Population dynamics and genetic structure of locally dominant species on coral reefs: a case study of the soft corals *Sinularia flexibilis* and *Clavularia koellikeri*

Thesis submitted by

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ABSTRACT

The population genetics and demography of soft corals, the second most abundant benthic invertebrate group on the Great Barrier Reef (GBR), were investigated to identify the proceses that determine their abundance and distribution. The study focusses particularly on the interplay between the demographic proceses and life history strategies of soft corals that commonly lead to their dominance in many coral reef communities. My general objective was to identify the mechanisms that allow soft coral species, specifically *Sinularia flexibilis* and *Clavularia koellikeri*, to dominate nearshore communities and to determine the likely time scales involved.

One potential mechanism to attain high cover is rapid colonisation of newly opened substrata, thus pre-empting space and preventing recruitment by potential competitors. The mortality caused by the 1998-bleaching event constituted an opportunity to evaluate the role that recruitment plays in the dynamics of recovering soft coral assemblages. Living cover declined by half at study sites on nearshore reefs in the Palm Island group (central GBR) that had been dominated by soft corals prior to the bleaching. In contrast to the common expectation that soft corals rapidly colonise substrata, a slow recovery was documented in the three years following the mortality, with soft coral cover increasing by only 16% between 1998 and 2000. The slowness of this recovery indicates that high cover is neither the result of rapid recruitment through sexual nor asexual recruits, at least in the time frame of this study.

Colonies of *Sinularia flexibilis* (Alcyoniidae) had size-dependent growth and mortality rates, and a high population turnover mostly derived from asexual replication. Small colonies generally increased in area by three-fold per year, whereas large colonies decreased in size mainly by binary fission. Despite the ability of small colonies to grow relatively rapidly, a matrix modelling study showed that population growth was variable among localities and time intervals, but all casese leading to increasing populations. Also, this study indicates that changes in the rates of colony growth, fission and stasis all have the potential to contribute equally to population growth. This finding is in stark contrast to studies of most other clonal species, which have found that stasis, especially of the largest sizes, largely controls their demography. Thus, although most vital rates in

Sinularia flexibilis were characteristic of a clonal species, the finding that demographic proceses in all size classses contribute similarly to population growth is novel.

Despite the larger contribution of asexual compared to sexual reproduction to population increases found in the demographic study, population genetic structures were not highly clonal at small spatial scales. Small-scale mapping of genotypes indicated that more than 60% of genotypes were unique, with the largest genet being represented by only nine daughter colonies. A high genetic diversity was also characteristic of populations of this species surveyed on 12 reefs and of *Clavularia koellikeri* (Clavulariidae) on six reefs, including both inshore and midshelf reefs along the length of the GBR. For both species, the population genetic structure was in agreement with that of a sexually reproducing species, when species were sampled at intervals ≥5 m for *S. flexibilis* and ≥3 m for *C. koellikeri*.

Genetic differentiation among populations of the larval brooder *Clavularia koellikeri* was four to thirty times that found for the gamete broadcaster *Sinularia flexibilis*, depending on the spatial scale compared. It is likely that differences in genetic differentiation among populations of these species reflects differences in the duration of their larval phases, and consequently their ability to disperse.

PUBLICATIONS ARISING FROM THIS THESIS

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

15/03/02

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THESIS OUTLINE

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1 General Introduction

The study of processes determining the distribution and abundance of organisms, such as life history strategies, demography and historical events, and the interactions among them constitutes the core of plant and animal ecology. Despite major advances in ecological research, the current knowledge of the interplay of these processes is still generally poor for many groups of organisms. In coral reef environments, the need to understand the fundamentals of processes that increase (*e.g.* recruitment and growth) and decrease (*e.g.* mortality caused by physical disturbances, competition, predation, etc) the abundance of organisms is becoming critical because of the number and magnitude of threats to reef communities (*e.g.* Bryant *et al.* 1998; Wilkinson 1999). Coral reefs have been particularly affected by the increasing intensity and frequency of bleaching, as well as by overfishing, diseases and other anthropogenic sources of mortality that, with different degrees of evidence, have been linked to global change and/or to the effects of land-based activities on the sea (Done 1992a; Hughes 1994; Buddemeier and Smith 1999; Hoegh-Guldberg 1999; Porter and Tougas 2001; Aronson and Preton 2001). Given the likelihood of increasing disturbances to coral reefs in the next few decades, it is imperative that we gain a better understanding of the population dynamics and life histories of key reef organisms in order to interpret their patterns of abundance and make decisions about their conservation.

Knowledge of the spatial and temporal extent of natural variability in the abundance and distribution of species, including the propensity for some species to dominate local assemblages, provides the framework with which to evaluate whether or not changes in community structure are a reason for concern. Lack of such understanding has meant that it has only been recently, after reef communities have failed to recover, that the global scale consequences of human-related changes to the environment have been recognised (*e.g.* Jackson *et al.* 2001; Scheffer *et al.* 2001). The potential effects of those changes to the communities have added a level of complexity to the study of the factors affecting natural variability. This study aims to contribute to the understanding of the effect of the interplay between life history and demographic processes on the variability in abundance of clonal sessile organisms.

Soft corals (Cnidaria: Octocorallia: Alcyonacea) are highly diverse (23 families and 90 genera in Fabricius and Alderslade 2001), and the second most abundant macro-benthic group on Indo-Pacific and Red Sea coral reefs (Benayahu and Loya 1981; Dinesen 1983). In the Red Sea, Benayahu and Loya (1987) have completed the longest study (12 y) on the colonization and successional processes of soft corals on artificial substrata. As these authors point out, this type of study in other geographic areas and on natural substrata is vital to determine the role played by soft corals during reef colonization and the partitioning of space in coral communities. On the Great Barrier Reef, it is known that the abundance, species richness and species composition of soft coral assemblages vary latitudinally and across the continental shelf (Dinesen 1983; Mapstone *et al.* 1998; Sweatman *et al.* 1998; Fabricius and De'ath 2000, 2001). Although these broadscale studies have begun to address gaps in our knowledge of soft coral distribution and abundance patterns, there is a paucity of ecological studies on soft corals compared with hard corals, which has led to a poor understanding of their relative importance in coral reef communities.

A common perception is that high soft coral abundance is associated with physically or anthropogenically disturbed habitats (reviewed in Fabricius 1997, 1998). However, long-term and large-scale studies on the Great Barrier Reef (GBR) indicate that where hard coral cover has decreased (*e.g.* as a result of crown-of-thorns predation or storm damage), algae cover increased, but little or no change occurred in soft coral cover (Sweatman *et al.* 1998; Ninio *et al.* 2000). Coral community surveys that have looked specifically at soft corals also indicate that their abundance changes little as a consequence of the history of *Acanthaster planci* outbreaks on middle and outer-reefs of the Central GBR (Fabricius 1997). Where a disturbance occurs and has no or little effect on soft corals (*e.g.* crown-of-thorns) but leads to a decline in hard coral abundance, it may result in a relative increase in soft coral cover compared to the total living cover in the community. Yet these changes are hardly supportive of concerns that soft corals may outcompete hard corals following disturbances (*e.g.* Endean 1976; Benayahu and Loya 1987; Endean *et al.* 1988), at least at large spatial scales on the GBR and on time-scales for most studies (< 30 years). In general, a relationship between high soft coral abundance and disturbance would be difficult to establish without information about the time frames required for presumed changes in a coral community to occur, and the

history of disturbances in the affected areas, among other factors which are generally unknown.

The fact that some genera may attain local dominance in some reef habitats could have also contributed to the perception that they dominate disturbed habitats. Hereafter, I will use the term local dominance interchangeably with monospecific or species-poor stands, and aggregations, to describe extensive areas of hundreds of square meters covered by one or a few species (*e.g.* Fabricius 1998). Soft corals that aggregate in this way include species of the genera *Sinularia*, *Clavularia*, *Pachyclavularia* and *Efflatounaria* on the Great Barrier Reef (Dinesen 1983; Karlson *et al.* 1996; Fabricius 1998) and *Sinularia*, *Cladiella*, *Sarcophyton* and *Lobophyton* in the Red Sea (Benayahu and Loya 1977; Benayahu 1985). Soft coral aggregations in the Pacific area have been reported from Guam (van Alstyne *et al.* 1994), Papua New Guinea (Tursch and Tursch 1982) and Japan (Nishihira and Yamazato 1974).

Furthermore, some soft corals have the potential to quickly colonise substrata (Benayahu and Loya 1981, 1984, 1987, Dinesen 1985; Karlson *et al.* 1996). However, the relationship between the ability of some species to attain local dominance and the species' capacity to quickly take over substrata is not clear, due to striking differences in growth between the studied tropical species of the families Xeniidae and Alcyoniidae, which are both able to achieve local dominance (Fabricius 1995 and references therein). Thus, relationships between soft coral abundance, formation of aggregations and disturbance regimes need further clarification. In this study, I examine the recovery of a soft coral dominated community following a mass bleaching event and estimate the time frame required for the formation of aggregations.

1.1 Factors controlling abundance and that can lead to local dominance

One of the most generalised features of communities is that most species are rare and only a few are extremely common (*e.g.* references in Brown *et al.* 1995). There is evidence that many species can locally dominate a community, but there is no consensus as to why this occurs. It also has been recognised that factors, based on both the function and interaction of species, and on the dispersal of species and stochasticity

of events, are relevant to the assembly and abundance of organisms in their communities (*e.g.* Drake 1990, reviewed in Hubbell 2001). However, the way in which these factors interact to result in high variability of local abundance of organisms is not completely established, and much of the biological and ecological significance of aggregations of organisms has yet to be uncovered (*e.g.* Parrish and Edelstein-Keshet 1999).

Various life history aspects of sessile species promote the aggregation of individuals (reviewed in Jackson 1985 and references below) that can lead eventually to high local abundance. Life history aspects associated with the dispersal of species include the aggregated recruitment by philopatric larvae or by planktonic larvae with gregarious behaviour; the attraction of larvae to adults, and the similar behaviour of larvae that are being subjected to the same oceanographic processes (*e.g.* Williams 1976; Roughgarden *et al.* 1991; Petersen and Svane 1995). Life history aspects associated with the function and interaction of species are: enhanced vital rates or stronger competitive abilities at local sites where the niche requirements of the species are satisfied (*e.g.* Ayre 1985); group benefit within an aggregation (*e.g.* Eckman and Okamura 1998; Gili and Coma 1998); and asexual replication by vegetative growth (*e.g.* McFadden 1986). In this thesis I will examine the effect of various life history aspects on the population growth of a soft coral species, and their potential to promote local aggregations.

1.2 Sexual and asexual reproduction in populations of clonal organisms

It is tempting to suggest that clonal species are more prone to forming local aggregations than aclonal ones, because of their greater capacity to spread through asexual replication, to recover from partial mortality, and to have a long lifespan (Hughes and Cancino 1985). However, there are many examples of aclonal species forming aggregations (*e.g. Mytilus* beds). Furthermore, among clonal organisms, the prevalence of sexual and asexual mechanisms of reproduction varies considerably, and consequently, the purported advantages of clonality also vary. This variability ranges from species that are virtually aclonal to species with no known sexual phase (*e.g.* obligate parthenogenesis). Sexual and asexual prevalence can also vary in response to environmental factors (*e.g.* Tsuchida and Potts 1994), or to interactions with

conspecifics (Karlson *et al.* 1996). In addition to these factors affecting the prevalence of sexual and asexual reproduction at the individual level, other factors produce variations of that prevalence in the population as a whole. Disturbance regimes, type of asexual reproduction, and historical events have been recognised as factors determining the proportion of sexually derived individuals in populations of clonal organisms (*e.g.* Hunter 1993; Coffroth and Lasker 1998). The study of species with mixed modes of reproduction and the processes that influence the allocation of energy between the two modes have increased our understanding of the ecological and evolutionary advantages of this life history strategy (*e.g.* Cheetham *et al.* 2001).

Studies of the relative importance of sexual and asexual reproduction in the life history of a species have involved both direct field observations and population genetic studies. Most field studies have very limited temporal and spatial scales, and in particular, studies of larval dispersal and recruitment are difficult. Population genetic studies provide an alternative means of inferring larval dispersal and the degree of asexual reproduction within a population. For example, a high level of dispersal among populations usually results in relatively little genetic differentiation, whereas low levels can lead to population differentiation. The occurrence of asexual reproduction can lead to gene frequencies that are skewed from those expected under random mating. Asexuality per se has no effect on allelic or genotypic frequencies, but by impeding genetic segregation and recombination, it maintains the genetic effects of selection, genetic drift, or founder effects (Black and Johnson 1979). A particular advantage of population genetic studies is that they integrate the impact of dispersal and recruitment processes on population structure through time. Consequently, population genetic approaches have been widely used in studies of marine invertebrates (reviewed in Neigel 1997 and Benzie 1999) and are the preferred approach for detecting relative success of sexual versus asexual reproduction (*e.g.* Ayre 1984; Edmands and Potts 1997). In this study, I used a genetic approach to examine the prevalent mode of reproduction and dispersal potential in populations of two soft coral species with contrasting life histories.

1.3 Aims

This study seeks to identify the processes that determine the distribution and abundance of soft corals on nearshore reefs in the GBR, focussing in particular on the interplay between demographic processes and life history strategies that commonly lead to their dominance in local communities. This study will contribute to the understanding of factors affecting the patterns of abundance and distribution of sessile marine organisms, particularly following the occurrence of local disturbances. The specific aims were:

1. To evaluate changes in coral community structure after a severe bleaching event in 1998. The severity of coral mortality caused by this event constituted a unique opportunity to evaluate recovery of the major benthic groups in a community where cover was dominated by soft corals (~ 50%) prior to the event. In Chapter 2, I document changes in cover and species composition that occurred during the 34 months immediately following the 1998 bleaching event on two nearshore reefs in the GBR.

2. To determine the demographic characteristics of *Sinularia flexibilis*, the dominant soft coral on two near-shore reefs in the GBR. In Chapter 3, I examine the population dynamics and relative importance of different demographic processes in this species, particularly in relation to its capacity to form extensive aggregations. Projected population sizes through time based on population growth rate estimations allowed me to infer time-scales for the formation of these aggregations.

3. To determine the potential for larval dispersal and the relative contribution of clonality to the population structure at various spatial scales of two soft coral species with contrasting modes of reproduction. In Chapter 4, I use population genetics to compare the dispersal potential of species having brooded versus planktonic larvae, and examine the implications of these alternative life history strategies for their distribution patterns and the establishment of local aggregations. This study also estimates the relative importance of sexual and asexual reproduction in these two soft coral species, *Sinularia flexibilis* and *Clavularia koellikeri*, which have contrasting mechanisms for asexual reproduction.

2 Response of a soft coral dominated community in the GBR after the 1998 bleaching event

2.1 Abstract

In this study I document changes during the 3 years following the 1998 bleaching event in a nearshore reef coral community of the GBR. This community was dominated by soft corals before and after the event, contributing >90% of the living cover with an assemblage of species from eight genera. A comparison with surveys made prior to the event indicated a 50% decrease in mean living cover (from 63% ± 4 to 33% ± 4 between November 1996 and December 1998). This change was most likely attributable to bleaching related mortality. Cover decreased significantly for hard corals (8% ± 2 to 1% ± 0.4), soft corals (50% ± 4 to 31% ± 3.5), and other invertebrates (2.5% ± 0.7 to 0.6% ± 0.1), but did not change significantly in macroalgae, which have a low cover in this community (<3%). Turf algae was the main group replacing the lost coral cover, and together with bare substrata, increased by 51% after the bleaching event. Within 34 months, the community showed slight signs of recovery, with overall living cover increasing from 33 to 38% ($p = 0.034$) from Dec-98 to Dec-00, although recovery differed among study sites. This increase resulted mainly from a change in soft coral cover during the first year (98-99). In contrast to soft corals, hard coral cover increased mainly during the second year, but it still remained low compared with pre-bleaching cover (< 3% vs. 8%). Overall, the density of colonies was relatively constant, although the turnover of colonies exceded 30% in all groups throughout the study. High mortality and slow recovery to previous levels of local dominance indicated that these communities will take far more than three years to recover, even where soft coral cover was still relatively high after the disturbance. Thus, not only the hard corals but also soft coral assemblages are likely to be severely affected by predicted future increases in the frequency and severity of bleaching events.

2.2 Introduction

Understanding processes that determine the distribution and abundance of species and the recovery of coral reef communities is gaining relevance as the intensity and frequency of bleaching events (*e.g.* Glynn 1993; Brown *et al.* 1996; Hoegh-Guldberg 1999) and other anthropogenic disturbances (e.g. Bryant *et al.* 1998) increase. The bleaching event in 1998 was the largest and most severe episode recorded so far (Hoegh-Guldberg 1999; Wilkinson 1999). On the Great Barrier Reef (GBR, Australia), broad-scale aerial surveys of 23% of reefs indicated that by April 1998, 87% of inshore reefs and 28% of mid- and outer-shelf reefs were bleached to some extent (Berkelmans and Oliver 1999). However, at present very little is known about the recovery of soft and hard coral assemblages severely affected by bleaching disturbance in the GBR.

In coral communities, patterns of occurrence of bleaching and disturbances in general, are much better described than processes of recovery. This is because major reef builders are relatively slow growing, only a few studies of coral communities have encompassed at least a decade (e.g. Connell *et al.* 1997), baseline data are scarce or absent, and the definition of what constitutes recovery varies (*e.g.* Done 1992a, 1997; Brown and Suharsono 1990). So far, when coral reef communities have been observed to recover from disturbances, the recovery has usually taken more than a decade. However, actual recovery times have varied greatly depending on the type of disturbance, type of community affected, and its history (*e.g.* Loya 1976; Done 1997, Brown *et al.* 1990; Tanner *et al.* 1994; Hughes and Connell 1999).

The most common phase shift in coral community structure following a disturbance has been the shift from coral to macroalgal dominance (reviewed in Done 1992b). Recently, shifts towards algal dominated communities have been reported to occur in less than five years following bleaching (Ostrander *et al.* 2000; McClanahan *et al.* 2001) and other types of disturbances (Lessios 1988; Hughes 1994). In some studies, soft coral dominated communities have been interpreted as a sign of recent disturbance (Endean 1976; Benayahu and Loya 1987; Endean *et al.* 1988), although evidence linking a shift towards soft coral domination with disturbance is lacking. On the contrary, large scale and long-term monitoring surveys on the GBR indicate that soft coral cover is stable

through time despite a variety of disturbances (Fabricius 1997; Sweatman *et al.* 1998; Ninio *et al.* 2000). Thus, it remains largely speculative to which extent local dominance of soft corals can be interpreted as a sign of recent disturbance.

The 1998 bleaching event provided a unique opportunity to evaluate how a soft coral dominated community responds to a major disturbance and to determine the time frame for such a response. In particular, if soft coral dominance in a community is established mainly as a result of disturbance, as is commonly implied, then soft coral recovery should occur relatively quickly, either in a time frame shorter than the disturbance frequency or shorter than the recovery rate of hard corals. Neither of these hypotheses has been previously examined.

In this chapter, I document changes in a soft coral dominated community over a 3 year period following a severe bleaching event, in order to gain insights into recovery processes in reef communities, and to determine if rapid recruitment and growth of soft corals contributes to their capacity to monopolise spatial resources. The specific aims of this study were (a) to estimate the percent living cover lost from two nearshore reef communities following the 1998 bleaching event in order to characterise its severity; and (b) to follow the recovery process over three years, comparing the responses of the major benthic groups in this coral reef community.

2.3 Methods

2.3.1 *Study site*

Study sites were established on fringing reefs surrounding the Palm Islands, a group of five islands 15 – 45 km off the coast in the Central Section of the Great Barrier Reef (GBR, Australia) (Figure 2.1), which experienced severe bleaching during the 1998 event (Marshall and Baird 2000; Berkelmans 2001). Hard and soft coral cover on these reefs ranged from 30 to 75% (depending on the habitat) before November 1996 (Thompson and Malcolm 1999; Berkelmans 2001). On the GBR, near-shore (or inner-shelf) coral communities in shallow waters can be dominated by alcyoniid soft corals which can make up to 80% of the total hard and soft coral cover (Fabricius 1997). I established two study sites (Figure 2.1) in areas that were known to have high soft coral

cover prior to the 1998 bleaching: the channels between Orpheus and Pelorus Islands (18° 34' S, 146° 29' E) and between Orpheus and Fantome Islands (18° 39' S, 146° 30' E). These two sites, henceforth referred to as sites **P** and **F**, are 11 km apart and 25 km from the mainland. Site **P** is located on the northern end of Orpheus Island, midway between the sheltered side (Iris Point) and the north-east end of the island that experiences high wave exposure. Site **F** is the fringing reef on the southern end of Orpheus Island, and also located midway between the sheltered and the relatively more wave exposed sides.

2.3.2 *Sampling methodology*

Twenty-one belt-transects, 5 m long and 1 m wide, were permanently established following the depth contour at the two sites: five transects at 2 m depth and five (site **F**) or six (site **P**) transects at 5 m depth. Combinations of site and depth will be labelled **P2**, **P5**, **F2**, and **F5** throughout this chapter. The starting point of each transect was haphazardly selected when it was first established. I monitored the belt-transects using still photography at 3 sampling times: December 1998, December 1999 and December 2000. The first monitoring of transects at site **F** was delayed until March 1999, but for the simplicity of tables and figures I refer to the first sampling date for all transects as December 1998.

In each transect, I used a tape measure attached to two permanent marks -at the beginning and at the end - as a guide to take the photographs at fixed distances from the starting point. A Nikonos V underwater camera with 28 mm lens and flash was attached to an aluminium frame, which provided a fixed height of 1.2 m from the reef substratum. Spirit levels were attached to the aluminium frame to orient the camera plane parallel to the substratum. At this height, each image covered 1.2 x 0.80 m of the reef, which resulted in a photo scale of 1:33 (1 mm in the slide is 33 mm in the field). The transect length approximated 5 m, ranging from 500 to 610 cm (N=21) in order to avoid anchoring the permanent marks into living colonies. Sizes of coral colonies were small compared to the transect length and width. Thus, the difference in length among the transects, as a consequence of not anchoring the stake in a colony, seems rather small to cause a biased in cover estimates. Among all transects, the area suitable for analysis (common to the three sampling times) varied between 3.85 m^2 and 5.76 m^2, and

averaged 4.70 m^2 ± 0.92 (SE). Parameters were calculated using the exact area of each transect. I took approximately 10 separate images along each tape, which provided an overlap of ~20 cm between images.

After digitising the photographs, I composed a single image for each transect by matching identifiable characteristics among consecutive photographs, and merging the pictures. For identification of taxa, I digitised the photographs at high resolution (350 pixel/inch, 20MB or 0.7 field mm /pixel), whereas transect images were composed of photographs with half this resolution. I gave real-world distances in metres to each transect image using ArcInfo, a Geographic Information System software package (ESRI, Arc), such that I could trace and calculate area, perimeter, etc for each colony, or patch (*i.e.* macroalgae, dead surfaces), or from the whole transect.

I traced each sessile invertebrate greater than 2 cm in diameter and identifiable in the images. Each colony of hard or soft coral was identified at least to the genus level. Different species were distinguished where possible and later confirmed by expert opinion (Dr. D. Fenner, Dr. K. Fabricius). Colonies of other invertebrates were identified to genus or higher taxonomic levels. Dead areas within colonies were traced and excluded from their total area. Among algae, only macroalgae and crustose coralline algae were traced. I grouped turf algae and other substrata suitable for coral colonisation (rubble, limestone or recently dead coral) into one category, as they were indistinguishable on the images. The area for this category was calculated as the entire area analysed minus the total living cover and the sand patches.

Each colony of coral or other invertebrate (defined as an identifiable individual or patch isolated from its neighbours) was given a unique number that was constant through time. In this way I calculated the number of colonies that died, appeared as new recruits, or survived from one sampling time to the next in the two time intervals: between Dec-98 and Dec-99, and between Dec-99 and Dec-00. For changes in colony numbers through time I only used colonies which were completely within the transect so edge effects would not affect the estimates. This procedure was not necessary for the cover estimates.

Three transects were photographed twice in the same sampling period to estimate the difference in cover caused by repositioning the transects and the natural expansion-contraction cycles of soft coral colonies. Summing the area of different colonies and patches across each taxon (species or genus) and across the three transects yielded 60 measurements of cover for each of the two sets of estimates of the same sampling: 22 measurements for hard corals, 25 for soft corals, 9 for other invertebrates, and 4 for algae. Mean net difference for the percent cover of all major benthic groups between the two estimates was 0.23% ± 0.18 SE (note that all error intervals presented throughout the text are standard errors). There were as many positive as negative net differences (median = –0.01%), however, the overall net difference was positively skewed by the influence of soft corals. Mean net difference was greatest for soft coral cover (0.66% ± 0.17) as compared to a mean net difference of –0.07% ± 0.03 for hard corals. Among all taxa, the soft coral *Sinularia flexibilis* had the largest net differences with 3%, 3% and 9% for the three transects. Since mean differences in percent cover for each major group, due to repositioning the transects and the natural expansion-contraction of soft corals were low (<1%), I have not incorporated these errors into the following analyses. At site **P**, three massive *Porites* spp. colonies > 2 m in height were avoided when establishing the transects for practical reasons, thus hard coral cover for this community is slightly underestimated.

2.3.3 *Pre-bleaching data*

As this study was set up after the 1998 bleaching event, Dr. K. Fabricius kindly provided pre-bleaching data from August and November 1996 to quantify the effect of the bleaching event and provide a baseline against which recovery could be evaluated. The cover of sessile invertebrates was calculated from a total of 13 line intercept transects, each 50 m in length, ranging between depths of 1.5 and 6 m at Orpheus - Fantome channel (n = 3 transects), Iris Point (n = 6) and Great Palm Island channel (n = 4). The first locality corresponds to site **F** in my study, Iris Point is less than 500 m from site **P**, and the third locality is 15 km from site **F**, in a very similar channel environment.

2.3.4 *Statistical analysis*

Because the transects were the same through time, I used a repeated measures ANOVA to analyse the changes in percentage cover and in number of colonies through time of the four major benthic groups (hard corals, soft corals, macroalgae and other invertebrates) in relation to site and depth. I used the Kolmogorov-Smirnov test (Lilliefors), the Levene test and the Mauchly test to evaluate normality, homogeneity of variances and sphericity, respectively. I transformed the data when necessary to meet these assumptions of the analysis. In particular, I used square root transformation for the percentage cover data; density of colonies did not require transformation.

To investigate the effects of depth and site on the number of colonies that died, recruited into the area, or survived from 1998 to 1999 and from 1999 to 2000, I used log-linear models for each of the categories: hard corals, soft corals, and other invertebrates. For each category, I first selected the model that best described the data by backward elimination of the factors (Depth, Site, Year Interval, and their interactions). For this I used the iterative proportional-fitting algorithm available in the SPSS v. 10.0.5, where the change in the likelihood ratio chi-square after a maxium of 10 iterations has an associated probability indicating how well the data fits a model without each term. Then, I evaluated the effect of the number of colonies of each category in the first year on the number of colonies that were new, had died or survived to the next year, incorporating it as a covariate to the best-fitted model. The degree of association of the colonies that recruited, died or survived between species was evaluated with the non-parametric Spearman's coefficient of rank correlation.

All statistical procedures were conducted with the statistical software package SPSS v. 10.0.5 and relevant information about them was obtained from Norušis (1994) and Sokal and Rohlf (1995).

2.4 Results

2.4.1 *Overview of coral community structure*

During the study period (1998-2000), the overall living cover of the two coral communities averaged 36%, with soft corals constituting 95% of this cover. Soft corals were thus clearly the most abundant group in these inshore communities. Hard corals ,

macroalgae and other invertebrates contributed 2.6%, 0.7% and 1.7%, respectively, to the living cover. Actual percent cover for each group was 0.86% ± 0.24% for hard corals, 33.8% ± 3.2% for soft corals, 0.61% ± 0.11% for other invertebrates and 0.25% ± 0.07% for the macroalgae group.

More than 2,000 colonies of soft coral were recorded in the transects, including 8 genera from four families (Table 2.1). *Sinularia* was the most abundant genus of soft coral and also the most speciose, with more than 10 species represented (taxonomic verification pending). Hard corals, although very low in cover, were diverse with 14 genera from 8 families. The categories of unidentified hard and soft corals mainly contained very small colonies for which identification was not reliable or possible. The category of 'other invertebrates' included mainly the zoanthid *Palythoa* sp., the bivalve *Tridacna* sp., sponges and anemones. The category labelled macroalgae included visible patches of crustose coralline algae and fleshy macroalgae, the most conspicuous of which was the green alga *Chlorodesmis* sp. The category hard substratum was comprised of a mixture of rubble and consolidated limestone, whereas the soft bottom was mainly coarse carbonate sand.

The total living cover was similar between the sites but cover of each group varied. Considering both depths together, soft coral and macroalgal cover were similar between sites, whereas the cover of hard corals and other invertebrates were different (Figure 2.2). More specifically, for square-root transformed data the cover of the latter two groups was higher at site **P** than at site **F** (hard corals: 1.125% ± 0.058 vs. 0.360% ± 0.023; other invertebrates: 0.959% ± 0.029 vs. 0.461% ± 0.017). Although these two groups had low cover (<3%), they contributed to a higher diversity at site **P** than at site **F** (*e.g.* Shannon's Diversity Index = 1.29 ± 0.01 vs 0.56 ± 0.01; Patch Richness = 15.18 ± 0.64 vs. 11.00 ± 0.55). This is mainly the result of a relatively high number of hard coral genera despite their low cover.

2.4.2 *Pre- vs Post-bleaching coral cover*

Overall mean living cover decreased from 63% ± 4% to 33% ± 4% between November 1996 and December 1998, most likely as a result of mortality caused by the 1998 bleaching event. Average percent cover decreased eight-fold for hard corals (from 8% ±

2 to 1% ± 0.4), nearly two-fold for soft corals (from 50% ± 4 to 31% ± 3.5), and approximately four-fold for other invertebrates (from 2.5% ± 0.7 to 0.6% ± 0.1) (Figure 2.3). Macroalgal cover also decreased but not significantly. The greater amount of sand recorded in the pre-bleaching transects could reflect the longer transects used (50 m vs. 5 m used here), which increases the probability of crossing over large sandy patches. If the sand category is subtracted to standardise cover to the amount of hard substrate available, the pre-bleaching cover was 10% for hard corals, 65% for soft corals, and 3.4% for other invertebrates. Turf algae and bare substrata increased by 51% after the bleaching event (or by 48% as standardised to hard substrate).

2.4.3 *Changes in overall living cover following the 1998 bleaching*

From Dec-98 to Dec-00, overall living cover increased by approximately 5% (*i.e.* from 33.2 to 37.9%). Total percent cover varied greatly among transects and there was a significant interaction between time and site ($F_{Time \times Site} = 4.103$, df=2, $p = 0.042$). Figure 2.4 shows this variability and the increase in median living cover at all combinations of sites and depths. This figure also shows that there is substantial overlap in percent cover at a given site between sampling times (as represented by the boxes in Figure 2.4), except at site **P5**, where boxes are well separated between the Dec-98 and Dec-00. Living cover increased significantly only in the first year of the study as indicated by the contrast of cover for each year with the preceding year (*i.e.* Dec-99 vs. Dec-98: $F_{Time \times Site} = 18.413$ df = 1, $p < 0.001$; Dec-00 vs Dec-99: $F_{Time \times Site} = 1.032$ df = 1, $p = 0.324$).

At both shallow sites, the total number of colonies of sessile organisms remained very similar through time, whereas it decreased at 5 m ($F_{Time* Depth} = 4.836$, df = 2, p = 0.015). This decrease, together with the increased living cover that mainly occurred at site **P**, resulted in an 1.6 fold increase in mean living patch size from 1998 to 2000 (from 136 ± 17 cm²/patch to 216 ± 14 cm²/patch: $F_{Time * Loc=} = 3.876$, df = 2, p= 0.030, data not shown).

2.4.4 *Changes in cover of major benthic groups following the 1998 bleaching*

Changes in abundance of soft corals determined the patterns of change in overall living cover, as they were the most abundant group in the community (Figure 2.5). Mean soft

coral cover for all combined sites and depths increased by 16% of initial living cover between 1998 and 2000 (*i.e.* from 31% ± 3.5 in 1998 to 36% ± 3.4 in 2000; p = 0.035, Table 2.2). The greatest increase occurred between the first two years (F = 8.868, df = 1, p = 0.008), whereas the increase was not significant between the later two years (F = 2.271, df = 1, p = 0.150). Increases occurred mainly at site **P** ($F_{Time * Site}$ = 12.432, df = 1, p = 0.003), where the mean soft coral cover for the two depths increased by nearly 30% (*i.e.* from 27% to 35% between 1998 and 1999), being largest in the deep transects (*i.e.* from 36% to 47%). In contrast to soft corals, the increase in hard coral cover occurred in the second interval (*i.e.* from 0.73% ± 0.22 in Dec-99 to 1.10% ± 0.35 in Dec-00; F = 6.672 df = 1, p = 0.019). However, mean hard coral cover remained at less than 1% for all but the deep transects at site **P** over the 2 years (Figure 2.5), and changes through the whole period were not significant (Table 2.2).

Macroalgae and other invertebrates changed significantly during the study period or between specific years and this occurred differently among sites and depths (Figure 2.5). For example, the cover of macroalgae decreased at 5 m at both sites, while it increased at 2 m only at site **P** (Figure 2.5). This interaction between site and depth for the cover of macroalgae over time (Table 2.3) resulted mainly from an increase in cover up to 3% from Dec-98 to Dec-99 in one transect while the mean for that time was 1%.

2.4.5 *Change in density of colonies of major benthic groups*

Overall, the mean density of colonies in each of the benthic groups remained very similar through time (Figure 2.6) but the small variations differed among sites and depths (Table 2.3). Hard corals had an overall mean density of 1.33 ± 0.18 colonies/m², with density being approximately twice as great at site **P** than at site **F** (1.80 ± 0.26 vs. 0.86 ± 0.25 col/m², Table 2.3). Changes were not consistent with depth, as hard coral density increased through time at 2 m whereas it decreased at 5 m (Table 2.3 and Figure 2.6).

The overall mean density of soft corals (12.6 ± 1.07 col/m²) was approximately ten times greater than that of hard corals. Density was nearly twice as great at 5 m (16.23 ± 1.48 col/m²) as at 2 m (9.04 ± 1.54 col/m²) at site **P** (Site * Depth p = 0.009, Table 2.3). Density of soft corals changed very little through time (Table 2.3). As with cover,

change mainly occurred during the first time interval for site **P** (contrast 1998 vs. 1999: $F_{Time \times Site} = 12.235$, df= 1, $p = 0.003$), but in contrast to the increase in cover, there was a decrease in the density of colonies. Density of other invertebrates and macroalgae had a larger variability compared with soft and hard corals and that precluded the detection of significant trends. Other invertebrates had an overall density of 2.3 ± 0.26 col/m², which did not vary significantly over time, between depths, or between sites. Similarly, macroalgae with an overall mean density of 1.23 ± 0.20 patches/m², decreased in number of patches particularly at 5m at both sites, but that difference was not significant (Figure 2.6, Time * Depth: $p = 0.084$ in Table 2.3).

2.4.6 *New, Dead and Surviving colonies of major groups between sampling times*

Although the total number of colonies remained relatively constant through time (as seen in the previous section), there was a large turnover of colonies between 1998 and 2000 for the groups analysed, *i.e.* a 58% ± 9.2, 38% ± 2.9, and 81% ± 5.3 turnover of colonies for the categories hard coral, soft coral and other invertebrates, respectively. Figure 2.7 shows the contribution of new, dead or surviving colonies to total density between sampling periods. This contribution varied significantly with site or depth in all groups (Table 2.4). For example, hard coral colonies had a 16% lower probability of surviving at site **F** than at site **P** (Figure 2.7). In most cases, however, there was a significant interaction between depth and site (Table 2.4). Therefore, the estimated odds on having a new recruit at 2 m depth are 3.3 times greater in **F** than in **P**.

There were, however, no major differences in the numbers of new, dead or surviving colonies when sampling interval alone was considered, except for the category of dead hard coral colonies (Table 2.4). More hard coral colonies died between Dec-98 and Dec-99 than between Dec-99 and Dec-00, a pattern that was particularly clear in the deeper transects at site **P** (Figure 2.7). For other groups, differences in the number of colonies that recruited, died or survived between time intervals showed an inverse trend between sites (see interaction terms Site * Time in Table 2.4). Hence, soft coral mortality at site **P** was 39% higher during the first year than during the second year, whereas at site **F** it was 68% lower. In summary, there was variability in the processes leading to generation and loss colonies between sites and depth, however they balanced

such that the densities of the groups were similar between the beginning and the end of the two time intervals.

The initial number of colonies during a one-year time interval, added as a covariate to the model decribing the number of new, dead and surviving colonies, did not help to explain the patterns, and did not change the relative importance of Site, Depth and Time. Only in other invertebrates did the initial number of colonies covary significantly with the number of new colonies, eliminating one of the interaction terms.

The number of colonies at the beginning of a time interval was positively correlated with the number of surviving colonies at the end of that year for all groups (Table 2.5). Also, the number of other invertebrates at the beginning of a time interval was positively correlated with the number of surviving hard corals. On the other hand, the number of new colonies of hard corals was negatively related to the initial number of soft coral colonies for the time interval. These correlations, however, do not seem to be very informative. Again, incorporating the number of soft coral colonies as a covariate in a log-linear model to help explain the number of new colonies of hard corals (as suggested from this analysis), did not improve the model and this term was not significant.

2.4.7 *Changes through time of the most common species*

Four taxa dominated at least one replicate transect, *i.e.* they comprised > 50% the living cover. *Sinularia flexibilis*, *Sinularia capitalis* type 1 and type 2, and *Clavularia koellikeri*. Cover in nineteen out of the twenty-one transects was dominated by one of these taxa for at least one sampling time, and in most transects (16 out of 21) throughout the whole study period. Their high relative contribution to cover was unrelated to the total living cover, which ranged from 8 to 66% among transects.

Sinularia flexibilis dominated most (71%) of the transects (15 out of 21), and this occurred at both sites (nine at site **F** and six at site **P**), and at both depths, although at site **P** it was preferentially in deep transects (five out of six, Figure 2.8). *S. capitalis* was dominant in two transects, with no clear pattern (ie, one at site **F** at 2 m shallow for *S. capitalis* type 1, and one at site **P** 5 m for *S. capitalis* type 2), and over all transects

comprised 15% ± 3 of the living cover. *C. koellikeri* had a relatively high cover in two transects, both at site **P** at 2 m. This species was almost absent from **F** at both depths (0.33% ± 0.13 of living cover), and at site **P** it was more abundant in shallow (31% ± 4) than in deep transects (4% ± 1).

S. flexibilis was the only species of these four dominant taxa that significantly increased its relative contribution to the living cover through time (repeated measures ANOVA for cover, defined as percentage of living cover in each transect, $F= 6.23$, $df=2$, $p = 0.006$ for Time, whereas $p> 0.05$ for Site and Interaction terms). As with soft coral and total living cover, this occurred mainly from Dec-98 to Dec-99 at site **P5**, where its contribution to the living cover increased from 66% ± 6 to 74% ± 6. Although the number of observations was insufficient to conduct a similar analysis for the other two species, it was noticeable that their cover decreased during the study period wherever their percentage of living cover was > 50%.

