of organisms slows when they become reproductive, due to energy being diverted away from growth towards the development of gonads. The size-structure of the population of *P. versipora* suggests that the growth rates of colonies larger than 5 cm² are slower than smaller colonies. Therefore, 5 cm² may be the size at which colonies can first become reproductive. Although *P. versipora* is gonochoric (Appendix IV), there may also be an effect of size, similar to some hermaphroditic corals, whereby male colonies become reproductive at a
smaller size than female colonies. Therefore, the following models were proposed with reference to General Model 1 (Chapter 1.4):

**MODEL E:** The reproductive biology of colonies changes as they grow, in that small colonies are not reproductive and the likelihood of larger colonies being reproductive increases as they grow.

He1) That only colonies larger than $5 \text{ cm}^2$ are reproductive.

He2) That the probability of colonies that have reached reproductive size containing gonads continues to increase as they grow.

**MODEL F:** That there is no distinction in size between male and female colonies.

Hf1) That male colonies become fecund at a smaller size than female colonies.

Hf2) That the proportion of colonies that is male is higher in smaller colonies than it is in larger colonies.

Finally, a lot of the variation between colonies of different sizes may be due to the rates that population processes occur in the smallest members of the population, namely single polyp recruits. Therefore, the rates of growth and survivorship of single polyp recruits were compared to the rates for larger colonies to test hypotheses related to the following model:

**MODEL G:** That most of the variation between colonies in their growth and mortality is due to the growth and mortality of very small corals (recruits).

Hg1) That recent (single polyp) recruits account for most of the differences in the rates of growth and mortality between colonies in size-class I ($> 1 \text{ cm}^2$) and colonies in size-class II ($1 < 5 \text{ cm}^2$).
Hg2) That the range of relative growth rates for corals that grow to become larger, and do not amalgamate with other colonies, is much greater for single polyp recruits than it is for colonies.

3.2 METHODS FOR SURVEYS OF FIXED QUADRATS

In choosing the best methods for measuring the rates of growth of this temperate hard coral I had to consider the following: 1) colony growth may be difficult to measure if colonies grow very slowly, 2) the growth rates of coral colonies are generally highly variable, therefore a large number of colonies needed to be included in this study and 3) disturbance to the population as a result of my research activities needed to be limited, as the population is small and it may take a long time for it to replace areas of lost coral.

Photographic monitoring of fixed quadrats through time allows the growth and mortality of a large number of colonies to be measured, while causing minimal disturbance to the population, and has the advantage of providing measures of other population processes, including recruitment, fission and fusion.

A quadrat of 29 cm x 20.5 cm was used to sample the population, as this size and shape fits within the area of most coral patches and was the largest quadrat that was logistically feasible for this study, given the underwater photographic equipment available and quality of image needed for measuring colony growth. A Nikonos V was attached to a four legged stand with a Nikonos 103 strobe set to directly illuminate the quadrat area beneath it. The camera had a 35 mm lens with a 12" close-up micro lens from ‘Aquasea’ fitted to it. The distance from the front of the micro lens to the ground perpendicularly below when the camera was attached to the stand was 30.5 cm. To give the best exposure and good depth
of field the camera aperture was set at F11 and the flash set on TTL. A diffuser attached to the flash helped to reduce backscatter. Fujichrome SENSIA 100 ISO (36 exp.) slide film was used.

Fixed quadrats were set up at Fairlight (n = 66) and Green Point (n = 33). There were fewer quadrats at Green Point as there is less coral at this site. Three sub-sites were sampled at each site. Descriptions of these sub-sites are given below:

Fairlight Sub-sites (n = 22 quadrats per sub-site):

A) Coralline alga area, 'barrens' (described in Chapter 2.2) - channel and boulders at the west end of the rock wall (directly out from the swimming pool at Fairlight Beach). Corals occur at 4 to 6 m depth.

B) Area along the base of the rock wall between sub-sites A and C. Corals occur at 5 to 7 m depth, where they are surrounded by turf algae, sponges, hydroids, and soft corals.

C) Similar assemblage of organisms as in area B. Corals occur on boulders and in channels at 4 to 6 m depth. This area is at the east end of the rock wall.

Green Point Sub-sites (n = 11 quadrats per sub-site):

All of the Green Point sub-sites had coralline algae or 'barrens' type habitats.

D) Connecting series of channels beneath an overhanging stand of the kelp Ecklonia radiata. This is the area of coral nearest to the beach. Corals occur at 2 to 3 m depth.

E) Area of coral patches occurring along the edge of the sandstone reef. Corals occur at 3 to 4 m depth.

F) Shallower area toward the end of Green Point (directly out from the World War II battlements). Corals occur amongst boulders and on sandstone ledges at 1.5 to 3 m depth.
The quadrats sampled were areas where the substratum was relatively flat, and contained coral (i.e. the quadrats were inside patches), and in places where the camera stand could fit. Only one quadrat was sampled per patch. The fixed quadrats were marked with two steel screws. These were drilled into the sandstone using a jig to position the holes and a pneumatic-drill. The distance between the screws was the same as the distance between the legs of the camera stand and the screws were used to position the camera. Quadrats were labelled with stainless steel tags. Laminated proof sheets were made from slides of the first survey of quadrats, and used as a reference for the orientation of quadrats on future dives.

The fixed quadrats were photographed at intervals of two months from April 1996 to April 1998 at Fairlight, and from December 1996 to April 1998 at Green Point. Unfortunately, due to repeated camera floods, there are no data for December 1997 at either site. The studies described in this chapter are based on measures of colonies at three time points: April 1996 (Fairlight only), April 1997 and April 1998. Data from surveys of quadrats at intervals of two months were used in further studies of partial mortality and the rates of colony injury, described in Chapter 5.

The photographic slide images of quadrats were converted to digital images using the Kontron Image Analyser at the Electron Microscope Unit, University of Sydney. The areas of individual colonies were measured by drawing around the perimeter of the digital image of a colony, and selecting the shape drawn for the computer to calculate the colony’s area. The area of each discrete colony was measured three times on each image, and the mean of these measures was used as the area for the colony at that time. The net growth of colonies at intervals of one year was calculated from these measurements. Colonies that were only partially in frame were also measured, but recorded as
3.3 POPULATION GROWTH

Population growth can be measured in two ways: 1) as the change in coral cover and 2) as the change in colony number. Coral cover is essentially a measure of the number of polyps the population has (Appendix D), hence it is a relevant and important population measure. The rate at which the cover of coral changes in the population is mostly due to the rates of growth and partial mortality of colonies in the population. In contrast, changes in the number of corals in the population are due to the rates of fission, fusion, whole colony mortality and the rates of recruitment to the population.

3.3.1 Methods

In this study I investigated Models A, B, and General Model 2c (described in Chapters 3.1.1 and 1.4) by measuring whether the population was growing, the effects of density (percentages cover) on the growth rates of corals in patches, and the amount of variation there was in the size-structure of the population at local sites over time.

The total area of coral and change in coral cover in each quadrat were calculated over intervals of one year to estimate population growth (as an area measurement). Both the area of colonies that were entirely within the quadrat and the area of colonies that were only partially within the area of the quadrat were measured.

Population growth could not be calculated.
were included in these calculations. The changes in the area cover of quadrats each year were also used to investigate whether there were any relationships between the percentage cover of coral in a patch and the change in coral cover over a year.

Measures of the rates of growth, mortality, recruitment and fission of colonies, and estimates of the rates at which colonies grew into contact with each other and could, potentially, fuse (Appendix II), generally only used data from colonies that were entirely within the area of the quadrat.

The data used for the size-frequency distributions of colonies in the population at each site, in each year, included both whole colonies and colonies at the edge of the quadrat that had been recorded as a part measure (P) only, but that had more than 20 cm² of their area inside the frame, so were known to be in size-class V. This was done to reduce the likelihood of underestimating the number of large colonies in the population, as large colonies are more likely than small colonies not to fit within the area of a quadrat.

3.3.2 Results

Overall, the percentage cover of coral in quadrats was highly variable, ranging from 0.6% to 82%. In contrast, the mean percentage cover of coral in patches at each sub-site was much more consistent, ranging from 14% to 23% (Appendix II).

Sub-site B was the only sub-site that had an overall loss of coral area over a year (1996-97). However, the area lost was regained, and increased upon, in the following year (Figure 3.1). The number of sub-sites that increased their coral
Figure 3.1: Percent change in area cover at each sub-site, a) Fairlight (1996 to 1997), b) Fairlight (1997 to 1998) and c) Green Point (1997 to 1998).

There were 22 quadrats in each sub-site at Fairlight, and 11 quadrats in each sub-site at Green Point. Error bars represent standard deviations.
a) Fairlight 1996-97

b) Fairlight 1997-98

c) Green Pt 1997-98
cover compared to the number of sub-sites that decreased their coral cover was greater than is expected by chance (Binomial test, \( p < 0.02, k \leq 1 \)). Therefore, in terms of area cover, the population was growing during the course of this study.

There was no significant difference in the percentage change in coral cover between quadrats of five different coral densities, at any site, in either year sampled (separate one factor ANOVA balanced, \( n = 3 \) to 8 replicates, \( p > 0.43 \)). However, there was a general trend of increasing variability in the percentage change in coral cover with increasing cover (Figure 3.2). Much of this variability was due to some patches losing some of their coral area. The proportion of quadrats that lost some of their coral area was greater for quadrats with more than 10% cover than for quadrats with less than 10% cover (Table 3.1).

The annual rates at which different population processes occurred in the population, at each site, are summarised in Appendix II (Table II.1). Most colonies (66% to 71%) had a net increase in area over a year. The proportion of colonies that grew was similar between the two years sampled at Fairlight, and between sites in 1997-98. The rates of whole colony mortality were almost twice as high at Green Point in 1997-98 (14%), as in either of the years sampled at Fairlight (8% and 7%, respectively). In contrast, the annual rates of recruitment were higher at Fairlight (32 recruits in 1996-97 and 26 recruits in 1997-98) than at Green Point (3 recruits in 1997-98). Fission of colonies was recorded only at Fairlight, where it produced 4 new discrete colonies over two years. The rate at which colonies grew into contact with their neighbours was higher at Green Point (18%) than at Fairlight (10% in 1996-97 and 11% in 1997-98).
Figure 3.2: Mean percent change in area cover for quadrats with different densities of coral at a) Fairlight and b) Green Point.

The number of quadrats of each density, in each interval sampled, are given in Table 3.3. Error bars represent standard deviations.
a) Fairlight 1996-97

![Chart showing mean % change in coral cover for different initial coral covers at Fairlight 1996-97.](chart_a)

b) Fairlight 1997-98

![Chart showing mean % change in coral cover for different initial coral covers at Fairlight 1997-98.](chart_b)

c) Green Point 1997-98

![Chart showing mean % change in coral cover for different initial coral covers at Green Point 1997-98.](chart_c)

Key of Initial Coral Cover:
- □ 0 < 5%
- ■ 5 < 10%
- □ 10 < 20%
- □ 20 < 30%
- □ > 30%
Table 3.1: Percentage of quadrats sampled that had a loss of coral area in one year, for quadrats with different amounts of coral cover.

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<tr>
<td></td>
<td>% Negative Growth</td>
<td>n</td>
<td>% Negative Growth</td>
<td>n</td>
</tr>
<tr>
<td>0% &lt; 5%</td>
<td>14</td>
<td>7</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>5% &lt; 10%</td>
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<td>10% &lt; 20%</td>
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<td>15</td>
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<td>20% &lt; 30%</td>
<td>46</td>
<td>13</td>
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<td>17</td>
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<tr>
<td>&gt; 30%</td>
<td>33</td>
<td>12</td>
<td>42</td>
<td>12</td>
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Contact between colonies results in the colonies amalgamating to form a single discrete colony, and thus reduces the number of discrete colonies in the population without causing a reduction in coral area. In 1996-97, there were 29 incidences of colonies having amalgamated with a neighbouring colony at Fairlight. A further 29 colonies at Fairlight, and 20 colonies at Green Point, grew into contact with their neighbours in 1997-98 (Appendix II, Table II.1 shows data for whole colonies only). These incidences of colonies growing into contact and amalgamating with their neighbours resulted in 12 and 13 discrete colonies at Fairlight in each of the years sampled, respectively, and 9 discrete colonies at Green Point in 1997-98. (Some of these colonies were only partially within the frame, so were not included in the whole colony data).

At Fairlight, the number of colonies ‘lost’ due to whole colony mortality or colonies having grown into contact with their neighbours, almost balanced the number of colonies ‘gained’ as a result of recruitment or fission. Over the 66 quadrats at Fairlight there was a gain of 3 colonies in 1996-97, and a loss of 1 colony in 1997-98. In contrast, the 33 quadrats at Green Point lost 20 colonies in 1997-98 (Appendix II, Table II.1).

At Fairlight, between 5% and 6% of the initial area of coral was lost each year. Most of the area lost at Fairlight was due to colonies shrinking; less than 1.5% of the area lost was due to whole colony mortality. In contrast, at Green Point whole colony mortality and partial mortality resulted in a total loss of 1.2% of the initial coral area (Appendix II). (These measures do not include the area of partial mortality due to lesions, measured in Chapter 5). Overall, the total area gained by whole colonies within the quadrats at Fairlight was 333 cm$^2$ in 1996-97 and 695 cm$^2$ in 1997-98. At Green Point the population gained 280 cm$^2$ within the quadrats in 1997-98 (Appendix II). Only half as many quadrats were sampled at Green Point as at Fairlight.
The relative growth rates of whole colonies are shown in Figure 3.3. The frequency distributions of relative growth rates of colonies were significantly different between sites in 1997-98 (Kolmogorov Smirnov test, $\chi^2 = 26.2$ with 2 df, $p < 0.001$). However, the frequency distributions of relative growth rates for colonies at Fairlight were not significantly different between the two years sampled (Kolmogorov Smirnov test, $\chi^2 = 1.31$ with 2 df, $p > 0.5$).

In each of the intervals measured, most colonies had relative growth rates of 10% to 100%. At Fairlight, 36% of colonies in 1996-97 and 44% of colonies in 1997-98 had 10% to 50% growth. At Green Point, 32% of colonies in 1997-98 had 10% to 50% growth. At Fairlight, 7 to 9% of colonies lost more than 10% of their area in a year, whereas only one colony at Green Point shrank, and that colony lost less than 10% of its area. Seven colonies had more than a sevenfold increase in area in a year (Figure 3.3).

Generally, colonies grew more quickly at Green Point than at Fairlight. At Green Point 51% of colonies more than doubled their area in a year, whereas only 21% of colonies at Fairlight (in each year) had similar increases in area. However, the colonies with the highest rates of relative growth were at Fairlight. The maximum relative growth measured at Fairlight was 13 in 1996-97 and 33 in 1997-98 whereas, at Green Point the maximum relative growth measured was 7.5. The fastest growing colonies at each site were all smaller than 1 cm$^2$; and the colony at Fairlight that grew thirty-threefold in a year went from 3 mm$^2$ to 99 mm$^2$.

The size-frequency distributions of whole colonies in the fixed quadrats at each site, in each year sampled, are shown in Figures 3.4 and 3.5. There were no significant differences in the size-frequency distributions of the population in any combination of years at Fairlight (Kolmogorov Smirnov test, $X^2 < 2.5$ for
Figure 3.3: The frequency distributions of relative growth rates of colonies at Fairlight and Green Point, in each year sampled.

Relative growth was measured as the increase in colony area in a year divided by the colony area at the start of that year.
Figure 3.4: The size frequency distributions of discrete colonies in each year sampled at Fairlight.
Figure 3.5: The size frequency distributions of discrete colonies in each year sampled at Green Point.
a) Green Pt 1997

b) Green Pt 1998
each comparison, df 2, p > 0.2). However, the size-frequency distributions were significantly different between the two years sampled at Green Point (Kolomogorov Smirnov test, $X^2 = 15.8$, df 2, p < 0.001).

These differences in the stability of the size-frequency distributions of the population between sites are likely to be due to differences in the rates of growth, mortality and recruitment of corals at these sites, and are likely to be partly explained by the fact that smaller colonies generally have faster rates of growth and lower rates of survivorship than larger colonies, which have increased rates of partial mortality (see Discussion in Section 3.9). This was investigated in sections 3.4 and 3.5, with reference to Models C1, C2, C3 and General Model 2d (Chapters 3.1.1 and 1.4).
3.4  EFFECT OF COLONY SIZE ON GROWTH RATE

Studies on corals from tropical locations have shown that smaller colonies grow more quickly than larger colonies, and that most of the variation in the growth rates of colonies of different sizes is due to the growth of very small colonies (Connell 1973; Hughes 1984). Therefore, I wanted to determine how much of the variation in the growth rates of colonies of *P. versipora* is due to their size, and the effect this has on the size-structure of the population. The hypotheses tested in this study were derived from General Models 1 and 2a and are presented in Chapter 1.4.

In this study, growth was not only measured in terms of the change in coral area, but also as the rate of linear extension. Thus, growth was measured as both the change in the number of polyps in a colony and the change in the number of rows of polyps at the periphery of a colony.

The rates of linear extension were used to estimate the rates at which colonies are expected to grow into contact with their nearest neighbours and potentially fuse (Chapter 4.3.5). Linear growth rates were also used to estimate the ages of colonies of different sizes to gain some indication of longevity in *P. versipora* and the age structure of the population (Appendix III).

3.4.1  Methods

Data obtained from image analysis of photographic slides from surveys of fixed quadrats were used in this analysis (Chapter 3.2). Only colonies that were entirely within the area of a quadrat and that did not die, fuse or split (undergo colony fission) during the year in question, were included in this study. These
colonies had positive, negative or zero net growth, over intervals of a year. Colonies were grouped into size-classes as defined in Chapter 2.6.

Colony growth was calculated as: 1) the mean change in area of colonies in each size-class in a year, 2) the mean relative change in area, where relative growth is the change in area in a year divided by the colony area at the start of that year and 3) the rate of linear extension (increase in radius) in a year. The area measurements of colonies were converted to linear dimensions (radii) using the assumption that colonies are circular ($A = \pi r^2$). This assumption is reasonable, as most of the colonies in the population are elliptical in shape and the length to width ratio of colonies smaller than 100 cm$^2$ is close to 1 (Appendix II, Figure II.3).

3.4.2 Results

The results are shown in Figures 3.6 and 3.7, and the numbers of colonies in each size interval are given in Table 3.3. Larger colonies had higher mean absolute increases in area, and greater variability in their absolute growth rates, than smaller colonies. The relative growth rates of the colonies showed the opposite pattern, with smaller colonies having higher mean relative changes in area and greater variability in their relative growth rates than larger colonies.

The relative growth rates of colonies were significantly different between colonies of different sizes at each site, in each year sampled (Table 3.2). SNK tests on the results of each analysis showed that the relative growth rates of colonies in size-class I were significantly different from those of colonies in size-classes II, III, IV and V, and at Green Point the relative growth rates of
Figure 3.6: The absolute growth rates of colonies in different size classes at Fairlight and Green Point, in each year sampled.

Absolute growth was measured as the increase in colony area in a year. The number of replicate colonies in each size class is given in Table 3.3. The error bars represent standard deviations.
a) Fairlight 1996-97

Change in Area (cm²)

Size Class

b) Fairlight 1997-98

Change in Area (cm²)

Size Class

c) Green Pt 1997-98

Change in Area (cm²)

Size Class
Figure 3.7  The relative growth rates of colonies in different size classes at Fairlight and Green Point, in each year sampled.

Relative growth was measured as the increase in colony area in a year divided by the colony area at the start of that year. The number of replicate colonies in each size class is given in Table 3.3. The error bars represent standard deviations.
Table 3.2a: ANOVA on Relative Growth Rates of Colonies of Different Sizes at Fairlight in 1996 to 1997 (data unbalanced)

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>SIZE</td>
<td>136.9</td>
<td>4</td>
<td>34.2</td>
<td>9.8</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>RESIDUAL</td>
<td>438.4</td>
<td>126</td>
<td>3.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>575.3</td>
<td>130</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

snk: I > II, III, IV and V, (p < 0.05).

Table 3.2b: ANOVA on Relative Growth Rates of Colonies of Different Sizes at Fairlight in 1997 to 1998 (data unbalanced)

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
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<td>57.8</td>
<td>7.4</td>
<td>&lt; 0.0001</td>
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<tr>
<td>RESIDUAL</td>
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<td>173</td>
<td>7.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>1587.3</td>
<td>177</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

snk: I > II, III, IV and V, (p < 0.05).

Table 3.2c: ANOVA on Relative Growth Rates of Colonies of Different Sizes at Green Point in 1997 to 1998 (data unbalanced)

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
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<td>SIZE</td>
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<td>17.5</td>
<td>11.1</td>
<td>&lt; 0.0001</td>
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<tr>
<td>RESIDUAL</td>
<td>91.4</td>
<td>58</td>
<td>1.58</td>
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<td>TOTAL</td>
<td>161.2</td>
<td>62</td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

snk: I > II, III, IV and V; and II > V, (p < 0.05).
colonies in size-class II were also significantly different from those of colonies in size-class V.

The maximum and minimum growth rates of different sized colonies are given in Table 3.3 and show that the range of growth rates increases with colony size. At Fairlight, in each year, some colonies in every size-class shrank, whereas at Green Point only one large colony shrank. At Fairlight, the greatest change in the area of colonies in size-classes I, II, III and IV was due to colonies increasing their area whereas, the greatest change in the area of a large colony (> 20 cm²) was due to it shrinking. At Green Point the greatest change in the area of a large colony resulted in an increase in area that was ten times greater than the area lost by the one colony that shrank.

The linear growth rates of colonies of different sizes are shown in Figure 3.8. These results do not show a relationship between colony size and estimated growth (ANOVA unbalanced, p > 0.7 at Fairlight, each year; and p > 0.2 at Green Point). The mean increases in radius at Fairlight were estimated to be 1.83 ± 2.54 mm in 1996-97 and 1.92 ± 3.99 mm in 1997-98. At Green Point the mean increase in radius was 4.04 ± 2.10 in 1997-98.

Preliminary estimates of the ages of colonies of different sizes were extrapolated from the growth rate data for colonies at Fairlight (Appendix III). Colonies at Green Point grew twice as quickly (on average) as colonies at Fairlight, and are therefore expected to be half as old in each size-class. The extrapolations suggest that colonies at Fairlight grow out of size-class I into size-class II one to two years after recruitment, and on average, colonies are expected to grow out of size-class II at 5 to 6 years of age. If a colony continued to grow at the average rate it would grow into size-class IV when it was 7 to 8 years old, and be > 20 cm² by 11 to 12 years of age. Based on average growth
Table 3.3: Range of absolute growth rates for colonies in different size classes

<table>
<thead>
<tr>
<th>Colony Size Class</th>
<th>Colony Size (cm²)</th>
<th>Minimum Growth (cm²)</th>
<th>Maximum Growth (cm²)</th>
<th>Number of Colonies Sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fairlight 1996-1997</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>visible &lt; 1</td>
<td>-0.17</td>
<td>1.93</td>
<td>34</td>
</tr>
<tr>
<td>II</td>
<td>1&lt;5</td>
<td>-2.77</td>
<td>15.64</td>
<td>38</td>
</tr>
<tr>
<td>III</td>
<td>5&lt;10</td>
<td>-7.34</td>
<td>8.22</td>
<td>20</td>
</tr>
<tr>
<td>IV</td>
<td>10&lt;20</td>
<td>-2.81</td>
<td>11.70</td>
<td>13</td>
</tr>
<tr>
<td>V</td>
<td>&gt;20</td>
<td>-37.94</td>
<td>26.14</td>
<td>26</td>
</tr>
<tr>
<td><strong>Fairlight 1997-1998</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>visible &lt; 1</td>
<td>-0.05</td>
<td>2.27</td>
<td>26</td>
</tr>
<tr>
<td>II</td>
<td>1&lt;5</td>
<td>-0.57</td>
<td>2.37</td>
<td>42</td>
</tr>
<tr>
<td>III</td>
<td>5&lt;10</td>
<td>-2.58</td>
<td>5.67</td>
<td>24</td>
</tr>
<tr>
<td>IV</td>
<td>10&lt;20</td>
<td>-0.27</td>
<td>12.73</td>
<td>15</td>
</tr>
<tr>
<td>V</td>
<td>&gt;20</td>
<td>-115.03</td>
<td>42.98</td>
<td>30</td>
</tr>
<tr>
<td><strong>Green Pt 1997-1998</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>visible &lt; 1</td>
<td>0.02</td>
<td>3.01</td>
<td>22</td>
</tr>
<tr>
<td>II</td>
<td>1&lt;5</td>
<td>0.87</td>
<td>7.88</td>
<td>17</td>
</tr>
<tr>
<td>III</td>
<td>5&lt;10</td>
<td>0.71</td>
<td>7.06</td>
<td>6</td>
</tr>
<tr>
<td>IV</td>
<td>10&lt;20</td>
<td>3.14</td>
<td>12.17</td>
<td>5</td>
</tr>
<tr>
<td>V</td>
<td>&gt;20</td>
<td>-1.46</td>
<td>20.18</td>
<td>13</td>
</tr>
</tbody>
</table>
Figure 3.8  The growth rates of colonies in different size classes measured as estimated absolute increase in colony radius at Fairlight and Green Point, in each year sampled.

The number of replicate colonies in each size class is given in Table 3.3. The error bars represent standard deviations.
a) Fairlight 1996-97

b) Fairlight 1997-98

c) Green Pt 1997-98
only, colonies larger than 100 cm² (diameter of 11.2 cm) are expected to be 26 to 27 years old. These estimates are crude and do not factor in the effects of other population processes such as partial mortality, fission, and fusion, which were shown to affect at least 29% of the colonies surveyed each year.

3.5 EFFECT OF COLONY SIZE ON MORTALITY


This study primarily measured whole colony mortality; however, partial mortality in terms of colonies shrinking was also investigated. Separate studies on partial mortality and the presence of lesions on the surfaces of colonies are described in Chapter 5. The hypotheses tested in this study were derived from General Models 1 and 2a and are presented in Chapter 1.4.

3.5.1 Methods

Data obtained from surveys of fixed quadrats were used in this study (Chapter 3.2). Colonies were grouped into the size-classes as defined in Chapter 2.6, and the proportion of whole colonies that died in each size-class calculated. The proportion of colonies that shrank (lost area) was also calculated from the survey data.
3.5.2 Results

Most whole colony mortality occurred for colonies in size-classes I and II, with the annual rates of whole colony mortality being the highest for colonies in size-class I, where they ranged from 11% to 26%. No whole colony mortality occurred among colonies in size-class V (> 20 cm²). In 1997-98, whole colony mortality was higher at Green Point than at Fairlight (Figure 3.9 and Table 3.4).

The numbers of corals in each size-class that shrunk are also shown in Table 3.4. There was no clear relationship between colony size and the proportion of colonies that shrunk, except when the largest and smallest size-classes at Fairlight are compared. In 1996-97, 11% of colonies in size-class I shrunk, compared to 24% of colonies in size-class V. Similarly, in 1997-98, 7% of colonies in size-class I shrunk compared to 18% of colonies in size-class V. Only one colony at Green Point shrunk and it was in size-class V.
Figure 3.9: Number of whole colonies that died in each size class at Fairlight and Green Point, in each year sampled (data from all quadrats pooled).
a) Fairlight 1996-97

```
Size Class
I  II  III  IV  V
Number of Colonies
0  10  6  2  0
```

b) Fairlight 1997-98

```
Size Class
I  II  III  IV  V
Number of Colonies
0  10  2  0  0
```

c) Green Pt 1997-98

```
Size Class
I  II  III  IV  V
Number of Colonies
0  12  2  0  0
```
Table 3.4: Rates of mortality for colonies of different sizes

The total number of whole colonies in each size interval has been calculated from the size frequency data at the start of each interval. The percentage values were calculated within each size interval for colonies that lost some of their area over a year (shrank) or died.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Shrank</td>
<td>% Died</td>
<td>n</td>
</tr>
<tr>
<td>I</td>
<td>11.1</td>
<td>11.1</td>
<td>54</td>
</tr>
<tr>
<td>II</td>
<td>18.1</td>
<td>9.6</td>
<td>83</td>
</tr>
<tr>
<td>III</td>
<td>20.0</td>
<td>3.3</td>
<td>30</td>
</tr>
<tr>
<td>IV</td>
<td>15.0</td>
<td>5.0</td>
<td>20</td>
</tr>
<tr>
<td>V</td>
<td>24.3</td>
<td>0</td>
<td>37</td>
</tr>
</tbody>
</table>
3.6 EFFECT OF COLONY SIZE ON REPRODUCTION

Colonies from different size-classes were sampled to determine the minimum size at which colonies become reproductive (Model E), and to investigate whether male colonies become reproductive at a smaller size than female colonies (Model F). The relationship between colony size and fecundity was also investigated for colonies larger than 20 cm², to determine whether the likelihood of colonies being reproductive continues to increase as colonies, that are reproductively mature, grow (Model E).

3.6.1 Methods

a) Sampling design to determine colony size at onset of reproduction

Colonies in each of four different size-classes were sampled and fixed in 10% formalin. The size-classes used were: visible to 1 cm², 1 < 5 cm², 5 < 10 cm², and larger than 10 cm². At one sampling time a fifth size-class of “very large” colonies (> 100 cm²) was also included.

Five to six replicate colonies were sampled per size-class, at each of six sampling times (five at Fairlight and one at Green Point). Samples were collected in Spring and Summer, which is when colonies are most likely to be reproductively active (Appendix IV). The sampling dates were December 1996 (Fairlight and Green Point); September and November 1997 (Fairlight); and February and March 1998 (Fairlight). A perspex template with holes cut-out for the different sizes of colonies was used to identify colonies for sampling, and colonies were removed from the substratum with a hammer.
and chisel. Pieces were sampled from the larger sized colonies; for small colonies (< 5 cm²) the whole colony was sampled.

b) **Relationship between proportion of colonies reproductive and size for large colonies**

Data from samples collected in studies to investigate the timing of reproduction in this species (Appendix IV) were collated to investigate whether larger colonies are more likely to be reproductive than smaller colonies. The colonies used in this study were all larger than 20 cm².

**3.6.2 Results**

Of the colonies sampled, no colonies smaller than 5 cm² contained gonads. Only colonies larger than 10 cm² had at least one fecund colony at every time sampled and there were the same number of males as females in the 5 < 10 cm² size-class. Not all colonies larger than 100 cm² were fecund; however, colonies larger than 120 cm² were the most likely to be fecund (> 60%). There was no relationships between colony size and the sex of colonies, for colonies that were larger than the size of reproductive maturity. The results are shown in Table 3.5 and Figure 3.10.
Table 3.5: Results from experiments to determine the minimum size of colonies at onset of reproduction in *P. versipora*

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Rep.</th>
<th>(27/12/96)</th>
<th>(01/09/97)</th>
<th>(20/11/97)</th>
<th>(04/02/98)</th>
<th>(13/03/98)</th>
<th>(28/12/96)</th>
</tr>
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<tbody>
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<td>1</td>
<td>a</td>
<td>n</td>
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<td>b</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>&lt;1 cm(^2)</td>
<td>c</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
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<td>n</td>
<td>n</td>
</tr>
<tr>
<td></td>
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<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td></td>
<td>f</td>
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<td>n</td>
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<td>n</td>
</tr>
<tr>
<td></td>
<td>b</td>
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<td>n</td>
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<tr>
<td>1&lt;5 cm(^2)</td>
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</tr>
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<tr>
<td></td>
<td>b</td>
<td>M-i</td>
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<td>M-i</td>
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</tr>
<tr>
<td>5&lt;10 cm(^2)</td>
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</tr>
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<td>M-i</td>
<td>F-m</td>
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</tr>
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<td>M-i</td>
<td>F-i</td>
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<td>&quot;very large&quot;</td>
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<td>M-i</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>M-i</td>
</tr>
</tbody>
</table>

Key:  
- **M** = male;  
- **F** = female;  
- **n** = no gonad;  
- **m** = mature and **i** = immature.
Figure 3.10: Percentage of colonies in different size intervals that contained gonad; data from October 1994 to March 1998.

Data from Fairlight and Green Pt have been combined. Where n is the number of colonies, ■: % of female colonies, □: % of male colonies, and : % with no gonad.
3.7 GROWTH AND SURVIVORSHIP OF SINGLE POLYP RECRUITS

The primary purpose of this study was to investigate whether (as proposed in Model G) most of the variation in the rates of growth and mortality of colonies is due to the rates that these processes occur for very small corals, namely recruits. For the purposes of this study single polyp recruits were considered to have 'recently' (within the last 12 months) arrived in the population. This was based on the fact that in previous studies, very small corals have been shown to have poor rates of survivorship (Babcock 1991), hence recruits were thought to be unlikely to survive as long as a year as single polyps.