2.5 Discussion

Living cover on inshore coral reefs of the Palm Islands, Central GBR, was reduced by half (from 63 to 33%) between Nov-96 and Dec-98, most likely as a result of the 1998 bleaching event. Cover was reduced for all major sessile macro-invertebrate groups in the community, *i.e.* soft corals, hard corals and other invertebrates, but not for fleshy macroalgae. Some of the variation between pre- (1996) and post- (1998) bleaching cover was likely to be due to differences in the methods employed and differences in study sites. However, a 30% net reduction in living cover is unlikely to result only from the combined effects of these two aspects limiting this comparison. Larger transects employed in 1996 (30 m in length) would result in lower living cover estimations than the 5 m long transect used in 1998 in which large sand patches were avoided. Thus, the reduction in living cover may have been underestimated due to the differences in methods used. Two of the three sites from 1996 do not correspond to the sites monitored in 1998 and onwards. Qualitatively, one of this sites is a very similar environment, whereas the other (Great Palm) has a similar soft coral cover, but more hard coral cover than the other reef sites of the study, potentially contributing to an overestimation of the reduction in hard coral cover. Except for bleaching, no other

disturbance that could have produced such a decrease in living cover (*e.g.* crown-of-thorns outbreaks, storms), had been reported for the central GBR in that period. Furthermore, results from other bleaching studies coincide with the magnitude of reduction in living cover in this study. A study showing that nearshore reefs in the Central GBR were the most severely affected communities (Berkelmans and Oliver 1999), provides corroborative evidence that the 1998 bleaching was primarily responsible for the dramatic change in cover at the Fantome and Pelorus channel sites. The 30% net reduction in living coral cover calculated for these sites is among the largest that has been reported for GBR reefs in recent years. Only 8 out of 47 reefs monitored in long-term studies lost more than 5% of hard coral cover between 1997 and 1999 (AIMS 2001). Five of these were inshore reefs in the Central GBR, where reduced cover was attributed to the 1998 bleaching event.

Although large-scale aerial surveys indicate that nearshore reefs of the Central GBR were the most severely affected by the 1998 bleaching event (Berkelmans and Oliver 1999), few studies have quantified the impact of bleaching on these communities. The 38% reduction in soft coral cover calculated ten months after the bleaching event for the Fantome and Pelorus channel sites, is consistent with a 30% soft coral mortality estimated by Fabricius (1999) three months after the event for five near-shore reefs of the Central GBR. Similarly, the 85% reduction in hard coral cover (8% to 1%) that I have attributed to bleaching is among the highest observed in other studies reporting changes up to eight months after the onset of the bleaching in the region of the Palm Islands (Thompson and Malcolm 1999; Berkelmans 2001). Thus it is likely that my monitoring sites, established ten months after the bleaching in December 1998, provided an appropriate baseline from which to monitor the recovery of these reefs.

My finding that living cover in December 1998 was lowest (18% ± 5) in the shallow (2m) transects at the Pelorus channel site (site **P2**) corresponds to previous studies where shallow water coral reefs have often been more affected by bleaching than deeper water reefs (*e.g.* Glynn 1993; Berkelmans and Oliver 1999; Marshall and Baird 2000). However, living cover did not differ significantly between 2 m and 5 m at the Fantome channel site (**F**), suggesting that bleaching could have affected these sites differently due to variability in local environmental conditions. Although I lack detailed pre-bleaching cover data to properly assess the latter, a number of other studies have found

that there is large variability in the impact of bleaching on reef communities associated with localised differences in environmental conditions (*e.g.* Lang *et al.* 1992; Glynn 1996; Berkelmans and Willis 1999).

Recovery of these inshore reef communities following the 1998 bleaching has been slow. Almost three years (34 months) after the event, mean living cover at all sites and depths, >90% of which is comprised of soft corals, increased by only 15%. The lack of recovery was particularly evident at the Fantome channel site (site **F**), where living cover remained at 37% ± 5 at both depths throughout the study period. Recovery was greater at the Pelorus channel site (site **P**), with nearly 25% increase compared to the pre-bleaching cover in the deeper water community. Similar initial cover in the two sites at deeper transects suggests that the recovery capacity differed between sites.

Hard and soft coral cover lost during the bleaching event was mainly replaced by algal turfs and coralline algae rather than by macroalgae, which are generally stronger competitors of corals (Jompa 2001). A similar pattern, of turfs and coralline algae replacing cover lost by corals instead of macroalgae replacing it, has been reported at two mid-shelf reefs following a crown-of-thorn starfish outbreak on the GBR, with turf and coralline algal assemblages comprising 4 – 18% of the total cover seven years later (Done *et al* 1991). Turfs and corallines have also been reported to colonise dead patches of massive *Porites* spp. after bleaching events (Diaz and McCook *in press*). In general, fleshy macroalgae on reefs of the Palm Islands have low cover compared to the much higher cover on other nearby inshore reefs (Jompa 2001; Diaz and McCook *in press*), with cover <3% both before and after the bleaching in this study. Given that turf and coralline algae provide a better substratum for the recruitment of corals than fleshy macroalgae (Morse *et al.* 1988; Slattery *et al.* 1999; McCook 2001), there is a better prognosis for the recovery of coral assemblages at the study reefs than at other inshore reefs. Thus, although their recovery has been slow (as discussed above), it could have been even slower if macroalgae had taken precedence over turf and coralline algae in the recovering assemblage.

This study is the first to demonstrate that disturbances such as bleaching events can have impacts on the soft coral assemblages over more than 3 years. Although short-term impacts such as bleaching-related mortality have been recorded for soft corals

(Fabricius 1999), there has been a lack of understanding about the longer term implications of bleaching disturbances for this group. This is in contrast to the growing body of evidence documenting long-term effects of bleaching on the reproduction and growth of hard corals (*e.g.* Szmant and Gassman 1990; Goreau and McFarlane 1990; Meesters and Bak 1993; Glynn *et al* 2000). It is clear from my study that more than three years are required for soft coral communities, such as those on inshore reefs in the Palm Island group, to regain their pre-bleaching living cover. These results are in agreement with studies that have shown that bleaching may reduce the reproductive output of soft corals for up to two years following bleaching (Michalek-Wagner and Willis 2001).

The similar or even slower recovery rate found at sites with higher initial soft coral cover, suggests that although asexual reproduction of surviving soft coral colonies contributed to the recovery rate (see Chapter 3), it did not necessarily translate into a fast recovery rate. Clonal propagation and allelochemical interactions have been indicated as the major potential mechanisms that allow soft corals to rapidly gain and maintain occupied space, conferring competitive superiority over hard corals (*e.g.* Aceret *et al.* 1995). Some Xeniidae and Nephtheidae genera have been shown to have very high rates of asexual reproduction. On the GBR, *Efflatounaria* is able to asexually produce 11 daughter colonies of 2 – 5 cm diameter per m^2 in less than 3 months (Dinesen 1985), and enhanced survival at high density suggests that they are able to maintain high cover in this manner (Karlson *et al.* 1996). *Dendronephthya hemprichi* in the Red Sea is able to produce fragments of 2 – 5 mm in length by autotomy within two days, and recruits from this mechanism on artificial substrata can reach > 1 individual per cm^2 in 52 days (Dahan and Benayahu 1997). However, such high rates of asexual reproduction cannot be extrapolated as a general feature of other species of soft corals (Order Alcyonacea). A population genetic study indicates that sexual reproduction constitute the main reproductive mode in *Sinularia flexibilis* when colonies are sampled at >5 m (Bastidas *et al.* 2001). Species of the alcyoniidae *Sinularia* and *Sarcophyton* on mid- and outer-shelf reefs appeared to reproduce largely aclonally (Fabricius 1995), and the same appears to be true for the 6 genera of Alcyoniidae monitored on near-shore reefs in this study.

Results from this study contrast with the perception that soft corals colonise disturbed sites quickly and, by doing so inhibit hard coral recovery (*e.g.* Endean *et al.* 1988). Although it has been shown that *Sinularia* and *Sarcophyton* (Alcyoniidae) from mid- and outer-shelf reefs in the GBR have a slow turnover rate (Fabricius 1995), these genera do not form extensive aggregations on these reefs (Fabricius 1998). Thus, I initially hypothesised that their domination of some near-shore reefs could be a consequence of higher growth and turnover rates in these environments. However, although I found that they have turnover rates of nearly 40% per year, this does not translate to a rapid change in biomass on the reef, at least for three years after a bleaching event. Growth rates and survivorship have also been shown to be variable among temperate alcyoniids. *Alcyonium acaule* in the Mediterranean was found to have a slow growth rate and there was little evidence of fission (Garrabou 1999), as was similar to findings for *Sinularia* and *Sarcophyton* on mid- and outer-shelf reefs in the GBR (Fabricius 1995). In contrast, *Alcyonium* sp. in the north-western Pacific had high turnover rates despite populations maintaining constant densities (McFadden 1991), similar to the results I found for *Sinularia* in the present study (see Chapter 3).

This study, combined with evidence from other large-scale and/or long-term studies (Fabricius 1997; Sweatman *et al.* 1998; Ninio *et al.* 2000), suggests that soft coral dominated communities are not a consequence of disturbances on reefs. On the GBR, six major bleaching events have occurred in the past 20 years (Berkelmans 2001) and considering the frequency of other events such as crown-of-thorn outbreaks (*e.g.* Moran *et al.* 1988) and cyclones (Done 1992a), the periodicity of major disturbances is relatively high. Given that the results of my study suggest that establishment of soft coral dominance may take as long as the frequency of these disturbances, or at least as long as it takes hard corals to recover, it seems unlikely that soft coral dominated communities are a consequence of disturbance. In contrast, shifts to communities dominated by turf algae and/or fleshy macroalgae have occurred within the first year of bleaching (*e.g.* Ostrander *et al.* 2000; McClanahan *et al.* 2001) or within five years of other major disturbances (*e.g.* Done 1992; Hughes 1994).

The occurrence of soft coral dominated communities, particularly on inshore reefs of the GBR (Fabricius 1997) may result from a combination of physical, and/or biological factors rather than being a consequence of the disturbance regime. For example, water

flow, concentrations of suspended particulate matter (*e.g.* Fabricius and Dommisse 2000), and strong pre-emptive substrate occupancy may favour soft coral rather than hard coral recruitment. Under these conditions, soft coral dominance may represent only one of several alternative phases in community structure, but the apparent stability of this state is more consistent with the conclusion that these are relatively undisturbed communities, rather than the opposite. While my study has demonstrated that inshore soft coral assemblages may recover slowly following a major disturbance, further studies of these soft coral dominated communities will provide insights into their stability and ecological role.

In summary, a near-shore, soft coral-dominated community on the GBR experienced a 30% decline in living cover, most likely as a result of the severe 1998 bleaching. Thirty-four months after the start of the event, this community has shown minor changes towards recovery and still appears to have a long way to re-establish its pre-bleaching cover. During the study period, this community increased between 7 and 11% in living cover at one site (**P**, the Pelorus channel site), but showed no signs of recovery at the other (**F**, the Fantome channel site), despite a >30% turnover of colonies at both sites. This study supports warnings about the potential long-term, damaging effects of bleaching on coral reef communities. It also suggests that local dominance by soft corals on near-shore reef environments in the GBR is likely to take more than three years to become established.

Table 2.1. Genera and Families of hard and soft corals recorded within the transects. Number of colonies refers to unique colonies observed during part or the entire study period.

	Family	Genus	No. cols
Hard Corals	Acroporidae	*Acropora*	81
		Montipora	9
	Agariciidae	*Pachyseris*	1
	Faviidae	*Favia*	25
		Favites	16
		Goniastrea	1
		Platygyra	9
	Fungiidae	*Fungia*	5
	Mussidae	*Symphyllia*	1
	Oculinidae	*Galaxea*	5
	Pocilloporidae	*Pocillopora*	2
		Stylophora	4
	Poritidae	*Porites*	23
		Goniopora	2
		Unidentified	94
Soft Corals	Alcyoniidae	*Klyxum*	1
		Cladiella	16
		Lobophytum	60
		Sarcophyton	52
		Sinularia	1770
	Briareidae	*Briareum*	17
	Clavulariidae	*Clavularia*	188
	Ellisellidae	*Juncella*	3
		Unidentified	77

Table 2.2. Repeated measures ANOVA testing for differences in cover of the major benthic groups over Site, Depth and Time. Bold numbers indicate significance at p <0.05. HC= Hard corals, SC= soft corals, OI= other invertebrates, AL= fleshy macroalgae.

		HC		SC		OI		AL	
Source	df	F	Sig.	F	Sig.	F	Sig.	F	Sig.
Between Subject Effects									
SITE	1	15.189	**.001**	.513	.484	19.320	**.000**	.002	.961
DEPTH	1	4.335	.053	2.437	.137	2.959	.104	5.740	**.028**
SITE * DEPTH	1	1.802	.197	4.756	**.044**	.304	.589	7.390	**.015**
Error	17								
Within subject effects									
TIME	2	3.068	.060	3.690	**.035**	1.210	.311	1.668	.204
TIME * SITE	2	2.524	.095	3.275	.050	.054	.948	4.060	**.026**
TIME * DEPTH	2	1.425	.255	1.072	.354	.675	.516	10.314	**.000**
TIME * SITE * DEPTH	2	1.797	.181	.502	.610	.274	.762	.487	.619
Error (TIME)	34								

Table 2.3. Repeated measures ANOVA testing for differences in colony density of the major benthic groups over Site, Depth and Time. Bold numbers indicate significance at p <0.05. Abbreviations as in Table 2.2.

		HC		SC		OI		AL	
Source	df	F	Sig.	F	Sig.	F	Sig.	F	Sig.
Between Subject Effects									
SITE	1	6.856	**.018**	1.840	.193	.380	.546	2.426	.138
DEPTH	1	.516	.482	11.305	**.004**	.600	.449	.439	.517
SITE * DEPTH	1	.322	.578	8.702	**.009**	1.408	.252	3.230	.090
Error	17								
Within subject effects									
TIME	2	3.037	.061	.999	.379	.575	.568	2.490	.098
TIME * SITE	2	1.684	.201	3.305	**.049**	2.125	.135	1.442	.250
TIME * DEPTH	2	8.439	**.001**	2.323	.113	1.320	.281	2.667	.084
TIME * SITE * DEPTH	2	1.850	.173	.300	.743	.203	.817	.700	.504
Error (TIME)	34								

Table 2.4. Effect of Site, Depth, and Time Interval (Dec-98 to Dec-99, and Dec-99 to Dec-00) on the New, Dead and Surviving (Surv) colonies between time intervals. Benthic groups abbreviated as in Table 2.2. The number of colonies in the 1st year of the time interval (N) was evaluated as a covariate in the model. Asterisks indicate significant terms in the log-linear model using the 95% confidence interval criterion.

	Group	No. cols (N)	No. cols in 1st year	Site (S)	Depth (D)	Time (T)	S*D	S*T	D*T
New	SC	867		*	*		*		
	HC	118							
	OI	327	*	*			*	*	
Dead	SC	937					*	*	
	HC	145			*	*	*	*	
	OI	356			*				
Surv	SC	1647		*			*		
	HC	134		*					
	OI	106		*			*		

Table 2.5. Correlation between the initial number of colonies and the number of new, dead and surviving colonies after one year. The beginning and end of each of the two time intervals (1998-1999 and 1999-2000) were pooled, and the analysis is based on individual transects. Hard corals= HC, soft corals= SC, other invertebrates= OI. Signs indicate the nature (positive or negative) of the significant associations, based on a p= 0.01 level of the Spearman's correlation rank test. Empty cells indicate no significant association.

		Group	No. of colonies at the beginning of a time interval		
			HC	SC	OI
No. of cols at the end of a time interval	New	HC	+	-	
		SC		+	
		OI			
	Dead	HC	+		
		SC		+	
		OI			+
	Surviving	HC	+		+
		SC		+	
		OI	+		+

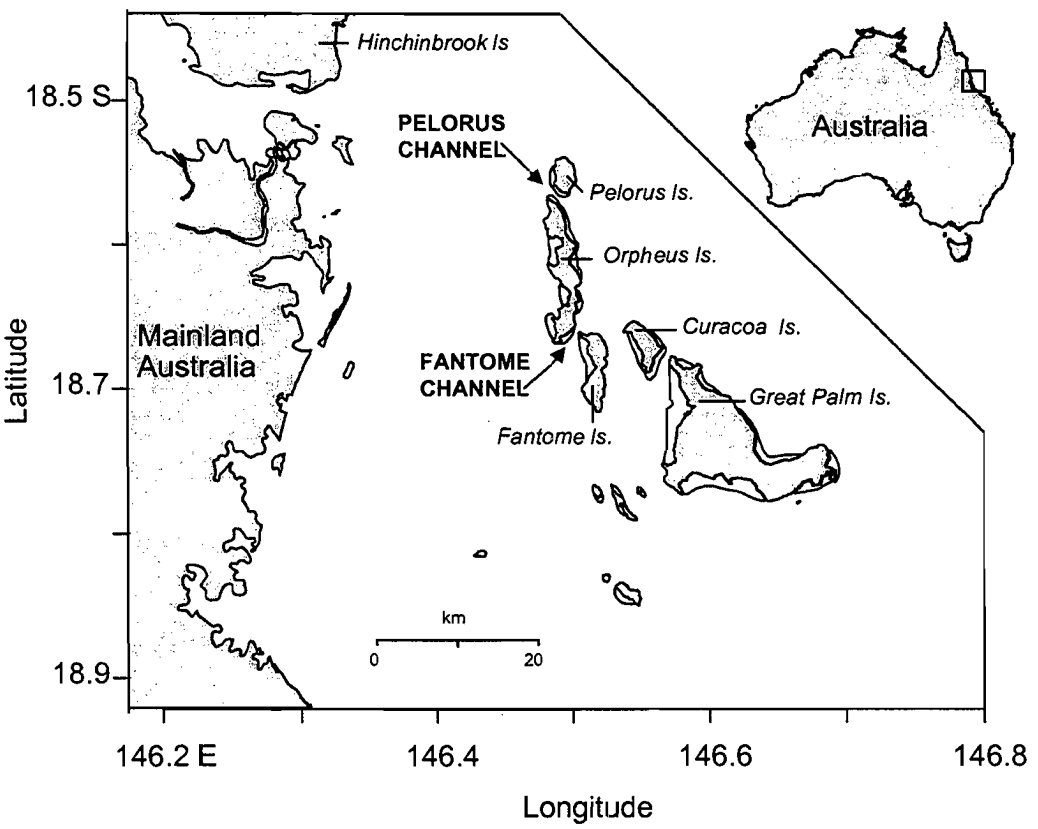

Figure 2.1. Study location within the Great Barrier Reef Australia and detail of the Palm Islands. Arrows point to the two study sites: Pelorus channel (P) and Fantome channel (F).

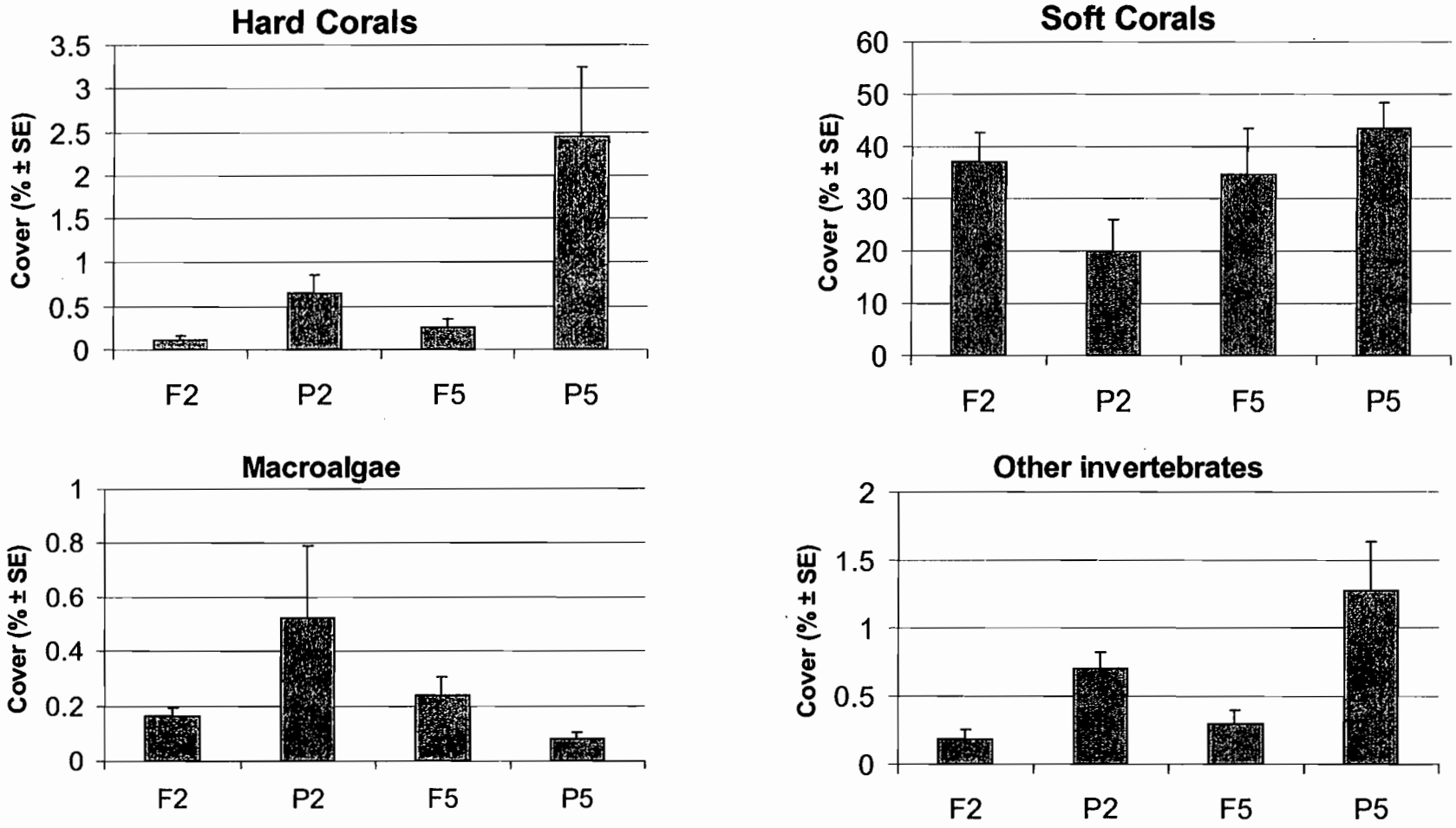

Figure 2.2. Percent cover of major benthic groups after the 1998-bleaching event, averaged over three sampling times to illustrate major trends among sites and depth. F = Orpheus-Fantome channel, P= Orpheus-Pelorus channel. Number in labels is depth in metres. N = 15 transects for each combination of site and depth (except P5: N = 18).

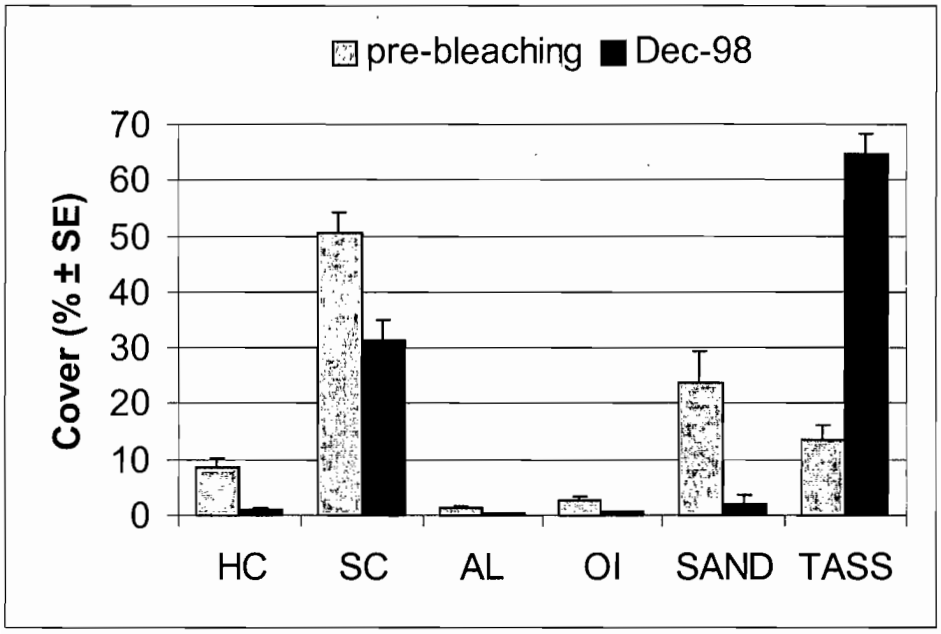

Figure 2.3. Percent cover of major benthic groups and substrata pre-bleaching (grey-bars), and 10 months after the onset of bleaching (black bars). HC = Hard corals, SC = soft corals, AL= fleshy macroalgae, OI = other invertebrates, TASS = turf algae and other suitable substrata.

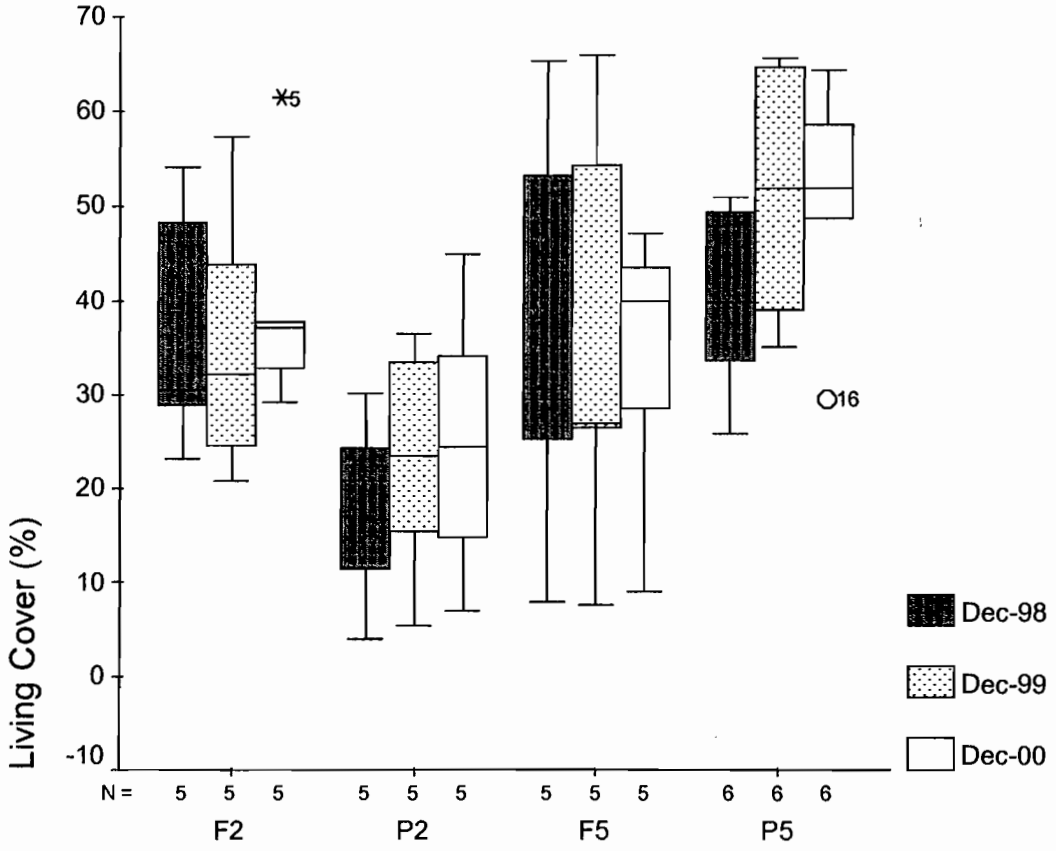

Figure 2.4. Change in total living cover over time at sites Fantome (F) and Pelorus (P), and at 2 and 5 m depths. Horizontal lines are the medians, boxes represent 50% of the data, and whiskers show extreme values (excluding outliers).

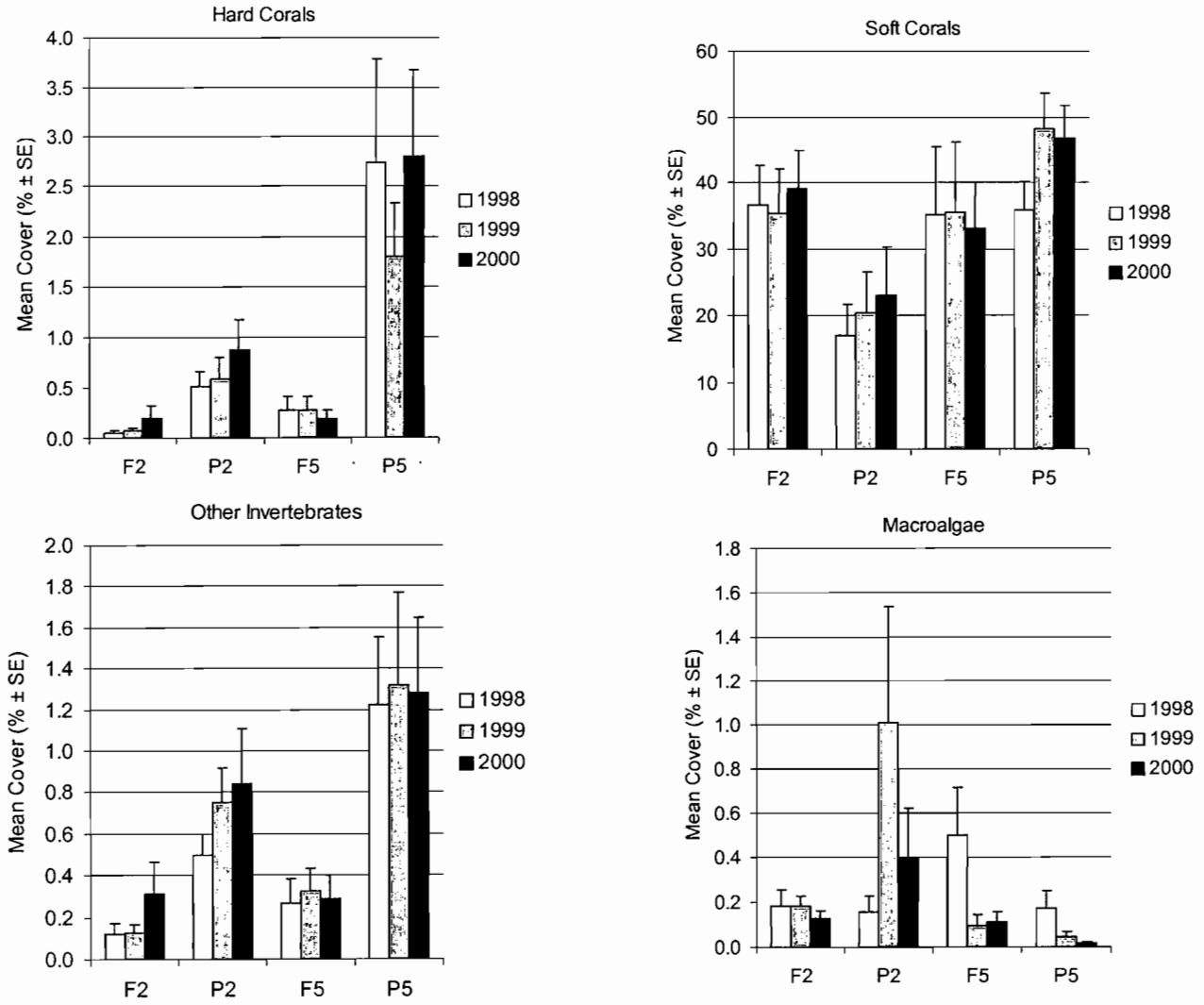

Figure 2.5. Change in cover of major benthic groups over time at sites Fantome (F) and Pelorus (P), and at 2 and 5 m depths.

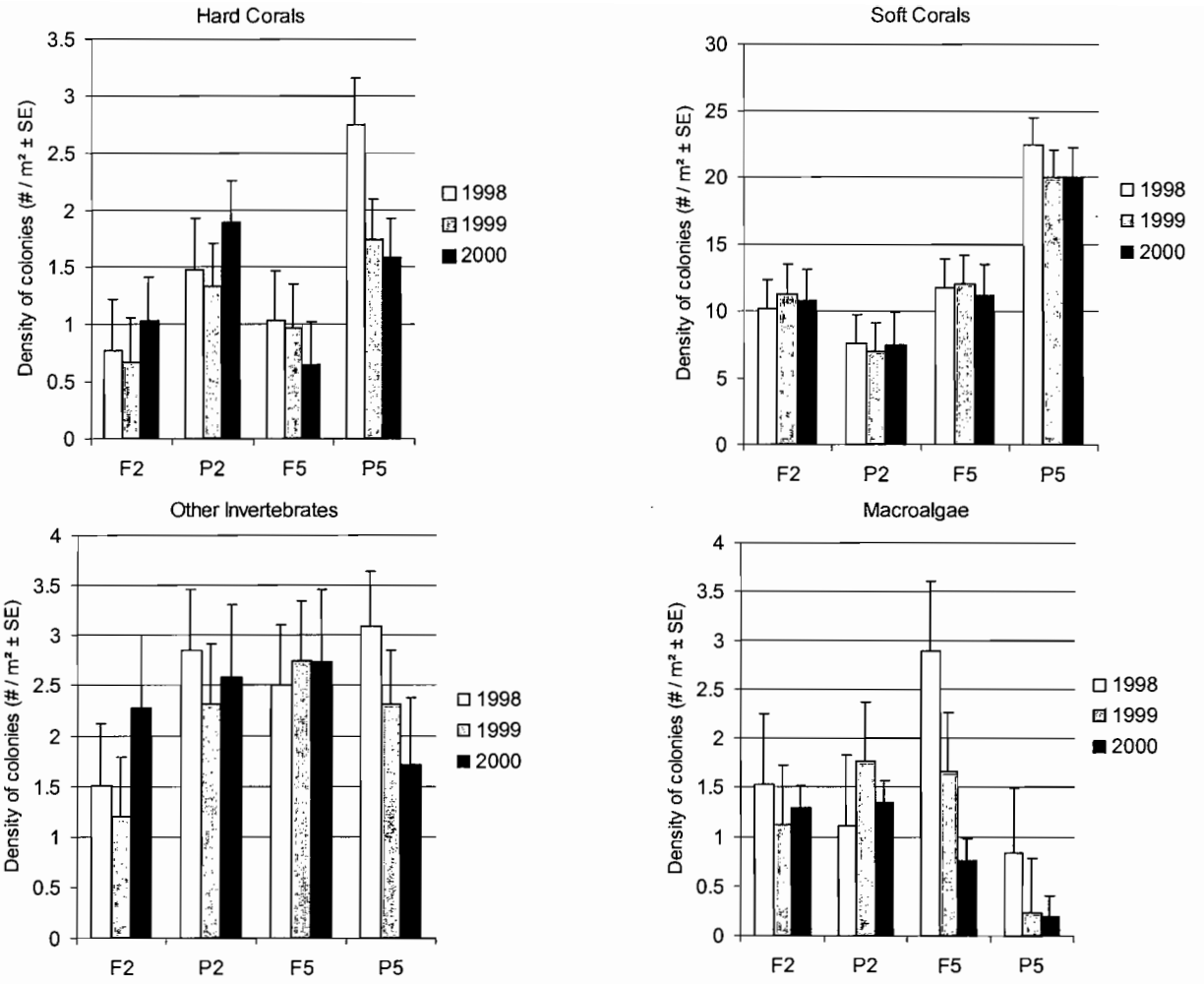

Figure 2.6 .Change in density of colonies of major benthic groups over time at sites Fantome (F) and Pelorus (P), and at 2 and 5 m depths.

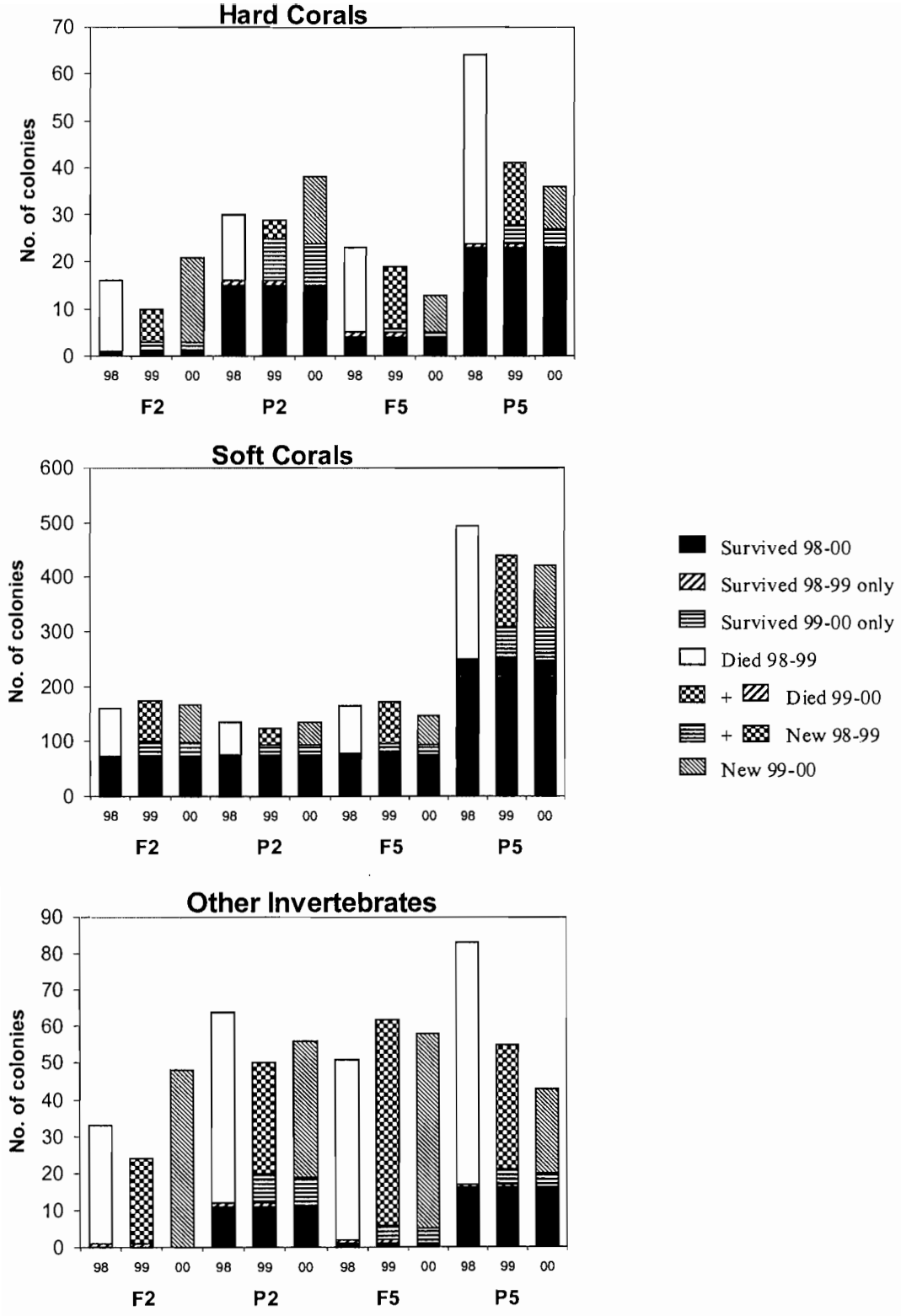

Figure 2.7. Number of colonies that survived, recruited and died between sampling times at sites Fantome (F) and Pelorus (P), and at 2 and 5 m depths.