Colony size and colony age are generally poorly correlated in corals due to partial mortality, fission and fusion. These processes can occur throughout the lifetime of a colony and can result in a dramatic change in colony size (Hughes & Connell 1987). Thus, the larger a colony is, the less reliable estimates of its age, based on its size, are likely to be. As a consequence of this, it is impossible to determine the age structure of a coral population without either damaging colonies by taking core samples of the skeletons, or monitoring individual colonies from the time of recruitment which, due to the longevity of most corals, is impractical. The surveys of fixed quadrats provided a record of the growth rates of recent recruits; this meant that the ages of colonies in size-class I could be estimated, and their rates of transition into size-class II directly measured. Thus, the age structure of these very small corals could be measured.

3.7.1 Methods

Direct measurements of single polyp recruits in the field had shown that they range from 0.5 mm to 7.5 mm in diameter (Appendix II). In the surveys of fixed
quadrats (Chapter 3.2), the image quality achieved was good enough that corals of 0.7 mm diameter could be seen in the slides; however, it was not always possible to see how many polyps these small corals had. Therefore, all corals measured in surveys of the fixed quadrats that were smaller than 50 mm$^2$ were assumed to be single polyp recruits.

The rates of recruitment, and rates of growth and survivorship of recruits, were measured at intervals of one year from the surveys of fixed quadrats. In the first year sampled at each site all colonies smaller than 50 mm$^2$ were included in these analyses. In the later surveys, the new recruits that had arrived in fixed quadrats and were not derived by fission, were included in the analysis (only two of these recruits were larger than 50 mm$^2$, and these are referred to separately in the results).

Although data were scored at intervals of twelve months, the surveys of fixed quadrats were actually done at intervals of 2 months. Therefore, in photographic slides where recruits may have been obscured due to sedimentation or back scatter in the image, the presence or absence of recruits was substantiated by checking slides taken in surveys before and after the time point being sampled.

3.7.2 Results

At Fairlight there were 35, 32 and 26 recruits in the permanent quadrats in 1996, 1997 and 1998, respectively. At Green Point there were 20 recruits in 1997, but only 3 recruits in 1998. Therefore, recruitment to the population was estimated to range from 6.6 to 8.9 recruits per m$^2$ per annum (within patches) at
Fairlight, and 1.5 to 10.2 recruits per m\(^2\) per annum (within patches) at Green Point.

More than 65% of recent recruits were smaller than 30 mm\(^2\), at each site, in each year. The two recent recruits that were larger than 50 mm\(^2\) were both from Fairlight, and had areas of 51 and 64 mm\(^2\) (and were measured in surveys in 1997 and 1998, respectively). After one year, 50% to 60% of recruits at Fairlight, and 82% of recruits at Green Point, were larger than 50 mm\(^2\) (data not shown).

The growth rates of recruits that grew without amalgamating with a neighbouring colony and did not die, are represented in Figure 3.11 and 3.12. In 1996-97, 27% of the recent recruits at Fairlight grew into size-class II. In 1997-98, 4.5% of the recent recruits at Fairlight, and 55% of the recent recruits at Green Point grew into size-class II. After one year of monitoring, all the recruits at each site, were still smaller than 3 cm\(^2\). After two years of monitoring at Fairlight, 65% of the 1996 recruits had grown into size-class II (1 < 5 cm\(^2\)), but none of these recruits had yet grown into size-class III (5 < 10 cm\(^2\)).

The relative growth rates of recent recruits are shown in Figure 3.13. The results show that most (65% to 86%) recent recruits had more than 100% growth in each year sampled at Fairlight, and that all the recruits at Green Point had more than 100% growth. Almost all the colonies surveyed in the fixed quadrats that had relative growth of more than 200% at Fairlight, and relative growth of more than 300% at Green Point, were recent recruits (compare Figure 3.3 to Figure 3.13).
Figure 3.11: The size frequency distributions of recruits at intervals of one year at Fairlight, for recent recruits measured in 1996 (n = 26), 1997 (n = 22), and 1998 (n = 26).
Figure 3.12: The size frequency distributions of recruits at intervals of one year
at Green Point, for recent recruits measured in 1997 (n = 11) and 1998
(n = 3).
a) 1997 new recruits

b) 1998 new recruits
Figure 3.13: Frequency distributions of the relative growth rates of recent recruits at Fairlight and Green Point in each year sampled.
a) **Fairlight 1996-97**

![Bar chart for Fairlight 1996-97]

Relative Growth in One Year

b) **Fairlight 1997-98**

![Bar chart for Fairlight 1997-98]

Relative Growth in One Year

c) **Green Pt 1997-98**

![Bar chart for Green Pt 1997-98]

Relative Growth in One Year
At Fairlight, recruits in 1996 had 14% mortality over a year, and 20% mortality (in total) over 2 years. Recent recruits in 1997 had 21% mortality at Fairlight, and 35% mortality at Green Point over their first year (Table 3.6).

Within a year of first being observed in a quadrat, between 4% and 18% of recruits grew into contact and amalgamated with a neighbouring colony (Table 3.6).

3.8 SUMMARY OF POPULATION PROCESSES MEASURED IN SURVEYS OF FIXED QUADRATS

The rates at which colonies in different size-classes increased their size-class, died or grew into contact with a neighbouring colony have been summarised in Table 3.7.

Most of the colonies surveyed either stayed in the same size-class or increased by one size-class, a few colonies decreased by one size-class. Almost all the colonies that amalgamated with other colonies became large (> 20 cm²) (see Chapter 4.3.6 for more details). Colony fission was rare.

To test Hypothesis C1 (Chapter 3.1.1), the rates at which colonies grow out of size-class I into size-class II were compared to the rates colonies grow out of size-class II into size-class III at each site for each year. These comparisons were done as two analyses: 1) for colonies that grew or shrank only, and 2) for all the colonies in each size-class. There were no significant differences in the rates of transition between these size-classes in either analysis ($\chi^2, \alpha = 0.05$).
Two recent recruits from Fairlight have been excluded from the data. One of these recruits was 51 mm$^2$ in 1997 and grew to a size of 1.3 cm$^2$ over a year. The second recruit was 64 mm$^2$ in 1998.

By 1998, 7 of the original 35 recruits at Fairlight in 1996 had died and 2 had grown into contact with a neighbouring colony. [nd = no data].
Table 3.7: Annual rates of transition between colony size classes

a) Fairlight 1996-1997

In this time interval the population gained 32 recruits and 3 new colonies formed by the fission of large colonies.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>No. Died</th>
<th>No. Contact</th>
<th>Size Class after One Year</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>6</td>
<td>3</td>
<td>I 25</td>
<td>II 16</td>
</tr>
<tr>
<td>II</td>
<td>8</td>
<td>8</td>
<td>I 2</td>
<td>II 39</td>
</tr>
<tr>
<td>III</td>
<td>1</td>
<td>6</td>
<td>I 0</td>
<td>II 2</td>
</tr>
<tr>
<td>IV</td>
<td>1</td>
<td>2</td>
<td>I 0</td>
<td>II 0</td>
</tr>
<tr>
<td>V</td>
<td>0</td>
<td>2</td>
<td>I 0</td>
<td>II 0</td>
</tr>
</tbody>
</table>

b) Fairlight 1997-1998

In this time interval the population gained 26 new recruits and 1 new colony formed by the fission of a large colony.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>No. Died</th>
<th>No. Contact</th>
<th>Size Class after One Year</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>10</td>
<td>6</td>
<td>I 32</td>
<td>II 13</td>
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<tr>
<td>II</td>
<td>3</td>
<td>7</td>
<td>I 0</td>
<td>II 42</td>
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<tr>
<td>III</td>
<td>1</td>
<td>5</td>
<td>I 0</td>
<td>II 0</td>
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<td>IV</td>
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<td>I 0</td>
<td>II 0</td>
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<td>V</td>
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<td>4</td>
<td>I 0</td>
<td>II 0</td>
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</table>
c) Green Point 1997-1998

In this time interval the population gained 3 recruits.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>No. Died</th>
<th>No. Contact</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>N</th>
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<tr>
<td>I</td>
<td>11</td>
<td>9</td>
<td>6</td>
<td>14</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>40</td>
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<tr>
<td>II</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>6</td>
<td>11</td>
<td>1</td>
<td>0</td>
<td>23</td>
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<td>III</td>
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<td>IV</td>
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<td>3</td>
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<td>V</td>
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<td>13</td>
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</table>
3.9 DISCUSSION

P. versipora colonies, like other species of coral, have highly variable rates of growth. As predicted some of this variation is due to the sizes of colonies and some to the site at which they are growing. There are strong relationships between colony size and the likelihood of whole colony mortality, and colony size and the probability of a colony being fecund. The results of these studies are discussed below, with reference to the models described in Chapter 3.1 and summarized in light of the general models proposed in Chapter 1.4.

3.9.1 Population Growth

Individual colonies can grow, shrink or die. Overall the population increased its area each year, but did not increase the number of colonies it contained. Thus, Model A (‘that the population is growing’) was only partially supported.

At Fairlight the area of coral increased by 6% to 15% over a year and at Green Point the area of coral increased by 28% over a year. This gain in coral area was over and above the area lost due to colonies dying and shrinking. At each site, in each year sampled, up to 1.5% of the area of coral present at the start of the year was lost due to the death of colonies. At Fairlight, a further 4% to 6% of the initial coral area was lost due to colonies shrinking. In contrast, at Green Point, the amount of area lost due to colonies shrinking was insignificant compared to the net area of coral gained (< 0.2% versus 28%).

The loss of coral area at Fairlight suggests that these colonies are damaged more often than colonies at Green Point. In contrast, however, the rates of whole colony mortality were higher at Green Point than at Fairlight, making it
surprising (and somewhat unlikely) that the reverse was true of the rates of partial mortality. This discrepancy occurred because colonies at Green Point grow more quickly and hence, are able to replace damaged areas faster than colonies at Fairlight. Studies in Chapter 5 on the rates of colony injury and lesion regeneration provide further evidence to support this model.

At Fairlight, the number of discrete colonies in the population changed by only a few colonies each year (≤ 1.4%). In contrast, the number of discrete colonies at Green Point dropped by 23% over a year (Appendix II). The loss of colonies at Green Point was partly because there were fewer new recruits than there were colony deaths in that year. However, many of the colonies ‘lost’ at each site did not actually die, but instead grew into contact and amalgamated with neighbouring colonies.

The average rates of coral growth in quadrats were not affected by the initial percentage cover of coral in a patch (Figure 3.2). However, the absolute amount by which the area of coral could change (range of growth) increased as the percentage cover of quadrats increased. Furthermore the likelihood of the quadrat losing area also increased as percentage cover increased. Quadrats with more than 10% cover were more likely than quadrats with less than 10% cover to lose some of their coral area (Table 3.1). Although these results are only partly consistent with Model B, they do seem to provide at least some explanation as to why few patches (< 19%) have more than 30% cover even though observations of colonies at local sites suggest that most patches could have close to 100% cover. These findings are discussed further in Chapter 6.

This apparent effect of percentage cover may be because patches that have a high cover of coral contain large colonies. Generally, large colonies have higher rates of partial mortality, so are expected to be more likely to lose some
of their area than small colonies (Hughes & Jackson 1980, 1985; Hughes 1984). However, the findings of studies described in Chapter 5 show that the relationships between partial mortality and colony size are more complex than described in this chapter and in previous studies.

3.9.2 Effect of Colony Size on Growth, Mortality and Reproduction

Consistent with Models C1 and C2, small colonies do have greater relative growth and greater whole colony mortality than larger colonies (Figures 3.7 and 3.9). On the other hand, larger colonies have greater absolute growth than smaller colonies (Figure 3.6 and Table 3.3).

Interestingly, when the growth rates of colonies were measured as the rates of linear extension, there were no significant differences between colonies of different sizes. This suggests that relationships between the rates at which colonies increase their area and their initial size reflect the simple geometric rule that, as a (circular) colony increases its radius linearly, its area increases exponentially. These relationships between the growth rates of colonies of different sizes, and the dimensions that growth is measured in, are not new and have been discussed before (Buddemeier et al. 1974; Maragos 1978; Hughes & Connell 1987). If growth is limited to fixed linear increments at the edge of a colony no matter what the size of the colony, then this suggests that colony growth is controlled by the rates of growth and development of polyps at the edge of the colony.

Colonies in size-class I had rates of growth that were much higher than all other size-classes. Thus, the growth rate data suggest that colonies in size-class I will grow into size-class II more quickly than colonies in size-class II will
grow into size-class III. This model is further supported by the fact that colonies require less linear growth to grow from size-class I into size-class II than colonies growing from size-class II into size-class III. However, direct measurements of the rates of transition of colonies in the field showed that the rates of transition were not significantly different between these different size-classes, thus rejecting Hypothesis c1 even though colonies in size-class I do grow faster than colonies in size-class II (Table 3.2). Therefore, these unexpected results must reflect the spread of colony sizes within these size-classes, in that colonies in size-class I were predominantly very small, whereas a large proportion of the colonies in size-class II must have been in the upper size range of that interval.

Previous studies on corals have found whole colony mortality to be highly dependent on colony size (Connell 1973; Pearson 1974; Glynn 1976; Loya 1976; Bak & Engel 1979; Highsmith 1980; Hughes & Jackson 1980; Hughes & Connell 1987; Babcock 1991; Johnson 1992). The mortality rates of *P. versipora* are also strongly linked to size, as proposed in Model C2. Consistent with the predictions of Hypothesis c2, colonies smaller than 5 cm$^2$ were more likely to die than larger colonies. Up to 26% of colonies in size-class I died and up to 10% of colonies in size-class II died. No colonies in size-class V (> 20 cm$^2$) died during this study (Figure 3.9 and Table 3.4).

At Fairlight, some colonies in every size-class shrank over a year. The greatest change in the area of a large colony (> 20 cm$^2$) was due to it shrinking. At Fairlight, 11% to 17% of whole colonies lost some of their area in a year, and colonies in size-class V were more than twice as likely to shrink as colonies in size-class I (Table 3.4). The one colony that shrank at Green Point was large. These results are consistent with Model C3, in that the rates of partial mortality increased with colony size.
Colony fission occurred at a very low rate in the population. Only four (small) colonies were produced by fission over two years at Fairlight. No fission was recorded in surveys at Green Point. These results show that fission is rare and therefore, unlikely to be of much consequence to the population. These low rates of fission meant that it was not possible to test Hypothesis c4.

As proposed in Model E, the reproductive biology of colonies does change as they grow. Consistent with Hypotheses e1 and e2 colonies smaller than 5 cm² are not reproductively active (Table 3.5) and the probability of colonies of reproductive size being fecund is greater in larger colonies than in smaller colonies. The largest proportion of colonies that were reproductive were larger than 120 cm² (Figure 3.10). However, contrary to Model F there was no relationship between the size and sex of colonies (Figure 3.10).

Although the colonies with the fastest rates of relative growth (size-class I) were non-reproductive (Figure 3.7), colonies do not actually become reproductive until they are in size-class III (> 5 cm²), which is the same size-class that colonies attain a sudden increase in survivorship (Figure 3.9). Similar findings were reported for the free-living coral Manicina areolata (Johnson 1992).

These results suggest that there is a change in the energetics of colonies related to their ability to recover from partial mortality, in that colonies larger than 5 cm² are more likely to have resources available to repair damaged areas (so are less likely to die) than smaller colonies. Hence, if colonies larger than 5 cm² are not injured then they may have the resources available to develop gonads. This effect of size is also likely to be related to
the fact that the polyps of small colonies are young, so may not have yet acquired the resources they need to be reproductively viable (Soong 1992).

If reproduction is linked to the energetics of colonies, then the size at which colonies attain reproductive maturity may vary between populations living under different environmental conditions.

It would be interesting to investigate the extent to which this link between the start of reproduction and increased rates of survivorship is a general characteristic of *P. versipora* and of other modular marine invertebrates. If it is general, then measures of the size-frequency distribution of a population, combined with sampling to identify the smallest size at which colonies first become fecund, could be used to obtain estimates of the rates at which mortality processes occur in different populations, and could also be used to detect shifts in the dynamics of populations. These methods could potentially avoid the need for the arduous and costly monitoring programs currently used to measure these parameters directly and could therefore, prove to be a useful tool in the management of reef environments. More studies are needed on different populations in an assortment of different habitats to investigate this model.

The difficulties of predicting when *P. versipora* colonies are most likely to be reproductive and the large proportion of colonies (39% to 67%) that did not contain gonads in each sampling interval (Appendix IV) meant that it was not practical to do studies to compare the fecundity (amount of gonad) of colonies of different sizes, due to the large number of samples that would have been needed relative to the size of the local population.
3.9.3 Growth and Survivorship of Recruits

The rates of recruitment to patches at Fairlight were low and ranged from 7 to 9 recruits per m² (within patches) each year. At Green Point recruitment was much more variable, with 10 recruits per m² (within patches) in 1997, but only 2 recruits per m² (within patches) in 1998. Thus, although recruitment was fairly stable between years at Fairlight, it did vary from year to year (as proposed by Model C5) at Green Point.

In surveys of recruits in the field (Chapter 4.3), no recruits were observed in areas that did not already contain coral colonies. However, one small colony (< 5 cm²) was observed in an area isolated from other colonies, at Green Point. This colony did not survive, suggesting that recruitment to ‘non-patches’ and the creation of new patches is very rare at these sites.

Corals that were only one polyp in size (< 50 mm²) were considered to be recent recruits; however, the surveys of fixed quadrats showed that not all colonies less than 50 mm² are less than a year old.

Consistent with Model G most of the variation between colonies in their rates of growth and mortality is due to the rates that these processes occur for recruits. In each year sampled at each site, the number of recruits that died was much higher than would be expected if mortality affected all corals in size-class I equally. Overall, between 31% and 54% of the corals that died in each year, at each site, were single polyp recruits. Similarly, the highest rates of relative growth measured in the population were almost entirely represented by the growth of recent recruits (Figures 3.3 and 3.13).
Recruits had higher rates of mortality and faster rates of growth at Green Point than at Fairlight. After one year, 55% of single polyp recruits at Green Point were larger than 1 cm², whereas at Fairlight recruits grew more slowly (on average) with, only 27% of the 1996 recruits, and 5% of the 1997 recruits growing into size-class II over a year (Figures 3.11 and 3.12).

Although recruits at Fairlight are less likely to die, they also grow more slowly, so are exposed to the risk of mortality due to being small for longer than recruits at Green Point. This result is interesting, as it suggests that, even though the annual rates of mortality of small colonies are higher at Green Point than at Fairlight, the cumulative risk of mortality for each generation at each site may actually be quite similar.

3.9.4 The Effect of Growth, Mortality, and Recruitment on the Size-structure of the Population

The size-structure of the population varies spatially and temporally. Preliminary surveys of the population showed that the size-frequency distributions of colonies varied significantly between Fairlight and Green Point (Chapter 2.4). Results from the surveys of fixed quadrats show that, as proposed in General Model 2c, the size-frequency distributions can also vary from year to year within sites.

In addition to this, the sizes at which the biology of colonies changed were chosen based on the size-structure of the population (Figure 2.2) and show that the frequency distributions of colony sizes can be used to predict biological differences between colonies (General Model 2a).
At Green Point the size-frequency distributions of colonies were significantly different between 1997 and 1998 (Figure 3.5); however, they remained stable over the three years surveyed at Fairlight (Figure 3.4). The greatest difference in the frequency distributions at Green Point were in the proportion of colonies that were smaller than 1 cm². This variation represented annual differences in the rates of recruitment at Green Point combined with the fast rates of colony growth and high rates of mortality, which meant that at Green Point colonies were quickly lost from the smallest size-classes if they were not replaced by more new recruits.

Between sites the greatest differences in the size-frequency distribution were in the proportion of colonies that were smaller than 5 cm² (Figure 2.2). These differences were also due to differences in the rates of growth, mortality and recruitment between sites.

The relative growth rates of colonies that grew to become large, and did not die, were similar between the two years sampled at Fairlight, but were significantly different between Fairlight and Green Point in the year both sites were sampled (1997-98), as predicted in Hypothesis d2 (Figure 3.3). On average, colonies grew much faster at Green Point than at Fairlight. Due to their faster growth rates, small colonies also had higher rates of growing into contact and amalgamating with neighbouring colonies at Green Point (19%) than at Fairlight (≤ 11%) (Table 3.7). Consequently, colonies were much more likely to increase their size-class at Green Point (41%) than at Fairlight (20% in 1996-97 and 18% in 1997-98) (Table 3.7). The higher rates of mortality and lower rates of recruitment also explain why there were fewer small colonies at Green Point than at Fairlight (Table 3.4).
In contrast, there was little variation in the proportion of colonies in size-classes that were larger than 5 cm$^2$ between sites and between years, due to the slower rates of growth, increased survivorship and increased rates of partial mortality of colonies in these larger size-classes.

The reason colonies grow more quickly at Green Point is probably because they occur in shallower water, so are exposed to more light and therefore, photosynthesize at a higher rate than colonies at Fairlight. However, increased irradiance is likely to also lead to increased growth of macroalgae and hence, increased competition for space unless algal growth is limited by grazing.

In the Sydney region, *P. versipora* occurs predominantly in 'barrens' habitats, although at Fairlight colonies also occur in assemblages with turf algae. Barrens habitats are recognised as areas of thin encrusting coralline algae and are intensively grazed by the urchin *Centrostephanus rodgersii* (reviewed by Jones & Andrew 1990). *C. rodgersii* has been observed grazing on *P. versipora* at night (Chapter 5.2). If, as these observations suggest, corals occur in areas which are grazed more intensively at Green Point than at Fairlight, then mortality is likely to be higher at Green Point than at Fairlight. Differences in grazing intensity may mean that recruits have higher rates of mortality and may also explain why the rates of recruitment were lower and more variable between years at Green Point than at Fairlight.
3.9.5 Concluding Comments

The results of the studies described in this chapter are consistent with models proposed by Jackson (1979) and with the findings of previous studies on other species of coral (reviewed in Chapter 1).

The changes in the biology of colonies as they grow are likely to reflect changes in their energetics due to the different rates at which colonies of different sizes are disturbed. Consistent with these models, small colonies have higher rates of growth and mortality than larger colonies. Some colonies in all size-classes at Fairlight shrank and large colonies had a higher rate of damage than small colonies. The types of damage colonies have on their surfaces and their rates of injury and repair were investigated in more detail in Chapter 5.

The greater survivorship of small colonies compared to larger colonies, and high proportion of colonies in the surveys that grew into contact with a neighbouring colony, suggest that the ability of colonies to amalgamate and form larger colonies quickly may also increase their survivorship and perhaps affect other aspects of their biology. Models about the importance of colonies forming amalgamations were investigated in Chapters 4 and 5.
3.10 SUMMARY

Similar to other corals and modular organisms, the biology of *P. versipora* colonies changes as they grow. Colonies smaller than 5 cm$^2$ have the highest mortality, whereas colonies larger than 20 cm$^2$ are highly unlikely to die. The relative growth rates of colonies decrease with increasing size. The rates of linear growth, however, do not change between colonies of different sizes. Only colonies larger than 5 cm$^2$ are reproductive, and colonies larger than 120 cm$^2$ are the most likely to be fecund. The sizes at which the biology of colonies is likely to change can be predicted from the frequency distributions of colony sizes in the population.

Colonies grow more quickly (on average) and have higher rates of whole colony mortality at Green Point than at Fairlight. However, colonies are much more likely to shrink at Fairlight than at Green Point. Rates of recruitment are higher and more consistent between years at Fairlight than at Green Point.

The size-frequency distributions of the population varied spatially and temporally, but only in the proportion of colonies that were small (< 5 cm$^2$). This variation was due to differences in the rates of recruitment, growth and mortality (all processes that affect small colonies the most). In contrast the rates of growth, partial mortality and colony amalgamation do not cause significant fluctuations in the numbers of colonies in the larger size intervals, although they will limit the maximal size colonies in the population attain.
CHAPTER 4: THE EXTENT TO WHICH FUSION OCCURS IN THE SYDNEY HARBOUR POPULATION

4.1 INTRODUCTION

In the preliminary population surveys (Chapter 2.4), some discrete colonies consisted of more than a single colony and were the result of multiple colonies having amalgamated. Of the discrete colonies surveyed, 15% of colonies at Fairlight and 21% of colonies at Green Point were composed of more than one coral. One discrete colony consisted of at least 52 corals, all in contact. From the surveys I estimated that about 48% of colonies at each site had amalgamated with other colonies, suggesting that colonies frequently grow into contact with each other. Furthermore, the Sydney Harbour population of *P. versipora* is unusual among corals in that it rarely occurs in patches with other clonal organisms (Plate 2.1). Consequently, *P. versipora* colonies are unlikely to grow into contact with colonies of other species, but are likely to be able to grow into contact with conspecific colonies (Plate 4.1).

Larger colonies have higher survivorship and more reproductive output than smaller colonies (Connell 1973; Hughes *et al.* 1992; Babcock 1991; Hall & Hughes 1996; this study, Chapter 3). If colonies that grow into contact can fuse to form a large colony, and these large colonies arise more quickly, yet have a similar biology to large colonies that have grown from a single recruit, then fusion may play a significant role in structuring the population at local sites (as proposed in General Models 3a and 3b, Chapter 1.4). However, the extent of the role it plays will depend on whether: a) colonies occur close enough together that they are likely to grow into contact, and b) colonies that grow into contact are likely to fuse.
Plate 4.1: An aggregation of colonies of *P. versipora* (blue colour morph) that have all grown into contact (c) at Fairlight.
4.1.1 Models and Hypotheses for Studies on Fusion and the Amalgamation of Colonies

Models proposed to investigate General Model 3b (Chapter 1.4):

MODEL A: Colonies frequently grow into contact with neighbouring colonies, and a large proportion of colonies that grow into contact fuse

Ha1) That colonies are likely (> 40% based on preliminary surveys of the population, Chapter 2.4) to grow into contact with a neighbouring colony.

Ha2) That recruits are likely (> 40% based on preliminary surveys of the population, Chapter 2.4) to grow into contact with a neighbouring colony.

Ha3) That some colonies (> 5%) grow into contact and amalgamate with their neighbours each year.

Ha4) That a proportion of colonies that grow into contact fuse (> 20%).

MODEL B: The histocompatibility reactions between colonies that grow into contact are stable (do not change over time)

Hb1) That the range of 'lengths of contact' are the same for all of the different histocompatibility reactions that occur between colonies.

MODEL C: Colonies that join amalgamations become larger (in total) and are not resorbed

Hc1) That colonies that grow into contact increase their size-class.

Hypotheses derived to investigate General Model 3c (Chapter 1.4), that only highly related colonies are able to fuse:
Hc1) That colonies that grow into contact and are of similar size are more likely to fuse than colonies of different sizes.

Hc2) That two small colonies are more likely to fuse than any other combination of colony sizes.

Hc3) That colonies always recognise their own tissue as ‘self’ and fuse with the tissue.

Hc4) That colonies sampled from the same patch are more likely to fuse than colonies sampled from distant patches.

These hypotheses were used as an alternative to genetic studies, which are the only way that relatedness between colonies can be definitively established.

Initially, I identified and described the different types of intraspecific histocompatibility reactions found between colonies in the population, and determined the frequency at which each of the different histocompatibility reactions occurs in the population. I then established whether the histocompatibility reactions are fixed or transient and investigated relationships between the combination of colonies that had grown into contact and the type of histocompatibility reaction.

Next, I needed to establish whether colonies are likely (> 40%, as measured in the preliminary population surveys in Chapter 2.4) to grow together and come into contact. To ascertain this I measured the distance between the growing edges of colonies and their nearest neighbours. Using frequency distributions of these nearest neighbour distances, combined with measures of the rates at which colonies grow towards each other (Chapter 3.4), I determined the proportion of colonies likely to be able to grow into contact with their nearest neighbour at different intervals of time.
I then set up experiments using histocompatibility assays, to find out the consequences of colonies growing into contact, the probability of colonies fusing, and whether fusibility between colonies has a spatial component, in that colonies sampled from further away are less likely to fuse than colonies sampled from near each other. Included in these experiments were assays to determine whether colonies always recognise and fuse with their own tissues ('self').

Finally, I compared the frequency at which each of the different historecognition reactions occurred in the within-patch histocompatibility assays (Chapter 4.4.3) with the frequency that they occur in the surveys of the field populations (Chapter 4.2.4). Significant deviations between these two sets of results would suggest that colonies involved in reaction types that are under-represented in the population surveys may have reduced rates of survivorship whereas, colonies over-represented in the population surveys may have enhanced rates of survivorship.
4.2 DESCRIPTION AND SURVEY OF HISTOCOMPATIBILITY REACTIONS OCCURRING BETWEEN COLONIES

4.2.1 Introduction

The primary purpose of this survey was to establish the importance of fusion in the population by measuring the proportion of colonies in the field that have grown into contact with a neighbouring colony, and fused. These data were used to test Hypothesis a4.

The results of the survey were also used to investigate General Model 3c. Colonies from the same recruitment event may be more highly related, and therefore, more likely to fuse than colonies from different recruitment events. At least to some extent, the ages and sizes of colonies are correlated, in that small colonies are likely to be young, and large colonies are likely to be older. Therefore, I predicted that colonies that grow into contact and are of similar size, are more likely to fuse than pairs of colonies of very different sizes (Hypothesis c1). Further, because size and age are likely to be more strongly correlated for smaller colonies than for larger colonies, I also predicted that amalgamations between two small colonies are more likely to result in the colonies fusing than amalgamations between two large colonies (Hypothesis c2).

Finally, a number of studies done over long time periods have shown that some histocompatibility reactions are unstable and transitory (Chadwick-Furman & Rinkevich 1994; Hidaka et al. 1997). Therefore, after identifying the different types of histocompatibility reactions occurring in P. versipora I needed to find out whether, as proposed in Model B, these reactions are stable.
The majority of colonies are circular or elliptical in shape. When colonies first grow into contact they touch only at a single point; this later forms a 'length of contact' between the colonies, that becomes longer as the colonies grow to fill the area between them. Therefore, the length of contact between colonies can be used as a measure of how long colonies have been in contact, and the range of contact lengths for each histocompatibility reaction will provide an indication of which reactions are likely to be transitory (unstable) and which are likely to be fixed (stable) - unless all the histocompatibility reactions are unstable. These were used to test Hypothesis b1.

From observations of the different histocompatibility reactions occurring between *P. versipora* colonies (described fully in the next section), it was predicted that the reactions that were most likely to be unstable were the 'partial rejection' responses of the distinct, alternate and mix reactions. This prediction was further supported by the fact that the alternate and mix reactions occur at a much lower frequency in the population than the other three types of reactions. Therefore, I predicted that if the distinct, alternate and mix contacts are intermediate or transitory reactions, they will occur only where contact between colonies is recent and therefore, involves only a few polyps (< 2 cm length), whereas the blend and ridge reactions will occur across the range of contact lengths measured, or only in contacts that are older (have lengths of contact > 2 cm).
4.2.2 Descriptions of the Types of Histocompatibility Reactions Identified in the Population

Preliminary observations identified five different types of histocompatibility reactions between colonies. I termed these reactions 'blend', 'distinct', 'ridge', 'alternate', and 'mix'. In each of these histocompatibility reactions the colonies were in direct contact with each other. To determine the type of histocompatibility reactions occurring between colonies, I ran a finger along the area of contact to cause the tentacles and tissue to retract, so that the structure of the skeleton between the colonies could be seen.

The 'blend' reaction appears to have complete fusion of the skeleton and tissue between the two colonies. The colonies appear to be completely integrated, as polyps near the area of contact contain a mix of the pigments from each of the colonies involved in the reaction. Blend reactions are also discernible between two colonies of the same morph due to variations in the brightness and depth of colour of the different colonies, and because colonies that form amalgamations generally lose their circularity. In blend reactions the skeleton is continuous between the colonies and the polyps are aligned and maintain their regular pattern of spacing (Plate 4.2b).

In the 'distinct' histocompatibility reaction the polyps are not aligned between the colonies in the area of contact, and the tissue is often discoloured, appearing pale or white, in the area of contact. There is no transfer of colour pigments between colonies in the association, and the tissues and skeletons (although directly adjacent to each other) are discontinuous between the colonies (Plate 4.2d and e).
Plate 4.2: Examples of the different historecognition reactions identified between colonies of P. versipora in the field (see text for full descriptions)

a) Interspecific 'stand-off' reaction between a P. versipora colony (Pv) and a Coscinaraea mcneilli colony (Cm). The tissue at the edge of the C. mcneilli colony is swollen in an aggressive/defensive response (x).

b) Blend reaction (fusion) between a blue and a green colony. The pigments from each of the colonies appear to have been transferred between them in the area of contact (c), and single polyps contain both blue and green pigments.

c) Ridge reactions between three blue colonies. A ridge has formed between the corals in the areas of contact (c).

d) Distinct reaction between two blue colonies. The colonies are in direct contact but the polyps of each colony have remained distinct in the area of contact (c), and there is no transfer of the pigments between the colonies.

e) Distinct reaction between a blue and a green colony. The tissues of the colonies remain distinct in the area of contact (c). In some places sweeper tentacles (S1) have been extended in an aggressive/defensive response.
In the 'ridge' histocompatibility reaction a suture forms between the colonies where the skeletons rise to form a crest or ridge between the colonies (Plate 4.2c). In colonies that have not yet developed an obvious ridge, this histocompatibility reaction can still be distinguished as the skeleton is jagged and sharp to the touch where the ridge is forming.

The last two histocompatibility reactions were termed 'alternate' and 'mix', and are much less common. The 'alternate' reaction appears to involve fusion between the skeletons of the two colonies, but there is probably incomplete fusion between the tissues as, although the tissue appears to have fused, the colouration of the individual colonies remains distinct. Each polyp is a single colour; thus, there is an alternate pattern of colouration along the zone of contact. In the 'mix' histocompatibility reaction the area of contact between the colonies has areas where the polyps appear to have blended, and other areas where the polyps appear distinct.

_Coscinaraea mcneilli_ is the only other colony-forming hard coral that occurs in local waters, and it has a very low abundance (< 10 colonies at Fairlight, and none at Green Point). There were a few instances of histocompatibility reactions between _P. versipora_ with _C. mcneilli_. In these interspecific reactions an area of separation of a few millimetres remained between the colonies, resulting in a 'stand-off' type of reaction (Plate 4.2a). Similar types of reactions have been described in Connell (1973) and Van Veghel & Bak (1996) between colonies of different species, and in Rinkevich & Loya (1983a) between two colonies of the same species.
4.2.3 Survey Methods

The frequency at which each of these histocompatibility reactions occurs in the population was measured in surveys at Fairlight and Green Point. The surveys were done for colonies occurring at between 2 and 8 m depth, by swimming from patch to patch. The surveys included a total of 150 incidents of contact between colonies at each site. Only one histocompatibility reaction was scored for each discrete colony (the reaction closest to me when I approached the colony), and a maximum of 3 randomly chosen discrete colonies was scored per patch. Due to the limit on diving bottom times, data were collected as three separate surveys at each site, each of about \( n = 50 \) incidences of contact between colonies.

For each reaction, the size and colour morph of the two colonies involved in the reaction were recorded. In two of the surveys at each site, the length of the contact zone between the colonies was also measured with a ruler. Colonies were assigned to the size-classes 'small', 'medium' or 'large', representing colonies of \(< 5 \text{ cm}^2\), \(5 < 20 \text{ cm}^2\) and \(> 20 \text{ cm}^2\) respectively. In the first survey at each site, the sizes of colonies were estimated by eye only, so those data have not been included in analyses involving colony size. In the later surveys the dimensions of colonies were measured with a ruler, and the sizes of colonies estimated using the formula for the area of an ellipse (given in Chapter 2.4).
4.2.4 Results from Surveys of Histocompatibility Reactions Between Colonies

The blend, distinct and ridge histocompatibility reactions were the most common, each with mean frequencies of between 24% and 35%. The alternate and mix reactions together made up less than 12% of the reactions surveyed (Figure 4.1).

There was no significant difference between sites in the proportions of different histocompatibility reactions ($\chi^2 = 3.3$, df 4, $p > 0.5$).

The blend, ridge, and distinct histocompatibility reactions had contact lengths that ranged from less than 2 cm to more than 6 cm (Figure 4.2). The mix reactions ($n = 5$ to 6 at each site) had short ($< 2$ cm) and very long ($> 8$ cm) lengths of contact. There were only 3 alternate reactions recorded at each site, and they all had contact lengths between 2 and 6 cm.

In Figure 4.3, the frequencies of blend, distinct and ridge histocompatibility reactions are shown for each of the different combinations of small, medium and large colonies recorded in the surveys.

The highest proportion of blend reactions occurred in combinations of two small colonies (50% at Fairlight and 50% at Green Point). Overall, there were fewer amalgamations involving two small colonies than two medium colonies, or two large colonies. At Fairlight, the smallest proportion of blend reactions occurred in reactions between two large colonies (7%). At Green Point, the smallest proportion of blend reactions occurred in reactions between a small and a large colony (14%) (Figure 4.3).
Figure 4.1: Frequency distribution of histocompatibility reactions at Fairlight and Green Point, where, □ represents Fairlight (n = 152) and ■ represents Green Point (n = 151). Graph shows the mean values of three surveys each of n = 50. Error bars are standard deviations.
Figure 4.2: Frequency distribution of contact lengths between colonies with different types of histocompatibility reactions at a) Fairlight and b) Green Point.

The blend, distinct and ridge reaction types are shown. For each reaction type the percentage frequency of colonies for each category of contact lengths was calculated. The alternate and mix contact types occurred at a very low frequency and have not been included on the graphs. The data from two surveys have been combined on each graph.
a) Fairlight

- Blend (n=21)
- Distinct (n=24)
- Ridge (n=40)

b) Green Pt

- Blend (n=31)
- Distinct (n=28)
- Ridge (n=33)

Length of Contact Between Colonies (cm)
Figure 4.3: Frequency of histocompatibility reactions for different combinations of small, medium and large colonies that have grown into contact at a) Fairlight and b) Green Point, where, small colonies (s) are $< 5 \text{ cm}^2$, medium colonies (m) are $5 < 20 \text{ cm}^2$ and large colonies (l) are $> 20 \text{ cm}^2$. The data from two sets of surveys have been combined.
a) Fairlight

![Bar chart showing frequency of histocompatibility reactions for Fairlight.

- Blend (n=29)
- Distinct (n=24)
- Ridge (n=40)

b) Green Pt

![Bar chart showing frequency of histocompatibility reactions for Green Pt.

- Blend (n=31)
- Distinct (n=28)
- Ridge (n=33)
The largest percentage of distinct histocompatibility reactions was recorded in the small-large size combination (63%) at Fairlight, and between the small-medium size combination (50%) at Green Point (Figure 4.3).

The largest percentage of ridge reactions occurred for the large-large size combination (57%) at Fairlight, and for the medium-medium size combination (58%) at Green Point (Figure 4.3).

The most common combination of colonies involved in histocompatibility reactions were the large-medium size combination at Fairlight (26%), and the large-large size combination at Green Point (40%) (Figure 4.3).

The mix and alternate contact types were excluded from Figures 4.2 and 4.3 as they occurred much less frequently in the population, and together made up less than 12% of the reactions surveyed.
4.3 SURVEYS TO MEASURE NEAREST NEIGHBOUR DISTANCES BETWEEN COLONIES

4.3.1 Introduction

If it is unlikely that colonies will grow into contact, then it is also unlikely that fusion between colonies will be of much significance to the population. Therefore, to investigate Models A and C, I needed to ascertain whether, 1) colonies occur close enough together and grow fast enough that it is likely that they will grow into contact (Hypotheses a1 and a2); 2) colonies frequently grow into contact (Hypothesis a3); and 3) contact between colonies increases the size-class of the colonies (Hypothesis c1) and therefore, could potentially change their biology.

Surveys were done at each site to measure the distance between the edges of nearest neighbouring colonies. There were two sets of surveys. The first survey measured the nearest neighbour distances of colonies in patches to estimate the frequency at which colonies are likely to grow into contact in the population. The second survey measured the nearest neighbour distances of single polyp recruits to estimate the size at which corals are likely to grow into contact with their nearest neighbour. Results from the surveys of fixed quadrats (described in Chapter 3), measuring the actual rate at which colonies in the population grow into contact, are also included to test Hypotheses a3 and c1.
4.3.2 Survey Methods

The surveys of nearest neighbour distances of colonies in patches were done at Fairlight (n = 48 colonies) and Green Point (n = 46 colonies), in October 1995. Colonies in patches were randomly chosen. The distance from the edge of each colony to the edge of the colony nearest to it was measured with a ruler. The longest diameter and the diameter perpendicular to the longest diameter of each colony in each pair were also measured to estimate their size. The colour morphs of the colonies were also recorded. No colony was included in the survey more than once, and no more than three pairs of colonies were measured per patch.

Surveys of the nearest neighbour distances of single polyp recruits were done as described for colonies. The substratum at each site was searched thoroughly by eye to locate all the recruits present in the population at each site, both inside and outside patches, in April of 1995, 1996, and 1997.

The results from the nearest neighbour surveys were then used to predict the rate at which colonies are expected to grow into contact with their nearest neighbouring colony. The mean increase in the radius of colonies at Fairlight each year was $1.83 \pm 2.54$ mm in 1996-97, and $1.92 \pm 3.99$ mm in 1997-98 (Chapter 3.4). The rate at which colonies at Fairlight grow towards each other was calculated from these linear growth rates (assuming that neighbouring colonies do not direct growth away from each other) and approximated to 4 mm per annum (representing the combined rates of linear growth of a colony and its nearest neighbour). At Green Point, colonies had a mean increase in radius of $4.04 \pm 2.10$ mm in 1997-98 (Chapter 3.4), so the rates at which colonies at Green Point grow towards each other were estimated to be about 8 mm per
annum (twice as fast as Fairlight). For consistency, however, the same rate of encroachment used for analysis of the Fairlight data was used for Green Point.

The size at which recruits would be expected to grow into contact with their nearest neighbours was calculated as the size that they would attain once they had increased their radius by half the distance to their nearest neighbour. This calculation assumed, that the initial size of recruits is $50 \text{ mm}^2$ (Appendix II), that there is no mortality or recruitment (both processes which could change the nearest neighbour distances of recruits) and, that corals all have the same rates of linear growth.

4.3.3 Results from Surveys of Nearest Neighbour Distances Between Colonies

Most colonies occurred very close to other colonies. Forty-six percent of colonies at Fairlight, and 26% of colonies at Green Point had nearest neighbour distances of less than 2 cm (Figure 4.4). Eighty-five percent of colonies at Fairlight and 72% of colonies at Green Point had nearest neighbour distances of less than 6 cm. All of the colonies surveyed were less than 21 cm away from their nearest neighbour at Fairlight, and less than 58 cm away from their nearest neighbouring colony at Green Point. There was no significant difference in the frequency distributions of nearest neighbour distances of colonies between sites (Kolmogorov-Smirnov, $d = 0.21$, $n = 48$, $m = 46$, $p > 0.05$) (Figure 4.4).

The mean nearest neighbour distances of colonies in different size-classes are shown in Figure 4.5. The size-classes are as defined in Chapter 2.6, and the data for colonies in size-classes III and IV have been combined to increase the number of samples. There were no significant differences between size-classes.
Figure 4.4: Frequency distributions of nearest neighbour distances at a) Fairlight (n = 48) and b) Green Point (n = 46).
a) Fairlight

Nearest Neighbour Distance (cm)

<table>
<thead>
<tr>
<th>Distance (cm)</th>
<th>Number of Colonies</th>
</tr>
</thead>
<tbody>
<tr>
<td>0&lt;2</td>
<td>20</td>
</tr>
<tr>
<td>2&lt;4</td>
<td>10</td>
</tr>
<tr>
<td>4&lt;6</td>
<td>5</td>
</tr>
<tr>
<td>6&lt;8</td>
<td>2</td>
</tr>
<tr>
<td>8&lt;10</td>
<td>0</td>
</tr>
<tr>
<td>10&lt;12</td>
<td>0</td>
</tr>
<tr>
<td>12&lt;14</td>
<td>0</td>
</tr>
<tr>
<td>14&lt;16</td>
<td>0</td>
</tr>
<tr>
<td>&gt;16</td>
<td>0</td>
</tr>
</tbody>
</table>

b) Green Point

Nearest Neighbour Distance (cm)

<table>
<thead>
<tr>
<th>Distance (cm)</th>
<th>Number of Colonies</th>
</tr>
</thead>
<tbody>
<tr>
<td>0&lt;2</td>
<td>10</td>
</tr>
<tr>
<td>2&lt;4</td>
<td>5</td>
</tr>
<tr>
<td>4&lt;6</td>
<td>3</td>
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<tr>
<td>6&lt;8</td>
<td>2</td>
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<tr>
<td>8&lt;10</td>
<td>1</td>
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<td>10&lt;12</td>
<td>0</td>
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<td>12&lt;14</td>
<td>0</td>
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<tr>
<td>14&lt;16</td>
<td>0</td>
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<tr>
<td>&gt;16</td>
<td>0</td>
</tr>
</tbody>
</table>
Figure 4.5: Nearest neighbour distances of colonies of different sizes at
a) Fairlight and b) Green Point.

The size classes shown are I: visible > 1 cm$^2$; II: 1 < 5 cm$^2$; III: 5 < 10 cm$^2$;
IV: 10 < 20 cm$^2$; V: > 20 cm$^2$. Error bars are standard deviations and for each size
class $n \geq 5$. 
a). Fairlight

![Graph showing mean NN distance (cm) for different size classes at Fairlight.]

b). Green Pt

![Graph showing mean NN distance (cm) for different size classes at Green Pt.]

Size Class: I, II, III and IV, V
in the nearest neighbour distances of colonies, at either site (ANOVA, unbalanced, p > 0.6 at each site).

4.3.4 Results from Surveys of Distances Between Single Polyp Recruits and their Nearest Neighbours

Results from the surveys of nearest neighbour distances of recent recruits are shown in Figure 4.6. More than 45% of single polyp recruits measured at each site, in each year, had nearest neighbour distances of < 2 cm. Less than 11% of recruits had nearest neighbour distances of more than 10 cm. All of the single polyp recruits surveyed occurred within 23 cm of their nearest neighbouring colony, and they all occurred in patches that contained some larger colonies.

There were no significant differences between sites in the nearest neighbour distances of single polyp recruits, in any year surveyed (Kolmogorov-Smirnov, p > 0.05).

4.3.5 Predictions of the Rates at which Colonies will Grow into Contact

From data obtained in studies described in Chapter 3.5, the mean increase in radius of colonies was estimated using the rate of change in surface area measurements, and the assumption that all colonies are circular (Figure 3.8). The mean increase in radius was about 2 mm per annum at Fairlight. From this, the rate at which colonies at Fairlight grow towards each other was estimated to be 4 mm per year (the annual increase in radius of a colony added to the increase in radius of its nearest neighbour). Colonies at Green Point approach
Figure 4.6: Frequency distributions of the nearest neighbour (NN) distances of single polyp recruits at Fairlight (a, c and e) and Green Point (b, d and f), in 1995, 1996 and 1997.
a) Fairlight 1995 (n=34)

b) Green Pt 1995 (n=38)

c) Fairlight 1996 (n=48)

d) Green Pt 1996 (n=41)

e) Fairlight 1997 (n=26)

f) Green Pt 1997 (n=23)
each other at twice this rate, as their linear growth rates are twice as fast as those of colonies at Fairlight.

Using the data obtained from the first survey of nearest neighbour distances (Chapter 4.3.3) and the assumption described in the methods, it was predicted that 19% of colonies at Fairlight and 13% of colonies at Green Point would grow into contact with their nearest neighbouring colony after a year; 46% of colonies at Fairlight and 26% of colonies at Green Point would be expected to contact their nearest neighbour after 4 years; 79% of colonies at Fairlight and 63% of colonies at Green Point would be expected to contact their nearest neighbour after 12 years (Figure 4.7).

However, if the rate at which colonies at Green Point grow towards each other is calculated at 8 mm instead of 4 mm, (which is a better estimate for that site), the frequency at which colonies would be expected to grow into contact is almost the same at each site (compare 1 and 2 years at Fairlight with 2 and 4 years at Green Point).

The rates at which single polyp recruits would be expected to contact their nearest neighbours were calculated to determine the size-class in which most corals are expected to grow into contact with their nearest neighbour. The predictions for recruits from 1995, 1996, and 1997 are shown as cumulative frequencies in Figure 4.8. At each site, more than 45% of the recruits from each year would be expected to have contacted their nearest neighbour colony by the time that they are 5 cm$^2$, and more than 89% of recruits would be expected to have contacted their nearest neighbour by the time that they are 100 cm$^2$.

Both these sets of predictions assume that whole colony mortality is independent of nearest neighbour distance. The consequences of whole colony
Figure 4.7: Percentage of colonies expected to contact their nearest neighbour in time intervals of 1, 2, 4 and 12 years, where □ are the estimates for Fairlight, and □ are the estimates for Green Point, assuming that colonies grow towards each other at a rate of 4 mm per annum.
Figure 4.8: Predictions of the sizes at which single polyps recruits will grow into contact with their nearest neighbour, shown as cumulative frequency distributions, for Fairlight (a, c and e) and Green Point (b, d and e), and estimated from separate surveys in 1995, 1996, and 1997.
a) Fairlight 1995

Size Class Grown Into (cm²)

% of Recruits

0 < 1  1 < 5  5 < 10  10 < 100

b) Green Pt 1995

Size Class Grown Into (cm²)

% of Recruits

0 < 1  1 < 5  5 < 10  10 < 100

c) Fairlight 1996

Size Class Grown Into (cm²)

% of Recruits

0 < 1  1 < 5  5 < 10  10 < 100

d) Green Pt 1996

Size Class Grown Into (cm²)

% of Recruits

0 < 1  1 < 5  5 < 10  10 < 100

e) Fairlight 1997

Size Class Grown Into (cm²)

% of Recruits

0 < 1  1 < 5  5 < 10  10 < 100

f) Green Pt 1997

Size Class Grown Into (cm²)

% of Recruits

0 < 1  1 < 5  5 < 10  10 < 100
mortality, partial mortality and the arrival of new recruits (all processes that could act to change the nearest neighbour distances of colonies) were not included in these calculations, as explained in the methods.

4.3.6 Rates at which Colonies in Fixed Quadrats Grew into Contact with a Neighbouring Colony

From the surveys of fixed quadrats used to measure growth, survivorship and recruitment (Chapter 3), the initial distance between colonies that grew into contact during the surveys was measured. At Fairlight, 45% of colonies that grew into contact with a neighbouring colony in a year were less than 4 mm apart at the start of monitoring, and 58% of colonies that grew into contact over 2 years were less than 8 mm away from the neighbouring colony at the start of monitoring. At Green Point, 47% of colonies that grew into contact with a neighbour were less than 4 mm away, and 87% of colonies were less than 8 mm away. All of the colonies that grew into contact within a year, at either site, were less than 1.8 cm from their neighbour, and colonies that grew into contact within two years, at Fairlight, were all less than 2.4 cm away from the neighbouring colony at the start of monitoring.

From Figure 4.8, (but using the rates of encroachment estimated for each site), it was estimated that about 20% of colonies at each site would grow into contact with their nearest neighbour after 1 year. At Fairlight, 10% to 11% of colonies surveyed grew into contact with a neighbour over a year, and at Green Point 18% of colonies contacted a neighbouring colony over a year.
At each site in each year measured, size-class III (5 < 10 cm²) had the greatest proportion of colonies that grew into contact with a neighbouring colony, ranging from 16% to 38% of the colonies in that size-class (Table 3.7).

Due to growing into contact with a neighbouring colony, 13 of the colonies surveyed at Fairlight (over 2 years) and 5 of the colonies surveyed at Green Point (over 1 year) increased one size-class; 6 colonies at Fairlight and 4 colonies at Green Point increased their colony area by 2 size-classes; another 4 colonies at Fairlight increased 3 to 4 size-classes, and 1 colony at Green Point increased 4 size-classes. Only 2 colonies, at each site, remained in the same size-class after growing into contact with a neighbour (3 of these were already in the largest size-class). None of the colonies decreased a size-class, which could happen if part of the colony dies after coming into contact with its neighbour. One colony at Fairlight did lose area overall due to having a large area of partial mortality on the side of the colony away from the contact area. Another 18 colonies were only partially within the area of the frame after growing into contact with their neighbours, so that their increase in size-class could not be measured. In each of the above measurements, the 'size-class grown into' refers to the total area of the new discrete colony formed.

It was not possible to identify confidently the different types of histocompatibility reactions occurring between colonies from the photographic slides of the fixed quadrats, so the frequency at which the different reactions types occurred between colonies that grew into contact was not measured.
4.4 MANIPULATIVE EXPERIMENTS TO INVESTIGATE FUSIBILITY BETWEEN COLONIES

4.4.1 Introduction

These experiments investigated General Model 3c and tested hypotheses c3 and c4, which were: 1) that colonies always recognise their own tissue as 'self' and fuse with the tissue, and 2) that the fusibility of colonies has a spatial component, in that colonies sampled from the same patch are more likely to fuse than colonies sampled from distant patches.

4.4.2 Methods

There were two sets of experiments in this study. The first was a preliminary experiment done at Green Point, which ran from December 1995 to October 1996, by which time all the assay pairs had grown together. Scoring of the assays from the first experiment continued until the end of the second experiment in July 1998, to determine whether there was any change in the histocompatibility reactions originally scored in the assays. The second experiment was larger than the first, in that corals were assayed from more patches and the experiment was done at two sites (Green Point and Fairlight). Experiment 2 ran from December 1996 to July 1998.

In Experiment 1, all the assay pairs grew into contact within 10 months. However, after 18 months, there were still some pairs of colonies in Experiment 2 that had not yet grown into contact. Only the results scored at the end of each
experiment are reported here (October 1996 for Experiment 1 and July 1998 for Experiment 2).

In each experiment self:self recognition was tested for both small and large colonies at each site, with five replicate assay pairs for each size of colony. Large old colonies have the potential for somatic mutation as they grow (Hughes et al. 1992), and this could result in one part of a colony not recognising a distant part of the colony as 'self'. Small colonies (< 10 cm²) were broken in half and the two growing edges placed in contact. In assays of large colonies (>> 100 cm²), samples (> 5 cm²) were taken from the furthest edges of the colonies and placed in contact. In Experiment 2, the assays of large colonies at Fairlight had very high mortality (4 of 5 died), so a second block of assays was made up in February 1997 (approximately 8 weeks after the start of the experiment), and the results from these assays are included in the results.

For the within-patch assays, pieces from the edges of nearest neighbour colonies that were large enough to sample (> 5 cm²) were placed in contact. For the between-patch assays, pieces of colonies from patches that were far apart (> 10 m) were placed in contact. No colony was assayed more than once. The coral pieces used in the assays were all of similar size (~5 cm²) at the start of the experiments.

Colonies sampled for the assays were transferred to dive buckets of seawater on land, where they were attached to large (> 500 cm²) flat sandstone blocks (obtained from a stone mason) using the epoxy resin Vepox CC57, from Vessey Chemicals, Australia. Each block had the full set of assays for each patch, that is 5 replicate pairs of sample colonies that were nearest neighbours from within a patch, and 5 replicate pairs of colonies consisting of one sample from within the patch and one sample from a far (> 10 m) away patch. The design of the
experiment and set-up of assays is shown in Figure 4.9. After the assays were set up, the blocks were immediately returned to the field, where they were wedged amongst boulders and in channels on the reef floor so that they would not be washed away.

The epoxy used is a two-part resin, consisting of a base and a hardener, and has a putty-like consistency when mixed. Underwater, it sets in a few hours and is fully cured in 7 days at 18°C. Until cured the epoxy is likely to be toxic. However, pilot studies in aquaria showed that it is not toxic enough to affect colonies noticeably. As the epoxy resin dries, gas bubbles collect and burst out of the mixture, sometimes pushing the assay pairs a few millimetres apart, thereby increasing the time needed for the corals to grow together.

A parallel experiment was set up to test fusibility between single polyp recruits. In the first year, assays were set up as outlined for adult colonies in Experiment 1, including within-patch and between-patch sets of assays, each with 3 replicate assay pairs per combination. Due to the small size of recruits, the assays were able to all be put on a single block. Unfortunately, this block was lost before the histocompatibility reactions could be scored. This experiment was to be repeated in the following year (1997), however due to the low rates of recruitment to the population in that year, there were not enough within-patch recruits to do the assays.

4.4.3 Results

The results of the self:self assays for small and large colonies are shown in Table 4.1. All of the self:self assay pairs that grew together and survived the experiment, fused (had the 'blend' histocompatibility reaction). The fusion of
Figure 4.9: Methods for Histocompatibility Experiments

a). Collection of Samples

In Experiment 1 there were only 2 sets of within \((P_x:P_x)\) vs. between patch assays \((P_x:P_y)\). In Experiment 2 there were 5 sets of within \((P_x:P_x)\) vs. between patch assays at each site \((P_x:P_y)\).

b). Set-up of within vs. between patch assays on sandstone blocks

Each \([P_x:P_x \text{ vs. } P_x:P_y]\) set of assays was set-up on a separate sandstone block, with 5 replicate pairs per combination. Each block had samples from 20 separate colonies.
Table 4.1: Results of assays to determine whether colonies always recognise ‘self’.

The rates of ‘self’ identification were measured for small colonies (small:small) and for large colonies (large:large).

<table>
<thead>
<tr>
<th>OUTCOMES</th>
<th>SMALL:SMALL</th>
<th>LARGE:LARGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>EXPERIMENT 1: GREEN PT</td>
<td>Blend 4  Dead 1  Not touching 0</td>
<td>3 2 0</td>
</tr>
<tr>
<td>EXPERIMENT 2: FAIRLIGHT</td>
<td>Blend 2  Dead 1  Not touching 2</td>
<td>6 4 0</td>
</tr>
<tr>
<td>EXPERIMENT 2: GREEN PT</td>
<td>Blend 0  Dead 4  Not touching 1</td>
<td>2 3 0</td>
</tr>
</tbody>
</table>
these coral pieces was so complete that, as the corals grew to fill the gap between them, the area of contact between the colonies became indistinguishable. The rates of mortality in these self:self assays, and the number of pairs that did not grow into contact, were quite high, ranging from 40 to 100% within each set of assays (Table 4.1).

The results from the experiments to test whether nearest neighbour colonies are more likely to fuse than colonies sampled from distant patches are shown in Table 4.2. High rates of mortality were recorded in each of the experiments, and in Experiment 2 one block of assays disappeared from Fairlight. Where one or both of the samples in a coral pair had died, the assay was scored as dead. For most (84%) of the assays scored as dead, the corals had died before they had actually grown together. As already mentioned, a large proportion of the self:self assays also died, or did not grow into contact before the end of the experiment. This suggests that these instances of mortality are not some sort of ‘fatal’ histocompatibility reaction, but rather represent the high rates of mortality of small corals (Chapter 3.6). Therefore, in interpreting the results of these experiments, assay pairs that died or did not grow together were excluded from the data (Figure 4.10).

In each experiment, a larger proportion of ‘blend’ reactions was recorded for the within-patch assays than for the between-patch assays. Further, in Experiment 2 there was a higher proportion of ‘blend’ reactions in the within-patch assays at Green Point than in the within-patch assays at Fairlight.

Conversely, there was a larger proportion of ‘ridge’ reactions in the between-patch assays than in the within-patch assays, in both sets of experiments. However, there was no discernible pattern in the proportion of ‘distinct’ reactions measured in the different assays.
Table 4.2: Results of histocompatibility Experiments 1 and 2 for the within- versus between-patch sets of assays.

Due to the high rates of mortality and 'non-contact' of the assay pairs, many of the replicates were lost from the experiment. Therefore, the results for separate patches were grouped to give two sets of comparisons at each site, in each experiment.

Experiment 1:

<table>
<thead>
<tr>
<th>OUTCOME OF ASSAY</th>
<th>GREEN POINT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. Within Patch</td>
</tr>
<tr>
<td>Blend</td>
<td>2</td>
</tr>
<tr>
<td>Distinct</td>
<td>2</td>
</tr>
<tr>
<td>Ridge</td>
<td>3</td>
</tr>
<tr>
<td>Alternate</td>
<td>0</td>
</tr>
<tr>
<td>Mix</td>
<td>0</td>
</tr>
<tr>
<td>Dead</td>
<td>3</td>
</tr>
<tr>
<td>Colonies not touching</td>
<td>0</td>
</tr>
</tbody>
</table>

Experiment 2:

<table>
<thead>
<tr>
<th>OUTCOME OF ASSAY</th>
<th>FAIRLIGHT*</th>
<th>GREEN POINT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. Within Patch</td>
<td>No. Between Patch</td>
</tr>
<tr>
<td>Blend</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Distinct</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Ridge</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Alternate</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mix</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dead</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Colonies not touching</td>
<td>2</td>
<td>4</td>
</tr>
</tbody>
</table>

[ * One block of assays disappeared from Fairlight].
Figure 4.10: Percentage frequency of different reaction types in Experiments 1 and 2 to compare the rates of fusion between colonies sampled from the same patch with the rates of fusion between colonies sampled from very distant patches.
WITHIN-PATCH ASSAYS

a) Experiment 1: GPt

b) Experiment 1: GPt

c) Experiment 2: FrIt
d) Experiment 2: FrIt

e) Experiment 2: GPt

f) Experiment 2: GPt

BETWEEN-PATCH ASSAYS
The results of each experiment were analysed to compare the proportion of colonies that 'accepted each other' (blend reactions) for the within-patch assays versus the between-patch assays, using Fisher Exact Tests. The within-versus between-patch assays were not significantly different in Experiment 1 at Green Point or Experiment 2 at Fairlight (p > 0.2). However, in Experiment 2 at Green Point the within-patch assays did have significantly more blend reactions than the between-patch assays (p < 0.05).

Only one assay pair had an alternate reaction, and none of the assays had a mix reaction. However, when colonies were first in contact (only 1 or 2 polyps in contact), some pairs were scored as having a mix reaction, but were later found to have either a distinct or blend reaction (n = 4). Similarly, 11 of the 22 ridge reactions recorded in the experiments were initially scored as distinct reactions, and the single alternate reaction was initially scored as a blend reaction. These apparent 'changes' in the types of histocompatibility reactions between colonies are almost certainly an artefact of the very short length of contact between the colonies when they first grow into contact, which makes it very difficult to distinguish between the different reaction types at this stage.

Assay pairs from the first experiment all grew together within seven months, and the results presented here were from 10 months after the start of the experiment. These assays were scored repeatedly for a further 19 months and did not change their histocompatibility reactions over this time, although more of the assay pairs did die.
4.5 DISCUSSION

4.5.1 Histocompatibility Reactions and the Prevalence of Fusion Between Colonies

Five different kinds of histocompatibility reactions have been identified in this study. The reaction types that occurred most frequently in the population were the blend, distinct and ridge reactions, which each had frequencies of about 30%. Two other reaction types, termed mix and alternate reactions, also occurred in the population, but each at a much lower frequency (approximately 6%). Overall, the frequencies at which the different reaction types occurred were similar between sites and, consistent with Model A, a large proportion of colonies in the population were found to have fused (had the blend reaction).

The different histocompatibility reactions all appear to be stable (as proposed in Model B). Each of the different types of reactions occurred between colonies that had been in contact for a long time as well as between colonies that had only recently grown into contact, as shown by the length of the contact zones between the colonies. Further, the pairs of colonies in the assays in Experiments 1 and 2, did not change their reaction type when monitored over long periods of time (> 19 months for assays in Experiment 1).

In corals, only highly related colonies are thought to be able to fuse. However, the results of this study suggest that fusion is much less specific in *P. versipora* than in other corals, as colonies of different morphs (Appendix V.5) and colonies sampled from distant patches were able to fuse.

To further investigate the specificity of fusion in *P. versipora*, it was predicted that colonies of similar size were more likely to fuse than colonies of very
different sizes, based on the assumption that colonies of similar size are more likely to have arisen from the same recruitment event and hence, are more likely to be related than colonies of very different sizes. In addition to this, small colonies were thought to be the most likely to fuse, as they were most likely to have arisen from the same recruitment event.

Surveys of the population showed that reactions between two small colonies did have the highest rates of fusion (blend reactions, 50%, supporting Hypothesis c2). Although, the rates of fusion were also high between some colonies of very different sizes. Thirty-eight percent of the small-large combination of colonies fused at Fairlight (rejecting Hypothesis c1).