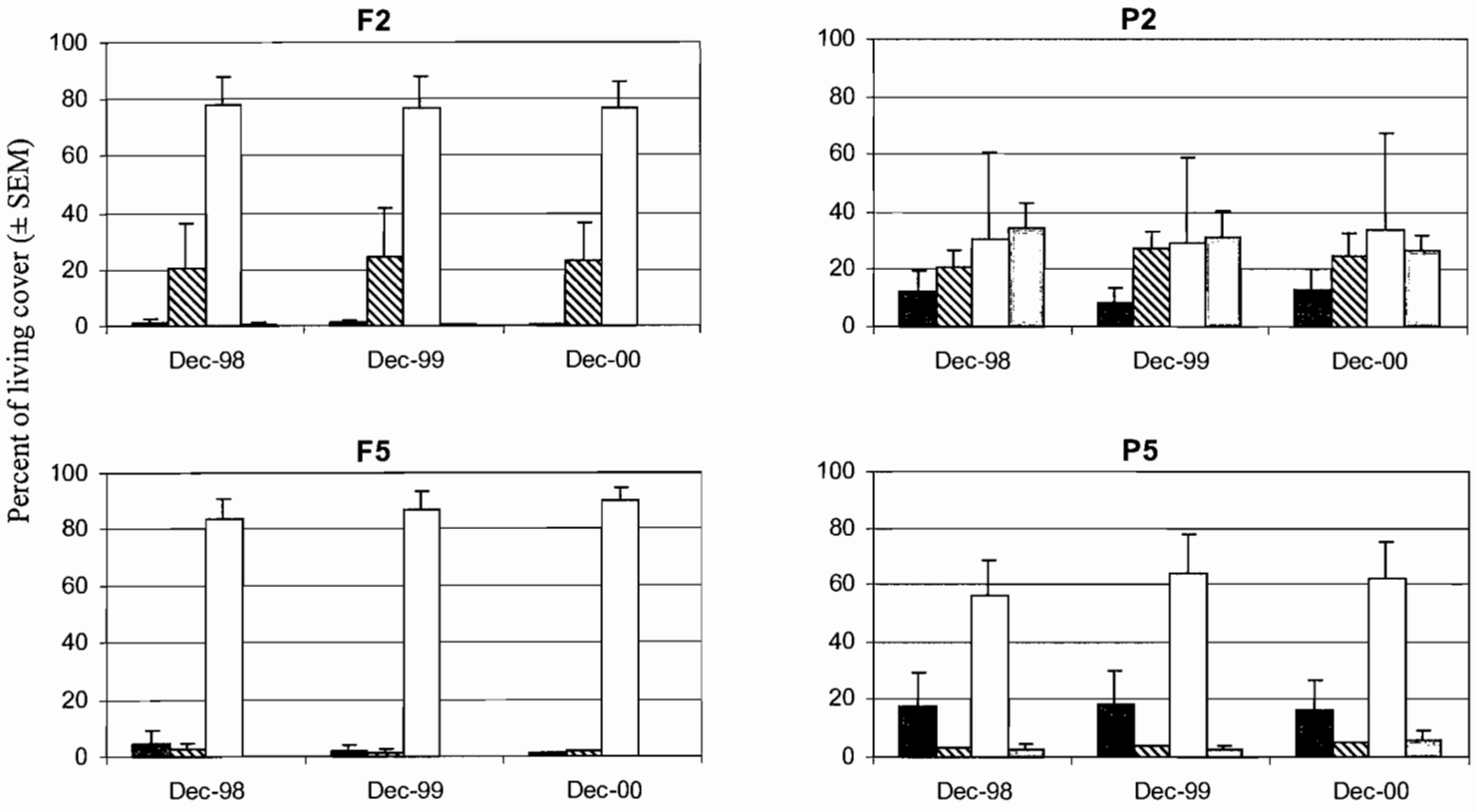

Figure 2.8. Contribution to living cover of the four most abundant taxa at sites Fantome (F) and Pelorus (P), and at 2 and 5 m depths. Solid black and diagonally striped bars = *Sinularia capitalis* type 1 and type 2; Solid white bar = *Sinularia flexibilis*; Grey bar = *Clavularia koellikeri.*

3 Demography of *Sinularia flexibilis*

3.1 Abstract

In this demographic study, I assessed the role that population dynamics plays in the formation of local aggregations of *Sinularia flexibilis,* a soft coral that commonly dominates nearshore coral reefs of the GBR. Two populations on nearshore fringing reefs of the Palm Islands were studied at three yearly samplings, starting 10 months after the 1998 bleaching mortality. Changes in size frequency distributions indicated that larger colonies were becoming more prevalent, with mean colony size increasing by 35% (from 276 cm^2 in 1998 to 373 cm^2 in 2000). Smaller colonies grew proportionally more than larger colonies. Growth data were fitted to a function of change in size in relation to initial size resulting in an expected mean annual growth of 128 cm^2 for a 50-cm^2 colony, in contrast to an expected decrease in size of 72 cm^2 for a 700-cm^2 colony (R^2 = 0.915). Zero growth was predicted for colonies having a mean size of 532 ± 21 cm^2, after which colonies would most likely undergo fission or shrink. Forty-three percent of colonies were undergoing fission at any given time at both localities. The majority of new colonies were produced by fission (70%, N = 285), but also by recruitment of sexual larvae (19%) and by the movement of colonies (11%). The density of sexual and asexual recruits was 0.24 and 1.0 recruits•m^{-2}•$year^{-1}$, respectively. Demographic parameters of *S. flexibilis* estimated from a time-invariant matrix model differed between time intervals and between localities. At both localities, the yearly growth rate of the populations (λ) was significantly higher in the first than in the second time interval (98-99 and 99-00). Assuming a constant growth rate through time, populations such as those in the present study (i.e. ~ 6 colonies•m^{-2}) could double in size in four or five years at the highest and at the lowest λ, respectively. By alternating matrices randomly through time on the assumption that observed differences between time intervals and localities are representative of temporal and spatial variability of λ, the projected population size would still increase even without sexual recruitment. In contrast to most studies on clonal species so far, changes in each demographic process (growth, fission and shrinkage, and stasis) could have the same relative contribution to changes in population growth for this species.

3.2 Introduction

The demographic study of the soft coral *Sinularia flexibilis* had two purposes. Firstly, I aimed to contribute to the understanding of demographic processes (growth, reproduction, and mortality) in sessile clonal organisms in general. Despite comprising a large group of species and being represented in most phyla, clonal animals have received little attention compared to aclonal animals or clonal plants (Hughes and Cancino 1985, Tanner 2001). Clonal species are characterised by morphological flexibility, and often by the potential to grow rapidly and attain large sizes. In sessile clonal species, these characteristics may result in a rapid production of many new clones allowing the formation of large aggregations, particularly for species that competitively acquire substrata (Hughes and Cancino 1985). However, the asexual propagules of some sessile species have the potential to be more mobile than previously thought (e.g. Stoddart 1983; Dahan and Benayahu 1997). The great capacity of clones to survive, recover from partial mortality, and have a long life-span confers many advantages to these species in comparison to aclonal organisms (Hughes and Cancino 1985, Jackson 1985). All these life history differences between clonal and aclonal organisms have led to major differences in their demographies (Hughes and Jackson 1980, Hughes 1984, Tanner 2001). However, these differences have not yet been fully explored in marine clonal organisms mainly due to their diversity and ample variety of life histories.

Secondly, I aimed to examine the population dynamics of a soft coral capable of forming extensive aggregations in inshore coral reef communities. In particular, population growth rates were used to determine the time-scales required for the formation of aggregations. I also evaluated the potential contribution of different demographic processes to the population growth rate. Opportunistic recruitment and growth following disturbances and the competitive abilities of soft corals are the main plausible mechanisms leading to local dominance. An understanding of the relative importance of these mechanisms, coupled with estimations of the time necessary for establishment of aggregations, would reveal the extent to which aggregations could be interpreted as a sign of disturbance in a reef community.

To accomplish these aims, I examined the demography of *Sinularia flexibilis* by repeated direct observation of colonies within permanent transects and by population projections using matrix models. Matrix projection models have been used to examine populations to determine the importance of demographic processes and to make recommendations for the management of many species (Heppel *et al.* 2000). Matrices provide a way to summarise life history information and compare population dynamics of species with very different strategies (Caswell 2001). In clonal marine organisms, such analysis has provided important insights into the life histories of anthozoan species (*e.g.* Hughes 1984, Done 1987, Gotelli, 1991, Lasker, 1990, McFadden 1991, Tanner *et al.* 1994, Tanner 1997, Hughes and Tanner 2000). I also used elasticity analysis to quantify the relative contribution of various demographic processes to population growth rate. Elasticity analysis is a powerful tool that has become popular in conservation biology to indicate which demographic parameters should be the focus of management (de Kroon *et al.* 2000). It can also be used to determine the effects of harvesting on populations and the effectiveness of control measures on pest and invasive species (de Kroon *et al.* 2000 and references therein).

Relatively few studies have examined demographic aspects of soft coral populations on the Great Barrier Reef (*e.g.* Dinesen 1985 and Karlson *et al.* 1996: *Efflatounaria*; Lasker 1988: *Nephthea* and *Xenia;* and Fabricius 1995: *Sinularia* and *Sarcophyton*) and all of them were conducted on mid- and outer-shelf reefs. Only one study (Gilmour 1994) has investigated the population structure of a soft coral species (*Sinularia capitalis*) on a nearshore reef. These studies have shown that there is large variability in the life histories of soft coral populations on offshore reefs as well as providing insights into their biology and ecology. However, there is a lack of similar studies of soft coral species on inshore reefs, which is also where soft corals of the Alcyoniina and Stolonifera groups tend to form the largest aggregations. The aim of this study was to use demographic data to estimate the population dynamics of the common inshore soft coral, *Sinularia flexibilis,* and to determine which life history characters of this species are important in the formation of aggregations on nearshore reefs of the GBR.

3.3 Methods

3.3.1 *Population size structure and estimates of vital rates*

Data were obtained at the sites described in section 2.3.1 and following procedures described in section 2.3.2. As in the previous chapter, study sites (or localities) will be hereafter referred to as Pelorus (or P) for the Orpheus-Pelorus channel and Fantome (or F) for the Orpheus-Fantome channel. Since the fate of colonies at the transect borders could not be reliably determined, to estimate the demographic parameters I selected only those colonies that were completely within the area of the transects on all three sampling occasions. Although this may lead to underestimate of the density of colonies it is necessary to determine the fate of the colonies.

To determine the appropriate number of size classes, I examined the size distribution of the species using 100 cm^2 increments up to the largest size class of 2100 cm^2 for each sampling year (Figure 3.1). I then established six size classes so as to have: 1. a roughly equal number of colonies within each class; and 2. an increment of at least 30% between the upper bound of a class and the midpoint of the next class to accommodate variable states of colony expansion and contraction. The 30% criterion was based on observations that *S. flexibilis* colonies can naturally contract by up to 10% of their size (see section 2.3.2), which was then arbitrarily increased three-fold to be conservative. These size classes thus accommodate natural contraction, i.e. without a specific perturbation to the colony, whereas a disturbed colony can contract to about 50% of its initial size. Soft corals naturally contract and expand in response to current strength (Fabricius *et al.* 1995, C. Bastidas, personal observations) or in diurnal, tide-related and seasonal cycles (Hartnoll 1978 and references therein). The largest size classes were pooled in some instances for statistical analyses to avoid empty cells per class, as specified accordingly throughout the text.

The size distribution of colonies was compared among sites, depths and sampling years with a log-linear model. This model analyses a contingency table in a similar way as an ANOVA analyses a continuous variable, by expressing the natural logarithm of the expected frequency of each cell as a function of the mean logarithm of the expected

frequencies of the factors of interest (Sokal and Rohlf 1995). The G-statistic (or likelihood ratio) is computed for the model with and without a term of interest, and the difference between the G values (or partial Chi-square) indicates the significance of that term (*i.e.* a factor or an interaction). For this particular analysis I used five size classes instead of six, by pooling the frequencies of the two largest size classes to avoid empty cells.

Of the 1,747 colonies analysed, I used those that were common to the three sampling times and those that had recruited by 1999, and by 2000, respectively, to estimate individual colony growth (Table 3.1). New recruits were assumed to settle soon after the mass spawning; thus, colony size at the end of a census interval was assumed to represent one year of growth. Annual growth estimates were based on measurements of 1,166 colonies: 589 from the 1998-1999 time interval (*i.e.* 448 colonies that survived from 1998 and 141 new colonies by 1999) and 577 from 1999-2000 (433 surviving from 1999 and 144 new colonies by 2000). Of the 1,166 colonies for growth estimation (589 + 577), 433 were common to both time intervals (353 present in 1998,1999 and 2000 plus 80 of the 285 new colonies that survived from 1999 until 2000).

To estimate the relationship between the change in size over a year in relation to the initial size of colonies, I used Francis' (1995) non-linear model, which describes growth as a function of size and estimates growth from mark-recapture data. For this I used a program provided by Ebert (1999). The parameters from the model (mean annual growth at two specified sizes, and the shape of the curve) were compared for various conditions. More specifically, I estimated the parameters under the following conditions: assuming the initial size of new colonies to be either zero or 20 cm^2 (conditions 1 and 2); excluding the five largest and five smallest outliers (condition 3); separating the two time intervals (conditions 4 and 5); excluding new colonies (condition 6); and excluding colonies that divided (condition 7). These conditions were cumulative, such that the base condition is the immediate previous one (*e.g.* condition 3 was applied using colonies 20 cm^2 of initial size, which is condition 2). An initial size of 20 cm^2 for recruits was based on an approximate detection limit of 2.5 cm of colony radius in the images. Although 69 colonies < 20 cm^2 were detected in the images, colonies smaller than this were difficult to see, either because of their small size, or due to overshadowing by bigger colonies.

Colony growth and its relation to time interval and initial size, were further investigated using log-linear models. To ensure independence of the samples, for one time interval I sampled randomly half of the colonies present in both time intervals, and used the remaining for the other interval (413 colonies in 1998-99 and 405 colonies in 1999-2000). Colony growth was defined as the annual change in size expressed as a proportion of the initial size, *i.e.* x = (Size at time 2 - Size at time 1)/ Size at time 1. Using five initial size classes (pooling the last two size classes in Table 3.1), I grouped colony growth into four categories, as follows: $x < -0.3$ (shrinkage); $-0.3 < x < 0.3$ (no growth); $0.3 < x < 1$ (growth); and, $1 < x < 100$ (rapid growth). Thus, the first growth category corresponds to shrinkage below 30% of the initial size. The second growth category was interpreted as no change in size through time. The third growth category indicates growth over the 30% of its initial size up to doubling in size, and the fourth category indicates growth above doubling in size.

The incidence of asexual reproduction (fission) was derived from the photographic record of the transects (see Section 2.3.2), as was most of the data in this chapter, but it was strongly supplemented by observations in the field. Additional field data from intermediate sampling times (within a year) were also used. To verify the existence of sexual reproduction, I assessed the presence and size of gonads by examining branch pieces of 1 – 2 cm in length under the dissecting microscope. Using this method, I estimated the number of eggs per polyp for three to four branches in each of three replicate colonies. Eggs in a late stage of maturity, from collections made one to three weeks before mass spawning, were measured under the microscope in four colonies. Histological preparation of branch tips was also done using standard embedding in wax and staining with the Mayer's Haematoxilin and Young's Eosin – Erythrosin procedure (Woods and Ellis 1994). In this case, between two and six branch tips were collected from each of 29 colonies comprising the range of sizes observed, prepared for histological serial sections and checked for the presence and size of gonads.

3.3.2 *Demographic analysis*

As a preliminary step in the demographic analysis of *S. flexibilis*, I used a simple transition matrix model (density independent and time-invariant, Caswell 2001) to project the population growth based on a constant matrix. This matrix was calculated

from the fate of colonies (size changes, death, recruitment) in one year interval (*i.e.* from data in Table 3.1). The previous analyses using log-linear models suggested that it could also be relevant to calculate the transition matrices for both localities and time intervals separately. The interdependence among the factors Time Interval, Locality, Size (at the beginning of the time interval), and Fate was examined by sequentially eliminating a term from a log-linear model that included these factors. Once a term was eliminated, the model was compared with the one that included all the terms (the saturated one) using the likelihood ratio as a measure of goodness-of-fit. For this I used the general log-linear analysis procedure in SPSS, and I used three size classes (< 75, <150, < 2100 cm^2) and an additional class that represented the dead colonies by the end of the time interval.

Matrices for the two Localities and the two Time intervals were calculated separately, resulting in four matrices: Fantome 1998-1999, Fantome 1999-2000, Pelorus 1998-1999, and Pelorus 1999-2000. The four matrices were used to examine the influence of Time Interval and Locality on the population growth using four size classes: < 75, < 150, < 250, and < 2100 cm^2, hereafter referred to as classes I, II, III, and IV respectively. These matrices were constructed based on the life cycle presented in Figure 3.2.

To determine the relative influence of sexual and asexual reproduction on the demography of *S. flexibilis*, three matrices were calculated: one without terms for fission and sexual fertility, one with a term for fission but not sexual fertility, and one with both fission and sexual fertility included (see Table 3.2 for full matrices used throughout this study and Table 3.3 for examples of calculations). I did not include the option of sexual but no fission fertility because it would result in an intermediate case between the first and second matrix, due to the way in which the fertility terms were calculated. I will use the term fission fertility to refer to the production per capita of daughter colonies by fission.

Sexual fertility was estimated using the number of recruits into the transects (regardless of their origin) as a proxy for the number of recruits that adult colonies in the same area would produce. It was calculated as the number of colonies recruited into size class I (not considered asexual recruits) divided by the total number of colonies in classes II,

III and IV at the beginning of the interval. Thus, larvae produced at the beginning of the interval (in the spawning of December) were assumed to be able to recruit into size class I in one year. The fission and sexual fertility were incorporated into the respective matrices by adding these terms to the shrinkage and survival probabilities (Table 3.3). I also compared, for the same number of sexual recruits, the projected population size obtained by using the sexual fertility incorporated into the matrix with that obtained by adding recruits to class I each year as an external input, *i.e.* comparing open to close populations.

Demographic statistics were calculated following procedures in Caswell (2001) and Roughgarden (1998) for Matlab (version 6.0.0.88, Math Works Inc.), and the software PopTools (version 2.2, G. Hood 2001). Time to extinction was assumed to be the time required for the initial number of colonies to be reduced to one individual. Life expectancy was calculated by adding up all the years an individual of class I was expected to spend in each size class. The 95% confidence interval of the population growth rate (λ) was estimated with the bias-corrected and accelerated method from 2,000 random resamplings (with replacement) of the appropriate data set (*e.g.* Fantome, 98-99). Each resampling was used to calculate a population transition matrix and its respective λ. Comparisons of the population growth rate among the four matrices and the calculation of their confidence limits were done only for projection matrices that included fission as the sole reproductive mechanism. I did this for these matrices only because the sexual fertility made a little contribution to λ; it was unlikely to change the variability among year intervals and sites; it is likely to vary in time, and it would facilitate the comparisons with studies of other anthozoans that have calculated λ this way. Population projections with random alternation of the four matrices were performed with calculations and software provided by Ebert (1999).

To determine the relative importance of the demographic processes to the population growth rate, the elasticities of λ were also calculated for the matrices. A proportional change to a demographic process (*e.g.* a 10% increase of a transition probability of the matrix) would produce a change in λ that would be reflected in the elasticity value of λ to that transition (Caswell 2001).

To examine the effect of the transitions on the variability of population growth rates under the different factors (locality and years), a life table response experiment was done. For this, I used the procedure for random designs described in Caswell (2001). Particularly, I examined the covariances among the transitions of the four matrices, as well as the contributions of these covariances to the variance of λ.

3.4 Results

3.4.1 *Population size structure and colony growth estimates*

The size frequency distribution of *S. flexibilis* colonies shows that more than 90% of the colonies recorded during the study were smaller than 800 cm^2, while the maximum size measured was 2018 cm^2 (Figure 3.1).

The number of *S. flexibilis* colonies varied significantly in response to all four factors analysed – Size class, Locality, Depth and sampling Time – either when they represented main factors, or when they interacted with another factor (Table 3.4). The term Time x Site x Size Class was the only significant third-order interaction, indicating that the number of colonies in different size classes varied differently through time between the two sites. This was mainly the result of a significant change in colony numbers through time at Pelorus but not at Fantome. The nature of these variations in size structure is exemplified in Figure 3.3. At Pelorus, the number of colonies in the larger size classes increased, while those in the smaller size classes decreased (Figure 3.3). The main difference between localities was a higher relative number of large colonies at Fantome compared with Pelorus. As the frequency of small size classes was similar, it is suggested that this difference may correspond to local conditions that favour larger sizes at Fantome than at Pelorus. Thus, during the study, colonies were on average 60% larger at Fantome (mean size ± SE = 380 ± 12 cm^2 , N= 762) than at Pelorus (232 ± 6 cm^2, N = 985).

The most important change through time was a sharp decline in colonies < 100 cm^2 after 1998 (Figure 3.1). Also, *S. flexibilis* showed an increase in the relative number of large colonies, mainly in the 750-cm^2 class, at both sites. As a result of changes in the size distribution of colonies through time, the size of colonies at all percentiles was displaced towards larger sizes, mainly during the first time interval. For example, mean size at percentile 50 (or median) was 208 cm^2 in 1998, 310 cm^2 in 1999, and 303 cm^2 in 2000, and at percentile 75 mean size was 347, 486, and 510 cm^2 in 1998, 1999 and 2000, respectively. For both localities, mean size was 276 cm^2 (95% CI 248 – 304 cm^2), 360 cm^2 (95% CI 333 – 388 cm^2), and 373 cm^2 (95% CI 342 – 403 cm^2) in 1998, 1999, and 2000, respectively.

The change in size as a function of initial colony size showed a curvilinear relation (Figure 3.4) indicating that small colonies grew proportionally more than large colonies, which on the contrary either underwent fission, shrank or maintained very close to zero growth. Expected growth at two sizes (50 and 700 cm^2), the shape of the curve (estimated parameters), and the amount of variation explained by the regression varied under different conditions (Table 3.5). The amount of variation in growth that was explained by the regression was improved by the assumption of an initial size of 20 cm^2 instead of zero cm^2 (R^2= 0.857 vs. 0.710, respectively). The mean expected growth of 50-cm^2 colonies ranged between 128 ± 7 for all colonies (condition 3) and 75 ± 10 $cm^2 \cdot y^{-1}$ with the exclusion of new colonies (condition 6), indicating that the new colonies had a higher growth rate than other colonies of the same size. Then, it is expected that after a year, a 50-cm^2 colony in the study sites will have on average a final size ranging between 125 and 178 cm^2, equivalent to 1.4 to 3.6 times its initial size, respectively. Similarly, it is expected that colonies of 700 cm^2 on average will reduce their size by 46 to 72 cm^2. Zero growth was expected to occur at colony sizes of 532 ± 21 cm^2 for all conditions (Table 3.5). From this size on, colonies are likely to reduce in size either by shrinking or by fission. The mean reduction in size of a 700 cm^2 colony was not different between years (–36 in 1998-1999 and –96 cm^2 in 1999-2000). Size reduction, however, was expected to be greater for colonies > 700 cm^2, but estimates towards the end of the size distribution are less reliable. Thus, colonies of 1,150 cm^2 are expected to lose approximately 4 times the size that a 700 cm^2 colony is expected to lose (-317 ± 16 cm^2 using condition 3 of Table 3.5).

Colony growth rates by locality were similar to results shown in Table 3.5 for the two sites combined, with one exception. Colonies 700 cm^2 in size from Pelorus decreased on average by -124 cm^2 in 1999-2000, similar to the general trend observed in Table 3.5, but colonies of that size increased on average by 204 cm^2 in 1998-1999.

A log-linear analysis of colony frequencies in relation to initial size, category of growth, and time interval, further supported the conclusion that initial colony size and annual growth are not independent (Table 3.6).

3.4.2 *Sexual and asexual reproduction of Sinularia flexibilis*

Sinularia flexibilis is able to reproduce asexually by fission and by the production of buds (Figure 3.5). The degree of fission assessed in 4,118 field observations of colonies in seven sampling times showed that 43% of colonies were clearly undergoing fission at any given time (fission categories 2 and 3 in Table 3.7). This percentage remained relatively constant throughout the sampling times (41 ± 3.4%, n = 7), and between the two localities (48 ± 4.8% at Fantome and 42 ± 1% at Pelorus). Fission was mostly binary, starting as an elongation of the colony stem between two or more branches. At the point where the colony stem elongated, branch initiation ceased. The height of the stem reduced as the process continued, until two (or more) physiologically separate colonies were produced (*i.e.* the connection at this point seemed to consist mostly of sclerites). The connection was eventually covered by sediment and disappeared, but the colonies appear to remain physically attached under recent soft substratum for some time. I considered colonies to be separated when tissue connecting them appeared as not having any physiological function. The slowness of the fission process coupled with the moderately rapid growth of colonies resulted in daughter colonies tending to be similar in size to parent colonies.

Buds were found protruding from the stems of colonies, mainly at the colony base (Figure 3.5). When present at the branching level of the stem, buds were difficult to differentiate from incipient branches. I observed a low incidence of budding (2% from 4,513 observations of colonies in the field throughout the study) that was similar between localities. However this is likely to be an underestimate as they are relatively inconspicuous and field observations of budding were time constrained. Buds mostly occurred on dividing colonies, indicating that these two asexual mechanisms for colony production are not mutually exclusive. The relative importance of budding as a successful mechanism to generate new colonies was not established in this study. Most colonies with buds produced only one (i.e. 75% of colonies), while the rest had between two and five buds.

Based on the observed rate of 43% of colonies being in an advanced state of fission (Table 3.7) resulting in the generation of one daughter colony per year, and assuming 50% survivorship of daughter colonies (from mortality rates observed), it would be

expected that 580 initial colonies (as in Table 3.1) could produce about 125 colonies per year. The observed number of colonies produced by fission each year from the photographic record of permanent transects was very similar to this estimation (95 in 1998-99 and 106 in 1999-2000). Colonies clearly undergoing fission (categories 2 and 3 of fission in Table 3.7) were able to complete this process within a year. Thus, the whole process of fission (*i.e.* from the initiation of fission on colonies in categories 0 and 1 through until daughter colonies are produced) is likely to take more than one year. Field observations indicated that 80% of the 1,178 colonies in categories 2 and 3 were dividing into two colonies (*i.e.* had the potential to generate one daughter colony), and 20% were dividing into more than two (Table 3.8). Of those dividing into more than two colonies, 0.4 % were dividing into between 6 and up to a maximum of 19 colonies (Figure 3.5). It is not known how long these conglomerates of colonies have taken to form, or how long it takes for them to completely separate, or if indeed they ever do.

The colonies that resulted from fission accounted for 70% of the 285 newly recruited colonies observed during the study, while the remaining 84 colonies were presumably recruited either by sexual larvae or by movement of neighbouring colonies into the transects (i.e. immigration). Fission was verified as the source of a large proportion of the asexual recruits from field observations (169 out of 201), and the remaining 16% were assumed to originate from fission because of close contact between presumed parent and daughter colonies in the photographs. The actual number of asexual recruits observed to originate through fission per colony varied between one and six (Table 3.9). Their mean size was larger than the size of sexual recruits and presumed immigrants together (190 ± 12 cm^2 vs. 123 ± 17 cm^2). Also, the size distribution of asexual recruits was less skewed towards the smaller size classes (Figure 3.6). I will hereafter refer to recruits that are not attributable to fission as sexual recruits if they are in size class I, and immigrants (presumed to have originated through the movement of colonies into the transects) if they are in larger size classes. According to colony growth estimations, however, some of the colonies in size class II could also have originated from sexual recruitment within a year.

Sinularia flexibilis also reproduces sexually and presumably releases its gametes during the mass spawning (K. Michalek-Wagner pers. obs., and C. Bastidas pers. obs). Examination of branch tips indicated that not all polyps contained eggs, the number of

eggs per polyp varied among colonies, and that this variability was higher than that within a colony (Table 3.10). Oocytes of two sizes were visible in small bunches in each mesentery and they most likely corresponded to a two-year period of oogenesis that seems to be common among species of the Alcyoniidae family (Benayahu *et al.* 1990). Mature eggs (*i.e.* collected a few days before spawning) were ellipsoid with a mean diameter of 211 ± 5.1 μm (n = 79 eggs from four colonies). The length of the major axis of the ellipse ranged between 170 μm and 500 μm. Egg sizes were smaller than the 900-1150 μm range reported for other *Sinularia* species (Benayahu *et al.* 1990), which probably reflects the smaller polyp size of *S. flexibilis*. In histological preparations of 129 branches, nine colonies out of a total of 29 had eggs, and only one of these 29 colonies examined had spermaries (Figure 3.7). The occurrence of female gametes appeared unrelated with colony size, as mature colonies were found across all sizes investigated. However, because only two out of these nine colonies were in size class I, and because the number of histological preparations was small, I preferred to assume class I colonies were unlikely to reproduce sexually in the matrix analyses. Between 24 and 400 eggs· cm^{-2} of branch tip were found in the nine mature female colonies.

3.4.3 Demographic analysis of *Sinularia flexibilis*

The change in size or death of *S. flexibilis* colonies (Fate) was dependent on the Locality, the Time interval considered, and the Initial Size of colonies (Table 3.11), in agreement with results from other analyses (*e.g.* section 3.4.1). Fate x Initial Size x Time was the only non-significant interaction, but other terms that included Fate were significant. Based on these results, it was apparent that demographic parameters would be better estimated from separate transition matrices for each time interval and locality.

The demographic parameters of *S. flexibilis* calculated from the separate transition matrices generally differed between time intervals and between localities (Table 3.12). In particular, the growth rate of the population per year (λ) was significantly higher in the 98-99 interval than in the 99-00 interval for both localities (Figure 3.8 for projections). Only during the 99-00 year interval did the growth rate differ significantly between the two localities. Thus, populations of *S. flexibilis* would be expected to increase in all cases assuming that growth rate is constant through time, there is no effect of species density, and no external sources of larvae. The highest λ suggests a

population doubling time of 2.6 years based on the per capita population growth rate (Table 3.12). However, shortest and largest estimated of doubling times were 4 and 6 years, respectively, when projecting population size with constant demographic rates through time and with the initial population observed in 1998 (*i.e.* 581 colonies, and size structure as in Table 3.1). Projections of the population size based on random alternation of the four matrices through time, on the assumption that differences between the time intervals and localities are representative of temporal and spatial variability in population growth rates of this species, also indicate that populations would tend to increase even in the absence of an external input of recruits (Figure 3.9). This indicates that the production of colonies by fission suffices to increase the population size; additional input of sexual recruits would accelerate the population growth beyond that shown in Figure 3.9. For example, the effect of 500 new annual external recruits to population projections based on the Fantome 99-00 matrix is illustrated in Figure 3.10.

Figure 3.10 also shows the effect of calculating sexual fertility and including it in the transition matrix to estimate of population size through time. Population size would increase similarly through time if the observed number of sexual recruits was added each year as an external input, or if it was used to calculate the per capita fertility, which was then incorporated into the matrix.

The rate of convergence to a stable size distribution (damping ratio ρ, Table 3.12) indicated that, if moved out of equilibrium (*e.g.* by a disturbance), a population would reach a stable size distribution in 3 to 10 years (estimated as ln 1000/ ln ρ, Ebert 1999). Similarly, the stable size distribution varied relatively little among localities and time, with the large size class being the most abundant in the population (Figure 3.11). The largest difference in stable size distribution between the two time intervals occurred at Pelorus, where the contribution of the largest size class dropped from 63% to 37%. As a result, the stable size distribution estimated from this locality in 99-00, at the lowest λ, is more evenly distributed among size classes. The initial size distributions at Pelorus in 1998 was dissimilar to the stable one predicted. Differences between observed and predicted size distributions were mainly due to excesses of colonies in size classes I, II and III, and a deficit in the largest size class (IV) in the initial populations. Initial and

stable size distributios were very similar at Fantome in the two years and at Pelorus in the last year (99-00).

A colony already recruited into the first size class (<75 cm^2) is expected to have a life expectancy varying between 2.8 and 8.2 years among localities and time intervals (Table 3.12). Survivorship increased with size, and so does the expected remaining life span. Thus, on average, a colony that has reached size class IV ($450 < x < 2100$ cm^2) will continue to live another three to 11 years. The expected lifetime production of daughter colonies dropped between 98-99 and 99-00 for all size classes at both localities (Table 3.12).

The elasticity of the population growth rate (λ) to the stasis of colonies in size class IV (transition a_{44}) was > 0.43 while the elasticity of λ to any other transition was < 0.09 among the four matrices (Fig. 3.12). This indicates that the effect of perturbations to this transition on the population growth rate would be at least five-fold of that expected from similar perturbations to any other transitions in the matrices. The elasticity of λ to the demographic processes also changed between time intervals within each locality (Figure 3.12). At both localities, the relatively large importance of stasis of colonies in class IV diminished from 98-99 to 99-00, and consequently, the elasticity of the population growth to other transitions increased. Particularly, the stasis of size classes II and III, and the transitions 'to and from' the largest size class increased from 98-99 to 99-00 (Fig. 3.12).

The elasticity of λ to the stasis of colonies in size class IV also diminished when including more size classes (Fig 3.13), and when including the fertility probabilities in the analysis (Table 3.13). Analyses of matrices using six size classes, with or without fertility terms, resulted in a more even distribution of the elasticities of λ to other transitions, rather than being strikingly high for the stasis of colonies in the largest size class. When using six size classes instead of four, the elasticities of λ to any element of the matrices did not exceed 0.22 (vs. 0.78 using four size classes), and to the stasis of colonies in the largest size class (transition a_{66}) did not exceed 0.02 (Fig. 3.13). Similarly, Table 3.13 summarises the relative importance of the demographic processes

of Fission and Shrinkage, Stasis, and Growth, by adding individual elasticities of the transition elements above the diagonal, along the diagonal, and below the diagonal, respectively. From this comparison, it is also clear that elasticities of λ to stasis decreased with the inclusion of fertility terms, with the increment of size classes (six instead of four), and with the time (in 99-00 they were smaller than in 98-99), while the elasticities of λ to fission or shrinkage, and to growth increased under those circumstances. Including fission alone resulted in larger changes in the elasticities than including fission and sexual fertility terms, when comparing them to the elasticities without reproductive terms (B vs. A > C vs. A in Table 3.13). This supports previous results indicating that fission was relatively more important in the production of colonies than sexual recruitment.

Figure 3.14a shows the variance and covariance of each of the matrix element among the four matrices that resulted from examining two localities and two years. Although there is a large variability among these variances and covariances, those that involved transitions from and to size class IV contributed to explained 62% of the variance of λ (Fig. 3.14b). The variance of stasis of colonies in size class IV among the four matrices was the single most contributing variance or covariance to the variance of λ (36%).

3.5 Discussion and conclusions

This demographic study of the soft coral *Sinularia flexibilis* revealed three fundamental aspects of its population dynamics, and provided new insights into its natural history. Firstly, *S. flexibilis* is clearly a clonal organism that relies primarily on fission for recruitment at the spatial scale of this study; it also has a relatively high colony growth rate at small sizes, yet its population growth is relatively slow. Secondly, all demographic processes (growth, fission and shrinkage, and stasis) may contribute similarly to the population growth rate. Thirdly, changes that occurred between the year intervals supported evidence from Chapter 2 and other studies, that these populations had been recently affected by a disturbance, most likely the 1998 bleaching event. A general shift towards stable size distributions during the study period indicated some population recovery. Finally, a number of demographic processes contribute to the formation of local aggregations in populations of *S. flexibilis*.

3.5.1 *Size Structure and Colony Growth*

The size structure of *S. flexibilis* at the study sites was characterised by a large abundance of small colonies and sharply declining numbers in the larger size classes. This indicated a considerable annual input of new, small colonies, produced either sexually or asexually. The marked decrease in the number of colonies in size class I that occurred in 1999 and 2000 compared with 1998, suggests a reduction in recruitment in 1999 and 2000, possibly as a consequence of the 1998-bleaching event. Michalek-Wagner and Willis (2001) demonstrated that experimentally induced bleaching had an impact on the reproductive output of the soft coral *Lobophyton compactum* over two annual spawning seasons. The results presented here support the prediction that sublethal effects of bleaching would also have consequences at the population level, altering the size structure and abundance of affected species.

Colony size in *S. flexibilis* was determinate, with growth reaching an asymptote at a mean size of 500 cm^2, although some colonies reached a maximum size of 2000 cm^2. Most clonal organisms have indeterminate growth, with more exceptions occurring among solitary (*e.g.* anemones) than among colonial animals (Sebens 1979; Hughes and Jackson 1985; Hughes *et al.* 1992). Restrictions to colony size have been explained by

biomechanical constraints imposed on organisms without a rigid supporting structure, and to surface-to-volume limitations for gas exchange (*e.g.* Cheetham *et al.* 1980). Many octocorals with erect growth forms have asymptotic size (*e.g.* Grigg 1974). Colonies of *S. flexibilis* have a shrub-like growth form that may well explain apparent growth restrictions. On the other hand, clones of *S. flexibilis* should be regarded as having virtually no limit to growth through the asexual replication of ramets, except through senescence or mortality. However, based on size specific mortality rates, no evidence of senescence was found in this study.

Individual growth rates of *S. flexibilis* were inversely related to size, as has been found for other clonal species. In particular, other octocorals species have been shown to have a similar pattern of relatively high linear or areal growth rates at small sizes (Table 3.14), with a few exceptions (*e.g.* Cordes *et al.* 2001). However, absolute growth rates are difficult to compare among species because the variability in growth forms necessitates the use of different type of measurements (Table 3.14).

A study of encrusting *Sinularia* on mid- and outer-shelf reefs in the GBR showed very little annual change in colony size over three years, nevertheless growth was also size-dependent (Fabricius 1995). Based on the midpoints of each size class representing the diameter of a circular colony, I calculated the average linear growth for a 44-cm^2 colony to be 1.0 ± 0.3 $cm \cdot y^{-1}$ in Fabricius' (1995) study. This is clearly much smaller than the maximum growth estimates in this study of *Sinularia flexibilis*, where a 50-cm^2 colony is expected to have, on average, a linear increase in colony diameter of 7 $cm \cdot y^{-1}$ (equivalent to a mean ± SE of 128 ± 7 $cm^2 \cdot y^{-1}$). This seven-fold difference in linear growth between species of *Sinularia* on the GBR suggests that great variations in the life histories can occur, even among closely related species. Differences in morphology, growth rates, fission and sexual recruitment between the *Sinularia* species in the two studies also indicate that they have contrasting dynamics, and thus the time to attain local dominance is likely to differ.

3.5.2 *Mortality*

Mortality of *S. flexibilis* colonies was also size-dependent, with smallest colonies having 2 to 5 times the mortality rate of the largest colonies. Most sessile benthic invertebrates

with clonality have shown to have decreasing mortality with increasing size (*e.g.* Tanner 2001). A size-independent susceptibility to some diseases and their related mortality is one exception (Ayling 1981; Antonius 1982; Gladfelter 1982, cited in Jackson 1985), as is likely to be the case for bleaching-related mortality.