*P. versipora* has planktonic larvae, which are likely to be widely dispersed. Recruitment from these larvae is unlikely to result in patches of highly related colonies of a wide range of different sizes. Therefore, the two most likely explanations for the relatively high rates of fusion between colonies of very different sizes are: 1) that fusion is not very specific in *P. versipora* and 2) that colonies in patches reproduce asexually.

*P. versipora* does have the potential to reproduce asexually if maintained in aquaria in conditions that are limiting; the contribution asexual reproduction makes to the field population is not known(Appendix IV). However, the fact that five different types of histocompatibility reactions were identified between colonies in the field population and the frequencies at which each of these reaction types occurred, suggests that patches are genetically diverse and not entirely (if at all) the product of local asexual reproduction.

Small colonies may have higher rates of fusion than other colonies due to their historecognition systems being immature. This model has been proposed
previously to explain why in some species very young corals (e.g. recent settlers) can fuse with other very young corals, whereas adult colonies of the same species cannot fuse at all (Duerden 1902; Hidaka 1985a; Hidaka et al. 1997; Jackson 1986). However, it is unlikely that the higher rates of fusion between small *P. versipora* colonies are due to these colonies being immature, as the small colonies (< 5 cm²) were not all 'very' small (propagules or recent settlers) and high rates of fusion (up to 42%) were also measured in some combinations of larger colonies at Fairlight.

The strongest evidence of a lack of specificity of fusion in *P. versipora* is from the results of the histocompatibility experiments. These experiments showed that the rates of fusion between colonies from the same patch, although higher, were not significantly different from the rates of fusion between colonies from distant patches, in 2 of 3 experiments. These results suggest that fusion is able to occur between many colonies in the population and therefore, contrary to General Model 3c, colonies do not need to be highly related to fuse.

Genetic studies are the only way to reliably measure relatedness between colonies. Such studies could determine the genetic structure of the population at local sites, both within-patches, and within- and between sites, so that the actual contribution sexual and asexual reproduction make to the population could be estimated and the processes controlling fusion in this species much better understood.
4.5.2 Likelihood and Consequences of Colonies Growing into Contact

*P. versipora* in Sydney Harbour has a highly aggregated distribution. The results of this study show that colonies are likely to grow into contact and that colonies frequently amalgamate with their neighbours, as proposed in Model A.

More than 70% of colonies were less than 6 cm away from their nearest neighbour. The distribution of colonies within patches was similar between sites, although there were fewer colonies that were less than 2 cm away from their nearest neighbour at Green Point (26%) than at Fairlight (46%) (Figure 4.4). There was no relationship between nearest neighbour distances and colony size (Figure 4.5), presumably because many of the larger colonies have already amalgamated with their original nearest neighbours.

Single polyp recruits were surveyed to estimate the likelihood of new corals amalgamating with their neighbours and the size at which colonies are most likely to contact their neighbour. In all of these surveys (*n* = 6) more than 45% of recruits were less than 2 cm away from their nearest neighbour (Figure 4.7). From these data it was predicted that more than 45% of colonies that survive (assuming survivorship is independent of nearest neighbour distance) will grow into contact with their nearest neighbour before they grow into size-class III (*5 < 10 cm²*).

From the results of the surveys of nearest neighbour distances combined with the mean rates of linear growth at each site, it was estimated that about 19% of discrete colonies will grow into contact with their nearest neighbour in a year, and that about 27% of colonies will contact their nearest neighbour in two years (Figure 4.7). The actual rates at which colonies grew into contact were 10% to 11% at Fairlight, and 18% at Green Point (Chapter 3.4). Therefore, although
these rates were comparable with the values estimated from the nearest neighbour distances for Green Point, they were 6% to 8% below the rates estimated for Fairlight.

*Stylophora pistillata* has intraspecific 'stand-off' reactions in which colonies are able to direct their growth away from each other if they come within 2 cm of each other (Rinkevich & Loya 1983a). Stand-off reactions do occur interspecifically in *P. versipora* (Plate 4.2a). If these reactions also occur intraspecifically, then this would explain why fewer colonies at Fairlight grew into contact than predicted, as it would mean that a proportion of the colonies that have nearest neighbour distances of only a few millimetres may not have actually been about to grow into contact with each other, but may instead have been maintaining 'stand-off' reactions.

If 'stand-offs' occur in *P. versipora*, then the proportion of corals very near others would be expected to be higher for colonies than for recruits, as some of the colonies would be expressing 'stand-off' reactions. However, in *P. versipora* the proportion of colonies less than 2 cm away from their nearest neighbour at each site was either similar or much less than the proportion of recruits less than 2 cm away from their nearest neighbour (Figures 4.4 and 4.6). Therefore, intraspecific 'stand-off' reactions do not account for the lower than expected rates of amalgamation at Fairlight.

The nearest neighbour distances of single polyp recruits were the same at both sites, in each of the 3 years measured. However, at Green Point fewer colonies were less than 2 cm away from their nearest neighbour than at Fairlight. This is probably because small colonies grow more quickly at Green Point, and therefore grow into contact with neighbouring colonies sooner, than recruits at Fairlight (Chapter 3.4). Some of this difference may also be because small
corals have higher rates of mortality at Green Point than at Fairlight (Chapter 3.5).

The slight differences measured in the frequency distributions of nearest neighbour distances of colonies between sites (Figure 4.5) appear to be reflected in the frequency distributions of discrete colonies measured in the preliminary population surveys (Figure 2.2). At Fairlight there were fewer discrete colonies in size-class II than in size-class III; given the nearest neighbour data this is likely to be at least partly explained by colonies in size-class II growing into contact with their nearest neighbours, and thus increasing their size-class. In contrast, at Green Point fewer colonies appear to be being 'lost' between size-classes II and III, and there were more discrete colonies composed of multiple corals in size-class IV than in the smaller size-classes. This observation suggests that colonies at Green Point are larger when they grow into contact with their neighbours as they were further apart than colonies at Fairlight, which is consistent with the nearest neighbour data.

The histocompatibility experiments showed that nearest neighbour colonies are more likely to fuse than colonies from two distant (> 10 m apart) patches, in each of three sets of experiments (Figure 4.10). However, this result was significant in only one set of assays (Green Point, Experiment 2). Conversely, in each experiment, the between-patch assays had a higher proportion of ridge reactions than the within-patch assays (Figure 4.10).

The proportions at which the different histocompatibility reactions occurred in the within-patch assays in Experiment 1 at Green Point and in Experiment 2 at Fairlight were consistent with the field surveys, although the rates of fusion were higher at Green Point in Experiment 2 than in the field surveys. This deviation at Green Point was almost certainly an artefact of the small number of
within-patch assay pairs that survived and grew into contact by the end of the experiment (n = 8, Table 4.2). The fact that the frequency of the different reactions were consistent between the field survey and assays suggests that none of these reactions is lethal and that fusion does not enhance the survivorship of colonies any more than any of the other reactions (if at all).

4.5.3 The Woes of Field Assays

The histocompatibility experiments used samples from a large number of colonies. In Experiment 2, 50 pairs (100 corals) were sampled at each site, but due to mortality and some assays not growing into contact, only 28 pairs at Fairlight and 18 pairs at Green Point could be scored at the end of the experiment (Table 4.2). Therefore, in terms of damage done to the population and the small proportion of assays for which contact reactions were scored, these field assays were not an efficient way of gaining information about the population.

Many of the corals used in the assays died, with up to 40% of the assays in each experiment being scored as dead. The coral pieces used in the assays were all small (~5 cm²). Results from the surveys of fixed quadrats (Chapter 3.5, obtained after these experiments were completed), showed that colonies of less than 5 cm² have annual rates of mortality of 19% to 35%. Therefore, considering that the corals in the assays were fragments from older colonies, and that small old colonies generally have higher rates of mortality than small young corals (Hughes & Connell 1987), the rates of mortality in the assays are (in retrospect) within the bounds of what might be expected.
In the Experiment 2, a large proportion of colonies (up to 28%) did not grow into contact with their assay partner. This was due to the assay pairs sliding a few millimetres apart before the epoxy had completely cured and some colonies then not growing quickly enough to make contact with each other before the end of the experiment. Although it could be argued that these assays were exhibiting a 'stand-off' reaction, it seems more likely that their slow growth rates were a consequence of the high rates of partial mortality in these colonies, as partial mortality reduces the growth rates of colonies (Bak 1983). These instances of partial mortality did not occur near the area of contact, so they were not histocompatibility responses; they almost always seemed to be due to grazing, as parts of the skeletons were often damaged or worn away.

In each set of assays per combination of patches, there were five replicate pairs of corals for the within-patch assays and five for the between-patch assays. The objective of this experiment was to compare the rates of fusion of colonies between different combinations of patches (i.e. P1:P1 vs. P3:P3 vs. P5:P5; and P1:P2 vs. P3:P4 vs. P5:P6). However, these comparisons could not be made due to many of the colonies in these assays either dying or not amalgamating by the end of the experiment.

Before the field experiments were done, pilot assays were set up in aquaria. These corals also took a long time to grow together (more than 8 months) and had high rates of mortality due to being overgrown by algae. Another method tested was to cut off pieces of tissue from colonies, maintain them in aquaria until they grew into polyps, and then use pairs of these laboratory reared polyps in histocompatibility assays. These tissue fragments also had very high rates of mortality, and larger pieces of tissue (which are more likely to survive) could only be removed from colonies that had a thick covering of tissue, thus
limiting the number (and type) of colonies that could be used in these experiments.

In future experiments, methods that assay tissue extracts might be a way of obtaining better quantitative data. In these assays, animal cells from different pairs of colonies could be dispensed into tissue culture multi-well plates and the association or disassociation between the cells from different corals scored as 'acceptance' or 'rejection'. Although this method may only distinguish between two types of reaction, it would have the advantage of providing quick results, could be easily repeated and would also allow cross-reactivity tests on 'acceptance' and 'rejection' between the cells of different pairs of colonies. This method would first need to be tested using colonies exhibiting different reactions in the field and assaying their cell extracts to find out whether the reactions observed between the cells are representative of the reactions observed between intact colonies.

The mechanisms controlling historecognition in corals are not known. The methods described above could, however, be used to obtain some insight into the genetic control of historecognition and fusion in P. versipora. In the ascidian Botryllus schlosseri, fusion occurs when colonies share one, or both, of the alleles at the historecognition locus (Schofield et al. 1982). By sampling pairs of colonies that have fused in the field and running assays of their cell extracts in a series of cross-reactivity tests, it may also be possible to determine the number of alleles at the historecognition locus of P. versipora.
4.5.4 Possible Advantages of Colonies Amalgamating

Fusion occurs relatively frequently in the *P. versipora* population in Sydney Harbour (in ~30% of encounters) and this not only enables colonies to become larger, but also appears to result in the two colonies becoming physiologically integrated. Buss (1982) and Grosberg & Quinn (1986) have described a number of possible advantages and disadvantages of fusion between allogeneic colonies (reviewed in Chapter 1.3). It would, therefore, be interesting to find out what, if any advantages *P. versipora* colonies gain from growing into contact with each other.

The advantages of contact reactions and fusion could fall into two separate categories. The first would relate to the geometry of colonies, and does not require the colonies to fuse. Larger colonies have smaller perimeter to area ratios than smaller colonies, and the more corals incorporated into one discrete colony, the smaller this ratio becomes for each individual coral in the amalgamation. Thus each coral in an amalgamation has a much smaller proportion of its tissues at risk of damage at the edge of the colony than if it was living independently of other colonies. Further, the aggregated distribution of *P. versipora* colonies and the fact that these colonies often live in direct contact with one another, mean that colonies have the potential to occupy all of the available space within an area, thus reducing the likelihood of interspecific competition for space, while perhaps increasing the fertilisation rates of gametes due to potential mates being very near.

Secondly, if corals that grow into contact fuse, and become physiologically integrated, then the new colony formed will, due to its larger size, have more metabolites available to it. This could result in the colony having higher rates of total growth, higher rates of recovery from injury, and higher rates of
colony fecundity. Further, when small colonies are incorporated into amalgamations, they may be able to become fecund sooner than if they were growing independently of other colonies.

In studies described in earlier chapters, I showed that the biology of *P. versipora* colonies changes as they become larger, in that larger colonies (> 20 cm²) have higher rates of survivorship than smaller colonies and only colonies larger than 5 cm² are likely to be reproductive (Chapter 3). This is consistent with the findings of previous studies on corals and other modular marine invertebrates. However, it is not known whether the biology changes in the same way for colonies that have grown large from a single recruit, as for colonies that have become large as a consequence of amalgamating with one or more neighbouring colonies. In experiments described in Chapter 6, I investigated this with regard to the rates of recovery of colonies of different sizes, that have arisen in different ways, from partial mortality.

Future studies could be done to investigate the extent to which colonies that fuse are integrated. Transmission and scanning electron microscope studies could be used to investigate the amount of integration there is between the cells of colonies that fuse (have a blend reaction). Radiotracers (carbon¹⁴) could also be used to investigate whether metabolites are transferred between apparently fused colonies.

Samples could be collected during the reproductive season to find out whether small colonies (< 5 cm²) incorporated into amalgamations contain gonads and are therefore, able to become reproductive sooner than small colonies that remain independent of other colonies.
The most interesting outcome of this study is the apparent lack of specificity of fusion in *P. versipora*. This is most clearly demonstrated by the fact that colonies sampled from distant patches, which are unlikely to be closely related, fused when they were put into contact with each other. Therefore, the histocompatibility system of *P. versipora* seems to act differently from those of other species of corals; however, genetic studies are needed to confirm that these colonies are not highly related. These results suggest that *P. versipora* would be a good organism for investigating models proposed by Buss (1982) and Grosberg & Quinn (1986) about the potential advantages and disadvantages of fusion between allogeneic colonies (reviewed in Chapter 1.2).
4.6 SUMMARY

The amalgamation of colonies is likely to be an important process in structuring the population as many colonies are likely to grow into contact with their nearest neighbour. Colonies that grow into contact generally increase their size-class, and almost a third of all contacts result in the colonies fusing.

Five different kinds of histocompatibility reactions were defined. They were termed blend (fusion), distinct, ridge, mix and alternate. Surveys of the lengths of the contact zone between colonies and repeated observations of reactions between colonies showed that these reactions are all stable and do not change over time.

The variety of reaction types occurring between colonies in the field suggests that colonies in patches are genetically diverse, and not all the product of a single genet.

The processes that control fusion in corals are not known. However, the results of this study on P. versipora suggest that colonies do not need to be highly related to fuse, although there was a general trend of colonies sampled from near each other being more likely to fuse than two colonies sampled from distant patches. Genetic studies are needed to estimate the level of relatedness between colonies that do fuse.

Colonies that amalgamate with a neighbouring colony may have both ‘geometric’ as well as ‘physiological’ benefits. These potential advantages, and any associated possible disadvantages, need to be investigated further if the ecological implications of fusion and contact between colonies, in populations of colony-forming organisms, are to be understood.
CHAPTER 5: COLONY INJURY AND RATES OF RECOVERY

5.1 INTRODUCTION

Corals have two types of partial mortality: a) the dieback of tissue around the edge of a colony, and b) areas of injury that form lesions on the surface of a colony. Partial mortality results in the biomass of colonies becoming smaller, and explains how colonies can have a net loss of tissue and shrink (Chapter 3). Extensive partial mortality can divide a colony, resulting in colony fission. The modular construction of many corals gives them the ability to regenerate some, if not all, of the area lost by partial mortality. The sooner damaged areas are regenerated, the less the impact of partial mortality is likely to be on the population.

In this chapter, studies investigating partial mortality in terms of the presence of lesions on *P. versipora* colonies in Sydney Harbour, are presented.

Lesions are areas where the tissue, and sometimes skeleton, of a coral has been injured or damaged. This can be due to biotic effects, such as grazing by fish, echinoids and molluscs, bioerosion by polychaetes and molluscs, or competition with macroalgae and other sessile marine invertebrates for space. Lesions can also be caused by abiotic effects, such as storm damage, sedimentation, temperature extremes, emersion at low tide, or diver scour (reviewed by Oren *et al.* 1997a and Hall 1997b).

Lesions can occur at the centre or edge of a colony. They can become permanent features of colonies, leaving damaged tissue open to invasion by pathogens and exposing bare skeleton to entry by bioeroders. Lesions also open
up space on the surfaces of colonies on which algae, sponges and other sessile invertebrates can settle.

The regenerative abilities of corals, whether they are able to regenerate areas of damage, the rate at which they regenerate areas of damage, and the sizes of lesions from which colonies can recover, are species-specific (Bak & Steward-Van Es 1980; Oren et al. 1997a). The ability of colonies to recover from injury is also affected by their physiological state, their history of previous injury, and the environment in which they live (Hughes 1984). Previous studies have shown that colonies that have bleached or been exposed to heavy sedimentation have poorer rates of recovery than control colonies (Meesters et al. 1992; Meesters & Bak 1993).

Regeneration requires metabolic energy. Colonies expending energy on recovery do so at the expense of other colony processes. Regenerating colonies have reduced growth (Bak 1983), reduced fecundity (Rinkevich & Loya 1979; Van Veghel & Bak 1994; Hall 1997b), and a reduction in their competitive ability and resistance to disease (Bak & Criens 1981).

The recovery rates of corals from instances of partial mortality are also affected by colony size, lesion size, and lesion shape (Connell 1973; Loya 1976; Bak et al. 1977; Buss 1982; Hughes 1984; Oren et al. 1997a). Small lesions (< 1 cm²) have a high probability of being completely regenerated, while larger lesions are less likely to be completely regenerated (Bak & Steward-Van Es 1980; Meesters et al. 1997). More than 40% of lesions occurring on corals in the Caribbean are less than 1 cm² (Meesters et al. 1996, 1997), and studies on these populations have shown that a large proportion of these small lesions are likely to be regenerated (Bak et al. 1977; Bak & Steward-Van Es 1980; Meesters & Bak 1993).
More recent studies have shown that the extent to which a lesion regenerates is not simply related to the size of the lesion, but is more dependent on the perimeter to area ratio of the lesion (Meesters et al. 1997; Oren et al. 1997a).

Meesters et al. (1996, 1997) proposed that limiting regeneration to smaller lesions may represent a trade-off against growth and reproduction, because smaller lesions require less energy to heal than larger lesions, so colonies that only repair small lesions may be less likely to have reduced rates of growth and fecundity. If the area damaged by larger lesions is unlikely to heal and therefore, likely to be lost from the population, then on an area cover basis large lesions could represent a huge amount of coral death.

In coral populations, large colonies generally have lower rates of whole colony mortality, but higher rates of partial mortality, than smaller colonies (Hughes & Jackson 1980, 1985; Hughes 1984; Bythell et al. 1993). Further, coral populations lose more tissue as a result of partial mortality than due to whole colony mortality (Hughes et al. 1992), suggesting that partial mortality is very important in determining the structure of coral populations.

Studies by Loya (1976) on Stylophora pistillata found that colonies of less than 80 cm² have poorer regenerative abilities than larger colonies, and that the rates of regeneration of colonies less than 8 cm² were worse still. Overall, however, the results from studies comparing the regeneration rates of colonies of different sizes are conflicting. Larger Montastrea annularis colonies do regenerate tissue lesions faster than smaller colonies (colonies of < 314 cm², 314 < 2 830 cm² and > 2 830 cm² were compared, Bak et al. 1977). However, Agaricia agarities and Porites asteroides were not shown to have a relationship between size and rates of lesion regeneration for colonies larger than 150 cm² (Bak & Steward Van Es 1980). This suggests that colonies need a minimum area before
they have the resources available to repair areas of damage, and that after that size is reached the effects of colony size and lesion type on rates of regeneration are species-specific.

Due to the cooler temperatures and reduced light intensity of high latitude environments, temperate corals are expected to have slower rates of growth than tropical corals. Populations of slow growing corals that have some large colonies must have long life-spans, if some colonies can grow to become large. Further, as long-lived colonies are exposed to the risk of being damaged for longer, they are likely to have more incidents of partial mortality in their lifetime than shorter-lived species. Therefore, large colonies of slow growing species must have good regenerative abilities to have recovered from the damage they are likely to have incurred while they were growing large. Furthermore, corals in temperate waters are likely to be exposed to higher rates of sedimentation and more competition with fast growing macroalgae than corals on tropical reefs, so are likely to have higher rates of damage. If populations of temperate corals have colonies that are able to survive to become large, these colonies must have a good ability to repair areas of damage and good rates of regeneration. Therefore, as the Sydney Harbour population(s) of *P. versipora* has some very large colonies (> 1 600 cm²), this species is expected to have good regenerative abilities.

In this study, I wanted to determine the impact of partial mortality at both the colony and population levels, to find out whether it plays an important role in structuring the population of *P. versipora* in Sydney Harbour. Therefore, I needed to assess the frequency and magnitude of injuries on colonies at local sites, and the ability of colonies to recover from these injuries. The models proposed to investigate this were:
MODEL A: There is a high turnover of coral tissue in the population due to colonies frequently having small areas of damage, sometimes the damaged areas are large.

Ha1) That most lesions are small (< 1 cm²).
Ha2) That colonies mostly regenerate the area of small lesions
Ha3) That some lesions are large (> 1 cm²).

MODEL B: The size of a lesion affects the rate and extent to which a lesion is regenerated, with smaller lesions being regenerated faster and to a greater extent than larger lesions.

Hb1) That colonies regenerate small lesions faster than they regenerate large lesions.

MODEL C: Lesions that have a larger perimeter to surface area ratio are regenerated faster than lesions with a smaller surface area to perimeter ratio. (Hypothesis given in section 5.3)

MODEL D: More coral area is lost from the population due to partial mortality than due to whole colony mortality.

Hd1) That lesions result in a greater loss of coral area from the population than whole colony mortality.

Data were presented in Chapter 3.5 that show that in *P. versipora* larger sized colonies have better rates of survivorship and are more likely to shrink than smaller colonies. These higher rates of damage on larger colonies could simply be because they are more frequently damaged than small colonies, as would be expected if the probability of damage is proportional to the area of substratum that colonies cover (Jackson 1979). Alternatively, it could represent the fact that larger colonies with lesions have better survivorship than small colonies.
with lesions; if that were the case, many of the small colonies with lesions would die and so would not be included in the survey. A third explanation could be that large colonies recover from lesions more slowly than small colonies; consequently, at any given time, the number of lesions remaining on large colonies would be greater than the number of lesions on small colonies. However, this last explanation conflicts with the results of previous studies on other species of corals, which suggest that large colonies generally recover from lesions more quickly than small colonies (Connell 1973; Loya 1976; Bak et al. 1977).

Therefore, the following models and hypotheses were derived to further investigate General Models 1 and 3a (Chapter 1.4):

**MODEL E:** Larger colonies have higher rates of partial mortality than smaller colonies

He1) That a greater proportion of large colonies have lesions than small colonies.

**MODEL F:** The regenerative abilities of colonies increase with colony size (hypotheses given in sections 5.3 and 5.4)

**MODEL G:** The effect of lesion size on the regeneration rates of colonies is greater in smaller colonies than in larger colonies (hypotheses given in sections 5.3 and 5.4)

**MODEL H:** Colonies that have amalgamated with other colonies to become large, have rates of regeneration that are similar to the rates of regeneration of large colonies that have grown from a single recruit (hypotheses given in section 5.4)
MODEL I: Colonies that form amalgamations and fuse with other colonies may have more resources available for repair, and therefore recover from injury more quickly than colonies that form amalgamations in which the colonies do not fuse (hypotheses given in section 5.4)

These models were investigated in two types of experiments. The first, involved surveys of colonies in the field to evaluate the frequency, size and recovery rates of naturally-occurring lesions on colonies in the field. The second, used experimental lesions to compare the regeneration rates of different types of colonies from lesions. This is the first study to quantitatively investigate the regenerative abilities of a temperate coral.

5.2 TYPES AND RATES OF NATURALLY-OCCURRING INJURY TO COLONIES IN THE POPULATION

For the purposes of this study 'lesions' are defined as areas of partial mortality on the surface of a colony, where the tissues have either been damaged or lost, and the skeleton of the coral is exposed. This definition does not include extensive areas of colony death where the skeleton is covered in sediment and colonised by macroalgae (when colonies shrink).

5.2.1 Observations of the Types and Causes of Lesions on Colonies in the Field

The types of lesions observed in the field included: 1) areas of colonies where tissue had died and sediment had collected, 2) areas of excavation by bioeroders
(tubeworms and molluscs), often surrounded by deposits of sediment, c) areas of abrasion probably due to the activities of grazers or from abiotic causes, and d) areas where nearby macroalgae have 'whipped' the corals, damaging or removing tissue from the colony.

On a night dive at Fairlight, two grazers were observed inflicting lesions on the surfaces of colonies. The first grazer was an urchin, Centrostephanus rodgersii, and the second grazer an opisthobranch mollusc, Berthellina citrina. These grazers only removed tissue from the centre of the colony, leaving a wounded area of 3 to 5 cm² where the surface tissue and upper parts of polyps were damaged. Polyps appeared to be able to avoid severe damage by retracting into the skeleton.

Damage on some P. versipora colonies was due to the presence of bioeroders in the skeletons of colonies. An assortment of bioeroders was found in the skeletons of colonies which were sampled and decalcified in studies on the reproductive biology of P. versipora (Appendix IV). The skeletons contained worms from the families Nereididae, Cirratulidae, Sylidae, Lumbrineridae, Sabellidae (Pseudopotamilla sp.) and Spionidae, as well as unidentified bioeroding sponge and bivalve species.

Therefore, P. versipora colonies are involved in a number of biotic interactions and associations that cause damage to their tissues and skeleton. Colonies at Fairlight and Green Point are also affected by human activities, particularly in the form of debris entering the waterways in stormwater and through beach, boating and fishing activities. These sites are also frequented by recreational divers and dive schools, exposing colonies to the risk of fin-damage from divers.
5.2.2 Survey Methods

The frequency of lesions occurring on colonies in the field and the recovery rates of colonies from lesions were measured from photographic slides of the surveys of fixed quadrats (see Chapter 3.3). The surveys were done at intervals of two months at Fairlight (April 1996 to April 1998) and Green Point (December 1996 to April 1998). More surveys of the fixed quadrats were done at intervals of less than two weeks in October 1996 (at Fairlight) and October 1997 (at Fairlight and Green Point). October was chosen for these surveys because this time interval fitted in with my other fieldwork commitments, and because diving conditions are generally relatively good then, so dives were less likely to be cancelled. Each survey included 66 quadrats at Fairlight, and 33 quadrats at Green Point. Due to repeated camera floods there were no data for December 1997.

Slides of quadrats were projected on to a screen at life size (1:1 ratio). Colonies with lesions were identified and the sizes of the lesions recorded. For each lesion the longest diameter and the length of the diameter perpendicular to it, were measured on the projected image. The area of the lesion was estimated using the formula for the area of an ellipse (see Chapter 2.3).

The sizes of lesions and occurrence of new lesions were recorded for each sampling time. At the start of monitoring, a few colonies had extensive areas where the colony was dead and large clumps of tubeworms were living in the skeleton. These colonies were not included in the surveys as the large dead areas were not considered examples of 'lesions' as defined for this study. These colonies did not show any signs of recovery during this study.
The surface areas of colonies in the quadrats had already been measured digitally at intervals of 12 months in the population growth studies (Chapter 3). These data were used to give measures of colony area in this study as a) it was convenient, b) in a year most colonies either stayed in the same size-class or increased one size-class only (Table 3.11), c) colonies that have partial mortality generally have reduced rates of growth (Bak 1983) so are less likely to change their size-class anyway, and d) due to the irregular shape of some colonies, this annual measure of colony area is likely to be more accurate (overall) than an estimate based on the bimonthly measures of the length and width of colonies measured directly on the projected image of a photographic slide.

5.2.3 Frequency of Lesions on Colonies in the Field

At each sampling time, 1.5 to 2% of total coral area at Fairlight had lesions, and 1 to 2% of the total coral area at Green Point had lesions. These measures are consistent with the estimate of 1.4% made in the preliminary surveys (Chapter 2.4).

a) Frequency of Lesions when Measured at Intervals of Two Months

Due to the sporadic and low frequency of injury to colonies, data from the surveys were combined at each site. The rates at which these lesions were regenerated are given in Chapter 5.2.5.

i) Fairlight, (n = 66 quadrats)

Between April 1996 and April 1998, a total of 79 lesions were found on the surfaces of colonies. In this period, 49 new lesions were measured. Some
colonies had up to six lesions during this period of sampling. Thirty percent of lesions at Fairlight occurred on the edges of colonies.

ii) Green Point, (n = 33 quadrats)

At Green Point, a total of 65 lesions were recorded between December 1996 and April 1998. Of these, 47 were new lesions. Twenty percent of lesions at Green Point occurred on the edges of colonies.

b) Frequency of Lesions when Measured at Intervals of Less than Two Months

In October 1996, quadrats at Fairlight were surveyed at intervals of 4 days on four sampling dates. Thirteen new lesions were measured in this period; the majority of these lesions (n = 8) were less than 1 cm².

In October 1997, the short time interval surveys were repeated, but due to poor weather conditions only three sampling times at intervals of 10 and 14 days were included. The 1997 surveys measured a total of 12 new lesions (3 at Fairlight and 9 at Green Point), and most of these lesions (1 at Fairlight and 6 at Green Point), were less than 1 cm².
5.2.4 The Size-frequency Distribution of Lesions on Colonies, and Relationships Between the Presence of Lesions and Colony Size

Lesions can increase or decrease in size through time, so the area of a lesion and the actual area of coral damaged are unlikely to be the same, except directly after the lesion has been inflicted. Therefore, the size-frequency distribution of lesions on colonies in the population at a given time is likely to be different from the size-frequency distribution of new lesions, unless the rates of colony recovery from lesions are very fast. Further, the size-frequency distribution of new lesions is likely to underestimate the average size of lesions, as some lesions may become bigger, and bigger lesions are expected to take longer to heal (Oren et al. 1997a; Meesters et al. 1997). Thus, the number of larger lesions could increase over time.

At Fairlight and Green Point, at the time points surveyed, between 37% and 67% of lesions were less than 1 cm$^2$, more than 60% of lesions were less than 3 cm$^2$, and more than 70% of lesions were less than 5 cm$^2$ (Figure 5.1).

Most lesions (92%) were found on large colonies (> 20 cm$^2$), and no lesions occurred on colonies in size-classes I, II and IV (Figure 5.2). In the surveys of fixed quadrats, less than 25% of colonies in the population were larger than 20 cm$^2$ (Figure 3.7). On an area cover basis, however, colonies larger than 20 cm$^2$ contribute to 92% of the coral area and have 95% of the total area damaged by lesions. This suggests that the amount of damage on colonies less than 20 cm$^2$ and greater than 20 cm$^2$ is directly proportional to their area cover.

However, colonies larger than 100 cm$^2$ are few in number (< 10%) and contribute about 77% of the area cover of the population, but account for only about 46% of the total area of lesions in the population. This means that the
Figure 5.1: Frequency distributions of lesion size in April of each of the years sampled, at Fairlight (a, b and c) and Green Point (d and e).

Data obtained from surveys of fixed quadrats, where ‘n’ is the number of lesions measured.
a) Fairlight, 1996 (n=30)

b) Fairlight, 1997 (n=43)

c) Fairlight, 1998 (n=38)

d) Green Pt, 1997 (n=21)

e) Green Pt, 1998 (n=11)
Figure 5.2: Number of colonies in each size class that had lesions on their surfaces in April of each of the years sampled at Fairlight (a, b and c) and Green Point (d and e).

The size intervals shown are I: < 1 cm$^2$; II: 1 < 5 cm$^2$; III: 5 < 10 cm$^2$; IV: 10 < 20 cm$^2$; V: > 20 cm$^2$. Data obtained from surveys of fixed quadrats, where 'n' is the number of colonies measured.
area damaged on these very large colonies is not directly proportional to their area cover. If the biology of colonies changes as they grow, such that larger colonies are damaged less frequently or have faster rates of recovery from lesions than smaller colonies, then this effect of size would be expected to be most likely to occur in colonies larger than 100 cm².

Of the new lesions measured during monitoring, 4% at Fairlight and 2% at Green Point were larger than 5 cm² (Figure 5.3). Therefore, the frequency of large lesions being inflicted on colonies is much less than their percentage occurrence at any single time point (Figure 5.1). This may be because some new lesions become bigger over time. It may also represent the fact that larger lesions take longer to repair than smaller lesions, and so remain in the population longer. Hence, at any single time point, larger lesions are likely to be greater in number than the frequency at which they are actually inflicted.

5.2.5 Recovery Rates of Colonies from ‘Natural’ Lesions

The data for all new lesions recorded in surveys of the fixed quadrats were combined for each site, to measure the recovery rates of colonies from new lesions. In these surveys, a lesion was said to have regenerated when the colony had regained the tissue over all of the area where the lesion had been.

More than 38% of lesions regenerated their tissue after two months, while 55% of lesions at Fairlight, and 75% of lesions at Green Point had regenerated within 4 months. By 6 months, 66% of lesions at Fairlight and 93% of lesions at Green Point had regenerated (Figure 5.4).
Figure 5.3: Size frequency distributions of new lesions, measured in surveys of fixed quadrats between 1996 and 1998, at a) Fairlight (n = 49 new lesions) and b) Green Point (n = 47 new lesions).
a) Fairlight

b) Green Pt
Figure 5.4: Cumulative percentage frequency graphs of the rates of recovery of new lesions, measured in surveys of fixed quadrats between 1996 and 1998, at a) Fairlight (n = 49 new lesions) and b) Green Point (n = 47 new lesions).
a) Fairlight

b) Green Point
At the start of monitoring, 30 lesions were recorded at Fairlight; of these lesions, 25 persisted to the end of sampling. Similarly, at Green Point, 18 lesions were measured at the start of monitoring, 6 of which persisted to the end of sampling. This suggests that a large proportion of lesions that do not regenerate quickly may never regenerate, and that overall, more colonies regenerate at Green Point, at a faster rate, than at Fairlight (Figure 5.4).

At Fairlight, five colonies with lesions died during the course of monitoring. Two of these colonies had lesions at the start of monitoring, two had new lesions, and one had a new lesion which regenerated, but this colony died six months later. All the colonies that died were less than 20 cm² in area. None of the colonies that had lesions at Green Point died.

At each site, more than 76% of new lesions occurred on large colonies (> 20 cm²), and more than 68% of new lesions were less than 1 cm² (Table 5.1 and 5.2). There were too few colonies with new lesions to compare the recovery rates of colonies of different sizes from lesions of different sizes (Table 5.2). However, from the data obtained, larger lesions (> 1 cm²) did show a trend of being regenerated more slowly than smaller lesions (Table 5.1).

In many instances, lesion regeneration was not a steady process by which lesions became progressively smaller through time. Recovery often involved the lesions increasing and decreasing in size between sampling intervals before they eventually regenerated. Of the 37 new lesions that colonies recovered from at Fairlight, 18 increased in size during the regeneration process. Similarly, 11 of the 43 new lesions that colonies recovered from at Green Point increased in area before finally regenerating (data collected at intervals of 2 months).
Table 5.1: Recovery rates of new lesions of different size measured from surveys of fixed quadrats between 1996 and 1998, at a) Fairlight and b) Green Point. One lesion was excluded from the data at Fairlight as it was only monitored for 2 months, in which time it did not recover.
a) Fairlight

<table>
<thead>
<tr>
<th>Size of New Lesion</th>
<th>Months to Recovery</th>
<th>No Recovery (by 8 months)</th>
<th>Dead</th>
<th>Total n</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>&lt; 1 cm²</td>
<td>15</td>
<td>7</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1 &lt; 3 cm²</td>
<td>3</td>
<td>2</td>
<td>5</td>
<td>1</td>
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</tr>
<tr>
<td>&gt; 5 cm²</td>
<td></td>
<td></td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Totals</td>
<td>18</td>
<td>8</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

b) Green Point

<table>
<thead>
<tr>
<th>Size of New Lesion</th>
<th>Months to Recovery</th>
<th>No Recovery (by 8 months)</th>
<th>Dead</th>
<th>Total n</th>
</tr>
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<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td>17</td>
<td>18</td>
<td>9</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 5.2: Recovery rates of new lesions on colonies of different size measured from surveys of fixed quadrats between 1996 and 1998, at a) Fairlight and b) Green Point.

Some data points were excluded because the area of the colony measured was < 20 cm² but some of the colony was outside the frame, and therefore the total colony area could not be known. One lesion was excluded from the data at Fairlight as it was only monitored for 2 months, in which time it did not recover.
a) Fairlight

<table>
<thead>
<tr>
<th>Colony Size</th>
<th>Months to Recovery</th>
<th>No Recovery (by 10 months)</th>
<th>Dead</th>
<th>Total n</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt; 20 cm²</td>
<td>12 8 5 3</td>
<td>8</td>
<td>0</td>
<td>36</td>
</tr>
<tr>
<td>10 &gt; 20 cm²</td>
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<td>1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>5 &gt; 10 cm²</td>
<td>2</td>
<td></td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>1 &gt; 5 cm²</td>
<td>3</td>
<td></td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Totals</td>
<td>18 8 5 5</td>
<td>9</td>
<td>2</td>
<td>47</td>
</tr>
</tbody>
</table>

b) Green Point

<table>
<thead>
<tr>
<th>Colony Size</th>
<th>Months to Recovery</th>
<th>No Recovery (by 8 months)</th>
<th>Dead</th>
<th>Total n</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt; 20 cm²</td>
<td>13 14 7</td>
<td>2</td>
<td></td>
<td>36</td>
</tr>
<tr>
<td>10 &gt; 20 cm²</td>
<td>1</td>
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<td>2</td>
</tr>
<tr>
<td>5 &gt; 10 cm²</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>1 &gt; 5 cm²</td>
<td>2 1</td>
<td></td>
<td>1</td>
<td>4</td>
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<tr>
<td>Totals</td>
<td>17 17 8 1</td>
<td>3</td>
<td>0</td>
<td>46</td>
</tr>
</tbody>
</table>
There were two sets of lesion surveys done at short time intervals (< 2 months). The first survey was at Fairlight in October 1996 and recorded 13 new lesions. Five of these lesions (38%) had regenerated by 22 days, and 8 lesions (62%) had regenerated by February 1997. Most new lesions (8 of the 13) were less than 1 cm$^2$; four of these small lesions (50%) regenerated by 22 days, and six (75%) had regenerated by February 1997.

The second survey was in October 1997 at Fairlight and Green Point, and recorded a total of 12 new lesions. Five of the seven lesions less than 1 cm$^2$ and two of four lesions between 1 and 3 cm$^2$, regenerated within 24 days. There was one large lesion (> 3 cm$^2$); this lesion did not regenerate until April 1998.

Therefore, due to the fast recovery rates of some colonies from small lesions, surveys that measure the area of lesions in the field at intervals of two months will underestimate the actual amount of area ‘lost’ from the population due to this type of partial mortality. However, as these small lesions quickly regenerate, they are unlikely to be of much direct consequence to the population, so the exclusion of these data from analyses calculating rates of population growth are unlikely to affect the results significantly.
5.3 EXPERIMENT 1: RECOVERY RATES OF COLONIES OF DIFFERENT SIZES FROM EXPERIMENTAL LESIONS OF DIFFERENT TYPES

If the rates of partial mortality are dependent on colony size, and coral populations lose more tissue from partial mortality than from whole colony mortality (Hughes et al. 1992; and this study), then the regenerative abilities of colonies of different sizes are likely to be relevant to understanding the size-structure of coral populations. This is because small colonies are expected to have poor recovery from partial mortality and their reduced size (after partial mortality) is likely to reduce their survivorship, and therefore increase the likelihood of small colonies being lost from the population. However, the partial mortality of a large colony is much less likely to reduce the size of the colony enough so that its chances of continued survival are also reduced (Connell 1973; and this study).

Lesion size and lesion shape have been found to affect the rates at which colonies recover from lesions (Bak & Steward-Van Es 1980; Meesters et al. 1997; Oren et al. 1997a). In P. versipora at least 37% of lesions at Fairlight and 55% of lesions at Green Point were less than 1 cm². Previous studies on various species of coral have shown that colonies with lesions of this size mostly recover; however, colonies with larger lesions are much less likely to recover - unless the lesion has a high perimeter to surface area ratio (Oren et al. 1997a; Meesters et al. 1997). Studies on Montastrea annularis showed that for complete regeneration of a lesion to occur, lesions had to have less than 4.7 mm² per millimetre of lesion perimeter (Meesters et al. 1997).

As there were relatively few incidents of damage on smaller colonies (< 20 cm²) in the lesion surveys, the relationships between size and the rates at which colonies recover from lesions were investigated using manipulative
experiments with artificial lesions, to simulate the partial mortality caused by grazers (Chapter 5.2.1).

Thus, the following hypotheses were tested to investigate proposed models (see Chapter 5.1 for models):

Model F:
Hf1) That more large colonies (> 20 cm²) recover from experimental lesions than small colonies (< 5 cm²).
Hf2) That large colonies (> 20 cm²) recover from experimental lesions faster than small colonies (< 5 cm²).

Model B:
Hb2) That colonies regenerate small lesions (1 cm²) faster than they regenerate larger lesions (3 cm²)

Model G:
Hg1) That the effect of lesion size on rate of recovery is greater in small colonies (< 5 cm²) than in large colonies (> 20 cm²).

Model C:
Hc1) That lesions of Type C regenerate at a faster rate than lesions of Type B (refer to methods for descriptions of these different types of lesions).
5.3.1 Methods

This experiment was set up at Fairlight and Green Point, using colonies located near the fixed quadrats (Chapter 3). It included 36 colonies at each site, and each colony had a single experimental lesion. The recovery rates of small ($< 5 \text{ cm}^2$), medium ($5 < 20 \text{ cm}^2$) and large ($> 20 \text{ cm}^2$) colonies were compared, and there were three different types of lesion. For each type of lesion there were four replicate colonies, in each size-class of colony.

As in previous chapters, the size-frequency distributions obtained in preliminary surveys were used to choose the size-classes of colonies relevant for investigating the proposed models (Chapter 2.6).

The sizes of lesions relevant to the population were chosen using the size-frequency distributions of new lesions (Figure 5.3). The maximum size of experimental lesions was constrained, in that lesions could not be larger than small colonies ($< 5 \text{ cm}^2$). Therefore, the lesion sizes used in the experiment were $1 \text{ cm}^2$ and $3 \text{ cm}^2$. The lesions used were: Type A (1 cm$^2$ circles), Type B (3 cm$^2$ circles), and Type C (3 cm$^2$ oblongs of 2.5 cm length and 1.2 cm width). Lesions of Type C have the same area as lesions of Type B, but they have a larger perimeter to surface area ratio.

The colonies used in the experiment had no lesions on their surfaces before the start of the experiment, and all appeared to have arisen from a single recruit (they were not 'amalgamated colonies'). Colonies were tagged using plastic 'Dymo' labels attached with 20 mm 'Ramset CW420' concrete nails hammered into the sandstone substratum next to the colony.
Lesions were made toward the middle of colonies, using a denture toothbrush. The coral was scrubbed until the skeleton and calices appeared white and completely bare of tissue. This caused only minor damage to the skeleton, and appeared to simulate the damage caused by grazers (Chapter 5.2.1). A perspex template of each lesion type was used to restrict the size and shape of each lesion and protect the surrounding tissue from damage.

The regeneration of lesions was recorded photographically, using a Nikonos V camera fitted with an Aquasea 3:1 extension tube and framer, and mounted with a Nikonos 103 strobe. Fujichrome 'sensia' 100 ISO film was used, and the camera aperture was set at f/22.

The recovery of individual colonies from experimental lesions was measured in two ways. The first method was quantitative, done by counting the number of bare calices on the surface of the colony remaining in a lesion at each time interval, and calculating the percentage of the lesion that had regenerated from the number of calices scrubbed bare at the start of the experiment. The second method was a qualitative assessment of recovery, in which colonies that had regenerated all the polyps and tissue over the lesion area were assessed as to whether or not the tissue was discoloured, or whether the lesion area had "completely recovered" in that it could no longer be distinguished.

Colony growth was not included as a factor in the experiment, as the expected duration of the experiment (a few weeks) was too short to measure growth. However, some of the small colonies used in the experiment did increase in polyp number during the course of the experiment (3 months), as may have some of the medium and large sized colonies. The growth rates of experimental colonies could not be calculated a posteriori, as most of the macro photographs taken of lesions did not include a whole colony within the frame.
This experiment was done in summer (December 1996 to March 1997), as conditions then are more suitable for the extended dive times required to set up and monitor the experiment than at other times of the year.

The experiment ran for 96 days and was sampled five times at 0, 8, 20, 40 and 96 days. A sixth sample at 60 days was included, but due to the camera flooding these data are incomplete, so were not included in the results.

5.3.2 Results from Lesion Experiment 1

The results of the experiment are shown in Figure 5.5. The lesions of a few colonies became larger than the area originally damaged at the start of the experiment.

The data are incomplete through time for some replicates. Missing data toward the end of the experiment were most probably because some colonies had completely recovered from their lesions and lost their labels, so were not recognised as an experimental colony during sampling. This explanation is reasonable as at earlier sampling times these colonies had rates of recovery comparable with other colonies that had recovered from their lesions by the end of the experiment. Other instances where a colony was missed at multiple (sporadic) time points, were due to the colony being intermittently missed during sampling because of its cryptic location. None of the missed samples are likely to have died, as colonies of the sizes that were missed have very high rates of survivorship (Chapter 3.5). On the final day of the experiment four medium sized colonies (two from each site) and one large colony from Fairlight were “missed” in sampling.
Rates of recovery of different sized colonies with lesions of Types A, B, and C on:

i) small colonies at Fairlight,
ii) small colonies at Green Point,
iii) medium colonies at Fairlight,
iv) medium colonies at Green Point,
v) large colonies at Fairlight,
vi) large colonies at Green Point.

Each treatment had 4 replicate colonies (although some samples were lost, see results), and each colony had a single experimental lesion. Error bars represent standard deviations.
i) SMALL COLONIES AT FAIRLIGHT

a) Lesion Type A

- Days Since Start
- % Area Recovered

b) Lesion Type B

- Days Since Start
- % Area Recovered

c) Lesion Type C

- Days Since Start
- % Area Recovered
ii) SMALL COLONIES AT GREEN POINT

a) Lesion Type A

b) Lesion Type B

c) Lesion Type C
iii) MEDIUM COLONIES AT FAIRLIGHT

a) Lesion Type A

b) Lesion Type B

c) Lesion Type C
iv) MEDIUM COLONIES AT GREEN POINT

a) Lesion Type A

b) Lesion Type B

c) Lesion Type C
v) LARGE COLONIES AT FAIRLIGHT

a) Lesion Type A

Days Since Start

b) Lesion Type B

c) Lesion Type C
vi) LARGE COLONIES AT GREEN POINT

a) Lesion Type A

![Graph for Lesion Type A]

b) Lesion Type B

![Graph for Lesion Type B]

c) Lesion Type C

![Graph for Lesion Type C]
By 96 days, all of the small colonies (n = 24) at each site had regenerated 100% of the tissue over the lesion area, regardless of the type of lesion. The recovery rates of small colonies from lesions were faster at Green Point than at Fairlight.

The recovery rates of medium sized colonies from experimental lesions were different between sites, in that all the experimental lesions on colonies at Green Point regenerated during the course of the experiment, whereas at Fairlight only colonies with lesions of Type C regenerated 100% of their area on all 4 replicate colonies. By the end of the experiment at Fairlight, 2 of the 3 colonies with lesions of Type A, and 1 of the 2 colonies with lesions of Type B, had regenerated all their lesion area (some samples were missed in sampling, n = 4 at start). Overall, medium sized colonies recovered faster from lesions at Green Point than at Fairlight.

All of the large colonies at Green Point had regenerated 100% by 96 days. At Fairlight, three of the large colonies with lesions of Type B, and two of the colonies with lesions of Type C had regenerated 100% (n = 4 per lesion type). However, none of the large colonies at Fairlight with lesions of Type A (n = 3 replicates, because of lost samples) regenerated all their tissue area. Two of the large colonies with Type A lesions had wounds that were larger than the original lesion.

Overall, the results show a trend of lower rates of recovery with increased colony size, and this trend is stronger at Fairlight than at Green Point.

There was no clear relationship between the extent of recovery and lesion type, except for the large colonies at Fairlight, which showed very poor recovery from the Type A lesions compared to the rates of recovery from lesions of Types B and C. Due to the loss of data for some of the medium sized colonies, there are
too few replicates to discern any relationships between the rates of recovery of medium sized colonies and lesion type.

For colonies that regenerated 100% of the tissue damaged in the lesion, a qualitative assessment of recovery was made, by noting whether the tissue was discoloured, or whether the colony had "completely recovered" from the lesion, so that the area damaged was no longer discernible. At the end of the experiment, all of the small colonies at Green Point showed complete recovery, 70% of the medium colonies had completely recovered from their lesions, but only 25% of the large colonies had completely recovered from their lesions. At Fairlight, a larger proportion of colonies had discoloured lesions, with only 50% of small colonies, 20% of medium colonies, and 18% of large colonies completely recovering from their lesions.

The faster rates of recovery of colonies from lesions at Green Point compared to Fairlight are consistent with the results from the surveys of fixed quadrats (Figure 5.4).

The results were expressed as the proportion of colonies in each size-class that had recovered or had not completely recovered from their lesions (for both quantitative and qualitative assessments), and analysed using Fisher Exact Tests. The results of these analyses showed differences in the recovery rates of colonies of different sizes at some time points (Table 5.3). Where significant differences occurred, more small colonies had recovered from their lesions than large colonies.

Therefore, the results of this experiment do not support any of the models proposed. Large colonies did not have higher or faster rates of recovery than small colonies (contrary to Model F). Small lesions regenerated at the same rate
Table 5.3: Analysis of Results from Lesion Experiment 1, 1996-97

Comparisons were made between the proportion of small versus large colonies that had recovered all the area damaged by experimental lesions at different sampling dates, for each site. Medium colonies were not included in this analysis because many of the replicates for the medium sized colonies were lost.

The recovery rates of colonies with different types of lesions were combined to investigate the effects of colony size. Data were only analysed for the sample days on which two or more colonies had 100% recovery in quantitative measures. Differences between size classes using the qualitative measures were calculated for the last sampling date only.

Data were analysed using the Fisher Exact Test with the level of significance set at $\alpha = 0.1$. NS: not significant, Sig: significant ($p < 0.1$), and V.Sig: very significant ($p < 0.001$). In all of the comparisons that gave a significant result the small colonies ($<5 \text{ cm}^2$) had recovered from their lesions more quickly than the large colonies ($>20 \text{ cm}^2$).

<table>
<thead>
<tr>
<th>Site</th>
<th>Quantitative Measure of Recovery</th>
<th>Qualitative Measure of Recovery</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20 days</td>
<td>40 days</td>
</tr>
<tr>
<td><strong>Fairlight</strong></td>
<td>NS</td>
<td>Sig</td>
</tr>
<tr>
<td></td>
<td>$p = 0.1$</td>
<td>$p = 0.02$</td>
</tr>
<tr>
<td><strong>Green Point</strong></td>
<td>NS</td>
<td>Sig</td>
</tr>
<tr>
<td></td>
<td>$p = 0.5$</td>
<td>$p = 0.02$</td>
</tr>
</tbody>
</table>
or more slowly and less completely than larger lesions (contrary to Model B). Small lesions had poorer rates of regeneration on large colonies than on small colonies at Fairlight whereas, both small and large colonies had similar rates of recovery from small lesions at Green Point (contrary to Model G). Finally, there was no difference in the rates of recovery of 3 cm$^2$ lesions with different perimeter to surface area ratios (lesions of Type B and C), and lesions with the highest perimeter to area ratios (1 cm$^2$ circles) had the lowest rates of regeneration at Fairlight, and similar rates of regeneration to the other types of lesions on colonies at Green Point (contrary to Model C). Possible explanations for these unexpected results are given in the Discussion.
5.4 EXPERIMENT 2: RECOVERY RATES OF COLONIES OF DIFFERENT SIZES FROM EXPERIMENTAL LESIONS

The results from Experiment 1 suggested that there were differences in the recovery rates of colonies of different sizes. However, the differences were not as predicted, as small colonies were found to recover more quickly from lesions than large colonies. In order to test Model F more stringently the experiment was repeated using more replicates in each size-class.

Experiment 2 was expanded (at Fairlight only) to include a fourth size-class of ‘very large’ colonies, which were colonies larger than 100 cm². Results from the surveys of fixed quadrats had shown that colonies of this size have fewer lesions (on an area cover basis) than smaller colonies (Chapter 5.2.4). This suggests that these colonies are injured less often and/or to less of an extent (per unit area) or have faster rates of recovery from injuries. If the effects of partial mortality change as colonies grow, then the greatest difference is likely to be measured when the recovery rates of these very large colonies (> 100 cm²) are compared to the recovery rates of small colonies.

Finally, to further explore the model that the biology of colonies changes as they grow (General Model 1), I investigated whether small colonies that have become large as a result of having amalgamated with a neighbouring colony have a biology similar to large colonies that have grown from a single recruit. Therefore, two more treatments were included in Experiment 2 which had small colonies that had become large through amalgamating with their neighbour(s). One of these treatments consisted of corals that had a blend histocompatibility reaction between the colonies, and the other treatment had corals that had a ridge or distinct histocompatibility reaction between the colonies (descriptions of these reaction types are given in Chapter 4.2.2). These new treatments
provided the opportunity to investigate whether amalgamated colonies joined by different types of histocompatibility reaction have different rates of recovery. This could be because: 1) Colonies that express the blend reactions appear to be physiologically integrated, so may be able to share resources between the colonies in the amalgamation. Consequently, these colonies may be able to repair damaged tissues faster than colonies in amalgamations joined by distinct or ridge reactions; and/or, 2) maintaining the ‘aggressive/defensive-like’ ridge and distinct reactions may require more resources than maintaining the ‘passive-like’ blend reactions. Hence, colonies in amalgamations with blend reactions may have more resources available for repairing damage, so regenerate lesions more quickly, than colonies in amalgamations joined by ridge or distinct reactions.

The number of colonies that could be used in the experiment was limited by the small size of the population, the limited number of colonies located in places where they could be readily photographed, the logistics regarding diving “bottom times” and the number of exposures in a roll of film. This meant that only 36 colonies at Green Point and 72 colonies at Fairlight could be included in Experiment 2. Therefore, to increase the number of replicates in each size-class, comparisons between the recovery rates of colonies from different types of lesions were excluded from the experiment, allowing me to have 12 replicate colonies in each size-class, at each site.

Models investigated in Experiment 2:

Model F:
Hf1) That more large colonies (> 20 cm²) recover from experimental lesions than small colonies (< 5 cm²).
Hf2) That large colonies (> 20 cm²) recover from experimental lesions faster than small colonies (< 5 cm²).

Model H:

Hh1) That, like large colonies (> 20 cm²) that have grown from a single recruit, large colonies (> 20 cm²) formed by the amalgamation of a small colony (< 5 cm²) with another colony, regenerate from partial mortality faster than (independent) small colonies (< 5 cm²).

Model I:

Hi1) That small colonies (< 5 cm²) that are joined into amalgamations and have a blend historecognition reaction have faster rates of regeneration from experimental lesions than small colonies (< 5 cm²) that are joined into amalgamations and have a ridge or distinct reaction.

5.4.1 Methods

The experiment included 36 colonies at Green Point and 72 colonies at Fairlight. Each colony had a single experimental lesion of type C. The recovery rates of small (< 5 cm²), medium (10 to 20 cm²) and large (> 20 cm²) colonies were compared at Fairlight and Green Point. Three additional classes of colonies were included at Fairlight; these were: 'very large' (colonies > 100 cm²), 'small corals that had grown into contact with a neighbouring colony to become large (> 20 cm²) and had a blend histocompatibility reaction type', and 'small corals that had grown into contact with a neighbouring colony to become large (> 20 cm²) and had a ridge or distinct histocompatibility reaction'.
In this experiment lesions of type C were used (see methods of Experiment 1), as these oblong lesions were the easiest to inflict on colonies. A piece of underwater paper with the shape of the experimental lesion cut out was used as a template. This worked better than the sturdy perspex template used in Experiment 1, as it could be moulded over the surface of the colony, making it easier to scrub the defined area. A similar template was used by Hall (1997).

The methods used to set up the experiment were the same as for Experiment 1, except that colonies were monitored over 137 days, and data were collected on six sampling dates (at 0, 14, 27, 55, 80 and 137 days after lesions were made). The experiment was done in summer and autumn (December 1997 to May 1998), as conditions at this time of the year are more suitable for the extended dive times required. As in Experiment 1, the recovery of colonies from lesions was assessed both quantitatively and qualitatively.

Colonies from Experiment 1 were not reused in Experiment 2. Therefore, due to the large number of colonies needed for the experiment at Fairlight, the second experiment was set up in an area which had not been previously sampled, at the far east end of Fairlight Reef, in water of 5 to 7 m depth.

5.4.2 Results from Lesion Experiment 2

The results from this experiment are shown in Figure 5.6. As in Experiment 1, a few colonies had lesions that became larger, rather than healing over time.

All of the small colonies, at each site, had regenerated their lesions by 80 days. However, at 137 days, on two small colonies, one from each site, part of the
Rates of recovery of different types of colonies from 3 cm² lesions.

i) Small, Medium and Large colonies at Fairlight

ii) Small, Medium, and Large colonies at Green Point

iii) Extra-large colonies, 'small colonies that have grown into contact with their neighbour(s) to form a discrete large colonies connected with a blend reaction', and 'small colonies that have grown into contact with their neighbour(s) to form a discrete large colonies connected with a ridge or distinct reaction', at Fairlight.

Each treatment had 12 replicate colonies, and each colony had a single experimental lesion. Error bars represent standard deviations.
i) COLONY SIZE TREATMENTS AT FAIRLIGHT, PART I

a) Small Colonies

b) Medium Colonies

c) Large Colonies
ii) COLONY SIZE TREATMENTS
AT GREEN POINT

a) Small Colonies

b) Medium Colonies

c) Large Colonies
iii) COLONY SIZE TREATMENTS AT FAIRLIGHT, PART II

a) Extra Large

b) Blend Reaction

c) Distinct/Ridge Reaction
lesion area opened up again, due to it having been colonised by tubeworms (presumably when the skeleton was exposed).

The regeneration of lesions was slower in the medium and large colonies than in the small colonies, with this relationship being stronger at Green Point than at Fairlight. The worst rates of recovery were shown by the medium sized colonies at Green Point, which had poor recovery up to 80 days, and had one colony that increased the size of its wound 6.5 times. By 137 days, almost all of the area damaged on medium sized colonies had regenerated, to the extent that ten of the twelve colonies had regenerated all of the tissue removed by the experimental lesions.

The large colonies had slower rates of recovery at Green Point than at Fairlight (Figure 5.6). At the end of the experiment each site still had three colonies yet to recover from their lesions. These colonies each had ≤ 40% of their original lesion area still to regenerate at Fairlight, and ≤ 6% of their lesion area left to regenerate at Green Point.

At Fairlight, the very large colonies showed similar rates of recovery to the medium and large sized colonies. The wounded area had not fully healed at the end of the experiment on two of the very large colonies. These colonies each had ≤ 5% of their original lesion area remaining.

Similarly, colonies with the blend reactions had rates of recovery comparable to those of large colonies at Fairlight. At the end of the experiment, colonies with the blend reactions all had ≤ 47% of their lesion area yet to regenerate.

The recovery rates of colonies with the ridge or distinct reactions were also similar to large colonies, although the amount of lesion area regenerated by the
amalgamated colonies was more variable within each time interval than for the large colonies. At the end of the experiment, the colonies with the ridge or distinct reactions all had less than 19% of their lesion area left to regenerate.

Between sites the recovery rates of small colonies were faster at Green Point than at Fairlight. However, the medium and large colonies had faster rates of recovery at Fairlight than at Green Point.

Overall, the results show a trend of reduced rates of recovery with increased colony size, with this trend being strongest at Green Point (Figure 5.6).

A qualitative assessment of lesion recovery at each site showed that at Fairlight 92% of the small, 55% of the medium, 45% of the large, 75% of the very large colonies, 58% of the 'blend' colonies and 55% of the 'ridge/distinct' colonies had completely recovered from their lesions at the end of the experiment. At Green Point, 92% of the small, 82% of the medium, and 25% of the large colonies had completely recovered from their lesions at the end of the experiment.

The results for the frequency of colonies in each size-class that had, and had not, recovered from their experimental lesions were analysed using Fisher Exact Tests; the results are given in Table 5.4. As in the previous experiment, small colonies were found to recover more quickly from their lesions than large and very large colonies. Small colonies that had amalgamated with other colonies to form a large, discrete colony had slower rates of recovery than small colonies that were independent of other colonies. No significant differences were found between the recovery rates of amalgamated colonies that had a blend reaction and amalgamated colonies that had a ridge or distinct reaction. Thus, the results of this experiment do not support any of the proposed models (Models F, H and I); possible explanations for this are given in the discussion.
Table 5.4: Analysis of Results from Lesion Experiment 2, 1997-98

<table>
<thead>
<tr>
<th>Colony Size Combination</th>
<th>Site</th>
<th>Days Since Start of Experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>27</td>
</tr>
<tr>
<td>Small vs. Large</td>
<td>Fairlight</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Green Point</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Qualitative)</td>
<td>Fairlight</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Green Point</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small vs. Extra Large</td>
<td>Fairlight</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small vs. Blend</td>
<td>Fairlight</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small vs. Ridge/Distinct</td>
<td>Fairlight</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large vs. Extra Large</td>
<td>Fairlight</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>NS</td>
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<tr>
<td></td>
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<tr>
<td>Blend vs. Ridge/Distinct</td>
<td>Fairlight</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>NS</td>
</tr>
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</tbody>
</table>

Fisher Exact Test analyses of the proportion of colonies that had recovered from their lesions for different colony size combinations. Unless otherwise stated, recovery was measured quantitatively. Data were only analysed for the sample days and treatments in which two or more colonies had 100% recovery in quantitative measures.

The level of significance was set at $\alpha = 0.1$. NS: not significant, Sig: significant ($p < 0.1$), and V.Sig: very significant ($p < 0.001$).
Surveys of naturally occurring lesions in the population suggest that *P. versipora* is good at regenerating, with a high turnover of damaged tissue. A large proportion of colonies regenerate their lesions quickly, with more than 55% of new lesions at Fairlight, and 75% of new lesions at Green Point regenerating within four months of occurrence (Figure 5.4). At each of the times surveys were done, no more than 2% of the coral area at each site consisted of lesions. Therefore, the total area of coral lost due to partial mortality (lesions and colony shrinkage combined, 6% to 8%) is greater than the area lost due to whole colony mortality (< 1.5%).

More than 70% of lesions occurred away from the edge of colonies, so only about a third of the damage occurring on colonies could be attributed to 'edge effects' such as competition with macroalgae or with other sessile marine invertebrates for space.

Most lesions (> 92%) occurred on large colonies (> 20 cm²). The total area of damage on large colonies was directly proportional to the large area of coral these colonies contribute to the population.

Most lesions occurring in the population were small (< 1 cm²) (Figure 5.1) and likely to fully regenerate (Table 5.1). In some time intervals, up to 30% of lesions were larger than 5 cm². These lesions had much slower rates of recovery and are less likely to completely regenerate. Thus, larger lesions represent the potential for a substantial amount of permanent damage to the population. These results are consistent with the findings of other, similar studies (Bak & Steward Van Es 1980; Meesters *et al.* 1997).
In the surveys of fixed quadrats, a large proportion of the lesions present at the start of monitoring were still present on the last day of sampling (83% at Fairlight and 33% at Green Point). Overall, the results from the surveys suggest that lesions that have not regenerated by 8 months at Fairlight, and 6 months at Green Point, are unlikely to ever regenerate. At Fairlight, a small proportion of colonies with new lesions died (4%). These colonies were all less than 20 cm². This represented a rate of mortality of 18% for smaller colonies (< 20 cm²) with lesions, suggesting that partial mortality reduces the survivorship of colonies, as the rates of mortality measured for all colonies of this size at Fairlight were less than half this rate (7% to 8.5%; Chapter 3.5).

5.5.1 Effect of Lesion Size on Colony Recovery

Results from the surveys of lesions in fixed quadrats showed that in *P. versipora*, large lesions do regenerate more slowly than small lesions (Table 5.1). This is consistent with previous studies on Caribbean corals (Bak & Steward Van Es 1980; Meesters *et al.* 1997) and is probably because the larger the area damaged, the more resources needed to heal it.