Based on field observations, I suggest that the turnover of colonies attached to relatively unstable substrata may be an important source of mortality in *S. flexibilis*, although on a few occasions, turnover may serve as a mechanism for the local movement of colonies. This is pertinent for the physical conditions of the study site, where tidal currents can reach more than 35 $cm \cdot s^{-1}$ (mean of 15 $cm \cdot s^{-1}$ measured over 3-4 d in winter, Fabricius and Domisse 2000), and where available substrata include unconsolidated dead fragments of hard corals. Coral detachment and abrasion have also been identified as an important source of mortality in other octocorals such as *Muricea fruticosa* and *M. californica* (Grigg 1977), and *Nephthea cupressiformis* and *Xenia lepida* (Lasker 1988). In addition, I observed some bite marks and heavy predation on a few colonies, but the relationship between predation and mortality could not be established. Predation-related mortality seems to be low in soft corals, mainly as a result of deterrent compounds found in their tissues, as well as their potential to repair injuries following partial mortality (*e.g.* Fabricius 1995; Slattery and McClintock 1995; Slattery *et al.* 2001). 'Crowding' by surrounding conspecifics, that restrict access to water flow and light, could constitute another potential source of mortality in *S. flexibilis*. All these sources of mortality would require more frequent observations to be properly quantified.

3.5.3 *Recruitment and colonisation by sexual and asexual mechanisms*

Asexual recruits made a greater contribution to the population growth of *Sinularia flexibilis* than sexual recruits during the study period. Sexual recruits into the first recordable size class accounted for 19% of the new colonies (0.24 $recruits \cdot m^{-2} \cdot year^{-1}$). This sexual recruitment rate was relatively constant between years and in marked contrast to fission rates, which accounted for 70% of new colonies throughout the study. The remaining 11% were attributed to the movement of colonies. As suggested by the reduction in numbers of colonies in the smallest size classes in 1999 and 2000 compared with 1998 (section 3.5.1), the bleaching may have had a sublethal effect on reproduction causing an underestimation of the relative importance of sexual

recruitment in this species (see also Chp 4). Furthermore, although at the individual level the asexual reproduction in *S. flexibilis* is clearly visible, the importance of asexual reproduction at the populations level in clonal organisms can be difficult to assess (*e.g.* Harrison and Wallace 1990). Jackson (1985 and references therein) suggested that a common pattern of clonal organism is a larger relative importance of asexual reproduction in comparison to sexual recruitment. However many studies since then have indicated that this pattern can be highly variable among species (examples of hard corals in Harrison and Wallace 1990, and also other groups in Chp 4). The relative importance of different reproductive mechanisms on recruitment would largely depend on the mode of development of the larval phase (and the potential for dispersal usually associated to it), post-recruitment mortality, and the occurrence and type of asexual reproduction. In soft corals, a short larval phase and relatively large contribution of sexual recruits has been observed either in species with brooded larvae, as in *Capnella gaboensis* (Farrant 1986), or species with external fertilisation but a short planktonic phase, as in *Leptogorgia virgulata* (Gotelli 1988). Also there are soft corals in which asexual reproduction is unknown, such as *Alcyonium acaule* (Garrabou 1999) and *Acabaria biserialis* (Ben-Yosef and Benayahu 1999). The type and occurrence of asexual propagules affect the success of asexual recruitment, as well as the ability and time involved in colonising available substrata.

Even when *S. flexibilis* showed more asexual than sexual recruitment, it colonised substrata slowly at the two study sites. This contrast with the traditional assumption that asexual replication is associated to rapid colonisation, because of its advantages over sexual reproduction in time and energetic requirements (*e.g.* Williams 1975). Many clonal organisms indeed produce daughter colonies by asexual means at high rates (*e.g.* Dinesen 1985). However, other studies have shown that the production of new colonies can occur just as rapidly by sexual means (*e.g.* Benayahu and Loya 1984; Ben-Yosef and Benayahu 1999). When dependent on clonal replication, the ability to rapidly colonise areas may well depend on the asexual mechanism.

Sinularia flexibilis reproduces asexually mainly by binary fission and very rarely relies on physical fragmentation, but instead initiation of division appears to be controlled endogenously. Soft corals show an ample variety of asexual mechanisms (Dahan and Benayahu 1997 and references therein), and they do not necessarily rely on physical

fragmentation or partial mortality for this. Rapid formation of daughter colonies in species of the family Xeniidae may be due in part to the formation of stolons (but see Lasker 1988). New colonies of 2-5 cm across generated by fission from established colonies commonly appear within < 2 months in *Efflatounaria* (Dinesen 1985). Also, the formation of fragments by autotomy of branches of *Dendronephthya hemprichi* (Nephtheidae) can provide a rapid means of replication (Dahan 1992). These fragments can be formed within two days and recruitment to artificial plates could be as high as one per cm^2 after 52 days, although mortality may be also high (Dahan 1992).

The clonal propagation of *S. flexibilis* has elements of the phalanx clonal strategy of resource exploitation (Lovett-Doust 1981), where a clone (a genetic entity, or genet) is composed of closely packed ramets (individual colonies) and spreads slowly as a front. Most of the contact and competition experienced by modules (polyps) and by ramets is expected to be intraclonal. With this type of growth, clones are expected to efficiently fill available space as they spread outwards (Waller and Steingraeber 1985). In *S. flexibilis*, however, I suggest that other processes, mainly, sexual recruitment and high mortality rates, and less importantly budding (that may serve as additional means for the dispersion of the clones), could make this 'front' more genetically diverse than expected from the phalanx strategy alone (see Chapter 4).

In *S. flexibilis*, the occurrence of colony fission was relatively high, with 43% of colonies in an advanced state of division throughout the year (*i.e.* colonies likely to complete division within the next year). The complete process of division takes approximately two years to be completed. Compared with studied species of the families Nephtheidae and Xeniidae, this process of division is relatively slow. However, fission in other tropical alcyoniid species studied was even slower and less frequent than in *S. flexibilis*. Fabricius (1995) reported that in the encrusting *Sinularia* of the mid- and outer-shelf reefs of the GBR, fission occurred mostly as a consequence of colony injury and suggested that these species more closely resemble an aclonal organism, with only 3.5% of colonies going through fission at any time. *Sarcophyton* in the GBR had a colony production of 8.8% per year, most likely by fission or budding (Fabricius 1995). In the Red Sea, *S. glaucum* was also considered to rely mainly on sexual reproduction, and to have poor colonisation capabilities of newly exposed reef surface (Benayahu and Loya 1986). The temperate alcyoniids species have shown mixed results, where

Alcyonium sp. from the coast of California had fission rates similar to *S. flexibilis* in this study (McFadden 1991), whereas the Mediterranean species *Alcyonium acaule* showed no fission in a two-year study (Garrabou 1999). In summary, *S. flexibilis* showed similar and higher rates of colony fission when compared with the other studied species of the family Alcyoniidae in temperate zones (McFadden 1991), and in the GBR (Fabricius 1995), respectively. However, the fission rates were lower than those of some Xeniidae species such as *Efflatounaria* (Dinesen 1985; Karlson *et al.* 1996).

3.5.4 *Population dynamics*

The demography of *S. flexibilis* was typical of a clonal organism, specifically with regard to size dependent vital rates and to the important contribution of asexual reproduction to recruitment. The relatively high colony growth rate and fission potential of this species were however counteracted by a correspondingly high mortality rate. As a consequence, population projections with a time-invariant matrix model indicated that the population growth rate was variable depending on locality and year (15% to 27% per capita per year), but all leading to increasing populations.

The population growth rates found in this study for *S. flexibilis* closely resembled those reported for a clonal Alcyoniidae species from temperate environments (McFadden 1991). To my knowledge this is the only other study on the population growth rates of an Alcyoniidae. However, similar analyses in other clonal marine organisms have also shown that population growth can vary amongst localities and years, rely on asexual reproduction, and be density dependent (Table 3.15).

Elasticity analysis in this study indicated that changes in each of the demographic processes of growth, shrinkage and fission, and stasis (staying in the same size class) could approximately have an equivalent effect on population growth. By contrast, other studies have shown that stasis commonly contributes more to population growth than any other demographic processes, both in clonal organisms (Gotelli 1991; Lasker 1991; Tanner 1997; Mandujano 2001), as in some long-lived aclonal species (*e.g.* Sæther and Bakke 2000). However, a large contribution of stasis has been mainly attributed to long-lived species, or to populations with low or declining growth rates (de Kroon *et al.* 2000).

The reduced contribution of stasis to population growth in *Sinularia flexibilis* was detected by increasing the number of size classes from four to six, which decreased the elasticity of λ to stasis such that it became more equivalent to, or less important than the processes of growing, shrinking and dividing. In other words, using six size classes, the elasticity of λ to the stasis of most size classes increased (becoming less exclusive of the largest size), as well as the elasticity of λ to the subdiagonal transitions (those transitions among adjacent size classes, which were also largely probable). Enright *et al.* (1995) also found that elasticities depend on the number of size classes used. In *S. flexibilis*, increasing the number of size classes reduced, in particular, the relative importance of stasis related to the largest size class. This occurs partly because every additional transition takes an additional year for the pathway to complete, and longer loops (the path a colony of a specific size takes throughout its lifetime) make a relatively smaller contribution than shorter loops in growing populations (de Kroon *et al.* 2000). The expected lifetimes of size classes IV, V and VI are similar, and consequently the contribution of the addition of size classes V and VI to the elasticity calculations associated with stasis is likely to be related to colony longevity. Thus, it is likely that elasticities derived from six size classes better represent the proportional contributions of the demographic processes to the population growth rate of *S. flexibilis*.

For *Alcyonium* sp., summed elasticities over the same demographic processes closely resemble those found in this study (data from McFadden 1991 recalculated by Caswell 2001). In both species, there was little variation in the relative effect of perturbations to the demographic processes in relation to the different population growth rates. Nevertheless, the contribution of stasis in *Alcyonium sp.* was negatively correlated with λ (0.60 for the lowest λ, and 0.47 for the highest λ), whereas stasis contribution was positively correlated with λ in *S. flexibilis* (0.52 and 0.71 for the lowest and largest λ, respectively). In this study, a positive correlation between the elasticity of λ to stasis and λ may be linked to the fact that the survival probability was combined with each one of the other demographic probabilities (and hence elasticities) within the matrices (see Mandujano 2001 for another positive correlation).

The relatively low (min 0.30, max 0.60) elasticity of λ to stasis in these two clonal species could correspond with: low population growth rate, a short lifespan compared with other clonal organisms for which elasticity has been calculated, and/or an early maturity and large reproductive output (clutch size in Sæther *et al.* 1996). Although there was considerable variability in population growth rates in these two species, the maximal λs of 1.312 and 1.152 for *Sinularia* and *Alcyonium* respectively, cannot be considered to represent a low rate of population growth. However, the expected remaining lifespan of the largest colonies of *S. flexibilis* is approximately 10 years, which again may not be considered a short longevity either among other clonal species (see Tanner 2001). The maturity of *Alcyonium* seems to occur rather late (McFadden 1991), however, *S. flexibilis* may have an early maturity (based on the observation of gonads in two <100 cm^2 colonies), and may produce a relatively high number of offspring considering that it possesses both asexual and sexual mechanisms. Thus, it could be possible that *S. flexibilis* is what has been described as a species with a bet-hedging strategy that may have large recruitments in favourable years (Sæther *et al.* 1996). Based on its life history characteristics, the latter could be the most likely explanation, among the three possible ones, for having a lower contribution of stasis to population growth than the other clonal species studied so far. However, other factors to consider include that the number of demographic studies of clonal species is limited, and that the number of size classes in other studies could has been insufficient for this pattern to emerge.

The population growth rate of *S. flexibilis* decreased during the last year of the study (between Dec 1999 and Dec 2000), the size class distribution of colonies shifted towards larger sizes, and the final size structure more closely resembled the stable distribution predicted from the matrix model. All these results indicate that the populations of *S. flexibilis* were in a transient state during the first time interval. This was, most likely, the result of the mortality that occurred during the 1998 bleaching event that affected the coral communities in both localities (see Chapter 2). Differences through time were consistent within localities and may have occurred as a consequence of the reduction in available space. During three years of censuses, the species cover in 5-m deep transects at Pelorus increased from 36% to 47%. Ninety percent of colonies at Pelorus occurred at 5 m, which also corresponded to 50% of all of the colonies used in

this demographic study. Thus, a decrease in available space from 60% to 49% at this site could partly explain the reduction in individual and population growth rates observed. Comparing the first and second year-intervals, fission and recruitment remained unchanged, whereas colony growth decreased at Pelorus. In addition, mortality rates increased for most size classes at both localities. In combination, these results suggest that space availability at the 5 m site at Pelorus may have limited both individual and population growth. Although other clonal species have shown a density-dependent mechanism to population regulation, this remains to be tested experimentally for aggregations of *S. flexibilis*, as it was only indirectly seen in the present study.

3.5.5 *Local dominance of Sinularia flexibilis*

This study has shown that the growth rate of *S. flexibilis* populations varies in time and space. This makes it hard to extrapolate from these results to determine the rate at which aggregations form in this species. Using the matrix that resulted in the highest λ (Fantome 1998-1999), a starting population of 580 individuals (equivalent to 25% in cover) could double in size in four years. This projection is dependent on the unlikely assumption that growth rate is constant through time, which was not borne out even in the following year of the study. Despite the variability of λ, the time required for the population to double was relatively similar from the different matrices, showing a maximum of six years. Thus, based on these estimates the formation of aggregations of approximately 50% in cover may vary between four and six years. Although these time estimates can be considered relatively short in ecological terms, it is meaningful to compare them with the frequency of disturbances at local scales, which is unknown for most communities. However, even at larger scales, current frequencies of disturbances appear to be greater than this time scale, taking into account, for example, that six bleaching events have affected the GBR in the last 20 years (*e.g.* Berkelmans and Oliver 1999), although there is evidence that the intensity of the 1998 was the largest so far.

The time scale for recolonisation and recovery of space occupancy by *S. flexibilis* suggests that aggregations in the order of 50% of cover over hundreds to thousands of m^2 could take from half a decade to form. These estimations clearly depend on the initial cover and density of organisms in the community, which in turn depend on disturbance intensity. Thus, contrary to suggestions that soft corals quickly overtake

available space after disturbances, results from this study suggest that this type of aggregations of *S. flexibilis* may be indicative of a coral community that has not been subjected to local scale disturbances for at least 5 years. In the case of disturbances that do not affect soft corals in general and *S. flexibilis* in particular (*e.g.* crown-of-thorns starfish predation), it would be necessary to determine the effect that intra-specific competition on the population at these 'aggregation' densities.

In conclusion, demographic rates of *S. flexibilis* were characteristic of clonal organisms, with size-dependent growth and mortality, and fission rates able to maintain growing populations. In contrast to clonal organisms studied so far, changes in the different demographic processes examined are expected to contribute equally to the population growth. From 1998 to 2000, the population growth rate decreased at both localities, the number of colonies in the first size class declined, and the size distribution was displaced towards the predicted stable one. These changes indicate that the population was affected by a recent disturbance event, most likely the 1998 bleaching that affected inshore reef communities in the GBR. At one locality, these changes were accompanied by a reduction in individual colony growth. In this study, a life history strategy of potentially limited sexual recruitment, a relatively slow rates of fission and binary fission as the main mechanism of asexual reproduction, contributes to a slow acquisition of space in *S. flexibilis*.

Table 3.1. Number of colonies of *S. flexibilis* in each size class, sampling year (1998,1999,2000), locality and depth. These numbers of colonies were used to calculate relative frequencies of Figure 3.3.

Year	Size Class upper bound (cm^2)	Fantome 2 m	Fantome 5 m	Pelorus 2 m	Pelorus 5 m	Total	Died	New by fission	New by sex or movement	Total New	N used for colony growth estimates
1998	75	11	25	6	87	129	57				
	150	14	22	11	85	132	34				
	250	21	12	6	76	115	19				
	450	35	29	8	47	119	18				
	750	23	19	1	9	52	3				
	2100	16	17		1	34	2				
						581	**133**				**448**
1999	75	24	19	7	39	89	40	19	24		
	150	13	19	6	63	101	24	29	11		
	250	21	21	11	52	105	30	19	5		
	450	31	31	14	75	151	36	19	4		
	750	34	30	1	35	100	22	7	2		
	2100	14	13		16	43	4	2			
						589	**156**	**95**	**46**	**141**	**433+141**
2000	75	18	21	5	44	88		29	24		
	150	19	11	9	68	107		35	6		
	250	19	14	10	57	100		16	2		
	450	28	28	13	69	138		18	3		
	750	27	29	7	36	99		8	2		
	2100	21	13		11	45			1		
						577		**106**	**38**	**144**	**144**
					Total	**1747**				**285**	**1166**

Table 3.2. Matrices used for estimating demographic parameters of *S. flexibilis* without (A) and with fertility terms (B for fission and C for fission and sexual fertility). Size-specific mortality rates (qx), input of colonies by fission into class x at time t + 1 (FF), and sexual input into class I at time t + 1 (SF) are shown. Calculations are exemplified in Table 3.3.

		Fantome 98-99 t				Pelorus 98-99 t				98-99, Localities pooled t			
		I	II	III	IV	I	II	III	IV	I	II	III	IV
A	I	0.194	0.140	0.059	0.004	0.215	0.058	0.000	0.000	0.209	0.085	0.017	0.003
t+1	II	0.132	0.139	0.094	0.025	0.215	0.167	0.123	0.024	0.196	0.159	0.116	0.024
	III	0.000	0.269	0.182	0.066	0.176	0.235	0.256	0.043	0.128	0.247	0.235	0.064
	IV	0.358	0.129	0.435	0.755	0.134	0.378	0.501	0.848	0.185	0.299	0.472	0.785
Σ		0.685	0.677	0.770	0.850	0.740	0.837	0.880	0.916	0.718	0.791	0.840	0.877
qx		0.528	0.250	0.273	0.129	0.409	0.260	0.122	0.076	0.442	0.258	0.165	0.112
B	I	0.194	0.177	0.096	0.152	0.313	0.083	0.049	0.073	0.251	0.117	0.060	0.119
t+1	II	0.132	0.157	0.186	0.191	0.215	0.313	0.270	0.146	0.196	0.233	0.232	0.172
	III	0.000	0.269	0.182	0.214	0.176	0.235	0.354	0.116	0.128	0.247	0.277	0.180
	IV	0.358	0.129	0.435	1.107	0.134	0.378	0.501	1.019	0.185	0.299	0.472	1.059
Σ		0.685	0.733	0.899	1.665	0.838	1.008	1.173	1.355	0.760	0.896	1.040	1.530
C	I	0.194	0.244	0.163	0.219	0.313	0.124	0.090	0.114	0.251	0.170	0.113	0.172
t+1	II	0.132	0.157	0.186	0.191	0.215	0.313	0.270	0.146	0.196	0.233	0.232	0.172
	III	0.000	0.269	0.182	0.214	0.176	0.235	0.354	0.116	0.128	0.247	0.277	0.180
	IV	0.358	0.129	0.435	1.107	0.134	0.378	0.501	1.019	0.185	0.299	0.472	1.059
Σ		0.685	0.800	0.967	1.732	0.838	1.049	1.214	1.396	0.760	0.949	1.093	1.583

(Continued)

Table 3.2. (continued)

		Fantome 98-99 t				Pelorus 98-99 t				98-99, Localities pooled t			
		I	II	III	IV	I	II	III	IV	I	II	III	IV
A	I	0.093	0.093	0.032	0.000	0.304	0.079	0.042	0.005	0.202	0.079	0.037	0.002
t+1	II	0.156	0.000	0.064	0.029	0.364	0.290	0.250	0.039	0.280	0.198	0.173	0.036
	III	0.105	0.175	0.214	0.058	0.075	0.232	0.222	0.122	0.087	0.213	0.219	0.092
	IV	0.250	0.358	0.340	0.588	0.000	0.203	0.309	0.709	0.113	0.236	0.316	0.646
Σ		0.605	0.626	0.649	0.674	0.743	0.804	0.823	0.876	0.682	0.726	0.744	0.777
qx		0.558	0.406	0.333	0.320	0.348	0.159	0.254	0.092	0.449	0.238	0.286	0.211
B	I	0.133	0.113	0.052	0.160	0.304	0.168	0.113	0.148	0.221	0.135	0.084	0.153
t+1	II	0.156	0.020	0.084	0.269	0.364	0.290	0.340	0.343	0.280	0.207	0.229	0.310
	III	0.105	0.175	0.214	0.178	0.075	0.232	0.222	0.301	0.087	0.213	0.219	0.243
	IV	0.250	0.358	0.340	0.948	0.000	0.203	0.309	0.834	0.113	0.236	0.316	0.882
Σ		0.645	0.666	0.689	1.554	0.743	0.893	0.984	1.626	0.701	0.792	0.848	1.588
C	I	0.133	0.188	0.126	0.235	0.304	0.194	0.139	0.174	0.221	0.183	0.132	0.201
t+1	II	0.156	0.020	0.084	0.269	0.364	0.290	0.340	0.343	0.280	0.207	0.229	0.310
	III	0.105	0.175	0.214	0.178	0.075	0.232	0.222	0.301	0.087	0.213	0.219	0.243
	IV	0.250	0.358	0.340	0.948	0.000	0.203	0.309	0.834	0.113	0.236	0.316	0.882
Σ		0.645	0.741	0.764	1.629	0.743	0.918	1.010	1.652	0.701	0.840	0.896	1.636

Table 3.3. Matrices showing calculations of the transition probabilities in each cell, abbreviated as Sta = stasis (not growing), Shr = shrinkage, G = growth, FF = fission fertility per colony, SF = sexual fertility per colony. For example, G21 is the probability of growing from class I at time t to class II at t + 1; FF1 is the contribution per colony of classes II, III, and IV into class I by fission. Three dots (...) indicate 'as in previous matrix'.

		I	II	III	IV
Without fission					
	I	Sta11	Shr12	Shr13	Shr14
	II	G21	Sta22	Shr23	Shr24
	III	G31	G32	Sta33	Shr34
	IV	G41	G42	G43	Sta44
With fission					
	I	... + FF11	... + FF12	... + FF13	... + FF14
	II	...	... + FF22	... + FF23	... + FF24
	III	...	...	... + FF33	... + FF34
	IV	...	...	...	... + FF44
With fission and sexual fertility					
	I	...	... + SF1	... + SF1	... + SF1
	II	...	...	...	...
	III	...	...	...	...
	IV	...	...	...	...

Table 3.4. Test of partial associations among Time (1998, 1999, 2000), Locality (Fantome, Pelorus), Depth (2 m, 5 m), and Size class (<75, <150, <250, <450, <2100 cm²) as factors affecting the number of colonies of *Sinularia flexibilis*.

Effect	Df	Partial Chi-square	Probability	
Size	4	20.027	0.0005	*
Depth	1	320.553	0.0000	*
Locality	1	28.336	0.0000	*
Time	2	0.070	0.9657	
Depth x Size	4	5.465	0.2428	
Locality x Size	4	116.534	0.0000	*
Time x Size	8	38.391	0.0000	*
Locality x Depth	1	307.129	0.0000	*
Time x Depth	2	2.353	0.3083	
Time x Locality	2	2.698	0.2595	
Locality x Depth x Size	4	4.542	0.3376	
Time x Depth x Size	8	9.852	0.2755	
Time x Locality x Size	8	26.885	0.0007	*
Time x Locality x Depth	2	0.339	0.8440	
Time x Locality x Depth x Size	8	11.448	0.1776	

Table 3.5. Estimation of colony growth parameters under different conditions as explained in the table footnote. Growth1 (cm^2) = annual growth as absolute change in size (± SE) for an initial size of 50 cm^2; Growth2 (cm^2) = annual growth as absolute change in size (± SE) for an initial size of 700 cm^2; No growth = expected size of zero growth in cm^2; b = shape of the curve; R^2 = proportion of total variation explained by the regression.

	Conditions						
Parameter	1	2	3	4	5	6	7
Growth1	148	132	128	133	123	75	68
↖size•y^{-1}	± 7	± 7	± 7	± 9	± 11	± 10	± 11
Growth2	-83	-79	-72	-39	-96	-64	-46
↖size•y^{-1}	± 12	± 12	± 12	± 18	± 16	± 13	± 15
No growth	492	518	512	594	448	567	595
b	0.77	0.47	0.63	0.54	0.75	-0.25	-0.22
R^2	0.710	0.857	0.915	0.965	0.965	0.949	0.967

1 New colonies have 0 cm^2 as initial size
2 New colonies have 20 cm^2 as initial size
3 As 2, without the 10 largest observed changes in size (5 growing and 5 shrinking)
4 As 3, only time interval 1998-1999
5 As 3, only time interval 1999-2000
6 As 3, without new colonies (sexually and asexually generated)
7 As 6, without colonies that went through fission

Table 3.6. Test of partial associations among Initial Size (<75, <150, <250, <450, <2100 cm^2), colony growth (shrinkage, no growth, growth, and rapid growth), and Time interval (1998-1999, 1999-2000) as factors explaining the number of colonies of *Sinularia flexibilis*. See text for a detailed explanation on colony growth categories.

Effect	Df	Partial Chi-square	Probability	
Initial Size	4	312.343	0.0000	*
Change in size	3	230.330	0.0000	*
Time	1	0.078	0.7796	
Time x Initial Size	4	119.204	0.0000	*
Change x Initial Size	12	452.726	0.0000	*
Time x Change in size	3	6.833	0.0774	
Time x Initial Size x Change	12	20.886	0.0521	

Table 3.7. Number of colonies at different categories of fission at Fantome and Pelorus for different sampling times. 0 = no sign of fission, 1 = incipient fission, 2 = fission , 3 = fission in advanced state. Note that colonies are not necessarily independent among sampling times.

	Fission Category								
	No Fission				Fission				
Time	0		1		2		3		Total
	Fantome	Pelorus	Fantome	Pelorus	Fantome	Pelorus	Fantome	Pelorus	
Dec-98		80		19		17		9	125
Mar-99	113	150	113	264	59	186	55	118	1058
Aug-99	47	101	63	148	56	119	31	54	619
Dec-99	77	91	70	99	67	71	40	46	561
Mar-00	21	84	29	94	57	94	45	54	478
Aug-00	27	100	67	165	58	115	61	69	662
Dec-00	53	88	83	114	70	90	58	59	615
Locality	338	694	425	903	367	692	290	409	4118
Category		1032		1328		1059		699	
			No Fission	2360 (57.3%)			Fission	1758 (42.7%)	

Table 3.8. Potential number of recruits to be generated from observations of colonies in the field in advanced degree of fission (categories 2 and 3 of Table 3.7).

	No. of colonies in categories 2 and 3 of fission (and %)	Potential number of recruits per dividing colony
	1406 (80.0)	1
	192 (11.0)	2
	100 (5.7)	3
	39 (2.2)	4
	13 (0.7)	5
	8 (0.4)	6-19
Total	1758 (100)	

Table 3.9. Observed number of recruits by fission per colony of *S. flexibilis* over two years into the permanent transects.

	Colonies that underwent fission (and %)	Recruits by fission per colony	Total recruits by fission over two years
	109 (75.7)	1	109
	24 (16.7)	2	48
	6 (4.2)	3	18
	2 (1.4)	4	8
	3 (2.1)	6	18
Total	144 (100)		201

Table 3.10. Number of eggs per polyp in three colonies of *S. flexibilis*

Colony (Size in cm²)	Subsample	No. of polyps	No. of eggs	No. eggs/polyp	Mean (SD)
1 (157)	1	85	71	0.83	0.74 (0.096)
	2	84	63	0.75	
	3	56	36	0.64	
2 (236)	1	48	14	0.29	0.27 (0.056)
	2	57	12	0.21	
	3	54	18	0.33	
	4	47	11	0.23	
3 (628)	1	74	0	0	0.05 (0.060)
	2	37	1	0.03	
	3	54	6	0.11	

Table 3.11. Evaluation of interactions between Fate (F), Initial Size (S), Time (T), and Locality (L) by comparing a model that excluded the three- and four-interaction terms listed, with a model that included all the terms. ΔG = difference between the goodness-of-fit G-values of the models compared; Df = degrees of freedom; P = probability.

Interaction terms excluded from the model	ΔG	Df	P
FST, FSTL	20.1	12	0.0658
FSL, FSTL	23.4	12	0.0244
FTL, FSTL	25.3	9	0.0027
STL, FSTL	28.9	8	0.0003

Table 3.12. Selected demographic statistics of *S. flexibilis* for the two localities and two time intervals. Results of the two time intervals, combining both localities, are shown in bold.

		Fantome 98-99	Pelorus 98-99	Fantome 99-00	Pelorus 99-00	**98-99**	**99-00**
Rate of population growth per year, λ		1.312	1.238	1.182	1.159	**1.285**	**1.157**
95 % CI of λ		1.272 – 1.374	1.224 – 1.265	1.152 – 1.236	1.123 – 1.225	**1.269 – 1.316**	**1.134 – 1.201**
Rate of population growth per individual, r		0.271	0.214	0.167	0.148	**0.251**	**0.146**
Damping ratio		5.15	2.94	10.20	2.72	**3.72**	**3.95**
Time for doubling population size							
a) from per capita growth rate		2.6	3.2	4.1	4.7	**2.8**	**4.8**
b) from projected pop size		4	4	6	5	**4**	**6**
Life expectancy (±SD)		4.7 ± 5.0	8.2 ± 9.8	2.8 ± 2.4	5.3 ± 5.6	**5.8 ± 6.5**	**3.7 ± 3.5**
Expected remaining life span for size class IV (±SD)		6.0 ± 5.4	11.1 ± 10.5	3.0 ± 2.5	7.0 ± 6.2	**7.6 ± 7.0**	**4.3 ± 3.7**
Expected lifetime production of new colonies per colony in each size class	I	2.26	2.86	1.05	1.48	**2.41**	**1.14**
	II	1.97	3.69	1.21	2.30	**3.00**	**1.49**
	III	2.86	4.15	1.23	2.62	**3.53**	**1.69**
	IV	4.34	4.67	1.40	4.02	**4.47**	**2.89**

Table 3.13. Proportional contribution of demographic processes to changes in the population growth rate (elasticity of λ to demographic processes). Each demographic process is the combined probability of the process listed and the related probability of survival (*i.e.* = Shrinking * Surviving). A, B, and C are matrices without fertility terms, with fission only, and with fission and sexual fertility included, respectively.

		Matrix			
		Four size classes		Six size classes	
	Demographic process	98-99	99-00	98-99	99-00
A)	Shrinkage	0.097	0.160	0.272	0.315
	Stasis (Not growing)	0.806	0.688	0.468	0.384
	Growth	0.097	0.152	0.260	0.302
B)	Shrinkage + Fission	0.158	0.202	0.311	0.340
	Stasis	0.672	0.582	0.372	0.311
	Growth	0.170	0.217	0.317	0.349
C)	Shrinkage + Fission + Sex	0.169	0.211	0.313	0.341
	Stasis	0.648	0.562	0.354	0.299
	Growth	0.183	0.227	0.333	0.360

Table 3.14. Growth rate estimates for octocorals. This table aimed to be exhaustive on members of the Stolonifera and Alcyoniina groups (*sensu* Fabricius and Aldersdale 2001), but shows only selected references from 'gorgonians' of the Scleraxonia group (see Coma *et al.* 1998 for more gorgonians references). L = Asymptotic growth.

Species (Family)	Growth rate (at size or age)	Units	Measurement of	Location, other observations	Source
Alcyonium siderium (Alcyoniidae)	2–12 (1st y recruits)	$mm \cdot y^{-1}$	Colony height	North western Atlantic, Gulf of Maine	Sebens (1983)
Parerythropodium f. fulvum (Alcyoniidae)	~30 (1st y recruits)	$cm^2 \cdot y^{-1}$	Colony area	Concrete plates, Red Sea	Benayahu and Loya (1987)
Sinularia Encrusting *Sarcophyton* (Alcyoniidae)	mean 0.5 (13.3 cm) max 1.4 (0.5-4.9 cm) min -1.5 (>20 cm) mean 0.5 (11.3 cm) max 1 (0.5-4.9 cm) min -0.7 (>20 cm)	$cm \cdot y^{-1}$	Colony diameter	Mid- and outer-shelf reefs GBR	Fabricius (1995)
Anthomastus ritteri (Alcyoniidae)	max 0.18 (8 y)	$cm \cdot y^{-1}$	Stalk or stem diameter	210-2050 m depth Baja California, L = 25-30 y (10 cm)	Cordes *et al.* (2001)
Alcyonium acaule (Alcyoniidae)	No change detected in two years (0–2000 mm^2)		Colony area	Medes Is. NW Mediterranean	Garrabou (1999)
Efflatounaria (Xeniidae)	max 5.2 min -2.3 72% of colonies < 1	$mm \cdot d^{-1}$	Stolon length	Mid-shelf reef GBR	Karlson *et al.* (1996)
Dendronephthya hemprichi (Nephtheidae)	max ~26 (< 1 y) max ~20 (1 to 2 y)	$cm \cdot y^{-1}$	Colony height	Red Sea, azooxanthellate	Dahan (1992)
Leptogorgia virgulata (Gorgoniidae)	12-42 (3 – 5 cm or 8 – 16 wk old)	$cm \cdot y^{-1}$	Colony branch length	Florida, No asexual reproduction	Gotteli (1988)
Plexaura kuna (Plexauridae)	1.99 (0-9.9 cm) 0.21 (10-19.9 cm) -0.43 (>20 cm) max 3.90 (0-9.9) min -3.60 (>20)	$cm \cdot y^{-1}$	Colony height	San Blas Is. Panama	Lasker (1990)
Paramuricea clavata (Plexauridae)	1.8 min 0.2 max 6.4	$cm \cdot y^{-1}$	Colony height	Medes Is. NW Mediterranean	Coma *et al.* (1998)
Muricea californica *Muricea fruticosa* (Plexauridae)	~ 2 (<20 cm) 1.69	$cm \cdot y^{-1}$	Colony height	Baja California, L = 78 cm (50 y) 40 cm (~20 y)	Grigg (1974)
Acabaria biserialis (Melithaeidae)	max 1 (3 cm)	$cm \cdot mo^{-1}$	Recruit height	Artificial substrata Red Sea, aclonal	Ben-Yosef and Benayahu (1999)
Briareum asbestinum (Briareidae)	16.6 (> 20 cm)	$cm \cdot y^{-1}$	Colony height	San Blas Island, Panamá	Brazeau and Lasker (1992)

Table 3.15. Some examples of population growth rates in studied marine clonal invertebrates based on the use of projection matrices.

Species	Summary	Authors, Observations
Agaricia agaricites	$\lambda = 0.887 - 0.982$	Hughes (1984) Only fission
Goniastrea aspera *Goniastrea favulus* *Platygyra sinensis*	$\lambda = 1.005$ $\lambda = 1.063$ $\lambda = 1.005$	Babcock (1991)
Montastrea annularis *Agaricia agaricites* *Leptoseris cucullata*	$\lambda = 0.388 - 1.074$ (recent – 70's) $\lambda = 0.330 - 0.673$ $\lambda = 0.503 - 0.801$	Hughes and Tanner (2000) Matrices only with fission; λ are over 5 y
Palythoa caesia	$\lambda = 0.095 - 1.15$	Tanner (1997) Density dependency
Plexaura A	$\lambda = 0.67 - 1.13$ (different months), average $\lambda = 0.99$	Lasker (1991) Large colonies having greatest elasticities (72%)
Muricea californica *Muricea fruticosa*	$\lambda max = 2.51$ (1.017 with larva mortality) $\lambda max = 4.26$ (0.921 with larva mortality)	Grigg (1977)
Leptogorgia virgulata	$\lambda min = 0.999$ $\lambda max = 1.009$	Gotelli (1991)
Alcyonium sp.	$\lambda min = 0.660$ $\lambda max = 1.152$	McFadden (1991)
Sinularia flexibilis	$\lambda min = 1.159$ (1.167 with sexual reproduction) $\lambda max = 1.312$ (1.339 with sexual reproduction)	This study

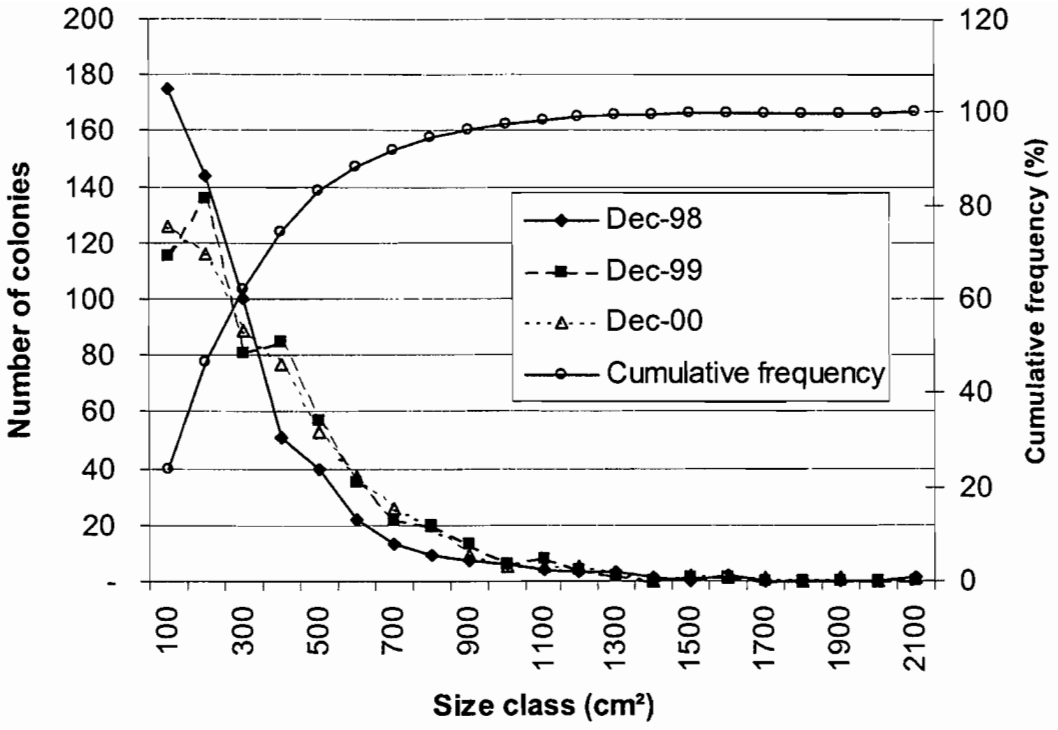

Figure 3.1. Size frequency distribution of *S. flexibilis* through time. The left y-axis represents the number of colonies in each size class for each year, while the right y-axis displays the cumulative frequency (%) for the three years.

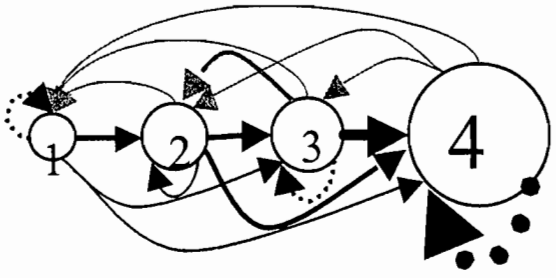

Figure 3.2. Representation of the *S. flexibilis* life cycle as used for the construction of the population transition matrices. Grey, black solid and black dotted lines represent shrinkage, growth, and stasis processes, respectively. Line thickness is scaled to transition probability values and nodes scaled to stable size distribution for 1998-1999 matrix with localities pooled.