Although large lesions occur less frequently in the population, the total area they cover is much greater than the area covered by small lesions. Therefore, the slower or less complete regeneration of large lesions compared to small lesions is likely to represent an important control on the long term growth of the population.

In Experiment 1, the rates of recovery of colonies of different sizes from three types of experimental lesion (A, B, and C) were compared. It was predicted that colonies would recover from the small Type A lesions most quickly, followed by
the large oblong Type C lesions, and then the large circular Type B lesions (Models B and C). The results, however, did not support this model. At Green Point, the three lesion types all showed similar patterns of regeneration, within each colony size-class. This was also true for the different types of lesions on small colonies at Fairlight. However, for the large colonies at Fairlight, more of the larger Type B and C lesions regenerated to a greater extent, sooner, than the smaller Type A lesions, which had poor rates of regeneration. Unfortunately, due to some of the medium sized colonies being missed on the last day of sampling, there are too few replicates to ascertain whether there were any relationships between the rates of recovery of medium sized colonies and the type of lesions.

Colonies can transport metabolites to sites of injury to aid in regeneration. This was demonstrated in an experiment by Oren et al. (1997b), in which the centres of *Favia favus* and *Platygyra lamellina* colonies were labelled with radioactive bicarbonate ($^{14}$C${\text{O}}_{3}$), and oblong lesions of approximately 1 cm$^2$, 2.5 cm$^2$, and 5 cm$^2$ were made on the colonies 10 cm away from the labelled centre. The results showed that metabolites were transported from the centre of the colony towards the large lesions and some of the intermediate sized lesions, but they were not transported towards the small lesions. This suggests that the regeneration of small lesions relies on nutrients from local polyps.

The faster recovery rates of large colonies from large lesions than from small lesions in Experiment 1 were unexpected, as results from the surveys of fixed quadrats suggested that large lesions regenerate more slowly than small lesions. This difference could reflect seasonal differences in the amount of energy colonies have available for regeneration, as the results for colonies in the fixed quadrats were compiled from data collected throughout the year, whereas
Experiment 1 was done in summer, when colonies (> 5 cm²) are likely to be using available energy in the development of gonads (see Appendix IV).

Therefore, in colonies which have limited resources available for regeneration, the rates of recovery of colonies from lesions of Type B and C may be faster than from lesions of Type A, due to the larger area of injury of Type B and C lesions stimulating the transport of nutrients from other parts of the colony to repair the injury, whereas the smaller Type A lesions may receive nutrients only from nearby polyps which may have already committed their available resources to reproduction.

Oren et al. (1997b) did not measure the rates of regeneration of the different sized lesions, so it is not known whether, in their experiment, the translocation of metabolites to sites of injury resulted in the larger lesions regenerating more quickly than the smaller lesions.

The treatments involving different types of lesions were not included in Experiment 2, due to logistical constraints. However, the relationship between the size and shape of lesions and the likelihood of a colony regenerating the damaged area is an interesting one, and warrants further investigation.

The lack of a strong difference in the recovery rates of colonies with different types of experimental lesions, could be because the experimental lesions had to be smaller than a small colony (< 5 cm²). This meant that the perimeter to surface area ratios of the different lesions were actually quite similar (3.5 for lesions of type A; 2 for lesions of type B; and 2.5 for lesions of type C lesions).

In future studies, it would be interesting to investigate the rates at which much larger lesions (> 5 cm²) regenerate, as data from the field surveys suggests that
these lesions have poor rates of recovery, so are of greater consequence to the population than small lesions, even though they occur much less frequently. The perimeter to surface area ratios of these larger lesions could also be varied much more. This type of experiment could be done if only large colonies were used in the experiment.

Most small lesions regenerate quickly, so have only a temporary (perhaps negligible) impact on the population, whereas larger lesions that have slower rates of regeneration have a longer term impact. The consequences of large lesions occurring on colonies need to be investigated further. If large lesions are repaired using resources from other parts of the colony, then the regeneration of large lesions may have a greater impact on the colony as a whole than the regeneration of small lesions, potentially reducing the fitness (e.g. rates of growth and fecundity) of the entire colony. On the other hand, small lesions may have a much more localised impact, as repair is probably supported by metabolites from adjacent polyps, reducing the fitness of polyps near the lesion. Therefore, the impact of small lesions on the fitness of the whole colony will be less for larger colonies than for smaller colonies.

5.5.2 Effect of Colony Size on Recovery

In each experiment, comparisons between small and large colonies showed that small colonies had significantly greater rates of recovery than large colonies (Table 5.3 and 5.4). Although this may not result in an overall difference in the proportion of small and large colonies that recover from their lesions, the slower rates of recovery of larger colonies does increase the potential of lesions on these colonies to result in a permanent loss of coral area. This is because the more frequently partial mortality occurs, and the longer a colony takes to
recover from a lesion, the greater the likelihood of the exposed skeleton being colonised by other organisms. Therefore, the higher frequency of lesions on large colonies, and the slower rates of recovery of large colonies from lesions, could act to increase the likelihood of damaged areas on large colonies being permanently lost from the population.

The higher frequencies of lesions observed on larger colonies can be attributed to the larger area covered by large colonies, the slower rates of recovery of large colonies compared to small colonies, and the fact that some small colonies die after they have been damaged.

The results from the surveys of fixed quadrats suggested that there may be an advantage in size for very large colonies (>100 cm²), in that the percentage area of coral that had naturally occurring lesions was much less on these colonies than on smaller colonies. In Experiment 2, the recovery rates of very large colonies were measured. There was no significant difference between the recovery rates of very large colonies and those of large colonies. Added to this, very large colonies, like large colonies, had significantly slower rates of recovery than small colonies 80 days after lesions were made on these colonies. Thus the fact that very large colonies have fewer lesions on their surfaces than large colonies is not because very large colonies have faster rates of recovery. The low rates of damage on very large colonies could, however, be linked to how these colonies occupy space. A colony of 100 cm² has a circumference to area ratio less than half that of a colony of 20 cm² (0.35 versus 0.79) and hence, per unit area, a greatly reduced likelihood of damage due to interspecific interactions at the periphery of the colony. Alternatively, the lower rates of damage could purely be related to the large amount of space very large colonies occupy. Jackson (1979) proposed the ‘disturbance model’ in which he attributes the different rates of partial and whole colony mortality of small colonies
compared to large colonies to the different ways these colonies occupy space. He hypothesised that, due to their small size, small colonies are less likely to be affected by a disturbance, but are much more likely to die as a result of being disturbed, than larger colonies. The results from the surveys described in this chapter support this model. However, the results also suggest a third scenario, in which very large colonies are able to avoid some kinds of disturbances. This could be due to very large colonies being so large that they act as a deterrent (e.g. by releasing large amounts of allelochemicals that deter grazers and settlers away from the colony), or it could simply be because these large colonies occupy so much space that bottom dwelling organisms simply avoid the areas where they occur. This suggests that there may also be an advantage in colonies having locally aggregated distributions, if these aggregations are similar to very large colonies in that they can also occupy a lot of space on the substratum and hence, also avoid some kinds of disturbances. A final explanation could be that very large colonies only occur in places that have low rates of disturbance, hence the colonies are able to grow to, and maintain, very large sizes.

The slower rates of recovery of larger colonies compared to small colonies is also likely to reflect differences in the energetics of these colonies. In *P. versipora*, colonies do not become reproductive until they are larger than 5 cm² (Chapter 3.6). Both of the lesion experiments ran over summer, which is when larger colonies are most likely to be reproducing (Appendix IV). Therefore, the different rates of recovery of small and large colonies could simply reflect the fact that most of the larger colonies were undergoing gametogenesis, and thus had fewer resources available to repair their injuries than small colonies. Van Veghel & Bak (1994) showed that the regeneration rates of *Montastrea annularis* colonies were reduced during the reproductive season, and this was attributed to the energy demands of reproduction. Similarly, Rinkevich & Loya
(1979) and Hall (1997b) found that the fecundity of colonies that had been
damaged was less than that of undamaged colonies. These results suggest that
the resources of colonies are allocated to different population processes in some
sort of priority. Therefore, the fact that there was a 'window' of difference in
the rates of recovery of small colonies compared to large colonies, after which
the large colonies recovered from their lesions to a similar extent to the small
colonies, could represent a period of 'catch-up' at the end of the reproductive
season when large colonies stop developing gonads and direct resources towards
colony repair.

If the effect of colony size on rates of regeneration is simply a seasonal
phenomenon, then in months when colonies are much less likely to be
reproductive (April to June), similar experiments would be expected to show
that large colonies either regenerate their lesions more quickly, or at the same
rate, as small colonies.

5.5.3 Recovery Rates of Amalgamated Colonies Joined by Different Types of
Histocompatibility Reactions

Small colonies that had amalgamated with their neighbours to form large
discrete colonies had rates of recovery that were significantly different from
the recovery rates of small independent colonies, eighty days after lesions were
made on the colonies. Interestingly, contrary to what was proposed in Model I,
the rates of recovery were not significantly different between colonies with
the blend reaction and colonies with the ridge or distinct reactions, in any of
the time intervals. This result is preliminary, and the experiment needs to be
repeated to establish whether this is a general pattern.
In colonies with the blend contact type metabolites may pass between colonies in the amalgamation, but the extra resources may be used for processes other than repair (for example, reproduction). Alternatively, the association of a small colony with a larger colony could result in a kind of parasitism, in which resources that would otherwise be used for repair are translocated away from the small coral to its larger partner.

Experiments using \(^{14}\text{C}\)-labelling could be used to determine whether metabolites are translocated between amalgamated colonies, and if they are, whether these metabolites are preferentially transported to sites of injury, growth or gonad development. Further, the energy expenditure of colonies involved in different types of histocompatibility reactions could be compared by measuring the respiration rates of these colonies (per unit area) to determine whether colonies joined by ridge or distinct reactions use more energy to maintain the association than colonies joined by a blend reaction.

If small colonies that amalgamate with their neighbours to become large have a similar biology to large colonies derived from a single recruit, even without the colonies in the amalgamation fusing, then some process must be acting to give these colonies a 'sense' of their increased size. When a small colony grows into contact with its neighbour the proportion of tissue it has at the periphery of the new colony changes dramatically. The consequences of this are that each coral in the amalgamation will have a shorter length of tissue exposed to damage at the edge of the colony and proportionately fewer polyps functioning for growth and defence in the colony. Therefore, these corals may have proportionately more polyps and more resources available for reproduction. As a result, the energetics of these previously small colonies may change, such that they suddenly become like large colonies. This model could be tested in manipulative experiments using colonies of the same size but with different...
lengths of perimeter, to investigate whether the biology (rates of growth, survivorship, fecundity and regeneration) of these colonies differs.

5.5.4 Comparison of Recovery Rates Between Sites

Although lesions were surveyed over a much smaller area of coral and a shorter period of time at Green Point (4,000 to 4,500 cm² for 16 months) than at Fairlight (7,200 to 8,600 cm² for 24 months), the total number of new lesions recorded during the surveys was very similar (47 at Green Point and 49 at Fairlight), and the total area of lesions in any time interval ranged from 38 to 87 cm² at Green Point, compared to 102 to 156 cm² at Fairlight. Therefore, the rates of damage to colonies were higher at Green Point than at Fairlight. However, this higher rate of damage on colonies at Green Point is offset by the faster rates of regeneration measured both in the surveys of fixed quadrats and from the results of Experiment 1. In Experiment 2 the medium and large colonies regenerated more quickly at Fairlight than at Green Point. These inconsistent results are probably because Experiment 2 was done on a part of Fairlight Reef away from the fixed quadrats and colonies used in Experiment 1 and where environmental conditions are likely to be different as corals occur in deeper water and are predominantly surrounded by assemblages of turf algae.
5.6 SUMMARY

There was a higher frequency of lesions on large colonies than on small colonies. This appears to be due to a combination of factors including: 1) the greater area cover of large colonies and, therefore, their greater risk of being damaged compared to small colonies, 2) the reduced survivorship of small colonies after partial mortality compared to large colonies, and 3) the slower rates of recovery of large colonies compared to small colonies.

Most lesions are small (< 1 cm²) and regenerate quickly. Larger lesions generally have slower rates of regeneration, are more likely to become permanent, and in total, cover much more coral area than small lesions. Therefore, larger lesions have a greater effect on the population than small lesions, as they represent much more coral death.

The long-term consequences of large unregenerated lesions collecting in the population through time is likely to represent an important control on the growth of large colonies and on population growth as a whole, limiting what may otherwise be the potentially endless expansion of coral colonies and coral populations.
CHAPTER 6: GENERAL DISCUSSION

In Sydney Harbour, _P. versipora_ maintains a viable, growing population, with reproductively active colonies and has influxes of new recruits each year.

The major findings of this study are 1) that the biology of colonies changes as they become bigger, 2) that the size-structure of the population can be used to predict biological differences among colonies, and 3) that the rates of partial mortality of very large colonies (> 100 cm²) are less than would be expected if mortality were purely random over any given area of substratum. The first of these findings is consistent with the model proposed by Jackson (1979); the second finding was not predicted by Jackson (1979), but similar preliminary findings have been described by Bak & Meesters (1998). The third finding is inconsistent with Jackson’s (1979) model for sheet-like colonies.

In this chapter, I discuss the results of my studies with reference to the general models presented in Chapter 1.4 and the models of Jackson (1979) about the physiological and ecological implications of size of colony. The growth and patchy distribution of colonies are then discussed in light of these results. Finally, suggestions for future studies of _P. versipora_ and of the population biology of other modular organisms are presented.
6.1 PHYSIOLOGICAL AND ECOLOGICAL IMPLICATIONS OF COLONY SIZE

General Model 1 (Chapter 1.4) proposed that the biology of colonies changes as they grow, so that smaller colonies have faster rates of growth and smaller rates of survivorship, fecundity and regeneration than do larger colonies. These models were supported, with the single exception that rates of regeneration were faster in smaller than in larger colonies. There were too few incidents of fission to test the model that larger colonies have faster rates of fission than do smaller colonies. The sizes at which the biology of colonies changed were as predicted, based on observations of the size-frequency distributions of colonies in the population (Chapters 1.4 and 2.6), thus supporting General Model 2a.

The relative rates of growth decreased with increasing size of colony, whereas the rates of linear extension were independent of size. Similar results have been reported previously (Connell 1973; Hughes & Jackson 1985; Kinzie & Sarmiento 1986). In *P. versipora*, this relationship represents the geometric constraints of colonies, in that they are elliptical and have most growth at their periphery. Therefore, relative to the total energy available, the amount of energy colonies can use for growth should decrease as they become bigger (Hall & Hughes 1996). This, in turn, means that larger colonies are likely to have more resources available for reproduction (Hall & Hughes 1996) and repair than do smaller colonies.

Mortality is highly dependent on size of colony. Most of the colonies that died were small (< 5 cm²). No colonies larger than 20 cm² died during the period of this study. The greatest mortality occurred among single polyp recruits (up to 35% died in a year).
Some colonies in all size classes shrank each year and large colonies (> 20 cm²) were much more likely to shrink than were very small colonies (1 cm²). In contrast, only colonies larger than 5 cm² had injuries (lesions) on their surfaces. Most injuries occurred on colonies larger than 20 cm². The absence of injuries on small colonies is probably because if small colonies are damaged they either die or shrink (due to the injuries inevitably including some of their edge). The fact that no large colonies died during this study suggests that large colonies do not die unless they suffer extensive partial mortality and shrink, thereby increasing their risk of death. Nonetheless, the death of large colonies will, most likely, be very rare.

If the rates of mortality are purely a matter of the amount of space that colonies occupy (their size) and the probability of damage, then the total mortality per unit area should be equivalent across size-classes. In contrast, the data showed that colonies larger than 100 cm² had less damage per unit area than did smaller colonies. This was not because larger colonies are better at recovering from damage (as shown in the manipulative experiments, Chapter 5), but rather because they are less likely (per unit area) to be damaged in the first place. These results suggest that very large colonies are better at maintaining space than are smaller colonies and that their larger size may act as some kind of ‘protection’ from some types of disturbances. Alternatively, these results could represent the fact that colonies can only become large if they occur in a place that has little disturbance.

Some polyps were degenerating (Appendix IV), probably due to senescence. If colonies are able to recover quickly from partial mortality (i.e. lesions < 1 cm², see Chapter 5) the polyps in a colony would be different ages. Thus it is unlikely that they would all senesce at the same time. This, in turn, could
increase the longevity of larger colonies and explain how very large colonies with a low rate of regular damage could potentially attain immortality.

*P. versipora* has a broadcast spawning mode of reproduction, is gonochoric, has a seasonal pattern of gametogenesis and is likely to have repeated spawning events each summer (Appendix IV). In addition to reproducing sexually, colonies have the potential to reproduce asexually; but, the relative contribution of each of these modes of reproduction to the population is not known.

In *P. versipora*, the smallest size at which colonies first become reproductive is the size which also has greatly increased survivorship (5 < 10 cm²). Similar findings were reported for the coral *Manicina areolata* (Johnson 1992), suggesting that this relationship may be widespread among corals. This relationship may represent a change in the energetics of colonies whereby colonies larger than 5 cm² are more likely to have the resources required to recover from partial mortality. If they reach this size without having been damaged, they will have resources available to start developing gonads.

The smallest size at which colonies can reproduce can be fairly readily measured, requiring little sampling effort, and could easily be used to predict quickly the size at which a colony is likely to have greatly increased survivorship. This information, combined with measures of the size-frequency distribution of colonies, could then be used to compare the dynamics of different populations.

The size at which colonies first become reproductive was recorded as the smallest size of a fecund colony in the population. The actual size at which
colonies first begin to reproduce is, however, likely to vary considerably between colonies. Therefore, in studies of the reproductive biology of colonies, it may be more useful to estimate the size at which colonies are most likely to be fecund. In *P. versipora*, the greatest fecundity (i.e. the largest percentage of colonies containing gonads) was recorded for colonies larger than 120 cm$^2$; more than 55% of these colonies were fecund. These results complement the rates of linear growth and partial mortality measured for very large colonies (> 100 cm$^2$), suggesting that these very large colonies were much more likely than are smaller colonies to have resources available for reproduction.

Fission of colonies was rare. Only three instances of fission were observed in the surveys of fixed quadrats and these occurred in colonies that had extensive dead areas (Chapter 3). This small number of fissions is probably because *P. versipora* has a hard skeleton and cannot readily divide and split the way some soft coral and ascidian species do. Thus, in hard corals, fission occurs only after extensive partial mortality.

Jackson (1979) proposed that colonies with a sheet-like morphology will have good regenerative abilities. Consistent with this model, *P. versipora* was shown to have very good regenerative abilities. More than 50% of new lesions had regenerated 4 months after colonies were damaged and more than 75% of new lesions had regenerated by 8 months (Chapter 5).

Because large colonies have more polyps and therefore more resources in total available for repair, I proposed that large colonies would replace lost area faster and more successfully than would small colonies. Contrary to this hypothesis, small colonies regenerated damaged areas faster and more completely than did large colonies (Chapter 5). These unexpected results are
probably a consequence of doing the experiments in summer, when large colonies are likely to be undergoing gametogenesis, so are least likely to have resources available for repair.

Variation among colonies in the rates at which different life-history processes occur may be due to the ages of colonies, their sizes, their past history of disturbance, or genetic and environmental differences among colonies. Much of the variation among colonies in *P. versipora* is due to their size. Therefore, my results are generally consistent with the findings of previous studies on other colonial marine species (Hughes 1984; Babcock 1991; Johnson 1992; Bythell *et al.* 1993) and show that size is a good way of categorising the variation among colonies in these populations.

In Sydney Harbour, grazing is the most likely cause of mortality in *P. versipora* (see Chapter 6.3), although sedimentation and the activities of bioeroders also cause damage to colonies (Chapter 5.2). Most grazing on temperate reefs is due to the activities of bottom-dwelling urchins (reviewed by Jones & Andrew 1990) and hence occurs across the surface of the substratum. Therefore, the small amount of damage to very large colonies is likely to be because these colonies are grazed less often than are smaller colonies.

If the energetics of colonies are directly related to the rates at which colonies are damaged and thus the rates of grazing they have been exposed to, then the sizes at which the biology of colonies are likely to change is also likely to vary among sites, due to variation in grazing intensity (for example). A recent study by Bak & Meesters (1998) showed that in comparisons among 14 species of coral the geometric mean size of colonies in populations was species-specific and conserved among four sites (although they did not give
any *a priori* reason why the mean sizes of colonies would be expected to vary). Thus, this model needs further investigation.

In future studies, it would be interesting to investigate the extent to which the relationships measured between size and the biology of colonies are conserved among a range of sites where corals are likely to be exposed to different environmental conditions, including different regimes of disturbance. The very wide geographic range of *P. versipora* make it a good species to use for these studies.

6.2 GROWTH DYNAMICS OF COLONIES

Colonies in the population ranged from smaller than 0.8 mm² to larger than 1500 cm². Most are, however, smaller than 10 cm² (Figure 2.4). Although there are few very large colonies (> 100 cm²), they constitute more than 50% of the area covered by the population (Figure 2.4). Therefore, they make a much larger contribution to the total growth and reproductive output of the population than do smaller colonies.

The fact that the rates of linear extension are independent of size suggests that the growth of colonies with a sheet-like morphology is limited by the rates of growth and development of polyps at the edge of colonies. These results also suggest that the growth of polyps at the edges of colonies is not supplemented with resources from other parts of the colony. If it were, large colonies would be expected to have faster rates of linear extension than do small colonies.
This constraint on the growth of colonies probably occurs because new polyps first have to grow to attain their maximal size (about 3 mm diameter, see Appendix I) before they bud to create more new polyps at the periphery of the colony and then finally start to develop gonad. In other words, a new row of polyps at the edge of a colony cannot form until after the polyps in the previous row have attained their maximal size. The fact that polyps at the very edges of colonies are often smaller than other polyps and are generally non-reproductive provides further evidence for this pattern of growth (Appendix IV).

These patterns of development of polyps, combined with the shape of small colonies, may explain why colonies do not become fecund until after they reach a certain size. In *P. versipora*, single polyp recruits must grow a total of about 8 polyps to grow from size class I (< 1 cm²) into size class II (1 < 5 cm²); the additional 7 polyps required to achieve this transition bud off the first polyp and encircle it. To complete the next row of polyps about 14 polyps then bud off the inner row of 7 polyps. Therefore, the amount of somatic growth required for the linear extension of the colony has changed from 7 polyps per polyp for colonies in size class I, to about 2 polyps per polyp for colonies in size class II. Colonies of 5 cm² only have about 4 rows of polyps and a total of about 30 polyps. Hence, based purely on the allometric evidence, polyps are not expected to become fecund until colonies grow large enough so that polyps have the opportunity to build-up the energetic resources that they need to grow, divide and then develop gonad.

In this project, I concentrated on the biological differences between colonies smaller than 20 cm² and colonies larger than 20 cm². Colonies larger than 20 cm² include colonies as large as 1 500 cm². Therefore, if the sizes of colonies
in a population are to be fully understood, the growth of very large colonies also needs to be considered.

The fact that only a small proportion of colonies in the population are larger than 100 cm\(^2\) suggests that recruits rarely grow to attain these very large sizes, unless they amalgamate with other colonies (Figure 2.2). Yet growth and mortality data suggest that a large proportion of colonies could (eventually) grow to be larger than 100 cm\(^2\) (Appendix III). This begs the question, what limits colony growth? Careful consideration of the growth of colonies explains this apparent anomaly.

The rates of partial mortality in the population (on an area cover basis) were estimated to be about 6% to 8% per annum and most of this mortality occurred on colonies that were larger than 20 cm\(^2\). Partial mortality on some colonies was extensive, with one colony losing 115 cm\(^2\).

Approximately 10% of colonies at Fairlight lost between 10% and 80% of their area each year. If a 101 cm\(^2\) colony shrinks and loses 80% of its area, it is still a large colony (> 20 cm\(^2\)). Assuming the colony has an average rate of growth (increase in radius of 2 mm pa) it will take about 15 years for it to regain its former size. In the much less likely event that a 1 000 cm\(^2\) colony loses 80% of its area, to become 200 cm\(^2\), then at an average rate of linear growth it would take more than 50 years for the colony to grow to its former size again, over which time the colony is likely to experience more partial mortality.

As a further example, if colonies in a 20 to 40 cm\(^2\) size interval have a 10% likelihood of damage each year and at an average rate of growth it takes 5 years for a 20 cm\(^2\) colony to grow out of this size interval, then the actual cumulative probability of damage to the colony is 50%. Depending on the
extent of any damage, it will take that much longer again before the colony grows out of the size interval (assuming it does not incur still more damage). Thus, the likelihood of large colonies being damaged and having their rates of growth impeded is actually quite large when the slow rates at which normal growth occurs are factored into the equation.

These examples show that partial mortality is likely to represent a significant constraint on the maximum size that colonies attain and this in turn may explain why so few colonies in the population are very large.

These patterns of growth show that answering a simple question such as whether it will be of less impact on the population to collect 100 cm$^2$ of coral by sampling of 10 to 20 small to medium colonies, a whole very large colony, or parts of a number of large colonies, is more complex than it at first appears.

Growth and mortality have different temporal scales, in that growth is continuous and mortality (injury or death) occurs as random, discrete events. The total new area of coral gained in the fixed quadrats at Fairlight over two years was less than half the area of the largest colony. *P. versipora*, like most other populations of corals, loses more tissue from partial mortality than from colonies dying (Hughes *et al.* 1992); hence the population will be limited by rates of partial mortality. Thus, the area gained by the continuous growth of colonies could quickly be lost from the population by sporadic instances of extensive injury and the rare deaths of large colonies.

In short, these results suggest that colonies do not grow indeterminately, but rather they grow to a size at which they can replace themselves, namely the
size at which the area of new growth is equivalent to the area injured (on average).

6.3 PATCHY DISTRIBUTION OF COLONIES

At local sites *P. versipora* colonies have a patchy distribution. The reduced rates of damage to much larger colonies (> 100 cm²) suggest that there may be advantages for colonies that occur in aggregations. For example, aggregations of colonies all very near each other may act as 'pseudo-large' colonies and hence, like very large colonies, have reduced rates of mortality. Thus, small colonies that are in aggregations (patches) may have greater survivorship than do small colonies that are distant and isolated from other colonies.

More than 45% of *P. versipora* in Sydney Harbour recruit within 2 cm of their nearest neighbouring colony. As a consequence, many colonies grow into contact and amalgamate with their neighbours. About 30% of colonies that grow into contact fuse. Colonies that join amalgamations become bigger and therefore, increase their rates of survivorship. If the amalgamation is very large, they will also reduce their rates of partial mortality.

For colonies composed of multiple, formerly separate, colonies that have coalesced, the more colonies amalgamated into the discrete colony, the more the ratio of the perimeter to the surface area is reduced for each coral in the amalgamation, to the extent that some corals may not have any of their edge at the periphery of the discrete colony formed. Although, the growth of corals located more centrally in these colonies will be limited, the trade-off is
that they are likely to have great survivorship, little damage, and potentially great fecundity per polyp.

The dynamics of aggregations or ‘patches’ are generally linked to changes in the density of organisms (Shorrocks & Swingland 1990). In populations of organisms that form encrusting colonies, changes in density can be measured as changes in area. Consequently, as the area of the Sydney Harbour population of *P. versipora* is predominantly contributed by larger colonies, the short-term dynamics of patches should be strongly correlated with changes in the cover of large colonies in the patch. Therefore, patches with a large area of coral would be expected to have reduced rates of partial mortality.

*P. versipora* mostly occurs in ‘barrens’ habitats at sites in Sydney Harbour. These habitats are likely to represent fairly hostile environments to solitary organisms, because they are characterised as being intensively grazed by urchins causing great mortality for the organisms living in them (reviewed by Jones & Andrew 1990). The ability of colony-forming organisms to recover from partial mortality is thought to enable them to exploit highly disturbed habitats, such as ‘barrens’, where solitary sessile organisms are unlikely to be able to survive (Jackson 1977; Buss 1979).

Within the barrens habitat *P. versipora* appears to have ample space for the population to grow. Colonies occupy only a small proportion of the available space (both inside and outside patches) (Plate 2.1). The percentage cover of coral in patches ranges from 2 to 76% and most patches have less than 30% cover, suggesting that the net growth of colonies in patches is limited. Consistent with this model, surveys of fixed quadrats showed that quadrats with more than 10% cover are more likely to lose some of their coral area.
than patches with less than 10% cover (Chapter 3). Thus, the size of patches and density of coral within patches are limited by mortality processes.

Jackson (1977) proposed that the abundance of coral represents the patterns of grazing. He proposed that, in habitats where there are many grazers, growth of macroalgae will be limited because the algae will be preferentially grazed. So, corals will grow without having to compete with macroalgae for space. In contrast, where there are very large densities of grazers, corals and algae will both be grazed, so the growth and recruitment of corals and algae, will be limited.

Around Sydney, not all places that have a barrens habitat have aggregations of colonies. One possible explanation for this is that grazing is more intense in some areas of the barrens than in other areas. The rates of grazing over the reef are probably related to the structure of the reef, in that places where recruitment is limited (i.e. where colonies do not form aggregations) may have many crevices into which urchins can retreat and thus, very high urchin densities and rates of grazing. In contrast, patches of coral could represent “spatial refuges”, in that they are places that are less frequently grazed, perhaps because there are fewer crevices nearby (within the grazing range of urchins). These models were not tested in my studies, although similar models were investigated by Andrew (1993) and Andrew & Underwood (1993). The absence of successful recruitment by P. versipora outside patches and the little mortality of recruits inside patches (less than 35%, which is small for a marine invertebrate), suggests that the intensity of grazing may vary across the reef.

If the distribution of patches reflects the distribution of urchins and hence, the distribution of crevices where urchins live, then the fact that crevices
are permanent structures in the sandstone substratum suggests that the rates of grazing over any given area of the reef will be similar from year to year. Consistent with this model, almost all the patches surveyed at each site (data taken from surveys described in Chapter 2.4) contained large/old (> 70 cm²) and small/young colonies (< 5 cm²). These data show that the turnover of patches is slow and that patches are likely to be maintained in the population for a very long time. Jackson (1985) proposed the model that colony-forming organisms predominate on subtidal, physically stable and/or long-lived hard substrata. This model appears to be true of P. versipora in that the old age of patches (presence of large colonies) suggests that the patchy distribution of P. versipora in Sydney Harbour does not vary much over time. These patches are not maintained by the asexual offspring of a once successful clone (as shown by his compatibility studies in Chapter 4), but are formed (at least to some extent) as a result of multiple recruitment events from larvae that are likely to have been dispersed from distant locations (Appendix IV).

The models that patches may act as ‘pseudo-large colonies’ and have reduced rates of mortality, yet that patches are also more likely to lose some of their area if the cover of coral is more than 10%, seem paradoxical and suggest that the advantages of being in an aggregation are complex. One explanation may be that, although patches may have reduced rates of grazing compared to non-patches, the rates of grazing may be fixed for each patch (e.g. due to the proximity of crevices) and hence, the maximal cover of coral in a patch constrained. Thus, as proposed for very large colonies, patches with a large cover of coral (> 30%) will only form in places that have a history of little disturbance.
The sizes of colonies in the *P. versipora* population in Sydney Harbour, varied temporally and spatially due to variation in the proportion of small colonies (< 5 cm²). The number of small colonies is a consequence of the number of new recruits arriving in the population each year, how quickly they grow into the next size class or are amalgamated into larger colonies, and their rates of mortality.

Variation between years in the rates of recruitment are not evident in the larger sizes due to the highly variable rates of growth and partial mortality. The fast rate at which colonies in the population grow into contact and amalgamate with neighbouring colonies also reduces the affects of inter-annual variation in recruitment in larger colonies. These population processes all act to decouple the relationship between the age and size of colonies (Hughes & Connell 1987). The older a colony, the greater is the range of sizes the colony could attain. The number of colonies in the population that are able to grow to become large (> 20 cm²) is limited by the rates of partial mortality. Partial mortality also limits the maximal size of colonies in the population and hence the variation of sizes of colonies.
6.5 FUTURE STUDIES

a) Implications of Size

It would be interesting to investigate the processes that lead to the relationships between size and rates of partial mortality of colonies (discussed in Chapter 6.2). Two models could be used to explain this relationship, both of which may be true. The first is that very large colonies are less likely to be damaged because their size acts as some kind of 'deterrent' (Model 1). The second is that very large colonies are less likely to be damaged because colonies only grow to become large if they occur in places that have little disturbance (Model 2).