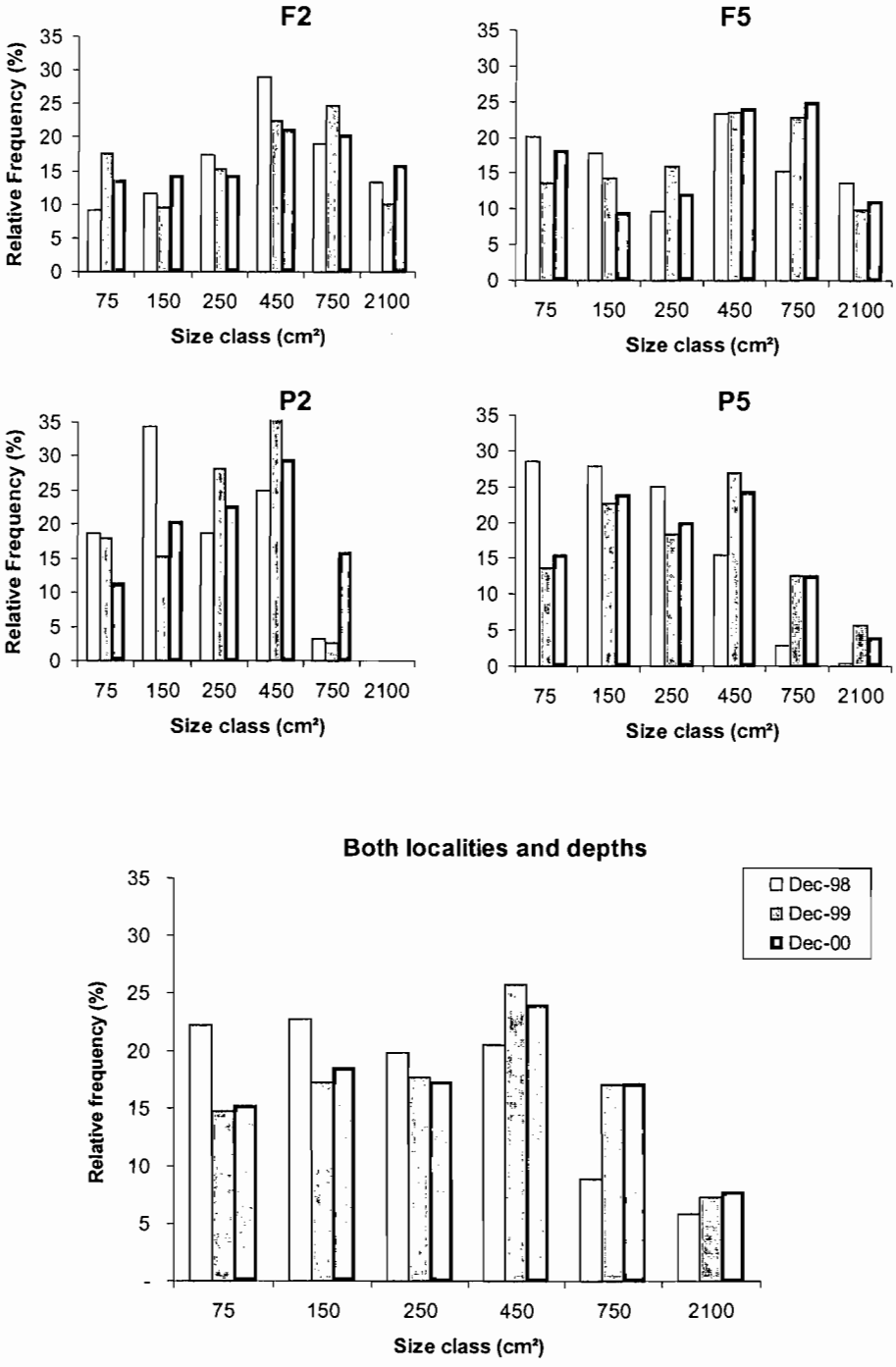

Figure 3.3. Size class distribution of colonies of *Sinularia flexibilis* (relative frequency in %) at Fantome (F) and Pelorus (P), at 2 and 5 m depth, and for both localities and depths combined. The three bars in each graph represent different sampling years (see legend).

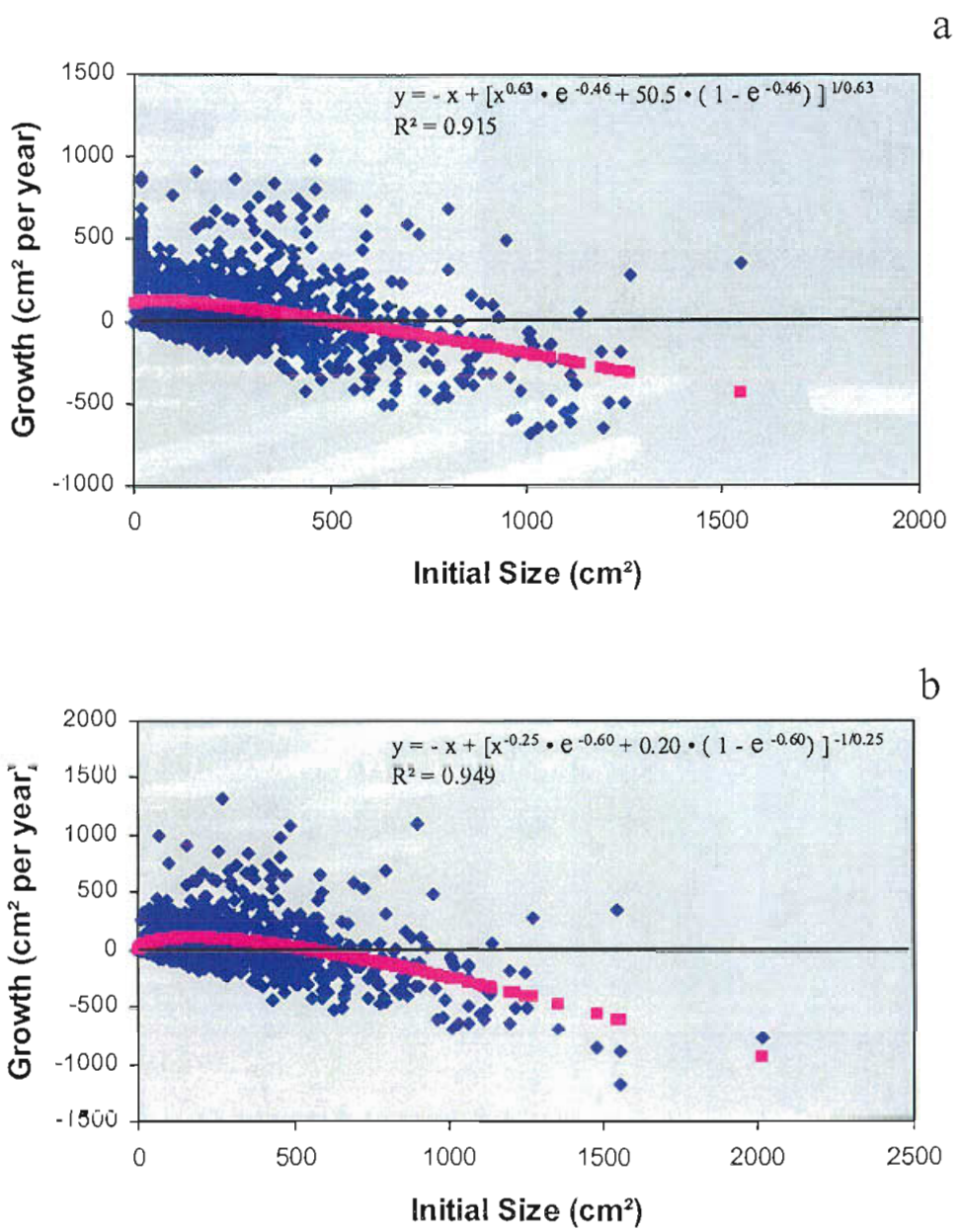

Figure 3.4. Colony growth function estimated for yearly change in size in relation to initial size at the beginning of that year. Non-linear fits to the model proposed by Francis (1995), with (a) and without (b) recruits (sexual and asexual).

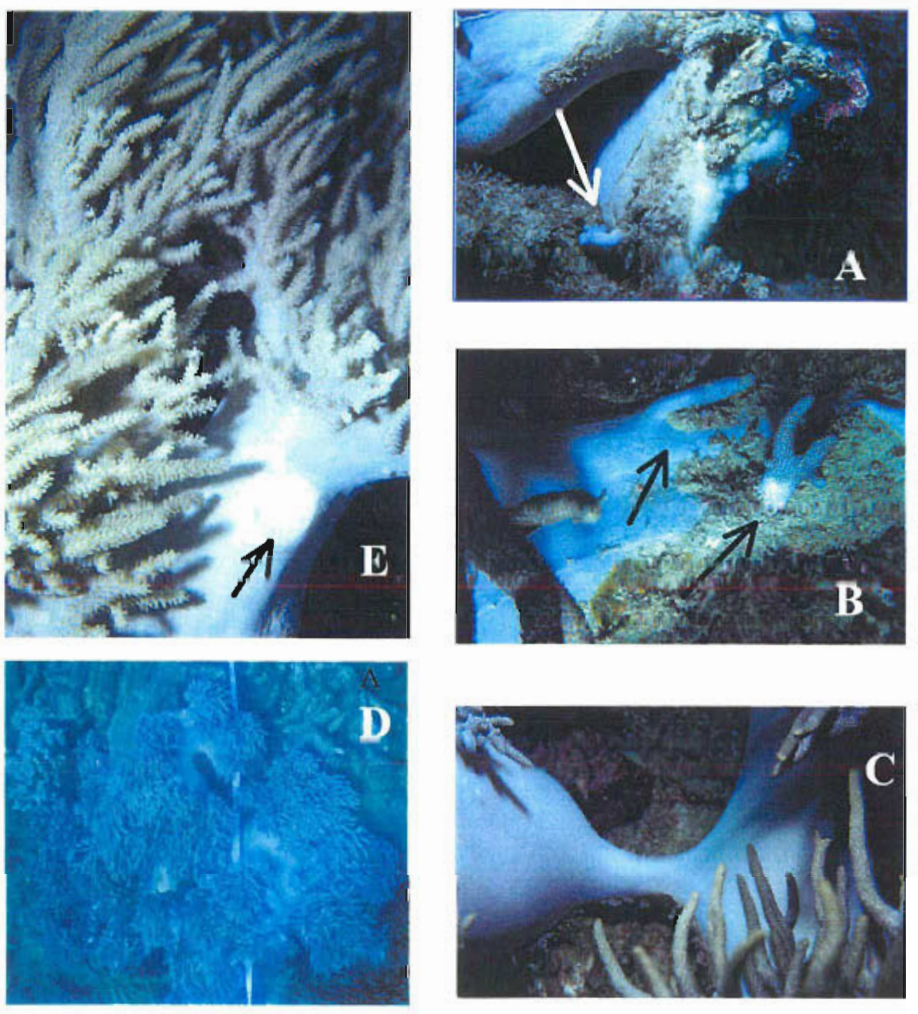

Figure 3.5. ***Sinularia flexibilis.*** **A) Bud of ca. 3 cm in height at the base of an overturned colony. B) Buds at the fission point between two colonies. C) Fission among three colonies. D) An individual colony that could generate up to 11 daughter colonies, here still showing connections among them (ca. 54 cm from top to bottom of image). E) Predation mark in a colony branch.**

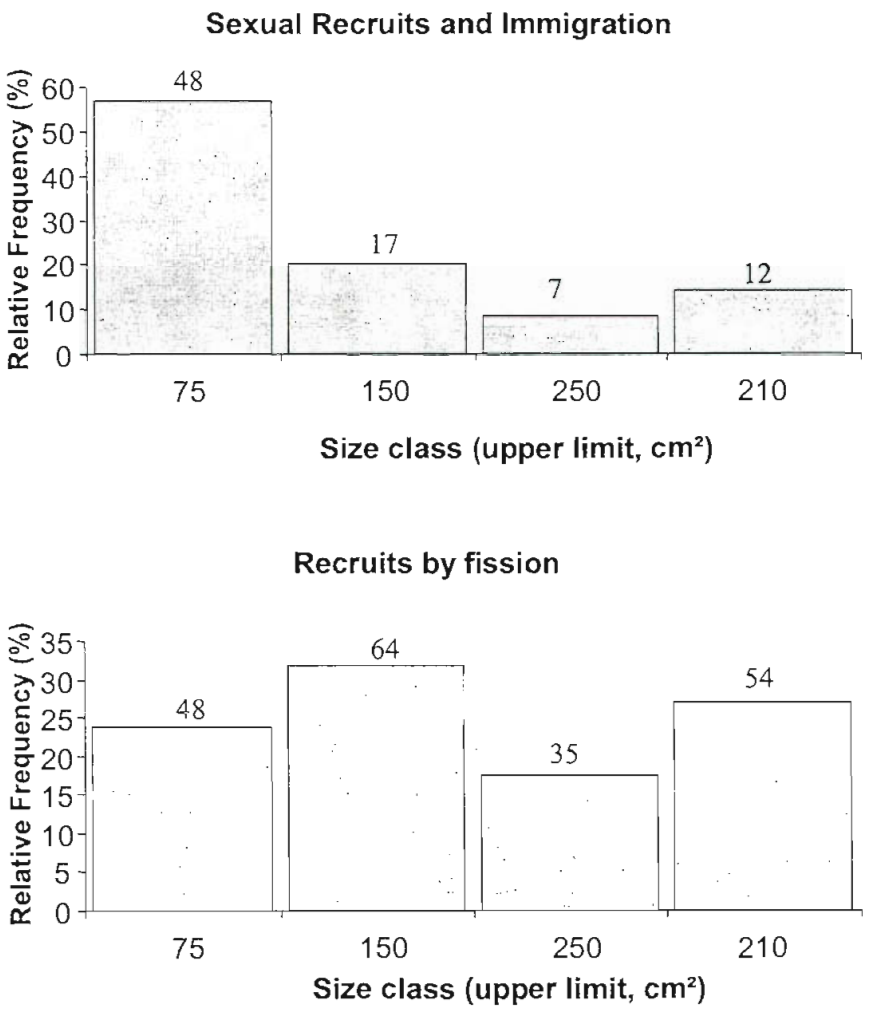

Figure 3.6. Relative frequency (percentage) of colonies recruited by sexual recruitment or movement, and by fission, into four size classes throughout the study. Numbers of colonies above each column.

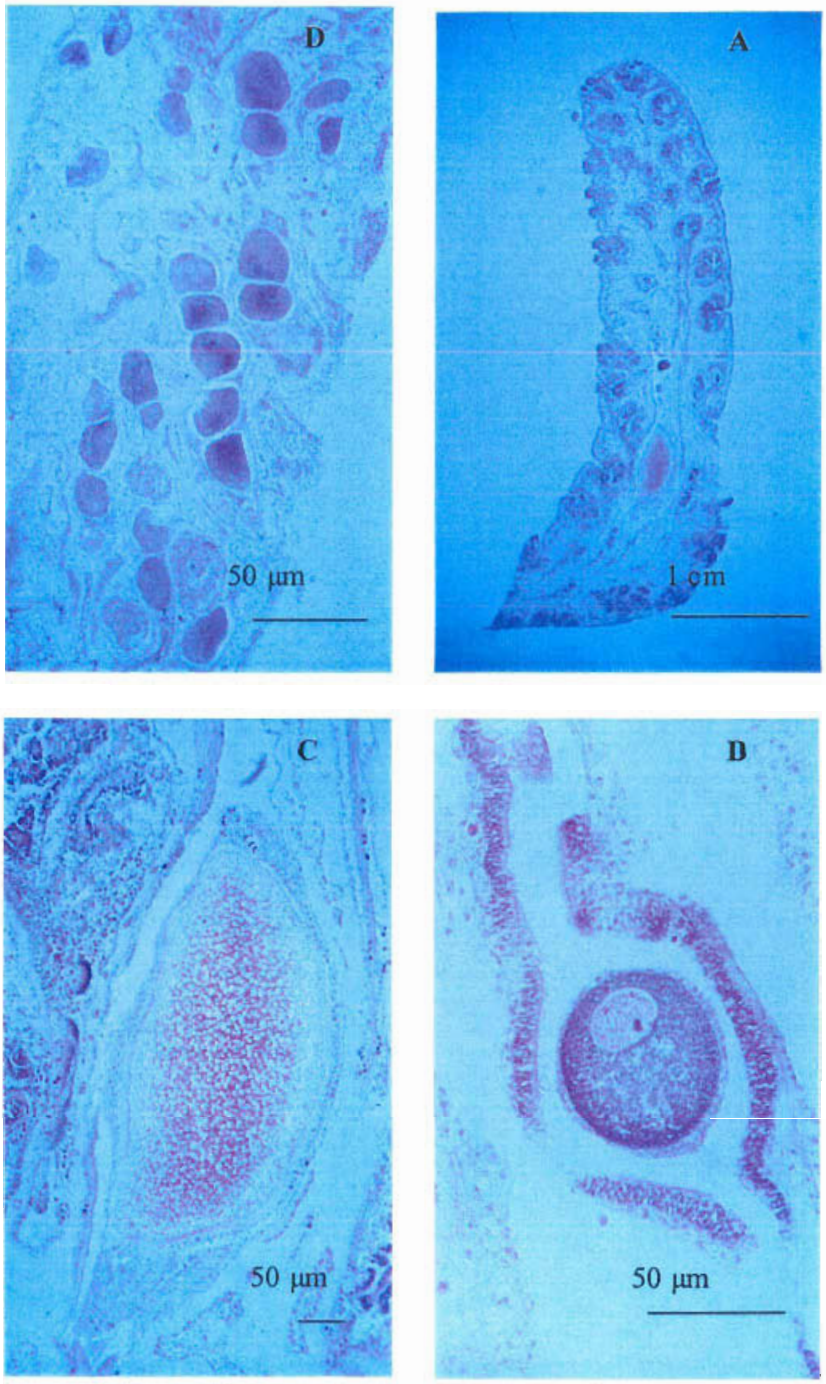

Figure 3.7. ***Sinularia flexibilis.*** **A) Branch tip showing distribution of polyps and a mature egg at the low centre. B) Oocyte in early developmental stage. C) Detail of egg in late developmental stage. D) Spermaries along a colony branch.**

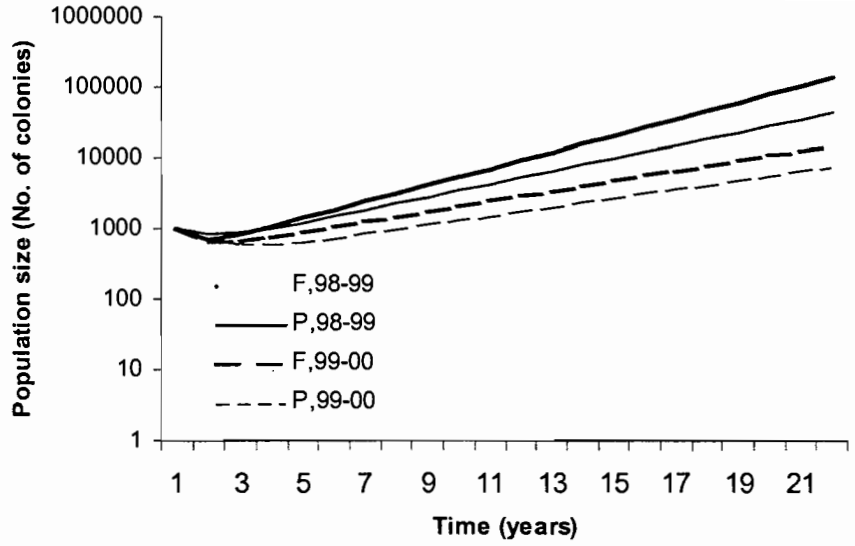

Figure 3.8. Population size of *S. flexibilis* through time assuming four constant growth rates, each calculated from data from two localities (F= Fantome, P= Pelorus) and two time intervals (98-99 and 99-00).

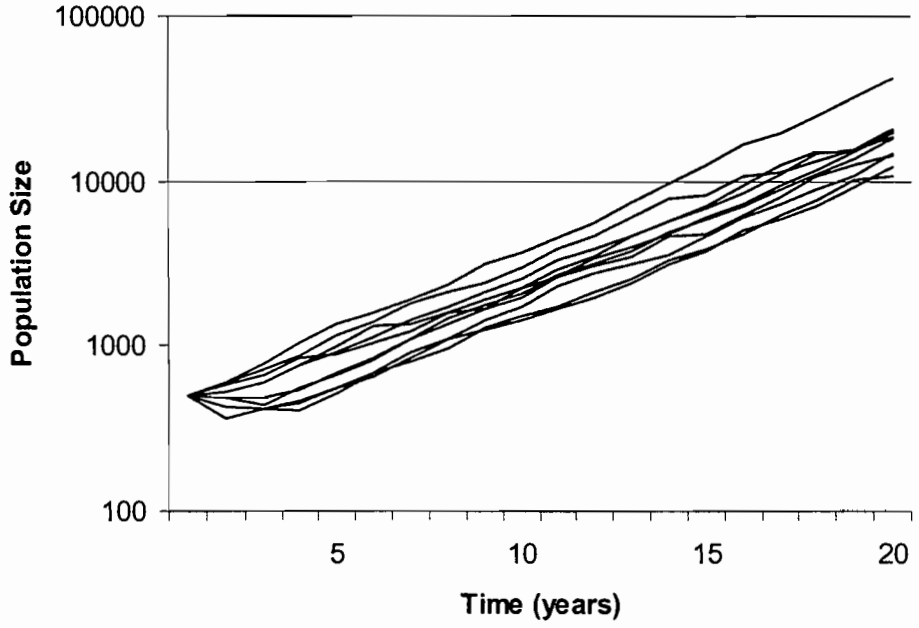

Figure 3.9. Population size of *S. flexibilis* (Number of colonies) through time (years) assuming that growth rate estimations from the four matrices (P 98-99, P 99-00, F 98-99, F 99-00) alternate randomly. Each line corresponds to one projection for a total of ten.

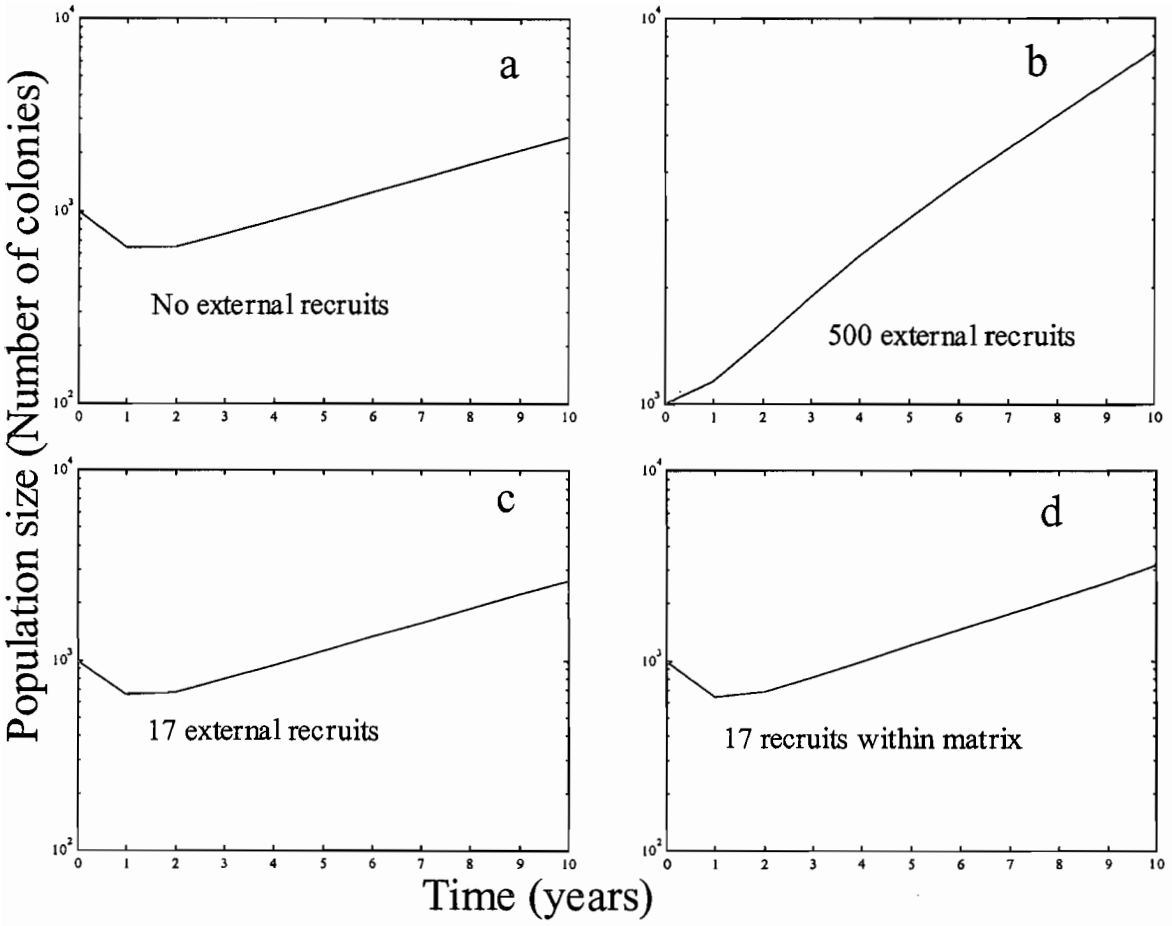

Figure 3.10. Population projection using Fantome 99-00 matrix with fission only (a). Same as (a) but adding 500 sexual recruits per year as an external input (b), and the number of sexual recruits observed also as an external input (c). The number of sexual recruits observed added as a fertility term within the matrix is also shown (d).

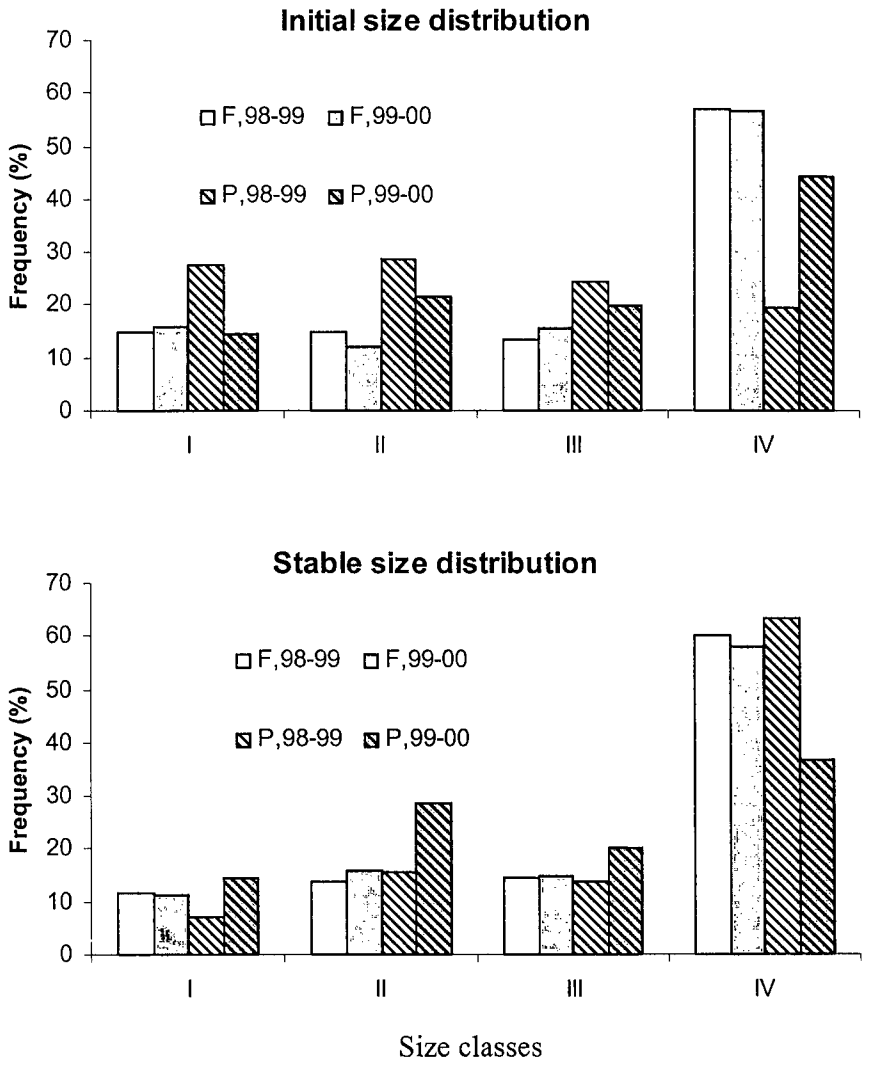

Figure 3.11. Observed size distribution at the beginning of each time interval (percentage of colonies in each size class), and stable size distribution for each of the four matrices in legend (F = Fantome, P = Pelorus).

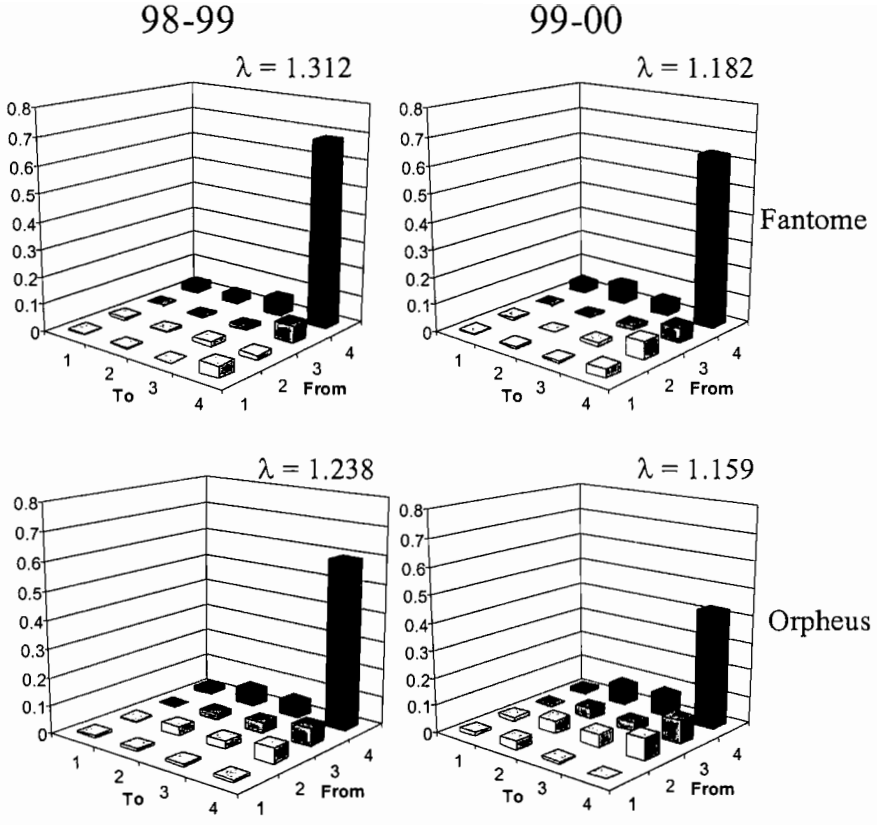

Figure 3.12. Elasticity of population growth (z-axis) to demographic process of each transition probability. The horizontal plane of the graph represents the matrix, with numbers in the x- and y-axis corresponding to the size classes, 'From' refers to time t, and 'To' to time t + 1 as in Table 3.2 and 3.3. Only matrices that include fission are shown for both localities and both time intervals.

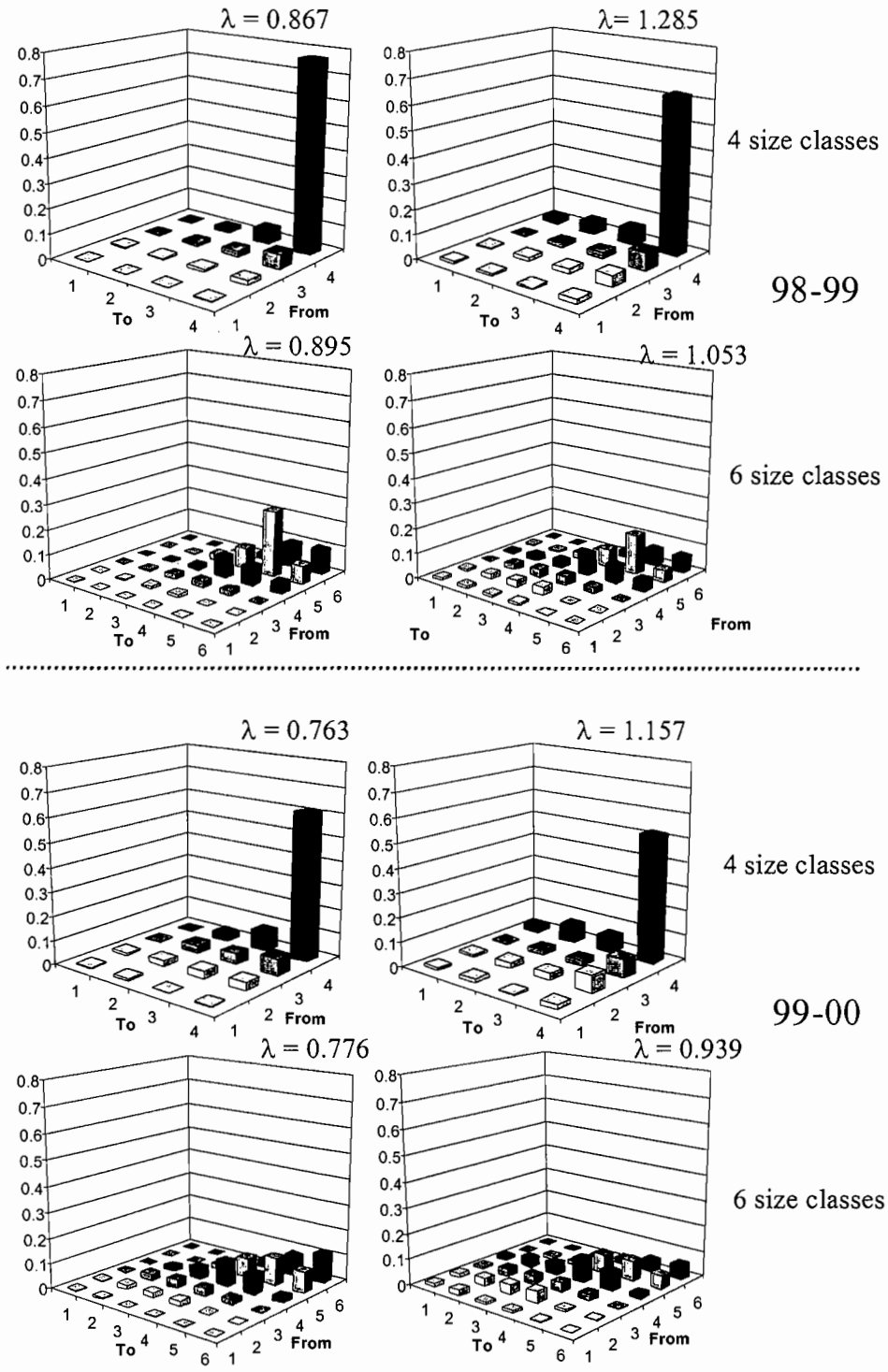

Figure 3.13. Elasticity of population growth (z-axis) to demographic process of each transition probability. Comparison between four and six size classes using matrices of year intervals 98-99 and 99-00, and both localities combined.Matrices on the left are without fertility terms, while matrices on the right include fission.

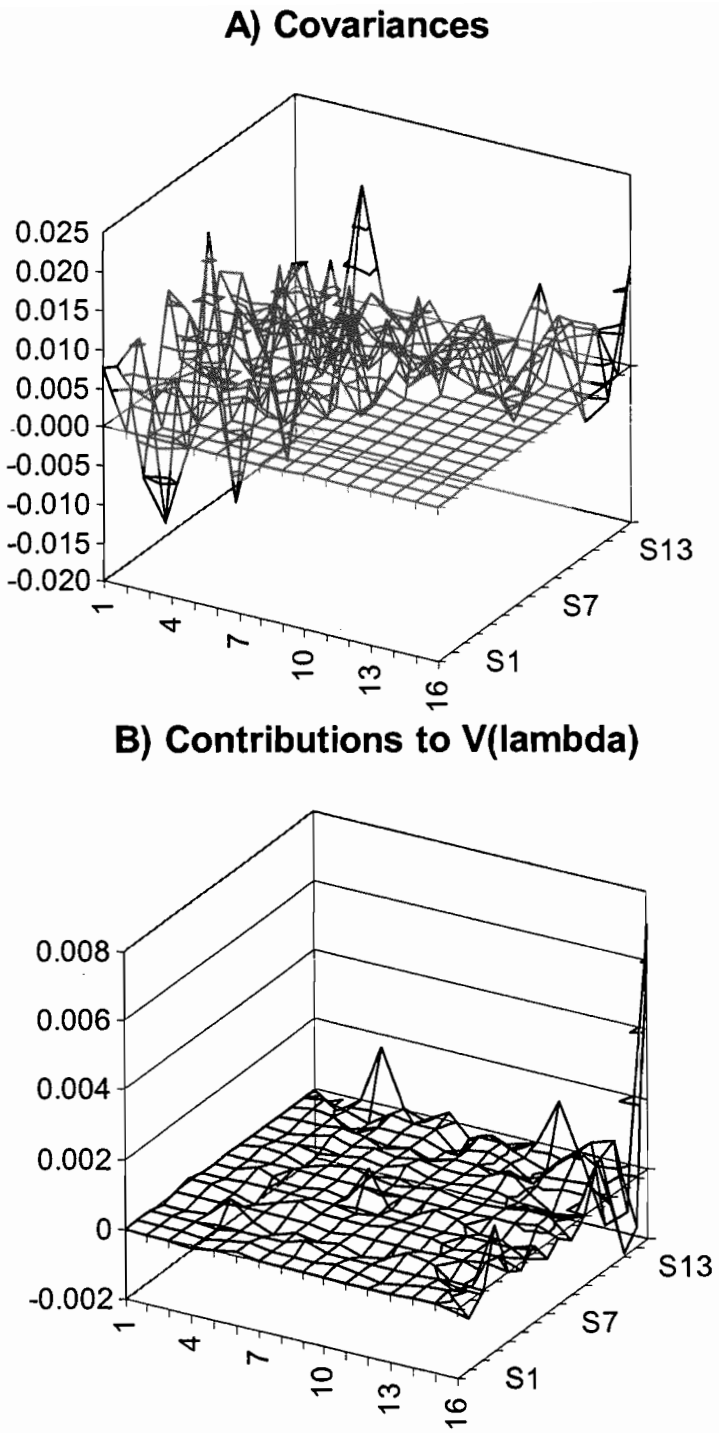

Figure 3.14. A) Covariances of the matrix elements among the four matrices (two localities and two sites. Only half of the covariances are represented as there is symmetry, with variances in the diagonal and covariances off-diagonal. B) Contributions of the covariances among matrix elements to the variance of the population growth rates (λ). Most of the variance in λ is due to variance in the stasis of colonies in the largest size class.