These models may also apply at the level of patches, in that patches with a large cover of coral may either act as a 'deterrent' to some kinds of disturbances and/or may occur only in places that have a history of little disturbance.

Very large colonies may not be subject to some kinds of partial mortality because the perimeter-to-surface-area ratio of these very large colonies is small and many types of disturbance occur at, or across, the periphery of colonies. Alternatively, large colonies may release more allelochemicals into their surrounding environment and hence be avoided by grazers. The release of allelochemicals is thought to deter grazers on tropical reefs (Coll & Sammarco 1988; Aceret et al. 1995).

These models could be investigated in experiments in which the densities of grazers are controlled and the rates of damage to colonies that occupy space in different ways compared. These experiments could be done using artificial
patches set up in sub-tidal area away from the sandstone reef, on to which colonies of different sizes or shapes are transplanted. The number of crevices around the artificial patches and the number of urchins introduced to the patches could then be used to alter the rates of grazing on these artificial patches.

The following hypotheses could be tested in such experiments using *P. versipora*:

To investigate Model 1:

H1) That, in artificial patches, very large colonies (> 100 cm²) are injured less (per unit area) than smaller colonies

H2) That, in artificial patches, very large colonies (120 cm²) with a large ratio of perimeter to area (e.g. long thin oblong or star-shaped colonies) have more injuries than do very large colonies (120 cm²) with a small ratio of perimeter to area (e.g. circular colonies).

To investigate Model 2:

H3) That colonies of different sizes have the same rates of damage (per unit area) in artificial patches

H4) That rates of damage on colonies of different sizes decrease at the same rate (per unit area) as the density of urchins is decreased

Further hypotheses comparing the rates of growth and fecundity of colonies of different sizes exposed to different rates of grazing could also be derived to investigate Models 1 and 2.
b) **Advantages in amalgamating**

It would be interesting to extend the studies I began on how the biology of small colonies changes after they have been incorporated into large colonies. In my studies, I compared the rates at which these different types of small colonies repair their injuries (Chapter 5). Future studies could investigate other changes in their biology, such as whether small colonies in amalgamations become fecund at a smaller size and/or have much greater survivorship than small colonies that remain independent of other colonies.

The results from my studies of the regenerative abilities of different types of colonies showed that small colonies in amalgamations were more like large colonies than like independent small colonies. The model I proposed to explain this finding was that the energetics of small colonies that join amalgamations change, due to the dramatic change in their perimeter-to-surface-area ratios (Model 3). It was also proposed that the energetics of colonies that are in amalgamations and fuse will change because resources can be shared between fused colonies (Model 4).

Model 3 could be investigated by comparing the energetics of colonies of the same size that have different perimeter to surface area ratios (i.e. are of different shapes). This could be done by using their rates of fecundity, growth and survivorship as indices for their energetics. Thus, the hypothesis that could be tested would be:

H5) That colonies with a large ratio of perimeter to surface area are less fecund and survive less well than colonies with a small ratio.
The effects of shape on growth are likely to depend on the size of the colonies used in experiments. If *P. versipora* from Sydney Harbour were used, colonies of 5, 10 and 20 cm² would be the most appropriate to investigate this model, because colonies of 5 cm² and 20 cm² have the greatest changes in their biology (Chapter 3).

c) Size as a species characteristic - variation among populations

These studies would involve the investigation of two models: a) that differences in the size-structure of populations represent differences in the energetics of colonies in these populations; and b) that the size at which colonies are first fecund is the same size at which they have dramatically increased rates of survivorship, and thus represents a fundamental change in the energetics of individual colonies of this size in a population.

If these relationships are general, they could be used to compare populations, and identify differences among the histories of populations (i.e. differences between sites) and/or of changes in populations (i.e. differences over time). Thus, the sizes of colonies when they are first reproductive could be used to provide fast measures of the dynamics of populations and be useful in the management of populations of modular marine invertebrates (discussed in Chapter 3.9.2). More studies are needed across a broad range of habitats and species to test the generality of these relationships. The wide geographic range and consequent diversity of habitats in which populations of *P. versipora* are found, suggest that *P. versipora* would be a good species to ascertain the extent to which the effect of colony size is conserved within a species so that the potential usefulness of such measurements could be established.
d) Are size and morphology enough to predict the biology of colonies?

Jackson (1979) proposed a series of models about how the biology of colonies of different sizes changes and proposed that these changes were interrelated with the morphology of colonies. Some of these models were investigated in my studies on *P. versipora*. One issue Jackson (1979) did not address is the issue of whether or not hard- and soft-bodied colony-forming organisms have different mechanisms for dealing with disturbances. Thus, the implications of size for sheet-like colonies may be different between soft- and hard-bodied species. For example, ascidians and some soft corals can split fairly readily. Some species even have the ability to move away from the parent colony and thus disperse locally (Stocker 1991). In contrast, hard colonies are limited to the location to which they recruited. Therefore, it would be interesting to investigate the models I have proposed for future studies using both hard- and soft-bodied colony-forming species.

e) Final Summation

Large and small colonies of *P. versipora* differ in many aspects of their biology. As a result, the area covered by a population is limited by processes that affect large colonies, whereas the dynamics of the population (turn-over of colonies) is controlled by recruitment and by processes that affect small colonies. The maximal size of colonies in a population is likely to be constrained by the rates at which colonies are injured, due to energy being diverted away from growth towards repair.

It is difficult to compare the variables measured in this study on a temperate coral with the variables measured in studies on tropical corals. The huge
diversity of tropical species and the array of different habitats that exist in tropical reef environments make the comparisons difficult.

Studies by Hughes (1984) concluded that the population of the coral Agaricia agaricites in the Caribbean may be regulated by larval input, recurring disturbance and density-dependent interactions. This is also likely to be true for a temperate population of P. versipora and suggests that generalities about the population biology of corals can be made across temperate and tropical habitats.

Furthermore, the implications of size of a colony will not apply only to corals, but are likely to apply across genera of different colony-forming species. Thus, my findings on P. versipora and models I have proposed for future studies are likely also to be relevant to tropical corals and other colony-forming species with a sheet-like morphology.
References


APPENDIX I: Polyp Size and Polyp Density

Polyps are the building blocks of colonies, and unlike colonies which generally grow to an indeterminate size, the size of polyps is thought to be determinate. Most coral growth is due to colonies increasing the number of polyps they contain, therefore, colony size and polyp number should be strongly correlated. However, the sizes of polyps can actually vary significantly between colonies within a species, due to colonies experiencing different environmental conditions or due to genetic differences (Stroemgren 1987).

Therefore, I wanted to measure the sizes and densities of polyps on different colonies to find out how conserved polyp size and polyp density are in P. versipora, and thus, the extent to which surface area measurements are representative of the number of polyps a colony has. Polyp size and polyp density were compared between colonies of different sizes and different morphs, and within different parts of large colonies, at each of my study sites.

1.1 Methods

The sizes and densities of polyps in colonies at Fairlight and Green Point were measured and compared between colonies of different sizes. The colonies compared in this study were in two different size classes only: a) small/medium colonies (< 10 cm²), and b) large colonies (>> 20 cm²).

At each site 6 small/medium colonies and 6 large colonies were sampled, and in each size class three of the colonies were of the green colour morph and three were of the blue colour morph. For large colonies, intra-colony variation in
polyp size was also measured, using photographs taken at both the centre and the edge of large colonies (one or two exposures needed depending on the size of the colony).

The surfaces of colonies were gently touched to retract the polyps, and each colony photographed using a Nikonos V underwater camera and Nikonos 103 strobe, with an Aquasea 3:1 extension tube attached to a 35 mm lens, and the camera aperture at 22. Fujichrome Sensia 100 ISO slide film was used. As a scale, a washer of known dimensions was placed on the surface of the colony being photographed, in the same plane as the polyps that were to be measured.

The sizes of the polyps were measured using the Kontron Digital Image Analyser at the Electron Microscope Unit, University of Sydney. Each photographic slide was placed on a light box and projected through a video camera on to a computer screen, to give a digital image of the colony. The digital image was calibrated to the known size of the washer. The sizes of individual polyps were measured by tracing around the edge of a corallite on the digital image, and the computer then calculated the area inside the shape drawn. Six polyps were measured on each of the small colonies, and for the large colonies six polyps were measured at the edge of the colony and another six polyps were measured in the centre of the colony. Only the largest polyps in the colony were measured, as I was in essence wanting to determine whether or not polyp size is determinate in that polyps have a maximum, conserved, size.

The density of polyps was also measured using the Kontron Image Analyser. A digital square quadrat of 3 cm² (calibrated to the real size of the coral image) was used to determine the density of polyps in the colony. Polyps on two perpendicular sides of the quadrat were counted, but polyps touching the other two sides were not. Only one quadrat could be sampled on each of the
small/medium colonies (due to their small size). However, for large colonies, four quadrats were sampled toward the centre of the colony. The densities of polyps at the edges of large colonies were also measured although, on many slides, there was not enough of the colony edge in the frame to sample four replicate quadrats.

1.2 Results

The results of the measurements of polyps sizes for colonies of different types are shown in Figure I.1. Analysis of the data showed that there was a four way interaction between the factors in the analysis, hence it was impossible to interpret the results for the two and three way interactions and the main effects (Four way ANOVA, $F = 64.5$, $p < 0.0001$). A Student-Newman-Keuls test found significant differences at the colony level in 7 of 8 comparisons, suggesting that a large proportion of the variation measured was attributable to differences between colonies. A summary of the results from the SNK tests is given in Table I.1. Overall, colonies at Fairlight tended to have larger polyps than colonies at Green Point, and small/medium colonies tended to have larger polyps than large colonies, with the effect of colony size being stronger at Fairlight than Green Point. The results of comparisons between colonies of different colour morphs show an inconsistent pattern. In three sets of comparisons the polyps of green colonies were larger than the polyps of blue colonies, and in three other comparisons the reverse was true. This suggests that the effect of colony morph is random, and that the differences measured are most likely attributable to other differences between colonies.
Figure I.1: The mean area of polyps on different types of colonies at
a) Fairlight, and b) Green Point.

On the x-axis: S = small/medium colonies, and L = large colonies, g = colonies of the
green morph (white bars), b = colonies of the blue morph (shaded bars). The areas
of six large polyps on three replicate colonies of each type (1, 2 and 3) were
measured. Error bars represent standard deviations.
a) Fairlight

![Bar chart for Fairlight showing polyp size (mm²) for different colony types.](image)

b) Green Pt

![Bar chart for Green Pt showing polyp size (mm²) for different colony types.](image)
There was no significant difference between the sizes of polyps at the centre and edges of large colonies (Binomial test of data about a constrained regression with the Y-intercept set at zero, \( p = 0.613, k \leq 6 \)) (Figure I.2).

The analysis to compare the densities of polyps of different sizes was limited due to the available data being very unbalanced, with few replicates for some comparisons. Therefore, the data were analysed as three separate analyses. The polyp size data suggested that the greatest difference between sites occurred between the small/medium colonies (Figure I.1). Therefore, in the first analysis, the density of polyps on small/medium colonies of each morph was compared between sites. Again, from the polyp size data, the greatest difference between colonies of different size occurred at Fairlight (Figure I.1). Therefore, in the second analysis, the density of polyps on small/medium colonies was compared to the density of polyps on large colonies, for colonies of each morph, at Fairlight. Lastly, as the analyses on polyp size attributed most of the variability measured to differences between individual colonies (Table I.1), the density of polyps was compared within and between large colonies of different morphs at Fairlight.

Each of these comparisons was done using two factor ANOVA. All of the comparisons passed Cochran’s test at \( p < 0.01 \) (Table I.2).

The densities of polyps on small/medium colonies was significantly different between sites (\( p < 0.05 \)), but not between colonies of different colour morphs (Table I.2a).

At Fairlight, there were no significant differences in the densities of polyps between colonies of different sizes or between colonies of different morphs (Table I.2b).
Figure I.2: Constrained regression on the mean size of polyps at the centre of a large colony against the mean size of polyps at the edge of the large colony, at Fairlight and Green Point.
Table 1.1: Results of Student-Newman-Keuls test of comparisons in polyp size for different types of colonies

The SNK test was run on the results of a four factor ANOVA. Cochran’s test (C = 0.2455). The factors in the analysis were:
SITE (Fairlight (FRLT) and Green Point (GPT)) - orthogonal and random;
SIZE (small/medium (S) and large (L)) - orthogonal and fixed;
MORPH (green (G) and blue (B)) - orthogonal and fixed;
and COLONY (3 colonies) - orthogonal and random;
with 6 replicate polyps measured on each colony.

<table>
<thead>
<tr>
<th>FACTOR</th>
<th>COMPARISON</th>
<th>NUMBER SIGNIFICANT (P &lt; 0.05)</th>
<th>NUMBER NOT SIGNIFICANT</th>
</tr>
</thead>
<tbody>
<tr>
<td>COLONY</td>
<td>3 colonies</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>SITE</td>
<td>FRLT &gt; GPT</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>SITE</td>
<td>GPT &gt; FRLT</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>SIZE</td>
<td>FRLT S &gt; L</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>SIZE</td>
<td>FRLT L &gt; S</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>SIZE</td>
<td>GPT S &gt; L</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>SIZE</td>
<td>GPT L &gt; S</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>MORPH</td>
<td>FRLT G &gt; B</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>MORPH</td>
<td>FRLT B &gt; G</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>MORPH</td>
<td>GPT G &gt; B</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>MORPH</td>
<td>GPT B &gt; G</td>
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<td>2</td>
</tr>
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Table I.2 a: ANOVA on Polyp Density for Small/Medium Colonies of Different Morphs at Each Site

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>SITE</td>
<td>138.1</td>
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<td>138.1</td>
<td>7.21</td>
<td>0.0198</td>
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<tr>
<td>MORPH</td>
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<td>1</td>
<td>3.1</td>
<td>0.16</td>
<td>0.6962</td>
</tr>
<tr>
<td>SITE X MORPH</td>
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<td>3.1</td>
<td>0.16</td>
<td>0.6962</td>
</tr>
<tr>
<td>RESIDUAL</td>
<td>229.8</td>
<td>12</td>
<td>19.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>373.9</td>
<td>15</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table I.2 b: ANOVA on Polyp Density of Colonies of Different Sizes and Morphs at Fairlight

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>SIZE</td>
<td>26.5</td>
<td>1</td>
<td>26.5</td>
<td>1.03</td>
<td>0.3261</td>
</tr>
<tr>
<td>MORPH</td>
<td>2.5</td>
<td>1</td>
<td>2.5</td>
<td>0.10</td>
<td>0.7618</td>
</tr>
<tr>
<td>SIZE X MORPH</td>
<td>61.3</td>
<td>1</td>
<td>61.3</td>
<td>2.38</td>
<td>0.1427</td>
</tr>
<tr>
<td>RESIDUAL</td>
<td>412.4</td>
<td>16</td>
<td>25.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>502.6</td>
<td>19</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table I.2 c: ANOVA on Polyp Density of Large Colonies of Different Colour Morphs at Fairlight

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>MORPH</td>
<td>42.0</td>
<td>1</td>
<td>42.0</td>
<td>0.9</td>
<td>0.3911</td>
</tr>
<tr>
<td>COLONY</td>
<td>334.0</td>
<td>4</td>
<td>83.5</td>
<td>26.3</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>MORPH X COLONY</td>
<td>182.1</td>
<td>4</td>
<td>45.5</td>
<td>14.3</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>RESIDUAL</td>
<td>95.3</td>
<td>30</td>
<td>3.18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>653.4</td>
<td>39</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
However, the densities of polyps on large colonies at Fairlight, with 4 replicate measurements of density per colony, were significantly different between colonies (Table I.2c). An SNK test of the results found significant differences at the colony level, and colour morph appeared to have a significant, but inconsistent effect. This result is similar to the SNK test on polyp size (Table 3.1), and suggests that the apparently random pattern of significant differences measured between colonies of different morphs, was due to differences between colonies other than their colour morphs.

The mean density of polyps in 3 cm$^2$ (data for both sites combined) was 22.9 ± 4.63 on small/medium colonies (n = 21 colonies); 25.8 ± 7.53 in the centres of large colonies (n = 16 colonies); and 26.3 ± 5.86 at the edge of large colonies (n = 15 colonies). The overall mean density of polyps was 24.2 ± 6.1 polyps per 3 cm$^2$.

1.3 Conclusion

There were some weak relationships between the maximum size of polyps in a colony and the size of the colony, and the maximum size of polyps and where the colony was sampled from. However, there was no consistent relationship between polyp density and colony size or polyp density and colony morph. There was, however, a relationship between the density of polyps on small colonies and site, in that small colonies at Fairlight have lower densities of polyps than small colonies at Green Point.

Therefore, the number of polyps in a *P. versipora* colony from Sydney Harbour can be estimated from the area of a colony, using the conversion of 8.1 polyps per cm$^2$. 
APPENDIX II: Additional Population Statistics

Miscellaneous data obtained from surveys of fixed quadrats (Chapter 3.2), preliminary surveys of the population (Chapter 2.4), and surveys that measured the sizes of single polyp recruits and small corals in the field directly.
Figure II.1: Mean percentage coral cover in fixed quadrats at each sub-site, at
a) Fairlight, and b) Green Point.

There were 22 quadrats in each sub-site at Fairlight, and 11 quadrats in each sub-site at Green Point. Error bars represent standard deviations.
a) Fairlight 1996

![Graph showing coral cover for sub-sites A, B, and C in Fairlight 1996.](image)

b) Green Pt 1997

![Graph showing coral cover for sub-sites D, E, and F in Green Pt 1997.](image)
Table II.1: Summary of population processes measured at Fairlight and Green Point, in each year the fixed quadrats were surveyed.

The numbers in brackets are the number of discrete colonies remaining after colonies grew into contact with each other.
<table>
<thead>
<tr>
<th></th>
<th>Number of Colonies</th>
<th>Percentage of Colonies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of colonies that grew</td>
<td>135</td>
<td>149</td>
</tr>
<tr>
<td>Number of colonies that shrank</td>
<td>34</td>
<td>23</td>
</tr>
<tr>
<td>Number of colonies that grew into contact with a neighbouring colony</td>
<td>21 (5)</td>
<td>24 (10)</td>
</tr>
<tr>
<td>Number of fissions</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Number of new recruits</td>
<td>32</td>
<td>26</td>
</tr>
<tr>
<td>Number of whole colonies that died</td>
<td>16</td>
<td>14</td>
</tr>
<tr>
<td>Total number of whole colonies in survey at start</td>
<td>206</td>
<td>210</td>
</tr>
<tr>
<td></td>
<td>Total area of whole colonies at start of time interval (cm²)</td>
<td>Total area of coral lost due to whole colony mortality (cm²)</td>
</tr>
<tr>
<td>------------------</td>
<td>-------------------------------------------------------------</td>
<td>-------------------------------------------------------------</td>
</tr>
<tr>
<td>Fairlight 1996-1997</td>
<td>3082.60</td>
<td>44.71</td>
</tr>
<tr>
<td>Fairlight 1997-1998</td>
<td>3255.54</td>
<td>13.19</td>
</tr>
<tr>
<td>Green Pt 1997-1998</td>
<td>966.21</td>
<td>9.81</td>
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</table>

Table II.2: Total change in coral area in surveys of fixed quarats at each site, in each interval surveyed. (Data includes measures of whole colonies only).
Figure II.2: Regression of the number of polyps in a small coral versus the estimated area of the small coral at a) Fairlight (n = 37), and b) Green Point (n = 13). Data from measurements of small corals in the field.
a) Fairlight, 1995

\[ y = 11.086x + 8.694 \]
\[ r^2 = 0.8143 \]

b) Green Pt, 1995
Figure II.3: Length versus width measurements of colonies measured in surveys of the population in March 1994, at a) Fairlight (n = 340) and b) Green Point (n = 219).
a) Fairlight

![Graph showing the relationship between length and width for Fairlight samples. The line of best fit is given by the equation $y = 0.63x$ with a correlation coefficient $r^2 = 0.77$.]

b) Green Point

![Graph showing the relationship between length and width for Green Point samples. The line of best fit is given by the equation $y = 0.73x$ with a correlation coefficient $r^2 = 0.78$.]

Appendix III: Estimations of Colony Age for *P. versipora* Colonies of Different Sizes in Sydney Harbour

The estimates shown are for colonies at Fairlight and assume that, on average, colonies increase their radius by 2 mm per annum (see Chapter 3). Colonies at Green Point grow twice as fast, so are assumed to be half the age of similar sized colonies at Fairlight. These estimates are likely to be poor due to partial mortality, fusion and highly variable growth rates all acting to decouple the relationship between age and size in colony-forming invertebrates (Hughes & Connell 1987).

<table>
<thead>
<tr>
<th>Colony Area (cm²)</th>
<th>Estimated Radius (cm)</th>
<th>Estimated Age (Years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>0.4</td>
<td>0</td>
</tr>
<tr>
<td>1.1</td>
<td>0.6</td>
<td>1</td>
</tr>
<tr>
<td>2.0</td>
<td>0.8</td>
<td>2</td>
</tr>
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<td>3.1</td>
<td>1.0</td>
<td>3</td>
</tr>
<tr>
<td>4.5</td>
<td>1.2</td>
<td>4</td>
</tr>
<tr>
<td>6.2</td>
<td>1.4</td>
<td>5</td>
</tr>
<tr>
<td>8.0</td>
<td>1.6</td>
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<tr>
<td>12.6</td>
<td>2.0</td>
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<tr>
<td>15.2</td>
<td>2.2</td>
<td>9</td>
</tr>
<tr>
<td>18.1</td>
<td>2.4</td>
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</tr>
<tr>
<td>21.2</td>
<td>2.6</td>
<td>11</td>
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<td>24.6</td>
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<tr>
<td>1000</td>
<td>17.8</td>
<td>87</td>
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APPENDIX IV: Patterns and Processes of Reproduction

IV.1 INTRODUCTION

Scleractinian corals exhibit an array of reproductive strategies. Colonies can be either hermaphroditic or gonochoric. Fertilisation can be internal and larvae brooded, or colonies can broadcast gametes for external fertilisation and external larval development. Many species also have the capacity to reproduce asexually, through a variety of different processes.

Temperate corals can have brooding and broadcasting modes of development, and generally have a seasonal cycle of synchronised gametogenesis (Szmant-Froelich et al. 1980; Fadlallah 1982; Fadlallah & Pearse 1982; Tranter et al. 1982; Ward 1992; Harriott 1992; Harriott & Banks 1995).

*P. versipora* is a member of the Faviidae. The Faviidae are amongst the most abundant corals, second only to the Acroporidae. Most Faviidae species are widely distributed (Veron 1995), almost all are broadcast spawners (Fadlallah 1983), and most are hermaphrodites (Harrison 1985; Harrison & Wallace 1990).

Hermaphroditism and gonochorism are generally conserved within Families; thus, sexuality is considered to have a phylogenetic basis (Harrison 1985). Therefore, *P. versipora* was expected to be hermaphroditic. The modes of reproductive development (brooding or broadcasting) do not, however, show systematic trends and are not conserved within families of scleractinian corals (Harrison & Wallace 1990).
The objectives of this study were to describe the reproductive biology of *P. versipora*. Primarily, to establish whether or not *P. versipora* in Sydney Harbour is sexually reproductive, and the modes by which colonies can reproduce.

The aggregated distribution of colonies at local sites suggested that *P. versipora* was either a brooder and/or had profuse asexual reproduction; however, family level generalities (Harrison & Wallace 1990) suggested that *P. versipora* would be hermaphroditic, produce mature eggs of 300 to 500 μm diameter, and might have a broadcast spawning mode of reproduction. Therefore, I wanted to find out whether the reproductive development of *P. versipora* conforms with these predictions.

Temperate corals generally have a seasonal cycle of gametogenesis, and in many corals (tropical and temperate) the gametogenic cycles of females is generally longer than the male cycles, which results in (apparent) changes in the sex ratio of populations during the course of a year. Therefore, I wanted to investigate the timing of gametogenesis and spawning in *P. versipora* to determine if it also has a seasonal cycle of reproduction and a delay in the onset of gametogenesis between the sexes.
IV.2 OBSERVATIONS OF REPRODUCTION IN *P. VERSIPORA*

IV.2.1 Laboratory Observations of Gamete Release and Larval Development

Eggs freshly collected after separate spawning events in aquaria, were measured under a light microscope, using an eyepiece graticule, and found to range in diameter from 300 to 540 μm. The mean diameters of eggs spawned from two separate colonies were $460 \pm 40$ μm and $490 \pm 50$ μm ($n = 38$ and 40 eggs, respectively).

Eggs were white and appeared to contain zooxanthellae. The eggs also contained a small amount of the green pigment present in adult colonies of the green morph. Images of a spawned egg taken under a light microscope, and under a fluorescence microscope are shown in Plates IV.6 and IV.7. Eggs were released individually from the mouth of the polyp. The eggs were buoyant, and in the still water of an aquaria tank, aggregated at the surface.

Over the years, there have been a number of observations in the laboratory of males spawning, particularly in spring and summer, whereas the release of oocytes have been observed only a few times. Sometimes spawning by colonies seemed to be 'induced' as a result of incubating colonies in warm water, or by changing the ion/salt concentration of the water. These observations suggest that mature spermares are maintained or stored in colonies longer than mature oocytes. During spawning spermatazoa are released freely into the water column.

In a spawning event in which both male and female colonies spawned (January 1994), the eggs and sperm were collected and mixed. Some of these eggs were successfully fertilised and developed into actively swimming
larvae. The larvae were about 0.7 mm in length and survived in aquaria for up to 6 weeks. They contained zooxanthellae, were ciliated, and had an oral pore.

IV.2.2 Observations of Asexual Reproduction

*P. versipora*, like many corals, has the potential to reproduce asexually. New colonies can form by colony fission, as the result of partial colony mortality in the field (this is rare, Chapter 5). Abrasion, bioeroding, or predatory activities, can separate tissue fragments from the skeleton, from which new colonies could regenerate (as has been observed in laboratory studies).

Corals maintained in closed aquaria for some months have been found to have small white bundles rolling around in the bottom of the tanks. These bundles were initially mistaken for sexually produced planulae, but are now considered likely to be asexual propagules (Ritchie *et al.* 1995). These can settle and form a polyp-like bud within a week. These propagules do not seem to be produced when colonies are maintained in flow-through aquaria.

In the laboratory, corals that are dying sometimes exhibit 'polyp bail-out', when the tissue degenerates, retreating back into the polyps to form balls of tissue, which they later release. These 'polyp balls' can form after colonies have been maintained in extremely limiting conditions (for example: after a cold shock of 4°C followed by many months of prolonged darkness without aeration). Polyp balls had a longer development time than other types of asexual propagules observed in this species and very poor survivorship. When polyp balls recently released from a colony were returned to light conditions in an aerated aquaria, it took more than three months for one of
the buds to differentiate and develop into a polyp-like settler. The rest of the propagules (n > 50) did not differentiate, and eventually degenerated and died.

Asexual propagules were mostly 2 to 4 mm in diameter, which is more than three times the size of sexually produced larvae. As rates of mortality are strongly linked to size in corals, the larger size of asexual propagules may increase their rates of survivorship over sexually produced larvae. Further, because asexual propagules have limited motility and are negatively buoyant, they are unlikely to disperse far and are not at risk from mortality in the plankton, which could also increase their rates of survivorship compared to sexually produced larvae. The limited dispersal of asexual propagules means that they are expected to settle near parent colonies, thereby creating aggregated patterns of distribution, similar to the patterns of distribution found for *P. versipora* colonies in the field. However, the extent to which colonies in the field produce asexual propagules is not known, nor is it known whether these propagules are able to grow to form successful recruits in the field.

A review of the modes of asexual reproduction observed for *P. versipora* is given in Ritchie *et al.* (1995).
IV.3 Studies of Reproduction for P. versipora Colonies in the Field

In this study I wanted to definitively establish the modes and patterns of reproduction present in the Sydney Harbour population(s) of P. versipora. This study included sampling to investigate reproductive development in this species by determining whether there are: a) seasonal patterns in the presence or absence of gonad in colonies; b) seasonal patterns of gonad maturation; and c) whether the start and duration of the gametogenic cycle is different between the sexes.

IV.3.1 Methods

a) Study area and collection of samples

Colonies were sampled from sites at Fairlight (5 to 7 m depth) and Green Point (2 to 4 m depth) in Sydney Harbour, N.S.W., Australia. Samples were collected between October 1993 and March 1998.

Small pieces were broken off colonies using a hammer and chisel. Generally, six separate colonies were sampled at a time, three colonies of each morph. Only six colonies was sampled at each collection time to limit the effects of destructive sampling on this slow growing population. All of the colonies sampled appeared to be healthy (were brightly coloured and did not have areas of injury) and were large (> 20 cm²) as large colonies were thought to be most likely to be reproductively mature. Previous studies on corals have shown that small colonies and colonies recovering from partial mortality can be non-reproductive or have reduced fecundity (Rinkevich & Loya 1985; Van Veghel & Bak 1994; Hall & Hughes 1996; Hall 1997). Colonies were generally
not re-sampled, except for a few of the very large colonies which were re-
sampled in subsequent years.

Collecting times were random in that samples were collected when I was in
the field, and had time available to collect them. Consequently, more samples
were collected in summer than in winter. When time permitted, sampled
colonies were measured so that the area of the colony could be estimated,
using the formula for the area of an ellipse (Chapter 2.4).

b) Processing of Samples for Dissections

Methods for the fixation, decalcification and dehydration of tissues were

Directly after collection, coral samples were placed in 25 ml glass
scintillation vials containing 10% buffered formalin (15 to 20 ml) to fix coral
tissues. After a minimum of three days immersion in formalin, samples were
decalcified in 15 to 20 ml of 5% formic acid solution containing 5% formalin.
The formic acid solution was replaced with fresh solution every 24 hours,
until the coral skeleton had completely dissolved. Some pieces of coral
required more than six repeats of formic acid. Samples were then soaked in
salt-water overnight to wash away the acid. Finally, tissues were dehydrated
in a graded aqueous ethanol series of 30%, 50% and 70% (minimum of 15
minutes each). Samples were stored in 70% ethanol.

To determine whether colonies contained gonad, larger sized polyps were
excised from the tissue samples at least four rows in from the edge of the
colony, and dissected under a binocular microscope. Edge polyps were not
used, as these polyps were often small, and dissections had shown that the edge polyps of fecund colonies often did not contain gonad. For each sample two polyps were dissected. In 87% of the samples, the amount of gonad was similar between the two polyps sampled. Gonad was defined as male or female, and the stages of gametogenesis were simply defined as mature, immature, or no gonad. Mature females were defined as colonies that had oocytes that were > 300 μm diameter, as this was the size of the smallest oocytes measured that had been spawned in the laboratory. A colony was scored as ‘mature’ if it had any mature oocytes in either of the polyps dissected. Immature females had oocytes < 300 μm diameter. The distinction between mature and immature male colonies was more qualitative than the distinction made for females. Mature male gonad was recognised by the spermaries being thickened, whereas the spermaries were much less pronounced in males that were scored as ‘immature’. Some large, very mature males had spermaries that appeared granular.

c) Histology

i) To confirm the sex and maturity of gonad observed in dissections

Samples from colonies (n = 20) with the different types of gonad observed in the polyp dissections were processed in a Miles Scientific Tissue-Tek VIP Automatic Tissue Processor to dehydrate the tissues, and embedded in paraffin wax for sectioning at 25 μm. Mounted sections were stained using Ehrlich’s haematoxylin and eosin (Drury & Wallington 1980).
ii) Electron Microscopy

Samples of freshly spawned sperm (n = 5) were fixed in glutaraldehyde and embedded in Spurr's resin for observation under the transmission electron microscope (TEM). Similarly, embryos that had developed from eggs that had spawned 20 hours earlier were processed for observation under both a light microscope and TEM, to find out whether the zooxanthellae shown in Plates IV.6 and IV.7 were actually inside the eggs or whether they were adhering to the surface of the egg.