4 Genetic structure of *Sinularia flexibilis* and *Clavularia koellikeri* populations

4.1 Abstract

The genetic structure of twelve and six populations respectively, of *Sinularia flexibilis* and *Clavularia koellikeri*, separated by up to 1300 km along the GBR were examined using allozymes. The genotypic frequency of most loci could not be considered different to expectations from a species with sexual random mating, for a sampling distance > 5 m between separated colonies. Also, in most populations, the observed number of individuals with the same multilocus genotype did not exceed the maximum expected from the sample size assuming sexual reproduction. There were 241 unique genotypes in 459 individuals for *S. flexibilis*, and 198 among 243 individuals for *C. koellikeri*. In four *S. flexibilis* populations, however, the spatial distribution of individuals with the same genotype was closer than expected from a random distribution. This was also true in a small-scale study where the genotype of each individual was mapped within 5 m^2. This indicated that based on their spatial distribution some repeated genotypes were likely to come from asexual reproduction. No such analysis was done for *C. koellikeri*. Some degree of genetic differentiation at all of the spatial scales analysed indicated that restrictions of gene flow occur in these two species. Genetic differentiation among populations of the larval brooder *C. koellikeri* was four to thirty times larger than that found for the gamete broadcaster *S. flexibilis*, depending on the spatial scale compared (F_{ST} values = 0.168 vs. 0.041 among sites within a reef, 0.176 vs. 0.026 among reef populations, 0.084 vs. 0.004 among regions in the GBR, respectively for the species). Differences between species most likely correspond to their dispersal capabilities, which is reflected in their different types of larvae. In *S. flexibilis,* I found some genetic differentiation at spatial scales of <10 km, more deficits than excesses of heterozygotes in four loci at some populations, and a low prevalence of clonality at < 5 m^2. All of these findings favoured genetic drift in populations with certain degree of gamete or larval retention, among other potential explanations of the pattern of genetic differentiation. In *C. koellikeri*, the amount of genetic differentiation between reef populations was related to the geographic distance between them.

4.2 Introduction

The ecological and biological data presented in the other two chapters of this thesis are limited to small-scale processes at two reef sites 11 km apart. The purpose of this chapter is to present results that broaden those findings and implications to a larger scale within the GBR. Here, I present data on the relative importance of sexual *versus* asexual reproduction, the genetic differences among populations, and the potential for dispersion in the GBR of two species of soft corals with different mode of reproduction.

Soft corals show a wide variety of life histories, including sexual and asexual reproductive modes, or a combination of both (*e.g.* Dinesen 1985; Lasker 1990; Benayahu 1997). The relative importance and specific roles of sexual and asexual reproduction as factors affecting their distribution and abundance are unknown for most species of soft corals, including *Clavularia koellikeri* and *Sinularia flexibilis*. *C. koellikeri* belongs to the Stolonifera group, within the family Clavulariidae (Fabricius and Aldersdale 2001). *S. flexibilis* from the family Alcyoniidae, order Alcyoniina, is a member of one of the most prolific soft coral genera in the Indo-Pacific (110 species: Verseveldt 1980). In *Clavularia* sexual larvae are produced by internal fertilisation, and are brooded on the surface of the polyps (Benayahu 1997). On the GBR, *C. inflata* is known to extrude a white planula within a mucus sheath approximately 20 days after the full moon of October or November that triggers the mass-spawning event in many hard (Harrison *et al.* 1984) and soft corals species (Alino and Coll 1989). *C. koellikeri* also appears to follow this pattern in the Central Section of the GBR (Bastidas pers. obs). Although no studies have been published on the reproductive biology of *S. flexibilis*, other species of *Sinularia* reproduce sexually by broadcast spawning of male and female azooxanthellate gametes (review in Benayahu 1997). Preliminary results on the reproductive biology of this species (Chapter 3) showed that eggs and spermaries are produced in different colonies, as with most *Sinularia* species studied so far (Benayahu 1997), and that this species presumably broadcasts its gametes during the synchronised mass spawning of other taxa on the GBR.

Both *Clavularia* and *Sinularia* differ in colony morphology (Fig. 4.1), sexual reproductive mode, and asexual mode of reproduction: *C. koellikeri* produces new polyps by the growth of stolons that can be excised from the mother colony, and *S. flexibilis* colonies divide by what appears to be an endogenously controlled mechanism (see Chapter 3). Also, both species are common in the GBR, varying in abundance across the continental shelf, with high abundances on inner-shelf to low abundance or absence on mid- and outer-shelf reefs (Fabricius 1998). Both species can also form monospecific stands or may occur as a dominant member of species-poor stands that can cover extensive areas of hundreds of square meters on inner-shelf reefs (Fabricius 1998).

Because *S. flexibilis* has planktonic larvae, while *C. koellikeri* broods its larvae, it is expected that these species could differ in their dispersal capabilities. However, the length of larval life for *S. flexibilis* is unknown, and recent genetic studies have demonstrated that even widespread marine species with relatively long larval lives may not meet their dispersal potential (reviewed in Palumbi 1994; Todd 1998; Benzie 1999), *i.e.* do not disperse as far as might be expected from the duration of their larval phase alone.

Larval dispersal and the degree of asexual reproduction have major effects on the genetic structure of populations of marine invertebrates (*e.g.* Neigel 1997, Bohonak 1999). High levels of dispersal among populations usually result in relatively little genetic differentiation among populations, whereas low levels can lead to population differentiation. The occurrence of asexual reproduction can lead to gene frequencies that are skewed from those expected under random mating or Hardy-Weinberg (hereafter HW) equilibrium. If the differences in abundance along the GBR of each of these species result mainly from differences in rates of asexual reproduction, abundant populations (inner-shelf reefs) would be expected to show less genetic diversity and more departures from HW equilibrium than reef populations with lower abundance (mid/outer-shelf reefs). On the other hand, if differences in abundance along the GBR result from species habitat preferences, either from larval settlement or individual survivorship, abundant populations would be expected to show similar or higher genetic diversity than reef populations with lower abundances. The level of dispersal among

populations may be detected by the degree and pattern of differences in gene frequencies among populations. To the best of my knowledge this is the first study of this kind for tropical soft coral species from the Alcyoniina and Stolonifera groups.

I investigated the genetic structure of *Clavularia koellikeri* and *Sinularia flexibilis* to infer the nature of reproduction and dispersal of these species, to help understand their patterns of distribution and abundance, and processes leading to local dominance. The aim of this chapter is to present findings for both species on: 1) the relative importance of sexual *versus* asexual reproduction; 2) the spatial pattern of genetic differentiation of reef populations, ranging from sites within reefs (<2 km apart) to regions (up to 1300 km apart); and 3) the degree of connectivity between those populations along the GBR.

4.3 Methods

4.3.1 *Genetic differentiation of* Clavularia *populations*

Sampling

Clavularia koellikeri was sampled from six reef populations along the Great Barrier Reef (GBR) between August 1999 and June 2000 (Figure 4.2). Three reef populations were sampled in the Torres Strait (~ 10° latitude South) and three in the Central Sector (~ 18° latitude South). Within each of these geographical Regions two populations were sampled from inshore and one from mid-shelf reefs (Table 4.1). I intended to duplicate the mid-shelf samples in each region. However, I had to exclude one of two populations in the Central Sector (Rib Reef 18°29' S 146°52' E) from the analysis because qualitative differences in the staining pattern, and fixed differences at various loci indicated that samples from that population probably belonged to a different species of *Clavularia*. In addition, only one mid-shelf population in the Torres Strait could be sampled. Between 15 and 50 individuals or colonies were sampled at each reef from similar back-reef habitats. At Wednesday Island, Zuna Island, Pandora Reef, and Orpheus Island, individuals were collected from two different sites between 0.34 and 3.8 km apart (N per site was 22 and 25; 9 and 33; 25 and 25; 19 and 25, respectively). A colony (here also referred to as an individual) was defined as a discrete patch of polyps connected by stolons, and only colonies more than ca. 3 m apart were sampled. I chose

this sampling distance as a first approach to examine the relative contribution of asexual reproduction in the formation of *Clavularia* aggregations in the order of 10-1000 m^2 in near-shore reefs. In an aggregation of size 10 m x 100 m, a sampling distance of approximately 3 m allows collecting ~ 33 samples within its maximum linear distance. Samples consisted of five to 20 polyps collected from each colony. Samples were transported in separate plastic bags, cleaned and snap-frozen in liquid nitrogen within a few hours after collection. Tissue homogenates were prepared by grinding approximately 0.3 g of tissue wet weight with 0.2 ml of 0.05 M Tris-HCl buffer pH 8.

Electrophoresis

From an initial screening for activity of ca. 25 enzymes using a variety of buffers, I selected eight enzymes for routine screening based on their resolution, polymorphism and reliability of scoring: GPI (glucose-6-phosphate isomerase E.C. 5.3.1.9), HK (hexokinase E.C. 2.7.1.1), FBP (fructose biphosphatase E.C. 3.1.3.11), LT (peptidase using leucyltyrosine as substrate E.C. 3.4.11/13), PGD (phosphogluconate dehydrogenase E.C. 1.1.1.44), PGK (phosphoglycerate kinase E.C. 2.7.2.3), PGM (phosphoglucomutase E.C. 5.4.2.2), and FLE (fluorescent esterase with methylumbelliferyl acetate as substrate E.C. 3.1.1.1). The number of samples reported in Table 4.2 corresponds to the number of samples for which all loci were scored effectively (as required in the analysis of multilocus genotypes), not the number of samples taken from the field. Allozyme electrophoresis was carried out on cellulose acetate gels (Cellogel^{TM}), using Phosphate 7 buffer (20mM Na phosphate, pH 7) for FLE, GPI, PGD, PGM and LT, and using TM 7.8 buffer (50mM Tris-maleate, pH 7.8) for HK, FBP and PGK, following the general procedures described in Ballment *et al.* (1997).

Data Analyses

Departures of genotypic frequencies from those expected under conditions of HW equilibrium were evaluated for each locus with an approximation to the Fisher's Exact test using a Monte Carlo method (TFPGA software, Miller 1997) at a level of significance of $\alpha = 0.05$, corrected for multiple comparisons (Weir 1990). Whenever p and its estimated standard error were close to the level of rejection, the number of permutations was increased (from an initial of 10,000 permutations per locus) to better evaluate the likely significance. For contingency tables, the Exact test does not have the

same restrictions in frequencies as the Chi-square analysis (i.e. no expected frequency less than one and no more than 20% of the expected frequencies less than five; Zar 1984). Thus, the independence among loci was evaluated by an estimation of the exact probability of linkage disequilibrium for all possible pairs of loci in each population (Lewis and Zaykin 2000). This analysis was performed to test for indepence of loci, ensuring that the loci used to estimate the genetic differentiation among populations were not redundant.

Sexual vs. asexual contribution to populations was further evaluated for multi-locus genotypes by calculating the ratio of the maximum number of individuals likely to be generated by sexual reproduction summed for all genotypes (N^*), to the number of individuals sampled (N). N^* was calculated using the allelic frequencies at each reef. The ratio of number of genotypes observed (N_{go}) to N also was calculated, and both ratios were estimated following standard procedures described in Johnson and Threlfall (1987) and Uthicke *et al.* (1998).

The degree of genetic differentiation was evaluated at three spatial scales with 10 Sites among six Reefs, which in turn were in two separate Regions. For this I used Wright's F-statistics (F_{ST}: standardised genetic variance), as described in Weir and Cockerham (1984), calculated by the TFPGA software (Miller 1997). For each locus, significant departures from Ho, $F_{ST} = 0$, were evaluated using a χ^2 test, where $\chi^2 = 2N\ F_{ST}\ (k-1)$ with (k-1)(s-1) degrees of freedom, and N is the total sample size, k is the number of alleles at the locus and s is the number of populations sampled (Waples 1987). Over all loci, rejection of Ho was evaluated using the 95% confidence intervals generated by bootstrapping. Genetic differentiation was further explored by examining differences in genotypic frequencies at the different spatial scales. For this I used the randomisation of genotypes (5000 permutations) and the log-likelihood G statistic implemented in the Fstat software (V. 2.9.3.2 Goudet 1995). To determine the relationship between genetic (pairwise F_{ST}) and geographic distances between reef populations I used a Mantel test with 1000 permutations.

4.3.2 *Genetic differentiation of* Sinularia *populations*

Sampling

Samples of *Sinularia flexibilis* (Quoy & Gaimard 1833) from twelve reef populations along the GBR, ranging from the Torres Strait to the Whitsundays Sector (maximum of 1300 km apart) were collected from December 1998 to Feb 2000 (Figure 4.3). Two pairs of reefs were sampled in each of four geographic sectors from north to south along the GBR. In two of these sectors, pairs of inshore and mid/offshore reefs were sampled to assess cross-shelf variability. Up to 60 individuals or colonies were sampled from two or three replicate sites at each reef. At each site, samples were taken at least 5 m apart along the swimming trajectory to avoid repeated collections. Tissue samples were cut from the top branches of the colony using scissors, transported in plastic bags numbered in the sequence of collection and frozen in liquid nitrogen within a few hours after collection. Tissue homogenates were prepared by grinding approximately 0.3 g of tissue wet weight with 0.2 ml of 0.05 M Tris-HCl buffer pH 8. Spicules, mucus and zooxanthellae were removed by centrifugation.

Electrophoresis

An initial screening for activity of 30 enzymes using different electrophoretic conditions showed that nine enzymes could be used for routine screening based on their resolution, polymorphism and reliability of scoring. They were (abbreviated as in previous section when common): GPI, HK, FBP, TPI (triose-phosphate isomerase E.C. 5.3.1.1), ME (malate dehydrogenase, oxaloacetate-decarboxylating E.C. 1.1.1.40), MDH (malate dehydrogenase E.C. 1.1.1.37), VL (peptidase valylleucine substrate E.C. 3.4.11/13), LGG (peptidase leucylglycylglycine substrate E.C. 3.4.11/13), and FLE. Allozyme electrophoresis was carried out using cellulose acetate gels (Cellogel^{TM}) for FLE in Tris- maleate buffer pH 7.8 (Richardson *et al.* 1986) and horizontal, 12% starch gels for the remaining enzymes. GPI, HK, FBP and TPI were scored from HC 6.5 buffer (Histidine- Citric acid) and ME, MDH and peptidases from TG 8.4 buffer (Tris-Glycine), following the general procedures of Ballment *et al.* (1997).

Data Analyses

Departures of genotypic frequencies from those expected under conditions of HW, and independence of loci were evaluated following procedures described in section 4.3.1. Genetic diversity and the sexual versus asexual contribution to populations were further evaluated for multi-locus genotypes using: a) the observed and expected genotypic diversity ratio (G_o:G_e) calculated as in Stoddart and Taylor (1988); b) the ratio N*:N as

defined in the previous section (in this case N^* was calculated using the allelic frequency at each reef and using the pooled allelic frequency over the whole data set); and c) the number of genotypes observed (N_{go}) over N (as in the previous section). Spatial autocorrelation of individual genotypes within reefs was investigated to detect spatial patterns of repeated genotypes within populations (*e.g.* Miller 1998; Ruckelhaus 1998). Each genotype was given a number and the relative position of the colony was assigned using its collection sequence within a site. Moran's I and Geary's c were calculated allocating an equal number of point pairs (pairwise distance between colonies) to five distance classes (SAAP software: Wartenberg 1989). Because both indices resulted in similar estimates, only Moran's I is shown. Analyses using multi-locus genotypes were based on seven loci instead of nine (*GPI** and *LGG** had missing data for many individuals and were excluded).

I evaluated the degree of genetic differentiation or population subdivision at four spatial scales: Sector, Cross-shelf position (Inner or Middle/Outer), Reefs and Sites within reefs, following procedures described in section 4.2.1. Genetic differentiation among reefs was also evaluated from differences in allelic frequencies for each pair of reef populations based on a Fisher's Combined Probability test, using a Monte Carlo simulation to obtain an approximation for the exact probability of differences (Miller 1997). Also, pairwise F_{ST} between reef populations were plotted against their geographic distance, and no further test was made after visual inspection of this graph.

4.3.3 *Small-scale mapping of* Sinularia *genotypes*

Sampling

To explore the genetic variability in a smaller sampling scale than the one used to study the genetic differentiation among populations (≥ 5 m), I collected samples from a total of 132 colonies in seven belt-transects 5 x 1 m in length, and recorded each colonies relative position in x, y coordinates. Four, two and one transect were sampled respectively at Border Island (Feb-2000; 20° 9' 15" S, 149° 1' 51" E), Orpheus Island (Nov-1999; 18° 34' 07" S, 146° 29' 15" E), and Low Isles (Dec-1998; 16° 23' 48" S, 145° 33' 25'' E), from the Whitsunday, Central and Cairns Sectors of the GBR. From the samples collected I effectively scored 128 individuals, 10 from Low Island (**LOW**), 77 from Orpheus Island (**ORP**), and 41 from Border Island (**BOR**). Samples were

collected and preserved as described in the previous section. Due to the small number of replicate transects, this study is rather limited and it should not be used to make generalizations.

Electrophoresis

Nine loci were routinely screened from seven enzymes (abbreviations as previous sections). They were common to those used in previous section except that PGM was scored instead of MDH. Allozyme electrophoresis was carried out using cellulose acetate gels (Cellogel^{TM}) for FLE in Tris- maleate buffer pH 7.8 (Richardson *et al.* 1986) and horizontal, 12% starch gels for the remaining enzymes. HK and FBP were scored from HC 6.5 buffer (Histidine- Citric acid) and PGM, ME, VL, and LGG from TG 8.4 buffer (Tris-Glycine).

Data Analyses

For every locus in each population (the individuals sampled in a reef), I tested the genotypic frequencies against expectations of HW equilibrium using an approximation to the Fisher's Exact test as described in Section 4.3.1. To evaluate the degree of genetic differentiation among transects within a reef and among reefs, I compared the homogeneity of allelic frequencies with a Fisher's Combined Probability test, using a Monte Carlo simulation to obtain an approximation for the exact probability of differences (Miller 1997). I also calculated the F_{ST} (as in Section 4.3.1) using only the two transects at Orpheus (N=28 and 49, respectively), due to sample size limitation in the other transects.

From 1,152 individual scorings (=128 individuals times 9 loci), there were 69 gaps (no successful scoring) distributed mainly in *ME1** (=29), *PGM** (=28) and *ME2** (=10). In the previous two sections individuals with gaps in any locus were eliminated from the analysis, because sample size was not as restricted as in the analyses within transects. In this case, analyses of multilocus genotypes were performed filling those gaps with homozygotes for the most common allele. Homozygotes will be favoured if the most common allele has a frequency of 0.67 or more, as is the case for the loci to which this procedure was applied. Thus, this assumption is conservative in that it reduces the diversity of multilocus genotypes instead of artificially increasing it. However, results

on allelic frequencies and differences among them, and F_{ST} analyses were calculated using the original data set (with gaps), and reported this way. To further evaluate the potential asexual origin of repeated genotypes, I calculated the spatial autocorrelation of multilocus genotypes within each transect as described in the previous section.

4.4 Results

4.4.1 *Genetic diversity and differentiation of* Clavularia *populations*

Genetic diversity in six populations of *Clavularia koellikeri*, measured by the average number of alleles and the observed heterozygosity, ranged from 1.5 to 3, and from 0.078 to 0.317, respectively (Table 4.1). Genetic diversity was higher in the Torres Strait than in the Central Sector based on allelic richness (2.43 vs. 1.18, $p < 0.01$) and gene diversity (0.29 vs. 0.15, $p < 0.01$). Although not significant the percentage of polymorphic loci and observed heterozygosity was also greater in the Torres Strait. The lowest mean number of alleles per locus and the lowest observed heterozygosity were recorded in the Britomart population (Central Sector) that had only three variable loci (not fixed for an allele), of which only one was polymorphic using the <95% criterion for the most common allele. Five loci were fixed in some populations of the Central Sector (*i.e.* no variation, Table 4.2). On the other hand, private alleles (i.e. alleles only present in that population) were found for *PGD** at Dungeness and for *PGM** at Wednesday Island (both in the Torres Strait).

Genotypic frequencies for most loci in each population did not differ significantly from those expected from HW predictions (Table 4.3). The only exception was the Wednesday Island population, where genotypic frequencies of *HK**, *PGK** and *FLE** had significant deficits of heterozygotes (Table 4.3).

The analysis of independence of loci showed that among 168 pairwise comparisons, 15 were significantly non-independent ($p < 0.0003$), all of them from the Wednesday Island population. This non-independence occurred mainly among loci which also showed departure from HW equilibrium, *i.e.* between *HK** and all other loci except *FBP**, between *FLE** and all other loci, and between *PGK** and other loci except *FBP** and *PGM**. Separate analysis for each site within this reef indicated that genotypic frequencies of *FLE** did not conform to HW predictions only at site 2. However, the power of the analysis to detect deviations decreased due to only having 22 and 25 samples in each site, and ranged from 9 to 64% (for $\alpha = 0.05$). Thus, deviations in this population are discussed further below.

The analysis of multi-locus genotypes indicated a relatively high genotypic diversity, with a total of 198 unique genotypes found among 243 individuals (overall N_{go}:N = 0.81). In each population, the number of repeated genotypes observed was not greater than that expected to have been produced sexually in those populations, with N^*:N close to unity (Table 4.4). Population on reefs from Torres Strait showed a higher proportion of unique genotypes relative to the number of individuals sampled than the Central Sector populations (N_{go}:N 0.83 ± 0.13 and 0.39 ± 0.24, respectively; mean ± SD for three reefs in each sector). The lowest number of unique genotypes was found in the Britomart population, where only six unique genotypes were found among the 45 individuals sampled (Table 4.4). In this population, although one genotype was repeated in 19 and another in 20 individuals, they were within the 95% confidence interval of the number expected on the basis of sexual reproduction using the allelic frequency of that population (Table 4.4).

The hierarchical F_{ST} analysis showed significant genetic differentiation among the reef populations (F_{ST} Reefs = 0.176; Table 4.5). Although allelic frequencies differed between regions (Exact test χ^2 = 260.2; d.f. = 16; $p < 0.001$), the hierarchical analysis showed no significant genetic differentiation between regions when differences between reefs were taken into account (F_{ST} Regions = 0.084, $p > 0.05$; Table 4.5). Six and four out of eight loci contributed significantly to the genetic differentiation found at the scale of Reefs and Regions, respectively (Table 4.5). Of the total variance of gene frequencies observed, differences between Regions explained 8.4%, differences among Reef populations within each Region explained 9.2%, and differences within populations explained 82.4%. Of the total variance attributable to genetic differentiation among Reef populations, 53% was among populations within Regions and 47% among populations between Regions.

A separate hierarchical F_{ST} analysis differentiating by sites showed significant genetic differentiation at all spatial scales: between sites <4 km apart within a reef, between reefs <30 km apart, and also between the two regions ~ 1000 km apart (Table 4.6). Eight, seven and five out of eight loci contributed significantly to the differentiation at the scale of Sites, Reefs, and Regions, respectively (Table 4.6). This analysis using sites as the smaller sampling scale is limited due to the number of samples, and consequently the results should be treated with caution. However, the trends and levels of genetic

differentiation are the same as in the previous analysis using reefs as the smaller sampling unit. Further exploration of the nature of differentiation, also showed that genotypic frequencies varied significantly among sites (Table 4.7). Sites within a reef only differed significantly at Wednesday Is. indicating that pooling the samples from sites within a reef, as done for the previous analysis, was appropriate except for this population.

Consistent with the pattern suggested from pairwise comparisons of genotypic frequencies among sites, there was a significant relationship between geographic separation and genetic distance between reef population pairs (Figure 4.4, $p < 0.05$). The pairwise comparisons cluster into two groups that correspond to the Regions because we had no data points between 200 and 1000 km apart. Within each of the two regions, analyses for those reefs with two sites indicated no significant relationship between genetic distance and geographical separation (Torres Strait $p = 0.54$; Central Section $p = 0.19$). Accordingly, in Figure 4.4 there is a large range of pairwise F_{ST} within each region, and more samples at intermediate distance would be necessary to suggest a mechanism for the pattern of differentiation found along this geographic range. The Britomart population was an outlier in the dendrogram that illustrates the genetic distance between populations (Fig. 4.5), and produced the two high F_{ST} values in nearest reefs in Figure 4.4, showing that marked genetic differentiation can exist within regions.

4.4.2 *Genetic diversity and differentiation of* Sinularia *populations*

Electrophoretic analyses of nine polymorphic allozyme loci showed consistent levels of genetic diversity in each population of *Sinularia flexibilis*, with the average number of alleles per locus ranging from 2.2 to 2.7, and observed heterozygosity ranging from 0.23 to 0.42 (Table 4.8). The percentage of polymorphic loci was high, as expected from *a priori* selection of enzymes that maximised the information to evaluate genetic differentiation (Table 4.8). The number of alleles per locus was relatively low in all populations, ranging from two to a maximum of four (Table 4.9).

In most cases genotypic frequencies for each population and locus did not differ significantly from those expected from HW predictions (Table 4.10). Genotypic frequencies for loci *MDH**, *FBP**, *LGG** and *TPI** were not in HW equilibrium in 10,

five, four and one population(s), respectively. For these loci there was a deficit of heterozygotes, with the exception of *LGG**. On a single-locus basis, all these loci showed a significant inbreeding coefficient consistent with the results that indicated deviation from HW expectations (F_{IS}, Table 4.13). When *MDH**, *FBP** and *LGG** were excluded from *F*-statistic analyses, the inbreeding coefficient (F_{IS}) over all loci remained significant, but barely.

Analysis of independence of loci showed that from 432 pairwise comparisons, 76 were significantly non-independent and 55 of these involved an association between *MDH** and another loci (data not shown). Further data exploration on the type of association between loci (using principal coordinate analysis, not shown) did not indicate that those associations were likely to have resulted from sampling different species. As exclusion of *MDH** from *F*-statistics did not result in a change in the main results, *MDH** was included in further analysis.

Analysis of multi-locus genotypes indicated an overall diversity of 241 unique genotypes in 459 individuals (N_{go}:N = 0.53), and an observed to expected genotypic diversity ratio G_o:G_e ranging between 0.72 and 1.37 (Table 4.11). The maximum expected number of individuals produced sexually belonging to the observed genotypes (N^*) was always equal to, or slightly smaller than, the number of individuals sampled (Table 4.11). Thus, all individuals may have been produced by sexual reproduction, whether calculations were performed using allelic frequencies for each reef population or for the population of all reefs pooled. Moreover, in each population the number of individuals per multi-locus genotype indicated that most repeated genotypes appeared once or twice, with few exceptions (Table 4.11). No population had a particularly high number of repeated genotypes. The relative spatial distribution of genotypes within reefs, however, indicated that in four out of twelve populations some repeated genotypes were closer than expected from a random distribution (Table 4.12). This suggests that some repeated genotypes could have been asexual in origin. In three out of four of these reefs (Undine, Agincourt and Cannon Bay) the overall significance of the correlogram was due to the significance of the autocorrelation value between all pairwise distances within the first distance class (*i.e.* the relatively closer colonies).

Hierarchical F_{ST} analysis nesting sites within reefs, and reefs within cross-shelf positions, demonstrated no significant differentiation between inner- and mid/outer-shelf reefs (F_{ST} = 0.006, Table 4.13). No genetic differentiation attributable to shelf position was detected even when: a) excluding loci showing HW disequilibria and high inbreeding coefficient consistently over most populations (*MDH**, *FBP** and *LGG**); and/or b) including only the Cairns and Central sectors that had pairs of reefs in each shelf position (Table 4.13).

However, there was significant genetic differentiation among reefs, and among sites within reefs (F_{ST} reefs = 0.026 and F_{ST} sites = 0.041, Table 4.13) which suggests restriction of gene flow at these scales. Genetic differentiation between sites within a reef occurred significantly at Hook Island and Undine Reef populations (F_{ST} sites = 0.029 and 0.038, respectively).

In a separate hierarchical analysis, nesting reefs within cross-shelf position and these within sectors (that correspond to a latitudinal gradient), no genetic differentiation over all loci was found among the four Sectors (F_{ST} = -0.004 95% CI -0.010 +0.002, data not shown).

The degree of genetic differentiation between each pair of reefs showed no relationship to the geographic separation of the reefs (Figure 4.6). However, pairwise comparisons of allelic frequencies between reefs over all loci indicated more significant differences among inner reefs (14 out of 15 pairs) than among mid/outer-shelf reefs (3 out of 15 pairs, Table 4.14). This pattern was also observed for pairwise F_{ST} values between reefs (data not shown). These results indicated more heterogeneity in allelic frequencies among inner-shelf reefs than among mid/outer-shelf reefs (F_{ST} inner reefs = 0.039 95% CI 0.019-0.060; F_{ST} mid/outer reefs = 0.015 95%CI 0.005-0.026). Also, 27 out of 36 comparisons between inner- and mid/outer-shelf reefs resulted in significant differences in allelic frequency (Table 4.14).

4.4.3 *Small-scale mapping of* Sinularia *genotypes*

An average of 120 individuals examined for each of the nine polymorphic loci yielded 28 presumed alleles. The percentage of polymorphic loci within transects ranged

between 55.6% and 88.9% (Table 4.15). Although loci chosen were variable, there was relatively high polymorphism considering the low number of individuals within transects, specifically at **LOW** and **BOR**. The maximum number of fixed loci within each transect was four, all at **LOW**.

The most common allele for each locus was the same between localities, with the exception of *HK** (Figure 4.7). For this locus the most common allele was *HK2** in **BOR** and **ORP**, and *HK3** in **LOW**, with frequencies of 0.54, 0.49, and 0.55, respectively. The most common allele for each locus was more variable among transects within a locality than among localities (Figure 4.7).

Allelic frequencies were heterogeneous within and among localities (Table 4.16). Hierarchical analysis of genetic differentiation at **ORP** also supported a higher variability in allelic frequencies among transects than among localities. This pattern also occurred after leaving only one copy of each multilocus genotype, to avoid potential effects of repeated genotypes. At this locality, there was still significant genetic differentiation among the two transects (N1 = 20 genets, N2 = 27 genets) separated by less than 100 m (F_{ST} = 0.088 95% CI + 0.014 to + 0.154).

Genotype frequencies did not differ significantly from those expected under HW equilibrium with nine exceptions out of 27 combinations of locus and locality (Table 4.17), or nine out of 23 after subtracting the number of fixed loci. Of those nine departures, eight were heterozygote deficiencies and one was a heterozygote excess. As a result of heterogeneity of allelic frequencies among transects, expected genotypic frequencies calculated from allelic frequencies of a locality (pooling across transects) contrasted with those calculated from allelic frequencies of each transect separately. For example in **BOR**, *LGG2** was fixed for allele *LGG2*-1* in three transects, while the remaining transect had a frequency of 0.93 for allele *LGG2*-2* (Figure 4.7). Similarly, at **ORP**, genotype frequencies of *PGM** deviated from HW with heterozygote deficiency, whereas within each transect this locus had an excess of heterozygotes, being non-significant at ORP1 and significant at ORP2. Thus, analysis of departure from HW equilibrium would be more reliable using the allelic frequencies of the transects, but on the other hand they are limited by the number of samples. Using allelic frequencies of each transect there were four out of 63 deviations from HW expectations.

In summary, using allelic frequencies either from a transect or pooled across transects in a locality, there were relatively few deviations from single-locus HW expectations, which indicated a predominantly sexual type of reproduction.

The genotypic diversity from the analysis of multilocus genotypes also indicated a low incidence of asexual reproduction. From 128 individuals scored, there were 79 different genotypes, of which 21 were repeated and 58 were unique. The estimated maximum number of individuals produced sexually was very similar to the number sampled ($N^*:N \sim 1$), indicating that most individuals with a repeated genotype could have been produced sexually (Table 4.18). A minimum $N^*:N$ of 0.89 was observed at ORP, and this ratio differed little whether calculated from the overall or the local allelic frequencies.

Despite little indication of asexuality from the $N^*:N$ ratio, the high exclusivity of repeated genotypes to a particular locality, and even to a particular transect suggested an asexual origin for some colonies (Table 4.19). For example, 13 and 17 out of the 21 repeated genotypes were exclusive to a transect, and to a locality, respectively (Table 4.19). Genotypes No. 8 and No. 11, mostly from transect ORP2, were in excess of the number expected to be produced sexually and were the only two genotypes contributing to lower the $N^*:N$ ratio in that transect (Table 4.19).

The potential asexual origin of some of the repeated genotypes was also emphasised by their spatial distribution within transects (Figure 4.8). The proximity of colonies of the same genotype was greater than expected from a random distribution, particularly at ORP and LOW (Table 4.20). There, significantly positive spatial autocorrelation of multilocus genotypes was obtained for closer colonies.

4.5 Discussion

This study of the genetic structure of *Clavularia koellikeri* and *Sinularia flexibilis* provided new insights into the nature of reproduction and dispersal of these soft coral species in the GBR. Firstly, genetic diversity and analysis of genotypes based on individual and multiple loci showed a predominantly sexual recruitment into the studied populations of these species that are also able to replicate asexually. Secondly, it showed that *S. flexibilis* populations could differ at all spatial scales analysed. This occurs despite potential for long distance dispersal from a planktonic larva, which is reflected in a low level of genetic differentiation. Genetic differentiation in *C. koellikeri* was larger than that found in *S. flexibilis* as expected from having a brooded larvae, which usually has more restricted dispersal. Finally, I will discuss potential explanations for the degree and pattern of genetic differentiation found.

4.5.1 *Sexual and asexual contribution to the genetic structure*

The genotypic diversity of six *Clavularia koellikeri* populations from two regions 1000 km apart, and of 12 populations of *Sinularia flexibilis* from four regions up to 1300 km apart in the GBR, indicated a predominance of sexual reproduction in all populations. In both species, this result is supported by genotypic frequencies that do not significantly deviate from those predicted by Hardy-Weinberg (HW) equilibrium for most loci within populations. For *C. koellikeri*, only three significant heterozygote deficits occurred, all in the Wednesday Island population (Torres Strait), which also showed a number of significant associations between alleles at different loci (see below for further discussion). For *S. flexibilis*, only one out of nine loci showed a significant deficit of heterozygotes in most populations.

The predominant contribution of sexual reproduction in both species was also supported by parameters based on multilocus genotypes (N:N^*, N_{go}:N, G_o:G_e), which for most populations were higher than those reported for highly clonal organisms (*e.g.* Ayre 1984; Stoddart 1984; Hoffmann 1986; Ayre and Willis 1988; Coffroth and Lasker 1998; Uthicke *et al.* 1998, 1999). The maximum estimated number of individuals likely to have been produced sexually, was always equal to or slightly smaller than the number of individuals sampled (N^*:$N \sim 1$), indicating that even repeated genotypes were likely

to have been produced by chance from sexual reproduction. In *C. koellikeri* the minimum value of $N^*:N$ in a population was 0.93, while in *S. flexibilis* it was one, both calculated from the allelic frequencies observed in each population. However, the ability to estimate clonal contribution to the population from $N^*:N$ greatly depends on the frequency of the most common allele, and on the number of variable loci. For example, *C. koellikeri* in the Britomart population had a small number of highly repeated genotypes but also low levels of genetic variation, with only one out of eight loci being polymorphic. Therefore, the number of highly repeated genotypes in the locus that was polymorphic, did not exceed the number of individuals that could be produced sexually ($N^*:N = 1$). This warns about the use of this ratio alone when there is reduced genetic diversity. The ratio of the number of unique genotypes relative to the number of individuals sampled ($N_{go}:N$) helps to complement results from $N^*:N$, as it is indicative of the minimum number of individuals that could have been produced sexually. Over all populations, both species showed a relatively high genotypic diversity for clonal species, with 241 unique genotypes among 459 individuals ($N_{go}:N$ 0.81 for *C. koellikeri*, and 0.53 for *S. flexibilis*). However, among populations, $N_{go}:N$ varied more in *C. koellikeri*, ranging between 0.13 and 0.93, than in *S. flexibilis* for which it ranged between 0.69 and 0.95. The lowest $N_{go}:N$ for *C. koellikeri* occurred in the Britomart population and showed a very reduced genotypic diversity, and further work will be required to determine the nature of this pattern. I suggest that genetic drift (changes in allelic frequencies due to random sampling of gametes to form the next generation) had strongly affected this population due to factors limiting its abundance (see below).

For *S. flexibilis* there is further evidence of the extent of sexual and asexual contribution. Spatial autocorrelation analyses of the genotypes of colonies separated by 5 m along the trajectory of sampling of ca. 300 m, indicated that in three out of 12 reefs, repeated genotypes were closer than they would be if randomly distributed. Similarly, the small-scale study of genotypes showed that in three 1 m x 5 m transects the colonies with the same genotype tended to be close together rather than in random association with any other genotype. Although repeated genotypes never exceeded 10 individuals within a locality at any of the two spatial scales, and most of them could have been produced sexually based on nine-locus genotypes, the spatial arrangement of colonies supports the contention that some of them are likely to have been produced asexually. This was expected, considering that at several reefs in the GBR as many as a

third of the observed colonies were going through fission (Chapter 3). Based on those observations, the relatively low contribution of clonality for *S. flexibilis* was unexpected. Alternatively to what the genetic structure suggests, if *S. flexibilis* has a higher incidence of asexual reproduction, other processes such as high local mortality, or mobility of clones, may open space to colonisation by sexually produced colonies, avoiding the dominance of a single genotype within 5 m^2. Sexual and asexual reproduction, and other factors that determine the population dynamic of a species affect the genetic diversity (*e.g.* Silander 1985; Hughes *et al.* 1992), and their relative contribution is generally unknown in clonal organisms. The demographic study of *S. flexibilis* has made an important contribution to calibrate between the inferred predominant mode of reproduction from field observations in a single-census with that inferred from the genetic structure of the populations (see general discussion).

For *Clavularia koellikeri*, this study also demonstrated a predominant role of sexual reproduction in the establishment of colonies ≥ 3 m apart in six reef populations. The major contribution of sexually produced recruits was supported by genotypic frequencies not deviating significantly from HW expectations and by the analysis of multilocus genotypes indicating that repeated genotypes could have been formed by sexual reproduction. The *Clavularia* study was more limited than that of *S. flexibilis* because the number of populations sampled for a similar geographic scale (1,000 km) was less, and small-scale mapping of genotypes was not undertaken. However, there were two additional aspects from the *Clavularia* study that deserve further discussion.

Firstly, the observed heterozygosity, number of alleles, and percent of polymorphic loci indicated a higher genetic diversity in the Torres Strait (~ 10° S) than in the Central Sector of the GBR (~ 18° S). The reef populations from Torres Strait showed a higher proportion of unique genotypes relative to the number of individuals sampled than the Central Sector populations (N_{go}:N 0.83 vs. 0.39). On the other hand, the southern distribution limit of *Clavularia* in the GBR is ~ 19° latitude South, and it occurs in lower abundances towards the outer-shelf reefs (Fabricius and De'ath 2000). These factors, considered together, suggest that in the Central GBR closer to its limit of distribution than the Torres Strait, *C. koellikeri* could have limited sexual reproduction and/or recruitment, particularly on mid-shelf reefs. The population at Britomart, a mid-shelf reef in the Central GBR, had the lowest genotypic diversity with one out of eight

loci polymorphic and six different genotypes from 45 individuals (N_{go}:N 0.13). Reduced genetic diversity, the genetic distinction from other populations, and the relatively low abundance of this species in the Britomart population (CB pers. obs.) may indicate restricted recruitment to that reef. A greater degree of self-seeding than on other reefs cannot be excluded as potential explanations for its genetic structure. It has been suggested that organisms may display a greater degree of asexuality in ecologically marginal habitats (*e.g.* Peck *et al.* 1998). There was no evidence to support this for *S. flexibilis* for which mid-outer shelf reefs could be suggested as marginal. However, small-scale genetic analysis and more replication on reefs with limited abundance will be required for a more accurate estimate of clonality of *C. koellikeri* in those marginal environments. Under the limitations of this study the formation of separate colonies in *C. koellikeri* remains mainly as the result of sexual reproduction. Thus, I speculate that differences in genetic structure between optimal and marginal environments (here only as limits of distribution) can be marked in *C. koellikeri* because of its more restricted dispersal (see next section), while such differences were not detectable in *S. flexibilis*.

Secondly, the Wednesday Island population (Torres Strait) showed three significant heterozygote deficits out of the eight loci examined, and there were 15 significant associations between alleles of different loci, all involving those three loci deviating from HW. The lack of evidence of a strong effect of asexual reproduction in this population (N_{go}:N = 0.68, N^*:N = 0.93) suggested that other processes leading to non-random association of alleles, such as local high reproductive success of only a few mating genotypes or population subdivision, may have occurred on this reef (reviewed in Lessios 1992). Between the two sites in this reef, population subdivision was suggested from genetic differences (F_{ST} = 0.103 95% CI 0.018 – 0.169); a potential mixing of populations from different gene pools (Wahlund effect) could be suggested from allelic differences, and heterozygote deficiencies for all three most deviating loci could indicate inbreeding. More replication would be needed to test rigorously any of the potential explanations for the pattern of genetic differentiation found at this locality.

4.5.2 *Gene flow at different spatial scales*

Some degree of genetic differentiation at all of the spatial scales analysed indicated that some restrictions in gene flow occur for both species. In *S. flexibilis*, gene flow seems

sufficiently restricted to maintain a significant genetic differentiation between some reef populations (minimum of 16 km apart), between some sites within reefs (0.8 to 2 km apart), and between transects in a site (< 100 m apart). However, gene flow seems large enough in other instances so that allelic frequencies did not differ significantly between some adjacent populations and some populations separated by several hundreds of kilometres.

The level of genetic differentiation of *Sinularia flexibilis* populations on different reefs was similar to that reported for other invertebrate species with a relatively long planktonic larvae phase in the GBR (*e.g.* Burnett *et al.* 1994, 1995; Ayre and Hughes 2000). However, in some other studies, organisms with a planktonic phase showed no significant genetic differentiation between widely separated populations in the GBR (*e.g.* Benzie and Stoddart 1992; Benzie and Williams 1992; Macaranas *et al.* 1992; Williams and Benzie 1993; Ayre *et al.* 1997). As these species are subject to the same hydrographic conditions within the GBR, differences in larval behaviour and/or larval residency times in the water column may explain the differences in their degree of genetic differentiation.

Genetic differentiation among populations of the larval brooder *Clavularia koellikeri* was four to thirty times larger than that found for the gamete broadcaster *Sinularia flexibilis*, depending on the spatial scale compared. Both species were sampled from similar leeward types of reef habitat, where they mostly occur. The F_{ST} value for *C. koellikeri* versus *S. flexibilis* respectively was, 0.189 versus 0.041 among sites, 0.134 versus 0.026 among reef populations, and 0.090 versus 0.004 among regions. Most likely, differences in the genetic differentiation among populations of these species reflect differences in the duration of their larval phases, and consequently their ability to disperse.

The level of genetic differentiation found in *Clavularia koellikeri* was similar to that of other sessile marine invertebrates with known limited larval dispersal, like the soft coral *Alcyonium rudyi* (F_{ST} = 0.23-0.46; McFadden 1997), and the viviparous corals *Seriatopora hystrix* (F_{ST} = 0.43; Ayre and Duffy 1994) and *Balanophyllia elegans* (F_{ST} = 0.28; Hellberg 1994). This finding is consistent with the view that brooded larvae are more likely to have limited dispersal. However, some marine invertebrate species with

brooded larvae or known limited larval dispersal, appear capable of considerable dispersal, judging from the relatively low amount of genetic differentiation found among populations. For example, *Anthipathes fiordensis* (Miller 1997), and the brooding species *Pocillopora damicornis* (Ayre *et al.* 1997), *Acropora cuneata*, *A. palifera*, and *Stylophora pistillata* (Ayre and Hughes 2000), all showed values of genetic differentiation (F_{ST}) less than 0.1 and most of them were not significantly different to zero. These results highlight the importance of other processes that, in addition to potential larval dispersal, affect the genetic differentiation among populations, and may result in a large variability of inferred dispersal for those species with known limitation from their larval phase.

4.5.3 *Potential explanations for the patterns of genetic differentiation*

The pattern of genetic differentiation of *S. flexibilis* along the GBR suggested a relatively high level of connectivity of populations separated by tens to hundreds of km while having some level of restriction in gene flow between some reefs and sites. This genetic differentiation, that did not show a relationship with geographic distance between 16 and 1300 km, suggests that populations of *S. flexibilis* are not in genetic equilibrium (balance between effects of loosing genetic diversity by drift and re-establishing them by gene flow) at the regional scale of the GBR. This pattern is common in some marine invertebrates due to the complexities of their life histories (*e.g.* Hellberg 1995; Ayre *et al.* 1997) but also in many other organisms (Hutchinson and Templeton 1999). It seems unlikely that natural selection has been responsible for the genetic differentiation in *Sinularia flexibilis* within and between some adjacent reef populations, because results were relatively consistent for all loci, and because this species tends to occur in similar habitat types, typically back reef areas (but see Ayre 1985). Instead, the observed pattern of genetic differentiation might have resulted mainly from the effects of genetic drift over populations with some potential restriction in dispersal at two spatial scales within the GBR.

Firstly, the genetic differentiation detected among some adjacent reefs, sites and patches within a reef may have resulted from greater retention of larvae or gametes at these reefs. For *S. flexibilis*, the mean amount of genetic differentiation among transects less than 100 m apart was 5.5 times greater than that found between sites within a reef.

Between sites <2 km apart genetic differentiation was 1.5 times greater than the average found between reefs 16 to 1300 km apart. Restriction of dispersal at these scales has been shown to occur in species with high dispersal potential, either as a result of local hydrodynamic conditions restricting dispersal (*e.g.* Sammarco and Andrews 1988), or through behaviour of planktonic larvae (*e.g.* Knowlton and Keller 1986), or both. Given that *S. flexibilis* predominantly occurs on the leeward side of reefs, the proportion of larvae retained on each reef may be increased (*e.g.* Black *et al.* 1990). However, the lack of information on its larval biology, or the time spent in the water column for development (*i.e.* pre-competence period), prevents any further discussion. In the GBR, modelling of planktonic larvae that spend 28 days in the waters of the Cairns Section, shows they disperse mostly to reefs in the proximity to their source, typically between 35 to 75 km away (Dight *et al.* 1990b). Self-seeding has been used to explain genetic differentiation of other species with high dispersal potential (*e.g.* Burton and Feldman 1982; Hedgecock 1986; Ayre *et al.* 1997). In this study, larval or gamete retention is preferred over other potential explanations for the differentiation pattern because it also leads to a certain degree of inbreeding. Because asexual reproduction may result in excesses as well as deficits of heterozygotes, and most deviations of genotypic frequencies from HW equilibrium were deficiencies, some degree of inbreeding could be a more important factor than asexual reproduction in contributing to the genetic differentiation. Favourable hydrodynamic conditions for some degree of retention of gametes or larvae, and a certain degree of clonality, such as observed in the 5 m^2 patches, could further increase the chances of self-fertilisation or fertilisation among related genotypes and contribute to genetic differentiation (*e.g.* Burke *et al.* 2000).

Secondly, despite the lack of a relationship between genetic differentiation and geographic distance, pairwise comparisons of F_{ST} or allelic frequencies between reefs suggested that there may be more restriction in gene flow among inner reefs, and between inner- and mid/outer-reefs than among mid/outer-reefs. Although oceanographic and population structure data have indicated the GBR can be regarded as a highly connected reef system (*e.g.* Williams *et al.* 1984; Benzie 1994), these differences may be explained by more detailed, smaller-scale patterns of currents. Hydrodynamic models have indeed predicted certain limitations in cross-shelf dispersal in the GBR, where also the net surface current drift is expected to be more restricted in

near-shore waters than in outer-shelf waters during summer, when this species reproduces (*e.g.* Dight *et al.* 1990a,b).

The amount of genetic differentiation between reef populations of *Clavularia koellikeri* was related to their geographic distance and the levels of gene flow are considerably restricted. The relation between genetic and geographic distance is weakened due to sampling of only two regions and a large within region variation, mainly due to the Britomart population. If, with more replication, a marked differentiation such as found for the Britomart population, occurs more commonly between reefs within regions, it would be no further valid to suggest isolation by distance as a mechanism that could be driving the genetic differentiation. Few studies have been able to support this mechanism of genetic differentiation, even though it can occur in marine organisms with limited dispersal potential at spatial scales similar to or smaller than the 25 - 1000 km in the present study (*e.g.* Hellberg 1995; Huang *et al.* 2000; Kusumo and Druehl 2000; Todd *et al.* 1998). Although several studies have shown genetic differentiation over a variety of spatial scales in marine organisms, isolation by distance has been reported to occur mainly over larger geographic distances (Palumbi 1994; Benzie 2000). The following factors have been discussed as responsible for this lack of relationship in other studies: a) larval dispersion was greater than assumed; b) low larval dispersal was compensated by high sperm dispersal; c) populations were not at equilibrium; d) the occurrence of complex current patterns; and/or e) low sampling replication within each spatial scale or the method of analysis used (*e.g.* Doherty *et al.* 1995; McFadden 1997; McFadden and Aydin 1996; Miller 1997; Ruckelshaus 1998; Hutchison and Templeton 1999; Benzie 2000). It is unlikely that the restrictions to gene flow found for *C. koellikeri* populations within the GBR were primarily determined by historical biogeographical factors, as hydrodynamic and population genetic studies (*e.g.* Williams *et al.* 1984; Benzie 1994) have shown that the GBR can be regarded as a relatively well-connected system of reefs at large spatial scales. Thus, I suggest that *C. koellikeri* has sufficiently restricted dispersal that it constitutes an appropriate model species to test the potentiality of different mechanisms that could drive the genetic structure of species within a relatively well-connected system as the GBR.

In conclusion, *Sinularia flexibilis* showed genetic diversity consistent with a predominance of sexual reproduction at all spatial scales sampled in the GBR. This

includes a scale of 5 m^2 within larger aggregations of *S. flexibilis* ($10^2 - 10^3$ m^2) in three localities. Most identical nine-locus genotypes could have been generated sexually but their spatial arrangement supported the idea that some of the repeated genotypes may have an asexual origin. Although this species has a high dispersal potential, it showed significant genetic differentiation between and within some reefs. For one locality, I also demonstrated that genetic differentiation could occur between genetically heterogenous patches less than 100 m apart. The spatial scales at which genetic differentiation can be found in *S. flexibilis* suggest that some degree of retention of sexual propagules can occur and/or some degree of inbreeding can occur in some reefs. Although genetic differentiation was not related to geographic separation at scales of 16 – 1300 km, there was some evidence that gene flow may be less restricted among mid/outer-shelf reefs in the GBR than among inner-shelf reefs.

Clavularia koellikeri showed genetic diversity consistent with a predominance of sexual reproduction at the spatial scales of sites and reefs in six reefs along the GBR. Significant genetic differentiation was found at all spatial scales, and the level of that differentiation is consistent with a species having considerable restriction to gene flow in a region without a major geographic discontinuity. Reduced genetic diversity in the southern populations suggested that these reefs close to the southern-most limit of *Clavularia* distribution may constitute a more marginal habitat for this species.

Genetic differentiation among populations of the larval brooder *Clavularia koellikeri* was four to thirty times that found for the gamete broadcaster *Sinularia flexibilis*, depending on the spatial scale compared. It is likely that differences in the genetic differentiation among populations of these species reflect differences in the duration of their larval phases, and consequently their ability to disperse.

A predominantly sexual mode of reproduction in the nearshore reefs studied, where both species attain local dominance in certain habitats, contrasts with expectations of clonal organisms aggregating mainly by the asexual replication of individuals. The present data demonstrate that aggregations of this species are not composed of a few widespread clones dominating those areas. Given that these species presumably reproduce sexually once a year, this study suggests that the formation of aggregations at

scales of hundreds of square meters in a few years would largely depend on high recruitment and fast growth rates.

Table 4.1. ***Clavularia koellikeri.*** **Sampling localities, dates of collections, and descriptive statistics for genetic variability in six reef populations of** ***Clavularia koellikeri*** **along the GBR. Averages for the Torres Strait and the Central Sector given with standard deviations in parentheses. N = number of individuals; n = mean number of alleles per locus; Polym = percentage of polymorphic loci for which the frequency of the most common allele < 95%. Note that these statistics are based only upon the variable loci analysed in this study and not on a random sample of loci**

Locality	Date	Shelf	Latitude	Longitude	N	n	Polym	Heterozygosity Observed	Heterozygosity Expected
Torres Strait					**35**	**2.83**	**91.7**	**0.260**	**0.299**
					(17)	**(0.14)**	**(7.2)**	**(0.056)**	**(0.008)**
Wednesday Island (WED)	Aug-99	Inner-shelf	10° 30' S	142° 18' E	47	2.75	87.5	0.205	0.290
Zuna Island (ZUN)	Aug-99	Inner-shelf	10° 44' S	142° 17' E	42	3.00	87.5	0.259	0.304
Dungeness Reef (DUN)	Aug-99	Mid-shelf	09° 53' S	142° 55' E	15	2.75	100	0.317	0.304
Central Sector					**46**	**1.88**	**41.6**	**0.177**	**0.155**
					(3)	**(0.38)**	**(20.0)**	**(0.089)**	**(0.080)**
Pandora Reef (PAN)	Apr-00	Inner-shelf	18° 49' S	146° 26' E	50	1.88	50	0.202	0.187
Orpheus Island (ORP)	Apr-00	Inner-shelf	18° 34' S	146° 29' E	44	2.25	62.5	0.250	0.214
Britomart Reef (BRI)	Jun-00	Mid-shelf	18° 14' S	146° 38' E	45	1.50	12.5	0.078	0.063

Table 4.2. ***Clavularia koellikeri.*** **Allele frequencies for eight loci and six reef populations (and sites) of** ***Clavularia koellikeri*** **in the GBR Locality abbreviations as in Table 4.1**

		WED			ZUN			DUN	PAN			ORP			BRI
Locus	Allele	Pooled	Site1	Site2	Pooled	Site1	Site2		Pooled	Site1	Site2	Pooled	Site1	Site2	
N		47	22	25	41	9	33	15	50	25	25	44	19	25	45
*HK**	1				0.02	0.05	0.02	0.03				0.05	0.03	0.06	
	2	0.11	0.16	0.06	0.06	0.06	0.06	0.07	0.09	0.08	0.10	0.10	0.08	0.12	0.01
	3	0.64	0.68	0.60	0.79	0.67	0.82	0.87	0.91	0.92	0.90	0.85	0.89	0.82	0.98
	4	0.26	0.16	0.34	0.13	0.22	0.10	0.03							0.01
*FBP**	1	0.03	0.04	0.02	0.05	0.11	0.03		0.01	0.02		0.01		0.02	0.04
	2	0.89	0.91	0.88	0.85	0.83	0.85	0.87	0.98	0.98	0.98	0.97	0.95	0.98	0.96
	3	0.07	0.05	0.10	0.11	0.06	0.12	0.13	0.01		0.02	0.02	0.05		
*PGK**	1	0.13	0.02	0.22	0.08	0.22	0.05		0.22	0.10	0.34	0.23	0.29	0.18	0.24
	2	0.39	0.25	0.52	0.63	0.78	0.59	0.30	0.78	0.90	0.66	0.76	0.71	0.80	0.76
	3	0.48	0.73	0.26	0.29		0.36	0.70				0.01		0.02	
*PGD**	1				0.01		0.02	0.03							
	2	0.93	0.89	0.96	0.95	1.00	0.94	0.73	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	3	0.07	0.11	0.04	0.04		0.04	0.20							
	4							0.03							
*PGM**	1	0.87	0.93	0.82	0.79	0.78	0.79	0.87	0.96	0.92	1.00	0.99	0.97	1.00	1.00
	2	0.12	0.07	0.16	0.21	0.22	0.21	0.13	0.04	0.08		0.01	0.03		
	3	0.01		0.02											
*LT**	1	0.98	0.96	1.00	0.94	1.00	0.92	0.87	1.00	1.00	1.00	0.94	1.00	0.90	1.00
	2	0.02	0.04		0.06		0.08	0.13				0.06		0.10	
*GPI**	1	0.01	0.02		0.06		0.08	0.07	0.24	0.28	0.20	0.27	0.24	0.30	
	2	0.91	0.98	0.86	0.86	0.72	0.89	0.83	0.76	0.72	0.80	0.73	0.76	0.70	1.00
	3	0.07		0.14	0.08	0.28	0.03	0.10							
*FLE**	1	0.18	0.07	0.28	0.25	0.33	0.23	0.13	0.54	0.54	0.54	0.63	0.50	0.72	
	2	0.09	0.04	0.12	0.05	0.06	0.04								
	3	0.73	0.89	0.60	0.69	0.61	0.71	0.83	0.46	0.46	0.46	0.38	0.50	0.28	1.00
	4				0.01		0.02	0.03							

Table 4.3. ***Clavularia koellikeri.*** **D- values ((Ho-He)/He) indicating heterozygote deficit (negative number) or excess (positive number) for eight loci and six reef populations. Bold indicates genotypic frequencies deviating significantly from HW expectations after Bonferroni correction (p< 0.001) for multiple tests. F = locus fixed for one allele.**

Location	*HK**	*FBP**	*PGK**	*PGD**	*PGM**	*LT**	*GPI**	*FLE**
Wednesday Island	**-0.46**	0.09	**-0.25**	-0.23	0.04	0.02	0.08	**-0.65**
Zuna Island	0.12	-0.21	-0.30	-0.48	-0.29	0.06	0.01	-0.12
Dungeness Reef	0.10	0.15	0.11	-0.05	0.15	0.15	0.14	-0.07
Pandora Reef	0.10	0.02	0.17	F	0.04	F	0.10	0.05
Orpheus Island	0.04	0.01	0.11	F	0.01	0.06	0.26	0.31
Britomart Reef	0.02	0.05	0.32	F	F	F	F	F

Table 4.4. ***Clavularia koellikeri.*** **Analysis of multilocus genotypes. N = number of individuals, N^* = estimated maximum number of individuals produced sexually using allelic frequencies for each reef, N_{go} = number of unique multi-locus genotypes.**

					Frequency of repeated genotypes										
Location	N	N^*:N	N_{go}:N	N_{go}	1	2	3	4	5	6	7	8	9	19	20
Wednesday Island	47	0.93	0.68	32	28	1		2					1		
Zuna Island	42	1.00	0.88	37	32	5									
Dungeness Reef	15	1.00	0.93	14	13	1									
Pandora Reef	50	1.00	0.46	23	13	5	3	1			1	1			
Orpheus Island	44	1.00	0.59	26	17	4	2	2	1						
Britomart Reef	45	1.00	0.13	6	3		1							1	1

Table 4.5. ***Clavularia koellikeri.*** **Hierarchical *F*-statistics for all reef localities. F_{ST} Regions = degree of differentiation between reefs from different Regions, F_{ST} Reefs = degree of differentiation between reefs within the total, F_{IS} = inbreeding coefficient, F_{IT}= overall inbreeding coefficient. N= number of individuals, n= number of alleles per locus.*= p< 0.05, **= p<0.001, H_0: $F_{ST} = 0$, H_1: $F_{ST} > 0$.**

				F_{ST}				
Locus	N	n	F_{IT}	Regions	Reefs	df	F_{IS}	df
*HK**	243	4	0.235	0.086 **	0.119 **	15	0.132 **	6
*FBP**	243	3	0.086	0.056 **	0.052 **	10	0.036	3
*PGK**	243	3	0.300	0.225 **	0.259 **	10	0.041 **	3
*PGD**	243	4	0.324	0.066	0.123 *	15	0.230	6
*PGM**	243	3	0.220	0.123	0.130	10	0.104	3
*LT**	243	2	-0.024	0.002	0.039 *	5	-0.066	1
*GPI**	243	3	-0.020	0.015 **	0.105 **	10	-0.140	3
*FLE**	243	4	0.306	-0.045	0.228	15	0.100	6
All loci			0.218 *	0.084	0.176 *		0.051	
95 % C.I	Upper		0.279	0.174	0.223		0.110	
	Lower		0.103	-0.005	0.100		-0.025	

Table 4.6. ***Clavularia koellikeri.*** **Hierarchical *F*-statistics for all sampled sites. F_{ST} Regions = differentiation among sites from different Regions, F_{ST} Reefs = differentiation between sites within reefs, F_{ST} Sites = degree of differentiation among sites within the total, F_{IS} = inbreeding coefficient, F_{IT}= overall inbreeding coefficient. N= number of individuals, n= number of alleles per locus, *= p< 0.05, **= p<0.001, H_0: $F_{ST} = 0$, H_1: $F_{ST} > 0$.**

				F_{ST}					
Locus	N	n	F_{IT}	Regions	Reefs	Sites	df	F_{IS}	df
*HK**	243	4	0.232	0.088 **	0.107 **	0.120 **	15	0.127	6
*FBP**	243	3	0.086	0.056 **	0.057 **	0.049 **	10	0.038	3
*PGK**	243	3	0.294	0.222 **	0.186 **	0.307 **	10	-0.018	3
*PGD**	243	4	0.319	0.071 **	0.116 *	0.116 **	15	0.230 **	6
*PGM**	243	3	0.220	0.123 **	0.124 **	0.133 **	10	0.100	3
*LT**	243	2	-0.025	0.003	0.010	0.053 *	5	-0.083	1
*GPI**	243	3	-0.029	0.021	0.071 **	0.112 **	10	-0.158	3
*FLE**	243	4	0.282	-0.027	0.169 **	0.219 **	15	0.080	6
All loci			0.212*	0.090 *	0.134 *	0.189 *		0.028	
95 % C.I	Upper		0.273	0.171	0.165	0.253		0.102	
	Lower		0.091	0.006	0.081	0.098		-0.049	

Table 4.7. *Clavularia koellikeri.* Pairwise comparison of genotypic frequencies among sites. Localities abbreviated as in Table 1, and numbers refer to sites within each locality. Asterisks showed significant differences among sites after adjustment for multiple comparisons ($p < 0.001$).

Site	WED_2	ZUN_1	ZUN_2	DUN	PAN_1	PAN_2	ORP_1	ORP_2	BRI
WED_1	*	*	Ns	Ns	*	*	*	*	*
WED_2		Ns	Ns	*	*	*	*	*	*
ZUN_1			Ns	*	*	*	*	*	*
ZUN_2				Ns	*	*	*	*	*
DUN					*	*	*	*	*
PAN_1						Ns	Ns	Ns	*
PAN_2							Ns	Ns	*
ORP_1								Ns	*
ORP_2									*

Table 4.8. ***Sinularia flexibilis.*** **Descriptive statistics for genetic variability in 12 reef populations along the Great Barrier Reef ordered from north to south. LOC= Site code used throughout the text, Date= date of sampling, I= Inner-shelf reefs, MO= middle or outer shelf reefs, *N*= Mean sample size per locus, n= mean number of alleles per locus (standard deviation in parentheses), P= Percentage of polymorphic loci (< 95% criterion for the most common allele).**

LOC	Name	Date	Shelf	Sector	Latitude		Longitude		*N*	n	P	Mean Heterozygosity	
												Observed	Expected
CUM	Cumberland	Aug-99	MO	Torres Strait	10°	04' S	143°	43' E	56.9 (13.5)	2.56 (0.53)	100	0.344	0.336
DUN	Dungeness	Aug-99	MO	Torres Strait	09°	53' S	142°	55' E	28.3 (3.3)	2.56 (0.73)	100	0.289	0.306
PIC	Pickersgill	Dec-98	I	Cairns	15°	52' S	145°	35' E	56.4 (6.5)	2.44 (0.53)	100	0.416	0.380
UND	Undine	Dec-98	I	Cairns	16°	06' S	145°	38' E	44.1 (20.5)	2.44 (0.73)	89	0.284	0.268
AGI	Agincourt	Dec-98	MO	Cairns	15°	59' S	145°	49' E	46.1 (10.9)	2.56 (0.53)	100	0.265	0.319
ESC	Escape	Dec-98	MO	Cairns	15°	49' S	145°	48' E	38.1 (3.7)	2.22 (0.67)	89	0.233	0.254
CAN	Cannon Bay	Dec-99	I	Central	18°	40' S	146°	35' E	45.7 (6.9)	2.67 (0.71)	100	0.355	0.396
ORP	Orpheus	Dec-99	I	Central	18°	34' S	146°	29' E	46.7 (10.9)	2.67 (0.71)	100	0.318	0.321
RIB	Rib	Mar-99	MO	Central	18°	29' S	146°	52' E	43.6 (9.8)	2.56 (0.53)	89	0.284	0.300
TRU	Trunk	Mar-99	MO	Central	18°	21' S	146°	46' E	52.8 (6.5)	2.67 (0.71)	89	0.304	0.315
DEL	Deloraine	Feb-00	I	Whitsundays	20°	09' S	149°	04' E	49.4 (0.7)	2.56 (0.53)	100	0.288	0.311
HOO	Hook Is	Feb-00	I	Whitsundays	20°	07' S	148°	53' E	49.6 (6.7)	2.67 (0.71)	100	0.309	0.359

Table 4.9. ***Sinularia flexibilis.*** **Allelic frequencies and number of samples for nine loci and 12 localities along the Great Barrier Reef. Alleles at each locus were labelled based on the mobility of the most common allele (=100). N is the number of individuals assayed for each locus. Table continues in next page.**

		Torres Strait		Cairns				Central				Whitsundays	
LOCUS	allele	CUM	DUN	PIC	UND	AGI	ESC	CAN	ORP	RIB	TRU	DEL	HOO
*GPI**	N	21	23	45	17	18	3	30	22	18	41	48	32
	109	0.048	0.152	0.056	0.441	0.139	-	0.167	0.046	0.056	0.049	0.021	0.172
	100	0.810	0.804	0.944	0.529	0.806	1.000	0.683	0.864	0.861	0.927	0.760	0.734
	91	0.143	0.044	-	0.029	0.056	-	0.150	0.091	0.083	0.024	0.219	0.094
*HK**	N	62	31	64	56	49	45	48	54	44	58	50	53
	107	0.040	0.097	0.141	0.027	0.020	0.011	0.000	0.009	0.034	0.078	0.010	0.066
	100	0.710	0.790	0.578	0.679	0.888	0.867	0.688	0.685	0.750	0.707	0.930	0.745
	95	0.250	0.113	0.281	0.295	0.092	0.122	0.292	0.296	0.216	0.207	0.060	0.170
	90	-	-	-	-	-	-	0.021	0.009	-	0.009	-	0.019
*FBP**	N	62	31	63	58	50	42	53	55	47	57	50	53
	105	0.202	0.258	0.230	0.078	0.170	0.179	0.151	0.200	0.181	0.254	0.090	0.264
	100	0.597	0.645	0.476	0.750	0.730	0.667	0.679	0.664	0.670	0.561	0.830	0.547
	92	0.202	0.097	0.294	0.172	0.100	0.155	0.170	0.136	0.149	0.184	0.080	0.189
*TPI**	N	61	29	58	49	43	34	50	44	48	52	49	50
	110	0.041	0.052	0.129	0.041	0.186	0.029	0.350	0.091	0.052	0.058	0.235	0.190
	100	0.861	0.948	0.802	0.939	0.767	0.941	0.550	0.818	0.906	0.846	0.735	0.730
	95	0.098	-	0.069	0.020	0.047	0.029	0.100	0.091	0.042	0.096	0.031	0.080
*ME**	N	62	28	55	53	52	42	48	54	50	57	50	53
	100	0.879	0.911	0.755	0.868	0.837	0.857	0.865	0.870	0.870	0.825	0.920	0.925
	95	0.121	0.089	0.246	0.132	0.164	0.143	0.135	0.130	0.130	0.175	0.080	0.076
*MDH**	N	61	28	57	55	51	43	48	52	47	57	49	51
	105	0.074	0.071	0.132	0.100	0.177	0.128	0.177	0.087	0.075	0.193	0.112	0.118
	100	0.926	0.929	0.868	0.900	0.824	0.872	0.823	0.914	0.926	0.807	0.888	0.882

Table 4.9. Continued

		Torres Strait		Cairns				Central				Whitsundays	
LOCUS	allele	CUM	DUN	PIC	UND	AGI	ESC	CAN	ORP	RIB	TRU	DEL	HOO
*VL**	N	61	23	54	51	52	45	43	47	44	57	50	51
	100	0.902	0.913	0.870	0.941	0.914	0.900	0.826	0.819	0.966	0.974	0.770	0.853
	92	0.098	0.087	0.130	0.059	0.087	0.100	0.174	0.181	0.034	0.026	0.230	0.147
*LGG**	N	61	31	49	1	50	44	41	38	47	43	49	51
	100	0.713	0.597	0.694	1.000	0.620	0.580	0.720	0.763	0.575	0.616	0.663	0.755
	90	0.287	0.403	0.306	-	0.380	0.421	0.281	0.237	0.426	0.384	0.337	0.245
*FLE**	N	61	31	63	57	50	45	50	54	47	53	50	52
	112	0.271	0.403	0.175	0.123	0.190	0.189	0.060	0.185	0.245	0.104	0.300	0.202
	100	0.623	0.548	0.635	0.754	0.790	0.811	0.780	0.787	0.681	0.849	0.680	0.740
	90	0.107	0.032	0.191	0.123	0.020	0.000	0.130	0.028	0.075	0.047	0.020	0.058
	80	-	0.016	-	-	-	-	0.030	-	-	-	-	-

Table 4.10. ***Sinularia flexibilis.*** **D- values ((Ho-He)/He) indicating heterozygote deficit (negative number) or excess (positive number) for each locus and population. Bold numbers indicate genotypic frequencies deviating significantly from HW expectations after correction for multiple tests. Empty cells indicate no data available.**

LOC	*GPI**	*HK**	*FBP**	*TPI**	*ME**	*MDH**	*VL**	*LGG**	*FLE**	All loci
CUM	-0.113	0.343	**-0.025**	-0.140	-0.014	**-0.640**	0.109	0.162	0.026	0.024
DUN	-0.337	-0.178	-0.111	-0.648	0.098	-1.000	0.095	**0.676**	-0.157	-0.057
PIC	0.059	0.213	**0.402**	**-0.384**	0.129	**-0.770**	-0.179	0.345	0.168	0.094
UND	0.234	0.225	-0.013	0.050	-0.013	**-0.697**	0.062		0.095	0.058
AGI	0.183	0.106	-0.393	-0.441	0.055	**-1.000**	0.095	0.273	-0.293	-0.169
ESC		-0.240	**-0.285**	-0.477	-0.028	-0.687	-0.629	**0.726**	-0.057	-0.083
CAN	-0.240	-0.104	**-0.070**	-0.009	-0.199	**-0.786**	0.050	0.148	0.080	-0.105
ORP	0.119	-0.121	-0.056	0.086	-0.016	**-0.879**	0.077	0.310	0.019	-0.009
RIB	-0.106	-0.008	-0.228	-0.402	-0.027	**-0.845**	0.035	**0.654**	-0.277	-0.053
TRU	0.060	-0.236	**-0.162**	0.063	-0.030	**-0.662**	0.027	0.524	0.134	-0.037
DEL	-0.163	-0.543	-0.123	-0.344	0.087	**-0.898**	0.299	**0.508**	-0.150	-0.074
HOO	-0.186	-0.311	-0.303	-0.152	0.081	**-0.811**	0.172	0.325	-0.010	-0.139

Table 4.11. ***Sinularia flexibilis.*** **Analysis of multilocus genotype (using seven loci). N= number of individuals, *N**= estimated maximum number of individuals produced sexually, N_{go} = number of unique multi-locus genotypes, G_o= observed genotypic diversity, G_e= expected genotypic frequency.**

		All reefs	Per reef		Frequency of repeated genotypes									
LOC	N	*N**:*N*	*N**:*N*	N_{go}	1	2	3	4	5	6	7	N_{go}:*N*	G_o	G_o:G_e
CUM	52	1.00	1.00	40	31	7	1	1				0.77	32.2	0.87
DUN	20	1.00	1.00	19	18	1						0.95	18.2	1.18
PIC	37	1.00	1.00	35	33	2						0.95	33.4	1.37
UND	41	0.99	1.00	30	26	1	1	1		1		0.73	18.5	0.76
AGI	39	1.00	1.00	31	27	2	1		1			0.79	22.0	0.79
ESC	27	1.00	1.00	19	14	4			1			0.70	13.3	0.78
CAN	33	1.00	1.00	31	29	2						0.94	29.4	1.00
ORP	41	1.00	1.00	38	35	3						0.93	35.8	1.12
RIB	34	1.00	1.00	25	19	4	1	1				0.74	19.3	0.78
TRU	45	1.00	1.00	38	32	5	1					0.84	33.2	1.01
DEL	48	0.99	1.00	33	26	4	1	1			1	0.69	19.9	0.72
HOO	42	1.00	1.00	36	32	3		1				0.86	29.4	0.84
	459													

Table 4.12. *Sinularia flexibilis*. Autocorrelation analysis of genotypes in each reef population using Moran's *I* index. Values are level of significance for the overall correlogram and for each distance class. Bold indicates significance at p< 0.05.

Locality	Overall	Distance classes				
		1	2	3	4	5
CUM	0.18	0.32	0.39	**0.04**	0.26	0.04
DUN	0.17	0.19	0.13	0.06	0.03	0.05
PIC	0.41	0.34	0.14	0.08	0.30	0.32
UND	**0.00**	**0.00**	0.36	0.46	0.10	0.01
AGI	**0.00**	**0.00**	0.10	0.12	0.47	0.11
ESC	**0.04**	0.37	**0.02**	**0.01**	0.31	0.37
CAN	**0.00**	**0.00**	0.13	**0.00**	**0.01**	0.19
ORP	1.00	0.47	0.37	0.49	0.31	0.46
RIB	0.52	0.11	0.10	0.35	0.44	0.25
TRU	0.16	0.09	0.24	0.32	0.08	**0.03**
DEL	0.84	0.20	0.33	0.17	0.42	0.44
HOO	1.00	0.32	0.33	0.38	0.41	0.44

Table 4.13. ***Sinularia flexibilis.*** **Hierarchical *F*-statistics for all localities with significance by chi-square per locus and over all loci by 95% CI. Separate results are shown for eight reefs in Cairns and Central Sectors for which *MDH**, *FBP** and *LGG** were excluded. F_{ST} Shelf, F_{ST} Reefs, F_{ST} Sites refer to the degree of differentiation between shelf position, among reefs, and among sites of a reef, respectively; F_{IS} = inbreeding coefficient; F_{IT} = overall inbreeding coefficient, N= number of individuals, n= number of alleles per locus.*= p< 0.05, **= p<0.001.**

				F_{ST}					
	N	n	F_{IT}	Shelf	Reefs	Sites	df	F_{IS}	df
*GPI**	299	3	0.168	-0.001	0.057 **	0.072 **	22	0.103	3
*HK**	590	4	0.060	0.002	0.032 **	0.044 **	33	0.017	6
*FBP**	585	3	0.125	-0.004	-0.002	0.040 **	22	0.089 *	3
*TPI**	548	3	0.250	0.029 **	0.074 **	0.075 **	22	0.189 **	3
*ME**	592	2	0.009	-0.004	0.009	0.011	11	-0.002	1
*MDH**	597	2	0.817	-0.003	-0.006	0.003	11	0.816 **	1
*VL**	559	2	0.011	0.030 *	0.036 **	0.050 **	11	-0.040	1
*LGG**	454	2	-0.376	0.018	0.012	0.033 *	11	-0.423 **	1
*FLE**	578	4	0.056	-0.001	0.029 **	0.027 **	33	0.030	6
All loci, All localities			0.084	0.006	0.026 *	0.041 *		0.045	
95 % CI	Upper		0.273	0.015	0.045	0.055		0.245	
	Lower		-0.086	-0.001	0.011	0.027		-0.127	
Six loci, Cairns and Central Sector			0.087 *	0.010	0.043 *	0.055 *		0.034 *	
95 % CI	Upper		0.156	0.027	0.062	0.086		0.090	
	Lower		0.039	-0.005	0.024	0.025		0.001	

Table 4.14. ***Sinularia flexibilis*****. Combined probabilities for each pairwise comparison of allelic frequencies between reefs (below diagonal) and geographic distances in kilometres (above the diagonal). Bold indicates allelic frequencies between reefs being significantly different based on an approximation to the exact probability test using p< 0.0008 after correction for multiple tests.**

	INNER REEFS						MID/OUTER REEFS					
	PIC	UND	CAN	ORP	DEL	HOO	CUM	DUN	AGI	ESC	RIB	TRU
PIC	----	28	330	316	611	600	676	725	30	26	323	308
UND	**0.0000**	----	304	289	589	575	702	752	24	36	296	280
CAN	**0.0000**	**0.0000**	----	16	320	303	1005	1056	310	328	38	40
ORP	**0.0000**	**0.0000**	**0.0003**	----	336	318	990	1040	295	312	44	40
DEL	**0.0000**	**0.0000**	**0.0000**	**0.0000**	----	20	1266	1328	585	602	307	323
HOO	**0.0000**	**0.0000**	**0.0005**	0.1054	**0.0000**	----	1260	1319	570	589	290	305
CUM	**0.0000**	**0.0001**	**0.0000**	0.2120	**0.0000**	0.0243	----	90	700	677	996	980
DUN	**0.0000**	**0.0000**	**0.0000**	**0.0002**	**0.0000**	0.0032	0.0224	----	750	734	1049	1034
AGI	**0.0000**	**0.0000**	**0.0000**	0.0015	0.0035	0.0144	**0.0000**	0.0109	----	19	298	283
ESC	**0.0000**	**0.0007**	**0.0000**	0.0170	**0.0003**	**0.0001**	0.0028	0.0310	0.0533	----	317	300
RIB	**0.0000**	0.0077	**0.0000**	0.0229	**0.0000**	**0.0004**	0.5527	0.3150	0.0195	0.2115	----	16
TRU	**0.0000**	**0.0000**	**0.0000**	**0.0003**	**0.0000**	**0.0000**	**0.0000**	**0.0001**	0.0015	0.0008	0.0713	----

Table 4.15. *Sinularia flexibilis* small-scale study. Descriptive statistics based on nine scored loci. Listed are values for the whole data set (ALL), each locality population (BOR, ORP, LOW), and each transect within locality in Border Island and Orpheus Island. *N*= average number of individuals among loci; Het. = heterozygosity, % Polym. Loci = percentage of polymorphic loci (*i.e.* with a frequency < 0.95 for the most common allele).