IV.3.2 Results

The polyp dissections confirmed observations that *P. versipora* is a gonochoric broadcast spawning coral. All of the polyps dissected that contained gonad, were a single sex - male or female. Within a colony, all polyps were found to be the same sex, although not all larger polyps were reproductive. There was no evidence to suggest that larvae are brooded. However, a single polyp, from a sample collected in February 1997, did contain what appeared to be an asexual propagule. This propagule had differentiated into a polyp-like form (Plate IV.12). It is assumed that this propagule was asexually produced as the histological sections of large oocytes (up to 500 μm diameter) all had a single nucleus and therefore, were not (multicellular) larvae. It is possible that the propagule was actually a recent settler that had been ingested by the colony. However, the propagule appeared to be free in the coral gastrovascular cavity, and had a piece of gastrodermal tissue attached to it, suggesting that it had been closely associated with the polyp. If it was being extracellularly digested by the
polyp, I would have expected to have found the propagule in the pharynx of the polyp.

a) **Identification of gonad types and structures**

The different types of gonad observed under the light microscope are shown in Plates IV.1 to IV.5.

The oocytes are surrounded by gastrodermis, which contains zooxanthellae. Plate V.1 shows what appears to be a single zooxanthellae being transferred from the gastrodermis to a large oocyte (although this could be an artefact of sectioning). Unfortunately, the egg has been sectioned quite thickly (25 μm), and the dense lipid droplets present in the ooplasm of the egg are similar in size, shape, and (after staining) colour to zooxanthellae, so it was not possible to determine whether there were other zooxanthellae already inside the egg.

Embryos fixed 20 hours after the (unfertilised) eggs were released from a colony, and observed under TEM, did not contain zooxanthellae. These embryos (n = 6 sampled) developed from eggs released from a coral that had been maintained in a closed aquarium. Therefore, it is likely that these artificial conditions induced the colony to spawn prematurely before the oocytes had been 'infected' with zooxanthellae. In contrast, the egg shown in Plates IV.6 and IV.7 was collected from a coral that had been maintained in flow through aquaria, in conditions more similar to what colonies experience in the wild.
Plate IV.1: Mature oocyte (Om) at the base of a gonadal packet

The ooplasm is full of lipid droplets. Zt: a single zooxanthella being transferred to the egg from the gastrodermis (G).

Plate IV.2: Small oocytes (Os) below a larger oocyte(Om) in a gonadal packet

The nutrients necessary for gonad development are transported via the trophonema (T). Mf: mesenterial filament.
gvc: gastrovascular cavity.
Plate IV.3: Gonad packets full of mature spermatozoa


Plate IV.4: Mature spermatozoa forming “fans” in mesentery

Plate IV.5: Germ cell (Gc), probably female, and sweeper tentacle (St) inside a *P. versipora* polyp

This sample was scored as containing ‘no gonad’ when observed under the stereo microscope.  
Plate IV.6: Light microscope view of a recently spawned egg

Zooxanthellae (z) can be seen, but it is not possible to determine whether the zooxanthellae are inside the egg or adhering to the outside of the egg.

Plate IV.7: Fluorescent microscope view of the same egg

Chlorophyll in zooxanthellae glows red. A green pigment is also present in the egg, which is likely to be the same pigment that occurs in corals of the green morph.
Plate IV.8: Transmission electron micrograph image of the edge of an embryo, 20 hours after the egg it developed from was released from a colony.

The surface of the embryo is covered in microvilli (Mv). There are many yolk/cortical granules (Y) near the surface of the embryo. Vacuoles near the surface of the egg suggests that the embryo is able to pinocytose nutrients from the water column (P). Cm: cell membranes.
Plate IV.9: TEM image from the centre of the embryo # 1

The centre of the embryo consists of many large cellular bodies. These may contain lipid/terpene molecules which act as sperm attractants or to deter predation. Vacuoles I, II and III appear to show the progressive stages of breakdown and release of these molecules from the cell bodies.
Cm: cell membranes.

Plate IV.10: TEM image from the centre of the embryo # 2

Large lipid terpene body (Ltb) contained within a single cell. It appears that the lipid is being transferred from the main vacuole into the cell cytoplasm, from where it is released from the cell as smaller granules (g). The embryo did not contain zooxanthellae. This may have been an artefact of laboratory conditions causing the premature release of gonad.
Cm: cell membrane.
Observations of embryos under TEM showed that the centre of the embryos were filled with dense cellular bodies (Plates IV.9 and IV.10). Similar structures were observed by Coll & Kelman (1997) in a study of eggs from the soft coral *Lobophytum crassum*. They hypothesised that these were lipid/terpene bound structures, and that eggs can contain two different types of terpenes, which are released from eggs and embryos to either deter predation or act as sperm attractants. A terpene that is a sperm-attractant has been chemically identified (Coll *et al.* 1995) and this terpene only occurs in eggs a few weeks prior to ovulation up until the embryos are five days old and does not occur in the tissues of adult colonies (Coll & Kelman 1997).

The surface of the *P. versipora* embryo is covered in microvilli and with numerous 'yolk' or 'cortical granules' just below the embryo's surface (Plate IV.7). The study by Coll & Kelman (1997) observed similar granules (as have a number of previous studies), and hypothesised that these granules migrate to the edge of the egg from where they release sperm-attractant terpenes into the water to aid fertilisation (Coll & Kelman 1997).

Unfortunately, the samples of spawned sperm observed under TEM had poorly fixed membranes and were heavily contaminated with bacteria. No intact spermatozoa were seen, although a single sperm capsule was found. This preliminary observation suggests that *P. versipora* spermatozoa have an ovoid nucleus, and that these sperm probably have a 'pear-shaped' morphology (Harrison & Wallace 1990). However, further observations are needed to confirm this very preliminary observation.
b) Results from polyp dissections

Of the 416 corals sampled between 1993 and 1998, 45% had polyps that contained gonad, and 6% had gonad in only one of the two polyps dissected.

In samples in which only one polyp contained gonad, there was no pattern of the gonad being of a particular sex, nor did these samples represent a set of smaller colonies. In the female colonies, the gonad was generally reduced (in number) to 1 or 2 oocytes in the fecund polyp, whereas in males the gonad did not appear to be reduced in the fecund polyp. In some samples, the absence of gonad in one polyp was probably attributable to polyp senescence, as they appeared to be degenerating.

Female colonies that contained mature gonad could have up to 80 eggs in a single larger sized polyp. However, most fecund female polyps contained less than 10 oocytes, and the oocytes were rarely all mature.

The data from the dissections for Fairlight and Green Point were combined and grouped into intervals of three months, from October 1994 to March 1998. These intervals were chosen as they fitted with local seasonal changes in seawater temperature and daylength and were April to June, July to September, October to December, and January to March.

The results from October 1994 to March 1998 show that there are annual cycles in the proportion of colonies that contain gonad in the population. The proportion of colonies containing gonad was lowest in the April to June interval of every year and highest in the October to December and January to March intervals (Figure IV.1).
Figure IV.1: Percentage of colonies containing gonad in intervals of three months from October 1994 to March 1998.

The data from samples collected at Fairlight and Green Point have been combined. Where, □: % colonies containing gonad, □: % colonies with no gonad. There were ≥ 10 colonies sampled in every interval (Total n = 398 colonies).
Concomitantly, there were seasonal patterns in the proportion of mature and immature gonad in the population. The largest proportion of mature gonad occurred in the October to December interval, and the largest proportion of immature gonad occurred in the April to June interval as did the largest proportion of colonies containing no gonad (Figure IV.2).

There was no delay in the start of gametogenesis in male colonies compared to female colonies. The proportion of female to male colonies in the population was similar in each of the time intervals (Figure IV.3).

The overall sex ratio for fecund colonies was 1.3 females : 1 male (n = 357). Within site, the sex ratio was not significantly different from a 1 : 1 ratio at Fairlight ($\chi^2 = 0.680$, 1 df, $p > 0.3$), but was significantly different at Green Point ($\chi^2 = 2.97$, 1 df, $p < 0.1$), (Table V.2a).

The proportion of mature and immature gonad measured in the population was similar at each site, and within each site these proportions were similar between colonies of different morphs (Table V.2b). At Fairlight the ratio of immature to mature gonad was 1 : 2.4 and at Green Point the ratio was 1 : 1.9.
Figure IV.2: Percentage of colonies containing mature and immature gonad at different times of the year, October 1994 to March 1998.

Data for samples from Fairlight and Green Point have been combined. Error bars represent standard deviations, (Total n = 398 colonies). Where, □ : % colonies with no gonad, ▼ : % colonies with immature gonad, ■ : % colonies with mature gonad.
Figure IV.3: Sex ratios of colonies at different times of the year, October 1994 to March 1998

The data for immature and mature colonies have been combined. Error bars represent standard deviations, (Total n = 398).
Where, ■ : % of colonies female, □ : % of colonies male, and ◊ : % of colonies with no gonad.
VI.4 DISCUSSION

*Plesiastrea versipora* has the potential to reproduce sexually and asexually. However, the relative contribution of each of these modes of reproduction to recruitment in the population, is not known.

VI.4.1 Sexual Reproduction in *P. versipora*

The fact that each colony contained gonad of only one sex and there was no correlation between sex and colony size (Chapter 3), provides good evidence of stable gonochorism in this coral (Figure 3.10 and Table 3.5).

Annual cycles in the proportion of colonies containing mature, immature and no gonad show seasonality, and the results suggest that *P. versipora* spawns more than once per year, with at least two spawning events occurring during spring and summer (October to March). It is not possible to determine whether this pattern is due to the same colonies spawning repeatedly, and/or whether colonies in the population spawn asynchronously. However, as *P. versipora* is gonochoric, at least some synchrony in spawning must occur between colonies if gametes are to be fertilised.

Female polyps often contain mature and immature oocytes simultaneously. This could be due to colonies having different rates of oocyte development in a single gametogenic cycle, or it could represent separate, overlapping gametogenic cycles. A few samples had polyps that were packed full of oocytes, all of which were mature, and therefore likely to be released in the same spawning event.
The fact that less than 50% of large, apparently healthy, colonies contain mature gonad in any given time interval provides further evidence to suggest that this population has repeated spawning events. Further, the fact that less than 63% of colonies were fecund in any given time interval suggests that a large proportion of adult colonies do not reproduce at all, each year. Only at a single sampling time were all six samples found to be fecund, and only four of those samples contained mature gonad. This lack of synchronicity in gametogenesis across the population again suggests that colonies do not all spawn at the same time.

Further studies are required to ascertain how many gametogenic cycles individual colonies have per year, and establish whether gametogenic cycles are distinct, or whether colonies have continuous gametogenesis with repeated partial shedding of mature gonad. This could be done by sampling the same colonies repeatedly through time, before and after spawning events.

Alternatively, synchronicity in the start of gametogenesis and timing of spawning may be limited to colonies that are near each other and hence, more synchronized within-patches than between-patches. For example, the coral Caryophyllia smithi achieves synchronized spawning due to the release of sperm acting as a stimulus for nearby female colonies to release their oocytes (Tranter et al. 1982). It would, therefore, be interesting to find out whether a similar mechanism to aid synchronicity occurs in P. versipora. To test this, colonies would need to be sampled at different spatial scales during summer (when colonies are likely to be reproductive) to ascertain whether colonies in the same patch are more likely to be at the same stage of gametogenesis than colonies sampled from other patches.
It is unlikely that *P. versipora* colonies spawn between April and June, as in this time interval less than 8% of colonies contained mature gonad. This small amount of mature gonad may represent ‘residual gonad’ left in the population at the end of the spawning season and maintained in the polyp until the next spawning season. Alternatively, it could represent continuous gametogenesis between years whereby the rates of development are slowed during winter and more rapid in summer when conditions are warmer and daylength is longer. In two of the four years sampled, there was a larger proportion of gonad in October to December than in January to March (Figure 2.1). In the two years in which there was more mature gonad earlier in the season, a larger proportion of colonies had gonad in the April to June interval of those years, than in other years.

If a gonochoric, broadcasting species with highly localised abundances is to maximise the probability of successful fertilisation, the population is expected to have a sex ratio of 1:1 (Williams 1975; Maynard-Smith 1978). *P. versipora* had a sex ratio of 1:1 at Fairlight, but had a significant deviation from this to a ratio of 1:1.5 at Green Point, where there were more female than male colonies (Table 2.1a). This deviation is unlikely to be enough to reduce the fertilisation success of the population, and depending on the spatial distribution of colonies of different sexes, could even enhance the rate of larva production at Green Point.

The proportion of mature and immature gonad measured in the population was similar between colonies from different sites. The ratio of immature to mature gonad was 1:2.4 at Fairlight, and 1:1.9 at Green Point. These data suggest that immature gonad becomes mature more quickly than mature gonad is spawned. However, these measures may also represent the combined effects of the pattern of gonad development in this species and the
scoring methods used in this study, in that many polyps contained both mature and immature gonad on the same mesentery (suggesting the colonies have multiple cycles of gametogenesis) and these were scored as 'mature' (see Appendix IV.3.1b).

VI.4.2 Asexual Reproduction in P. versipora

In clonal population biology, asexual reproduction is considered to be a means for colonising a favourable habitat and sexual reproduction is a means for dispersal between habitats (Williams 1975). However, in this study, asexual reproduction seemed to mostly occur when colonies were maintained in conditions that were likely to have been limiting.

Most of the instances of asexual propagation occurred when colonies were kept in closed aquaria. For example, corals maintained in deoxygenated water, and/or extended darkness, and/or exposed to low temperatures (4 °C) often had areas of tissue die-back and degeneration resulting in the eventual formation of polyp balls (Plate IV.11). Of the healthy colonies sampled from the field, 45% contained gonad, but only one colony had a polyp that contained what seemed to be an asexually produced propagule. This suggests that this type of asexual reproduction is rare. Further, the asexual propagules produced in aquaria were all either rounded or irregularly shaped and did not appear to be as well differentiated as the field propagule, which had more of a polyp-like form (Plate IV.12). This suggests that the kinds of asexual reproduction observed in the laboratory may be different (or even abnormal), as colonies in the field are never likely to experience the conditions that initiated asexual propagation in the laboratory. Further, the mortality rates of asexual propagules produced in the aquaria were very
high, suggesting that these forms of reproduction, are unlikely to contribute greatly to local recruitment.

The contribution of asexual reproduction to recruitment in the field population was not investigated, but could be estimated in genetic studies of the population. Asexual propagules like the one found in the field colony are more likely to recruit to the population than sexually produced larvae, due to their larger size and increased stage of development probably enabling them to grow into recruits much more quickly than sexually produced larvae. Further, as corals at Fairlight and Green Point occur in patches, often in discrete hollows or crevices amongst the rocks, unmotile asexual propagules are unlikely to be able to disperse more than a few metres from the parent colony. This means that they would not be at risk from predation in the plankton, and after being released from a parent colony would be able to settle, directly, in a favourable patch, which would also increase their likelihood of survival over sexually produced larvae.

*P. versipora* colonies may also reproduce asexually by tissue scission or abscission. In the laboratory, pieces of tissue were 'pinched-off' colonies using dissection scissors and these could then regenerate into polyps and grow to form new colonies. Similar processes could increase the rates of asexual propagation of *P. versipora*.

Partial mortality is commonly observed on colonies in the field, and occasionally colonies were observed that had bleached (turned white), yet no evidence of polyp bail-out on these colonies was seen. Polyp bail-out has, however, been observed in field *Seriatophora hystrix* (Sammarco 1982).
That asexual reproduction was common only when colonies were maintained in closed aquaria, in conditions unlikely to occur in the field, suggests that it is a rare phenomenon in the field and unlikely to contribute substantially to recruitment in the population, unless these propagules have very high rates of survivorship compared to sexually produces larvae. Genetic studies are needed to estimate the actual contribution sexual and asexual reproduction make to the population.

As only healthy corals were sampled in this study, it would be interesting to find out whether or not, colonies with extensive areas of partial mortality or that look to be degenerative are more likely to contain asexual propagules than healthy colonies. This could be done by sampling healthy and unhealthy colonies in the field during the reproductive season to compare the number of asexual propagules they contain. Alternatively, manipulative experiments could be done in which colonies are inflicted with different amounts of 'damage' and their fecundities and number of asexual propagules they contain, compared.

VI.4.3 Reproduction as a species characteristic in *P. versipora*

Many patterns of coral reproduction have been described in the literature. Generalities have been proposed relating different species of coral to their modes of reproduction from which predictions about the patterns of reproduction expected for *P. versipora* were made. Table IV.1 outlines the consistencies and inconsistencies in the reproductive biology of *P. versipora* with respect to these generalities.
Table IV.1: Consistencies and inconsistencies with what was expected for the reproductive biology of *P. versipora*, based on generalisations of scleractinian coral reproductive biology reviewed by Harrison & Wallace (1990).

**Consistencies**
- *P. versipora*, like most Faviidae, are broadcast spawners
- *P. versipora* have eggs that range in size from 300 to 540 μm diameter, this is consistent with the egg size of other species of Faviidae
- *P. versipora* like most gonochoric corals, have a seasonal pattern of gametogenesis
- *P. versipora* like most gonochoric corals, release gametes freely into the water column
- *P. versipora* like most broadcast spawning corals, have a seasonal pattern of gametogenesis
- *P. versipora*, like many species of coral, have a delay the onset of reproduction until colonies attain a certain size, (in *P. versipora* this size is 5 cm²)
- *P. versipora*, like most temperate corals, have an annual cycle of gametogenesis with marked seasonality
- *P. versipora*, like most species of coral, have smaller non-reproductive polyps at the margins of the colony
- *P. versipora* have the potential for asexual reproduction, as do almost all other species of coral

**Inconsistencies**
- *P. versipora* are gonochoric, whereas most other Faviidae are hermaphroditic
- The eggs of *P. versipora* are associated with zooxanthellae, whereas the eggs of most other broadcasting corals are not
- The larvae of *P. versipora* can are associated with zooxanthellae, whereas the larvae of most other broadcast spawning corals are not
- *P. versipora* do not have a delay in the onset of gametogenesis between the sexes, whereas most other species of coral start female gametogenesis a few months before male gametogenesis
- *P. versipora* do not appear to have the 'pear-shaped' sperm structure expected for gonochoric corals, but rather the 'ovoid' sperm structure expected for hermaphroditic corals (preliminary findings)
Some corals have been found to change their mode of reproduction at different latitudes. *Galaxea fascicularis, Goniastrea aspera* and *Heliofungia actiniformis* change from spawning to brooding modes of development nearer the equator, although there is some controversy surrounding these reports due to the difficulties in reliably identifying each of these species (reviewed by Harrison & Wallace 1990). This latitudinal change is unlikely to be a general rule, as both modes of development occur in temperate corals (van Woesik 1995; Ward 1992; Harriott 1992; Harriott & Banks 1995). As *P. versipora* occurs around the entire mainland coast of Australia, it would be interesting to investigate whether the modes of reproduction found in this study are conserved in other more distant populations, where the light and temperature regimes may be very different from Sydney Harbour.

Along the East Coast of Australia, there is a delay in spawning from early summer for corals on the GBR at 18° to 25° S, to late summer for corals at Lord Howe Island (31° S) (reviewed by Harrison & Wallace 1990). Therefore, it would also be interesting to compare the gametogenic cycles of *P. versipora* populations at different latitudes, to find out whether tropical colonies have more resources available to them, so reproduce year round.

Generally, gonochoric broadcast spawners have longer breeding periods and less tightly synchronised spawning events than their hermaphroditic counterparts. In some gonochoric corals only part of the population spawns during each event, and each colony can spawn on a number of occasions, resulting in a series of staggered spawning events during the reproductive season (Harrison & Wallace 1990).

Most species of coral have a delay in the onset of gametogenesis between the sexes, with female gametogenesis sometimes starting many months before
male gametogenesis begins (Harrison & Wallace 1990). This does not occur in
P. versipora. The proportion of colonies that were male or female was similar
in each of the intervals of three months (Figure IV.3), and it is unlikely that
a delay of less than three months is being masked as (from the raw data) both
male and female gonad were found to occur in samples throughout these
three month intervals.

The larvae reared in the laboratory contained algae, and had an oral pore
which could enable them to feed in the plankton. Planktotrophy and the
translocation of photosynthetic metabolites from algae would considerably
enhance the competency time and dispersal potential of P. versipora larvae.
Consistent with this, some of the larvae maintained in the laboratory
survived for up to six weeks, suggesting that they have the potential to
disperse long distances. Zooxanthellae inside larvae could play a role in the
phototaxic responses of larvae and be important in the selection of suitable
sites for settlement (Fadlallah 1983).
VI.5 SUMMARY OF FINDINGS FROM STUDIES ON REPRODUCTION

*P. versipora* has the potential for a mixed mode of reproduction using either sexually derived free swimming larvae or by propagating asexually through the release of asexual propagules and by colony fission. Genetic studies are needed to determine the relative contribution of each of these modes of reproduction to recruitment in the population.

*P. versipora* is gonochoric and there is no delay in the start of gametogenesis between male and female colonies. Gametogenesis is seasonal, probably with multiple spawning events over the summer months. Further studies are required to determine the exact timing of spawning in the population, and to establish whether spawning is fuelled by the same colonies spawning repeatedly, or whether there is a division between colonies in the timing of spawning across the population.
APPENDIX V: The Effect of Colour Morph on the Biology of Colonies

V.1 DISTRIBUTION OF COLONIES OF DIFFERENT COLOUR MORPHS

*P. versipora* occurs as green, blue and brown colour morphs. The green and blue colours arise due to the presence of pigments in the coral tissue, whereas, the brown colonies do not contain any blue or green pigment and the brown colour is directly due to the zooxanthellae. Individual colonies have been observed to change colour both in the field and in the laboratory. Green colonies can vary in colour from brilliant green through to yellow, and blue colonies can vary from bright blue, to grey, to almost translucent. Both green and blue colonies can become brown (lose the animal pigment), and in one instance a green colony was observed to change from green to yellow to blue. When the colours of colonies at a site change, many colonies are affected. Therefore, colour could provide a useful indication of changes in environmental and/or colony conditions.

Data from the preliminary surveys were analysed to see if any patterns exist in the colour morphs of colonies with patch type. Green colonies were most common in patches at 7 m depth; however, overall the percentage of green colonies in a patch was similar whether the patch was shaded, partially shaded, or fully exposed to sunlight (Figure V.1). Fifty-one percent of colonies at Fairlight and 45% of colonies at Green Point were green. None of the colonies surveyed in March 1994 were brown.
Figure V.1: Patterns of distribution for colonies of different colour morphs,
a) Percentage of colonies that are green in patches with
different light conditions; and b) Percentage of colonies that
are green in patches at 3, 6 and 7 m depth.

Graphs include data from Fairlight and Green Point. Data collected in March
1994. Error bars represent standard deviations, and ‘n’ is the number of
patches.
a)

Percentage of green colonies in patch

- Exposed: n = 4
- Part shaded: n = 15
- Shaded: n = 14

Light Type

b)

Percentage of green colonies in patch

- Patch Depth: 3m: n = 12
- Patch Depth: 6m: n = 15
- Patch Depth: 7m: n = 6

Patch Depth (m)
A study by Gleason (1993), found colour morph specific differences in the Caribbean coral *Porites astreoides*. Corals of the green morph were more abundant in shallow water (≤2 m) and had higher levels of UV-absorbing mycosporine-like amino acids, than brown colonies. However, in deeper water corals of each morph had similar abundances. Experiments in which colonies of each morph were transplanted to shallower water showed that brown colonies had lower rates of growth and lower algal mitotic indices than green colonies, whereas in deeper waters the green and brown morphs have very similar physiologies. Gleason (1993) proposed that these differences between the green and brown colonies represented differences in their ability to tolerate UV light and probably explains their different patterns of distribution.

*P. versipora* colonies occur at Fairlight occur in deeper water than at Green Point, so are likely to be exposed to different light regimes. As a result, the rates of growth and survivorship of colonies of each morph may vary between my two study sites. Therefore, I proposed the model that colonies of different morphs have different rates of growth and survivorship at different sites, and because there were slightly more green colonies at Fairlight than at Green Point, I proposed that green colonies grow faster and have higher rates of survivorship at Fairlight than at Green Point.

These different patterns of distribution suggest that there may be physiological differences between green and blue colonies of *P. versipora*, which could result in differences in their reproductive biology. Therefore, I also compared the sexuality and fecundity of colonies of different morphs. This has not been previously investigated in corals.
V.3 GROWTH, MORTALITY AND REPRODUCTION IN COLONIES OF DIFFERENT COLOUR MORPHS

Within each size class the growth rates of colonies were highly variable (Figure 3.9 and 3.10). Therefore, the growth rates of colonies of different colour morphs within each size class were compared, to determine to what extent colour morph contributed to the variability measured.

V.3.1 Methods

The data for these comparisons are from studies described in Chapter 3.3.1 and 3.4.1, with colonies sorted by colour morph (green or blue), as well as by colony size. In analyses of the data the differences between colour morphs in their rates of growth, if they occurred, would be most likely to occur in comparisons between small colonies as they have the fastest rates of growth.

The methods and data for comparisons of the reproductive biology of colonies of different morphs are from studies described in Appendix IV.

In these studies all the colonies used in these comparisons were either green or blue. Whole colonies that consisted of multiple colonies that had amalgamated and were a mix of different colour morphs were excluded from these analyses.

V.3.2 Results

There was no clear relationship between colour morph and the relative growth rates of colonies, except for a weak trend between morphs in comparisons.
between the smallest size classes at each site, consistent with the model (Figure V.2). However, this difference was not significant (2 factor ANOVA, n= 4, p > 0.07).

The rates of mortality for corals of different morphs are shown in Table V.1. In 1997-98 mortality was higher for blue corals than green corals, at each site. At Green Point, 77% of the colonies that died were blue. In contrast, at Fairlight the slightly higher rate of mortality of blue colonies (57%) in 1997-98, appears to cancel out the higher rate of mortality of green colonies (63%) in 1996-97. Therefore, the mortality rates of corals at Fairlight do not suggest any effect of colour morph on mortality, and the high rates of mortality of blue colonies (77%) at Green Point, seems only to represent the fact that there were many more blue colonies (74%) than green colonies, in the quadrats at Green Point.

There was no significant difference in the sex ratios of colonies of different morphs at each site (Fairlight: $\chi^2 = 1$; Green Point: $\chi^2 = 0.26$ with 1d f, p > 0.3), (Table V.2a).

The proportion of mature and immature gonad measured in the population was similar at each site, and within each site these proportions were similar between colonies of different morphs (Table V.2b).
Figure V.2: The relative growth rates of colonies of different colour morphs in each size class at Fairlight and Green Point, in each year sampled. Where, ■ represents blue colonies and □ represents green colonies.

Table of the number of replicates of each morph in each size class in Figure 3.13.

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>I b</td>
<td>15</td>
<td>10</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>I g</td>
<td>19</td>
<td>11</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>II b</td>
<td>9</td>
<td>11</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>II g</td>
<td>29</td>
<td>31</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>III b</td>
<td>9</td>
<td>9</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>III g</td>
<td>11</td>
<td>14</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>IV b</td>
<td>7</td>
<td>8</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>IV g</td>
<td>6</td>
<td>7</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>V b</td>
<td>8</td>
<td>10</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>V g</td>
<td>12</td>
<td>14</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>
Table V.1: Whole colony mortality for colonies of different morphs in different size classes each year

<table>
<thead>
<tr>
<th>Colony Size Class</th>
<th>Morph</th>
<th>Total No. Died</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>Fairlight 1996-1997</td>
<td>blue</td>
<td>2 2 1 1 0</td>
</tr>
<tr>
<td></td>
<td>green</td>
<td>4 6 0 0 0</td>
</tr>
<tr>
<td>Fairlight 1997-1998</td>
<td>blue</td>
<td>6 2 0 0 0</td>
</tr>
<tr>
<td></td>
<td>green</td>
<td>4 1 1 0 0</td>
</tr>
<tr>
<td>Green Pt 1997-1998</td>
<td>blue</td>
<td>6 4 0 0 0</td>
</tr>
<tr>
<td></td>
<td>green</td>
<td>1 2 0 0 0</td>
</tr>
</tbody>
</table>
Table V.2: Patterns of Reproduction in Colonies of Different Morphs

a) Number of colonies of each sex for colonies of different morphs at different sites (n = 357 colonies).

<table>
<thead>
<tr>
<th>SITE</th>
<th>MORPH</th>
<th>SEX</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>FEMALE</td>
<td>MALE</td>
<td>NO GONAD</td>
</tr>
<tr>
<td>Fairlight</td>
<td>blue</td>
<td>22</td>
<td>23</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td></td>
<td>green</td>
<td>29</td>
<td>20</td>
<td>51</td>
<td></td>
</tr>
<tr>
<td>Green Point</td>
<td>blue</td>
<td>21</td>
<td>12</td>
<td>54</td>
<td></td>
</tr>
<tr>
<td></td>
<td>green</td>
<td>19</td>
<td>14</td>
<td>45</td>
<td></td>
</tr>
</tbody>
</table>

b) Number of colonies with mature and immature gonad for colonies of different morphs, at each site (n = 357 colonies).

<table>
<thead>
<tr>
<th>SITE</th>
<th>MORPH</th>
<th>REPRODUCTIVE STATE</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>IMMATURE GONAD</td>
<td>MATURE GONAD</td>
<td>NO GONAD</td>
<td></td>
</tr>
<tr>
<td>Fairlight</td>
<td>blue</td>
<td>11</td>
<td>34</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td></td>
<td>green</td>
<td>17</td>
<td>33</td>
<td>51</td>
<td></td>
</tr>
<tr>
<td>Green Point</td>
<td>blue</td>
<td>11</td>
<td>23</td>
<td>53</td>
<td></td>
</tr>
<tr>
<td></td>
<td>green</td>
<td>12</td>
<td>21</td>
<td>45</td>
<td></td>
</tr>
</tbody>
</table>
V.5 CONTACT TYPES BETWEEN COLONIES OF DIFFERENT COMBINATIONS OF COLOUR MORPHS

If fusibility is related to morphotype, perhaps because colonies of the same morph are more likely to be related, then histocompatibility reactions between two colonies of the same colour morph would be expected to have a higher rate of fusion than histocompatibility reactions between two colonies of different colour morphs.

V.5.1 Methods

For survey methods see Chapter 4.2.3. Data sorted by combinations of colonies of different colour morphs.

V.5.2 Results

At Fairlight, 69% of the histocompatibility reactions surveyed were between colonies of different colour morphs, only 7% of the reactions were between two colonies of the blue morph, and 24% of reactions were between two colonies of the green morph. At Green Point, 50% of the reactions were between colonies of different colour morphs, 40% were between two colonies of the blue morph, and 10% were between two colonies of the green morph (Figure V.3).

The proportions of different histocompatibility reactions were compared between pairs of corals of the same colour morph, and pairs of corals of different colour morphs, at each site. There were no significant differences
Figure V.3: Frequency of different reaction types between two colonies of the same colour morph and two colonies of different colour morphs at a) Fairlight and b) Green Point.

Where, $\mathcal{S}$ is the blend reaction, ■ is the distinct reaction and □ is the ridge reaction.
a) Fairlight (n=101)

- Number of Incidents
- Different Morphs: 20
- Same Morphs: 15

b) Green Point (n=101)

- Number of Incidents
- Different Morphs: 15
- Same Morphs: 10
(Fairlight: $\chi^2 = 1.9$, df = 2, p > 0.05; Green Point: $\chi^2 = 1.2$, df = 2, p > 0.05). The results for the blend, distinct and ridge reactions are shown in Figure V.3. Colonies that fuse have the blend reaction. The mix and alternate reactions were excluded from Figures V.3 as they had a low frequency of occurrence in the population (< 12% of reactions).

V.6 DISCUSSION

Colonies in fixed quadrats did not change their colour morph through time. Even colonies that had grown into contact and amalgamated with corals of other colour morphs, did not change their colour during the photographic surveys. Colonies did, however, have seasonal variations in the intensity of colour they had. Over the summer months blue colonies often became paler in colour, turned grey-white (although still containing animal pigment), or became translucent (no apparent animal pigment), and green colonies became yellow-green. In winter, blue colonies would darken, sometimes even to a purple-blue colour, and green colonies often became a vibrant, bright green colour.

Corals of different colour morphs had similar rates of growth and survivorship at each site, suggesting that there was is unlikely to an advantage in being one colour over another colour morph at different sites, even though these sites are likely to have different light regimes. However, manipulative experiments are needed to substantiate this correlative data.

The sex ratios of *P. versipora* colonies were calculated for each of the blue and green colour morphs at each site, and found to be the same between colonies of
different morphs. Thus, colony colour is not an indicator of colony sex (Table V.2b).

The proportion of mature and immature gonad measured in the population was similar between colonies of different morphs at each site.

V.7 SUMMARY

Colonies of different morphs had similar rates of growth and mortality, and similar patterns of reproduction. No significant or consistent effect of colour morph on the biology of colonies was shown in these studies.