Population		*N*	Het. Expected	Het. Observed	% Polym. Loci
ALL		120.33	0.331	0.317	100
BOR		**37.00**	**0.423**	**0.356**	**100**
	BOR1	7.33	0.246	0.352	55.6
	BOR2	10.78	0.249	0.348	66.7
	BOR3	12.22	0.301	0.307	77.8
	BOR4	6.67	0.370	0.444	88.9
ORP		**74.11**	**0.275**	**0.306**	**88.9**
	ORP1	28.00	0.241	0.290	77.8
	ORP2	46.11	0.268	0.317	88.9
LOW		**9.22**	**0.173**	**0.211**	**55.6**

Table 4.16. *Sinularia flexibilis* small-scale study. Comparison of allelic frequencies at the level of transects within a locality and among localities. Asterisks indicate allelic frequencies at each comparison being significantly different using an approximation to the exact probability test at * = p < 0.05, ** = p < 0.01 *** = p < 0.001; Ns = non-significant difference in allelic frequencies.

	Transects within localities							Among localities pooling transects		
	BOR						ORP			
	1 vs. 2	1 vs. 3	1 vs. 4	2 vs. 3	2 vs. 4	3 vs. 4	1 vs. 2	BOR vs. ORP	BOR vs. LOW	ORP vs. LOW
*FLE**	.4423	.6430	**.0002**	.1128	**<.0001**	**.0001**	**.0296**	**.0004**	.6076	.3226
	Ns	Ns	***	Ns	***	***	*	***	Ns	Ns
*LGG1**	.1525	**.0262**	**<.0001**	.3782	**<.0001**	**<.0001**	1.0000	**<.0001**	**.0124**	**.0153**
	Ns	*	***	Ns	***	***	Ns	***	*	*
*LGG2**	1.0000	1.0000	**<.0001**	1.0000	**<.0001**	**<.0001**	.5367	**<.0001**	.0647	1.0000
	Ns	Ns	***	Ns	***	***	Ns	***	Ns	Ns
*VL**	**.0001**	1.0000	**<.0001**	.0001	**.0002**	**<.0001**	.4852	**<.0001**	**.0105**	.1343
	***	Ns	***	***	***	***	Ns	***	*	Ns
*FBP**	**.0006**	.2250	.2968	.0602	**.0029**	.0625	.8786	**<.0001**	.2736	**.0120**
	**	Ns	Ns	Ns	**	Ns	Ns	***	Ns	*
*HK**	**<.0001**	**.0008**	**.0299**	.3762	**<.0001**	**.0012**	**<.0001**	**<.0001**	**.0209**	.0990
	***	***	*	Ns	***	**	***	***	*	Ns
*PGM**	.4827	.1015	**<.0001**	.1688	**.0004**	**.0021**	**<.0001**	.3434	.0768	.3712
	Ns	Ns	***	Ns	***	**	***	Ns	Ns	Ns
*ME1**	**.0284**	.0673	.0722	1.0000	1.0000	.5442	**<.0001**	.1912	.5929	.2027
	*	Ns	Ns	Ns	Ns	Ns	***	Ns	Ns	Ns
*ME2**	1.0000	1.0000	.5032	.7387	**.0005**	**.0372**	**.0300**	**.0003**	.2748	.7533
	Ns	Ns	Ns	Ns	***	*	*	***	Ns	Ns
Overall	**<.0001**	**.0081**	**<.0001**	**.0040**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**.0007**	**.0131**
	***	**	***	**	***	***	***	***	***	*

Table 4.17. *Sinularia flexibilis* small-scale study. Estimated p-values for the exact test of genotypic frequencies. Bold indicates genotypic frequencies significantly different from those expected under HW equilibrium after correction for multiple comparisons ($p < 0.0019$). Genotypic expectations were calculated from the pooled allelic frequencies for each locality.

Locus	BOR	ORP	LOW
*FLE**	0.0263	**0.0005**	1
*LGG1**	**0.0000**	**0.0000**	0.3059
*LGG2**	**0.0000**	1	Fixed
*VL**	**0.0013**	0.3403	Fixed
*FBP**	0.2302	0.2667	1
*HK**	0.7941	0.7705	0.1139
*PGM**	**0.0007**	**0.0007**	Fixed
*ME1**	0.5023	1	Fixed
*ME2**	**0.0000**	**0.0004**	1

Table 4.18. *Sinularia flexibilis* small-scale study. Parameters from multilocus genotype analyses. N= number of individuals sampled; N_{go} = number of unique genotypes; N_{go}:N = minimum proportion of individuals produced sexually; N^*:N = maximum proportion of individuals produced sexually. N^*:N estimations using allelic frequencies of each 'Transect' and of each 'Locality' (pooling across transects).

				N^*:N	
	N	N_{go}	N_{go}:N	Locality	Transect
BOR	41	34	0.83	1.00	
ORP	77	43	0.56	0.88	
LOW	10	6	0.60	0.97	
BOR1	10	8	0.80	1.00	1.00
BOR2	14	11	0.79	1.00	1.00
BOR3	10	9	0.90	1.00	1.00
BOR4	7	6	0.86	1.00	1.00
ORP1	28	20	0.71	0.86	1.00
ORP2	49	27	0.55	0.85	0.95

Table 4.19. ***Sinularia flexibilis*** **small-scale study. Frequency of repeated multilocus genotypes and their distribution within Localities and Transects. MLG= multilocus genotype number. ALL= all data set, BOR= Border Is., ORP= Orpheus Is.; LOW= Low Isles; = repeated genotypes exclusive to a locality (=Unique/Loc) and to a transect (=Unique/Trans).**

	ALL	Localities				Transects							
MLG No.		BOR	ORP	LOW	Unique/Loc	BOR1	BOR2	BOR3	BOR4	ORP1	ORP2	LOW	Unique/Trans
1	2	2				1		1					
2	2	2				2							
3	3		1	2							1	2	
4	2	2					2						
5	2		2							1	1		
6	3		3							3			
7	2		2							2			
8	11	1	10				1			1	9		
9	3		3							3			
10	4		4								4		
11	7		7								7		
12	2		2							1	1		
13	5	3	2				3			2			
14	2		2								2		
15	6		6							2	4		
16	2		2								2		
17	2			2								2	
18	4		1	3							1	3	
19	2		2							2			
20	2	2						2					
21	2	2							2				
Count	21	7	15	3	17	2	3	2	1	9	10	3	13

Table 4.20. *Sinularia flexibilis* small-scale study. Moran's *I* autocorrelation coefficient of the multilocus genotypes present within transects in each locality. Distance pairs between colonies were assigned to five equal-interval distance classes. Bold numbers indicate significant association of the genotypes with $p < 0.05$. Numbers of pair distances at each class interval are shown in parentheses. Number of colonies of each transect as in Table 4.18.

Trans	Overall correlogram significance	1	2	3	4	5
BOR1	0.142	-0.14	-0.10	**-0.62**	**0.37**	-0.36
		(5)	(8)	(8)	(10)	(5)
BOR2	0.379	0.28	-0.20	-0.15	-0.16	-0.31
		(10)	(15)	(13)	(12)	(5)
BOR3	0.675	-0.13	0.08	-0.94	-0.09	-0.07
		(59)	(31)	(1)	(5)	(9)
BOR4	0.378	0.67	-0.34	-0.45	-0.14	0.38
		(2)	(4)	(8)	(5)	(2)
LOW	**0.003**	**0.56**	0.06	-0.04	**-0.71**	**-1.47**
		(10)	(13)	(11)	(7)	(4)
ORP1	0.085	**0.06**	-0.13	0.06	-0.10	**-0.56**
		(164)	(135)	(64)	(32)	(11)
ORP2	**0.000**	**0.08**	**0.10**	-0.08	**-0.20**	**-0.41**
		(423)	(219)	(343)	(122)	(69)

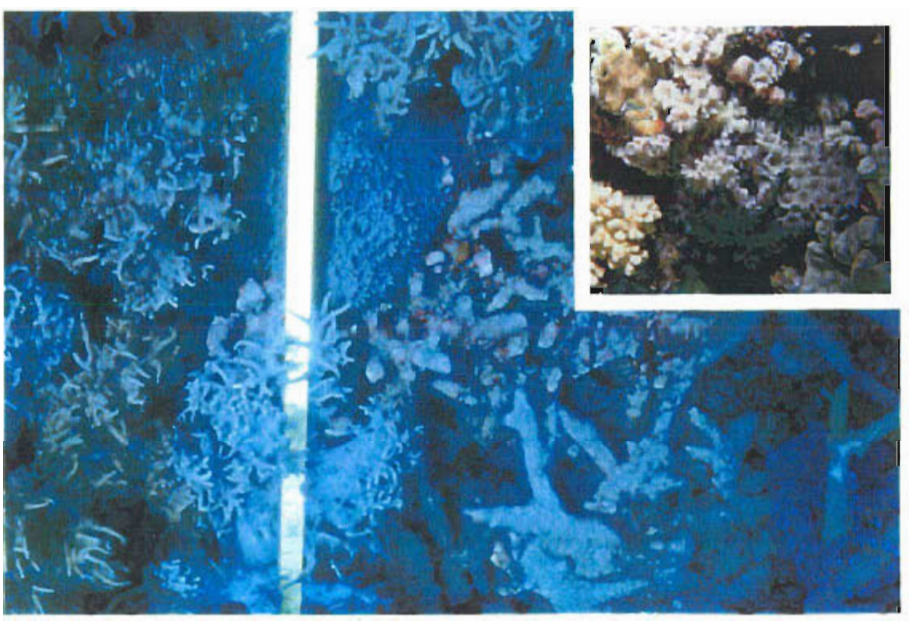

Figure 4.1. Colonies of the soft coral species *Clavularia koellikeri* and *Sinularia flexibilis*. Tape marks correspond to one centimetre. Inset: details of *C. koellikeri* polyps.

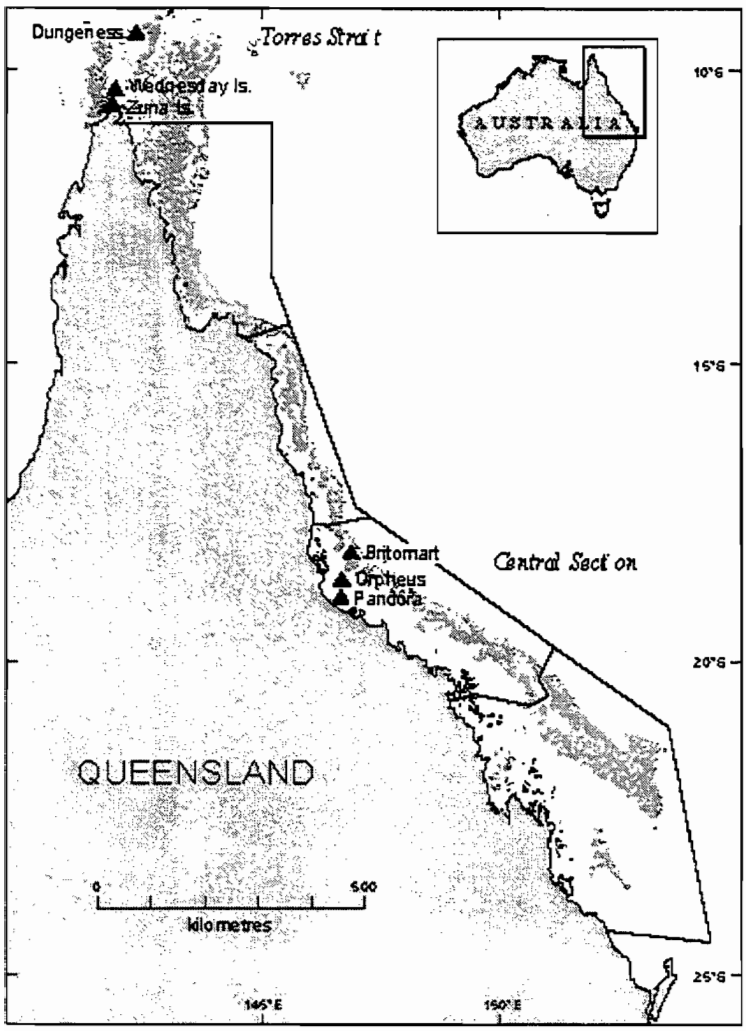

Figure 4.2. ***Clavularia koellikeri.*** **Map showing the six localities of collection along the Great Barrier Reef, Australia.**

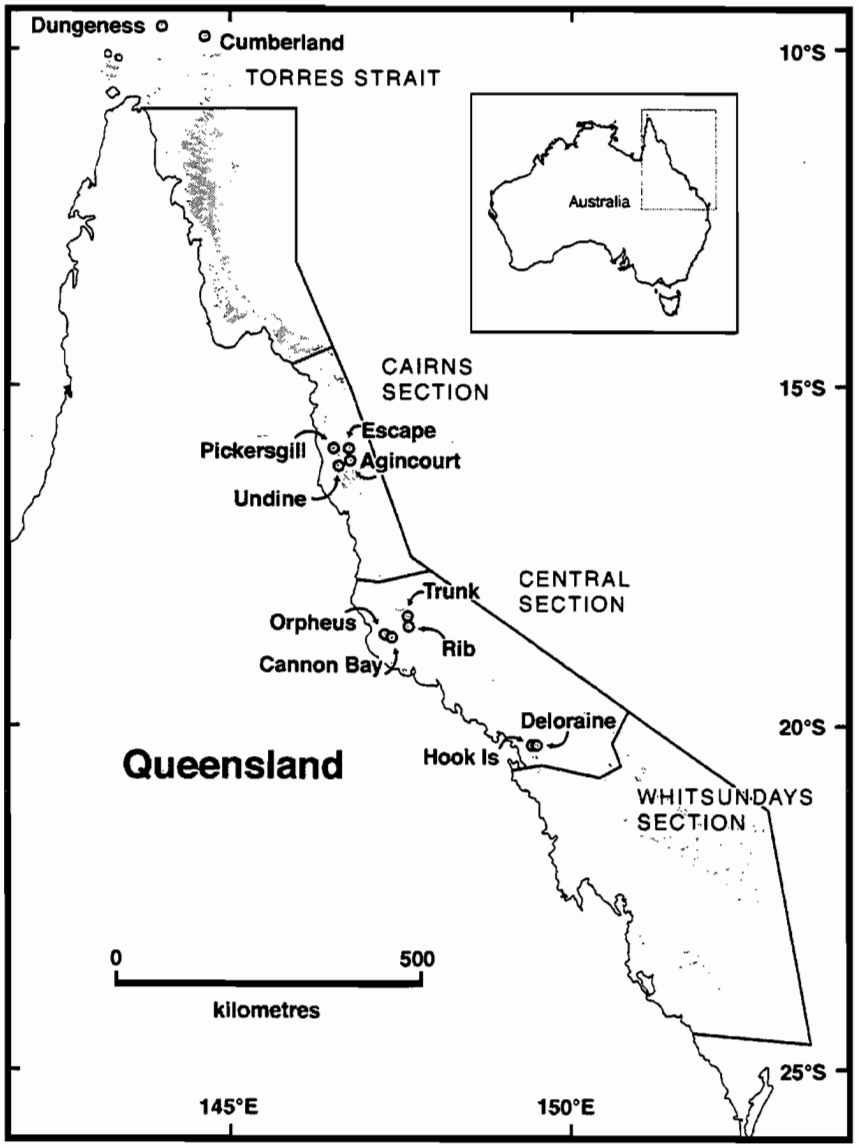

Figure 4.3. Map showing the 12 localities of collection of *Sinularia flexibilis* along the Great Barrier Reef, Australia.

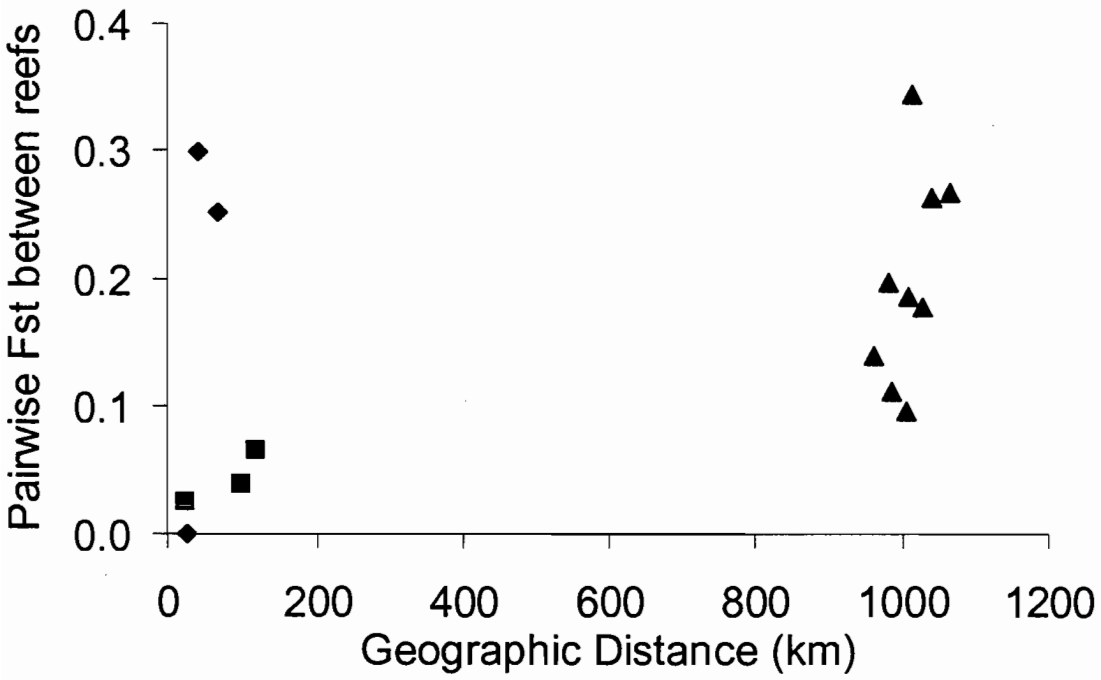

Figure 4.4. ***Clavularia koellikeri.*** **Genetic differentiation between reef populations (pairwise F_{ST}) plotted against the corresponding geographic distance for six reefs along the GBR. Symbols represent comparisons among "squares" = Torres Strait populations, "diamonds"= Central Sector populations, "triangles"= Torres Strait vs Central Sector populations.**

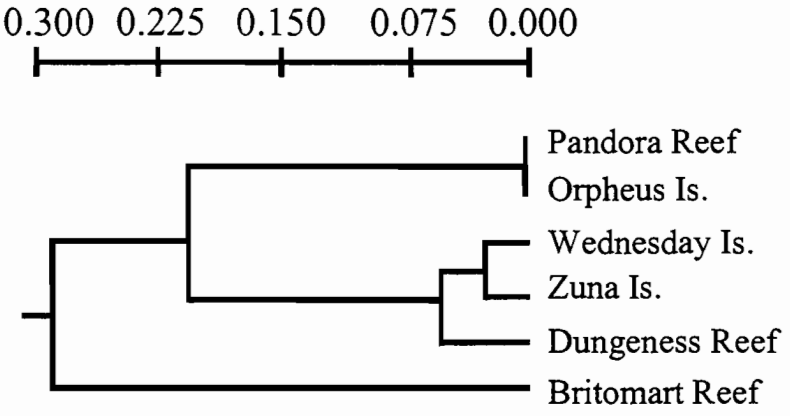

Figure 4.5. ***Clavularia koellikeri.*** **Graphic representation of the genetic distance (coancestry distance: Reynolds *et al.* 1983) between six reef populations along the GBR (UPGMA analysis).**

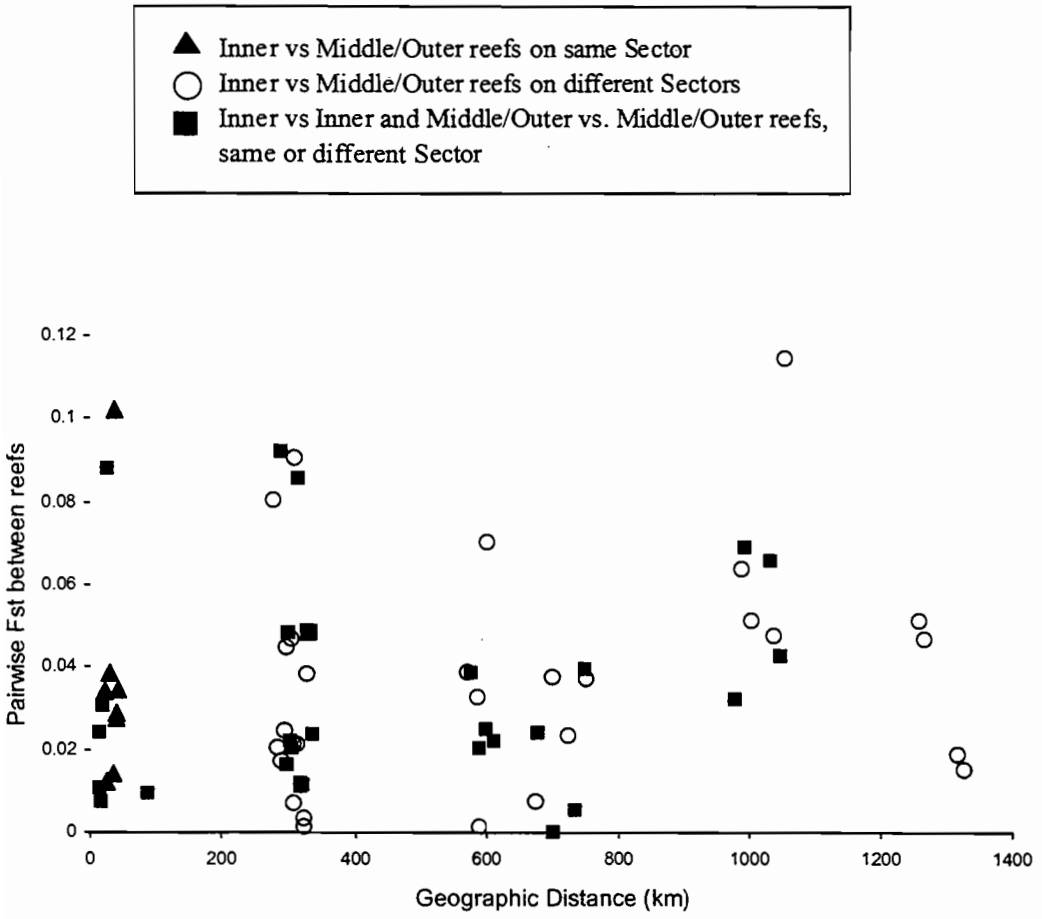

Figure 4.6. *Sinularia flexibilis*. Pairwise F_{ST} between reef populations plotted against their geographic distance in kilometres.

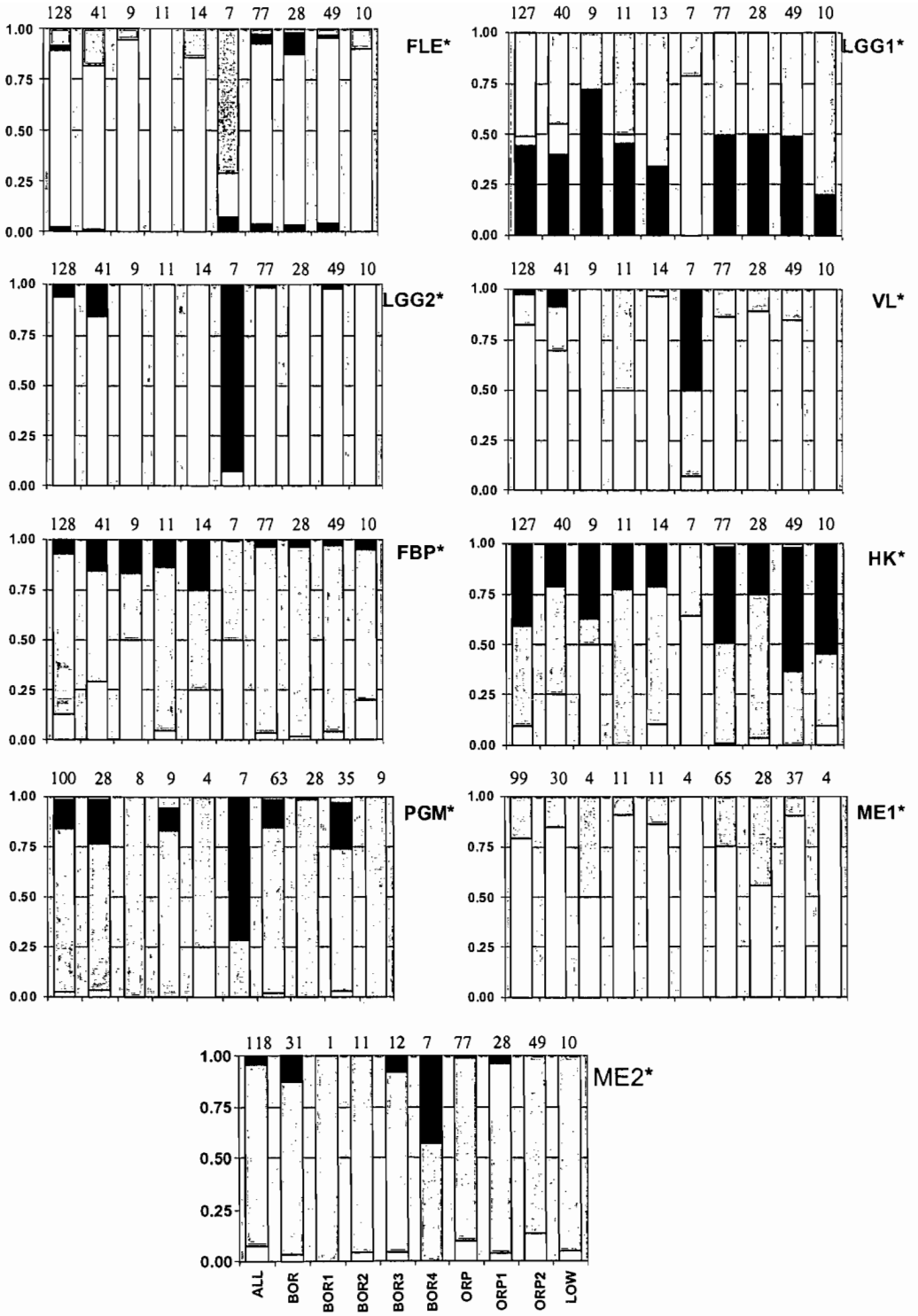

Figure 4.7. ***Sinularia flexibilis*** **small-scale study. Allelic frequencies of nine loci displayed for the complete data set (ALL), each locality (BOR, ORP, LOW) and each transect within locality (BOR1-BOR4, ORP1, ORP2, LOW). Numbers of individuals are shown on top of each bar. Shading in each bar represents different alleles.**

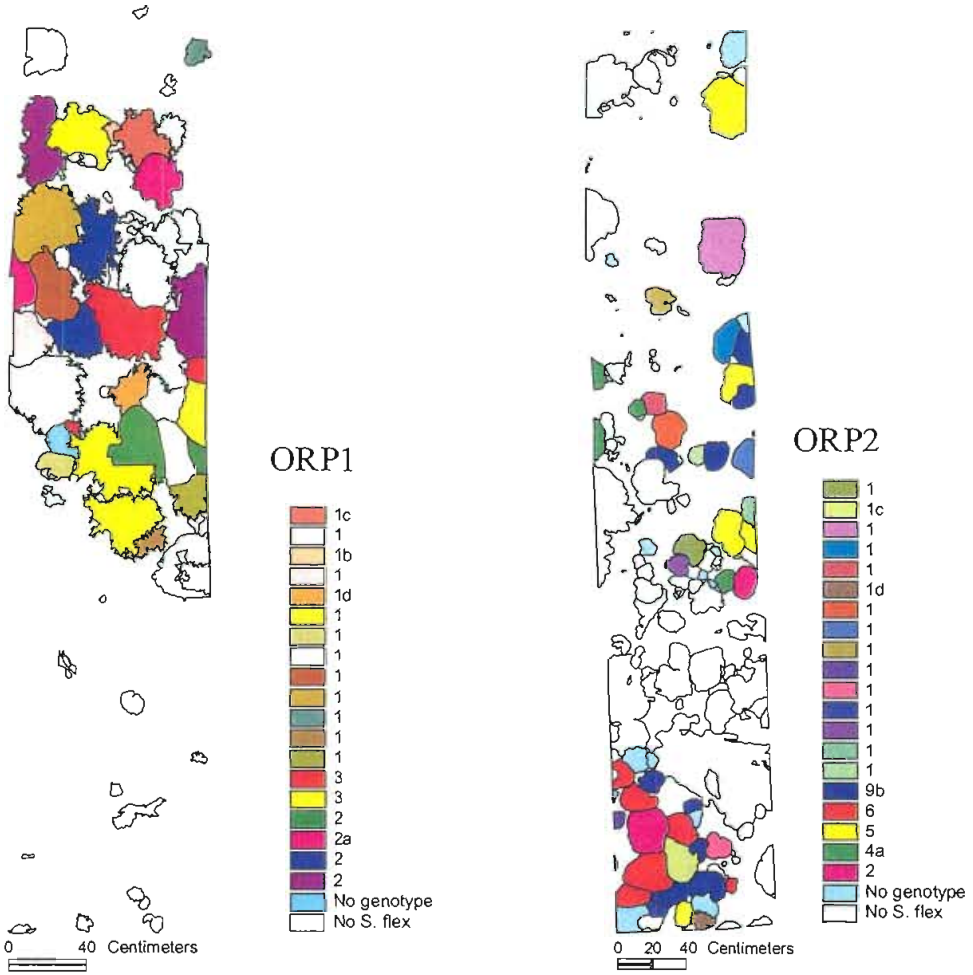

Figure 4.8. ***Sinularia flexibilis*** **small-scale study. Distribution of nine-locus genotypes over 5 m² in two transects at Orpheus Island (Central GBR). Genotypes are color-coded and numbers are their observed frequency within each transect. Letters indicate genotypes common to both transects.**

5 General Discussion and Conclusions

5.1 A clonal organism with local dominance but high genet diversity

Small-scale mapping and a modeling study show that inshore populations of *Sinularia flexibilis* rely primarily on asexual reproduction to compensate for high rates of mortality (~ 25% turnover of colonies annually) and that the species has the potential to slowly increase in population size in the absence of sexual recruitment. However, given that fission is the primary mode of asexual reproduction and that the rate of daughter colony formation is slow, clonal spread does not lead to rapid colonisation of newly opened space outside the immediate vicinity of parent colonies. A three-year census of *S. flexibilis* populations at two localities showed that approximately half (43%) of colonies were undergoing fission at any given time. Most colonies (~80%) underwent binary fission, although colonies could divide into more than two. Despite the high occurrence of fission, the combination of high mortality with the slow rate of fission suggests that it is unlikely that local populations are dominated by a small number of genotypes. This prediction is supported by the results of a small-scale genotype mapping study, in which more than 60% of genotypes (n=47) appeared only once in the 5 m^2 belt transects, with the largest genet being represented by nine daughter colonies. Thus, small-scale demographic and genetic studies support the conclusion that asexual reproduction does not lead to highly clonal population structures in this species.

Results of large-scale population genetic studies of *S. flexibilis* on 11 reefs and of *Clavularia koellikeri* on six reefs, including both inshore and midshelf reefs along the length of the GBR, indicate that both species have high genotypic diversity despite their potential to form clones. Since colonies were sampled at intervals ≥5 m for *S. flexibilis* and ≥3 m for *C. koellikeri*, the relative importance of sexual versus asexual reproduction refers only to population genetic structure at this scale. However, the concordance of the small- and large-scale genetic studies suggests that the primary role of asexual reproduction in these species is the replacement of parent colonies. Thus, even with the comparatively low rates of sexual recruitment found in the demographic study of *S. flexibilis*, the persistence of all genotypes through slow asexual proliferation maintains population genotypic diversity, which may then slowly increase with continuing

influxes of sexual recruits. Thus, the relatively high genotypic diversity of *S. flexibilis*, reflects both sexual recruitment and the maintenance of genotypes within populations through asexual reproduction.

The apparent contradiction between the high genetic diversity of *Sinularia flexibilis* revealed in population genetic studies and the predominantly asexual recruitment observed in belt transects, highlights the importance of identifying the appropriate scale of study. Local genotypic diversity of clonal animals and plants is generally assumed to be low, because asexually produced offspring tend to recruit locally and survive well in the parental habitat (Williams 1975). However, Williams predicted that species size, habitat characteristics, and the mode and frequency of both asexual and sexual reproduction would influence the size, persistence and distribution of clones. As predicted, many studies of clonal organisms have shown that genet diversity may vary with environmental conditions (*e.g.* stable versus unstable habitats) or according to the mechanism of asexual reproduction (see references in McFadden 1997; and Silander 1979; Coffroth and Lasker 1998; McFadden 1999; Burke *et al.* 2000; Gómez and Carvalho 2000; Reusch et al. 2000). Even for populations where sexual recruitment is rare, multiclonal populations of intermediate diversity are common among plants (Ellestrand and Roose 1987) and animals (Parker 1979). However, as my study demonstrates, it is critical to determine the appropriate sampling scale when characterising population genetic structure. For example, a large grid would be necessary to sample populations of *Zostera marina,* in which a single genet can dominate an area of 160 x 40 m (Reusch *et al.* 1999). In contrast, it is likely that a reduction of the scale of sampling from 5 m^2 to 1 m^2 in my study would have indicated a relatively higher importance of asexual reproduction, as expected from the close proximity of repeated genotypes. Importantly, combining studies across two scales provides insights that would not emerge through sampling at just one scale. Finally, it is also important to note that rates of sexual recruitment revealed in the demographic study could have been depressed because of long-term impacts of the 1998 bleaching on reproduction (*e.g.* Michalek-Wagner and Willis 2001) or simply as a result of natural variability in recruitment (*e.g.* Roughgarden *et al.* 1988).

It is generally expected that in clonal species genetic diversity will increase during the initial recolonisation period following a local extinction event, because relaxation in

selective processes allows a diversity of sexual recruits to colonise newly opened space (e.g. Stevens et al. 1999; Gómez and Carvalho 2000). However, when sexual recruitment is limited in comparison to asexual recruitment, clonal proliferation following a disturbance may result in relatively low genetic diversity. From the consistently high genetic diversities found for the 12 populations of *S. flexibilis* along the length of the Great Barrier Reef and from population growth estimates, it is likely that recent local extinction and recolonisation events have further contributed to the establishment of a diverse number of genotypes. Since daughter colonies proliferate at rates that are similar to rates of mortality, aggregations of colonies in this species are genetically diverse rather than predominantly clonal.

In summary, patterns in the abundance of *S. flexibilis* and *C. koellikeri* result from both sexual and asexual reproduction, but given the long timespan of fission coupled with the high turnover rate of colonies, the primary consequence of asexual reproduction in *S. flexibilis* is the maintenance of genotypes. In this latter species, a demographic model shows that colony growth and fission may slowly increase population size leading to local dominance in the absence of major disturbances. However, genetic population studies show that aggregations of these species are genetically diverse, reflecting slow rates of asexual proliferation and the potential effect of local disturbances.

5.2 Potential for dispersal inferred from larval type and genetic differentiation between populations

The population genetic study of *Sinularia flexibilis* revealed genetic sub-structure in a broadcast spawning species with a planktonic larva within a relatively well connected geographical range that encompassed the habitat of the species. Although a number of studies have shown genetic differentiation among populations of marine invertebrates with planktonic larvae (e.g. Nash et al. 1988; Burnett *et al.* 1994; 1995; Benzie and Wakeford 1997; Benzie 1999; Yu *et al.* 1999; Ayre and Hughes 2000), it is more commonly predicted that populations of such species will show little genetic subdivision. Thus, populations of the broadcast spawning species, *S. flexibilis*, were predicted to have no genetic differentiation, particularly given the predominance of sexual reproduction found at spatial scales as small as 5 m^2. However, I found genetic differentiation between populations separated by as little as 0.8 km, including

differences between sites within reefs, as well as between populations separated by up to 1300 km.

One explanation for genetic differentiation among populations of an outcrossing species with planktonic larva is that not enough time has elapsed to homogenise differences arising through genetic drift, particularly in small populations established following disturbance events. Alternatively, the dispersal of the species is more restricted than previously suspected. The former explanation seems unlikely to explain patterns of genetic differentiation in the present study, because populations of these species are large, implying that colonies have accumulated over long periods of time and there has been ample opportunity for homogenization. A more likely explanation for the genetic differentiation found among populations of *S. flexibilis* is that dispersal of larvae among populations is restricted to a certain level, even if low. Note that dispersal was most restricted between: 1. inshore populations, and 2. mid-shelf and inshore populations. The latter result suggests that restrictions to larval dispersal operate across the shelf. More genetic differences found for inshore reefs is consistent with the relatively low abundance and scattered distribution of inshore reefs in comparison to mid and outer-shelf reefs. (It is also expected that reefs in the proximity of the coast would have a more complex pattern of currents). The much lower differentiation between mid- and outer-shelf reefs in the same reef region suggests that these populations are relatively more connected through larval dispersal.

A number of studies suggest that local retention of gametes or larvae may play a much more important role than previously suspected, even for species with planktonic phases (*e.g.* Sammarco and Andrew 1988; Black *et al.* 1990; Jones *et al.* 1999; Hughes *et al.* 1999). However, so far the evidence to support local retention of larvae for coral populations is contentious. For example, patterns of recruitment found by Sammarco and Andrews (1988) do not distinguish between local retention of larvae and patterns that would result from very dispersive larvae from other sources. Also, patterns of recruitment found by Hughes *et al.* (1999) are consistent with dispersal occurring mainly among reefs within sectors in the GBR, which would contribute to explaining differences between reefs in different sectors but not within sectors. This highlights the need for greater understanding of local currents, the timing of spawning, but more importantly, the larval biology of species before dispersal patterns and distances can be

inferred. It has been largely assumed that there are no restrictions to the dispersal of planktonic larvae, apart from those imposed by local currents. Differences in the larval phases of species (e.g. in competency periods, in the duration of the planktonic phase, and in behaviour) undoubtedly help to explain why, within the same geographic region and subject to the same local current patterns, some species have shown genetic differentiation (Burnett *et al.* 1994, 1995; Benzie and Wakeford 1997; Ayre and Hughes 2000; Uthicke and Benzie 2001), while others have not (Benzie and Stoddart 1992; Benzie and Williams 1992; Williams and Benzie 1993; Ayre *et al.* 1997; Uthicke *et al.* 1998, 1999; Uthicke and Benzie 2000).

Larval ecology studies of soft corals exemplify that the common assumption of external fertilisation producing a long-lived, and consequently, very dispersive planktonic larvae is a matter of discussion. The planula of *Dendronephthya hemprichi*, a tropical broadcaster, developed within 45 hours after fertilization and in the presence of stony corals it is able to settle after 2 days (Dahan 1992). Also, in the broadcaster *Leptogorgia virgulata*, planula developed in 24 h after fertilisation and remains in the plankton for 2 – 3 d before settling, although settlement can be delayed up to 19 d (Adams 1980 cit. in Gotelli 1988). The above examples illustrate that the occurrence of oceanographic features that entrain larvae around reefs for 3-4 days could lead to greater genetic subdivision than previously thought. Whether such oceanographic features occur is still a matter of debate (e.g. Williams et al 1984; Willis and Oliver 1988; Black *et al.* 1990; Dight et al. 1990; Oliver et al. 1992; Black *et al.* 1995).

The second contribution of the population genetic study is to provide further evidence that species that brood their larvae have greater population genetic differentiation than those that broadcast spawn gametes for planktonic development. This is in contrast to several studies that have challenged the dogma that brooders should have greater genetic differentiation than spawners because of shorter competency periods. For example, the brooded larvae of *Alcyonium siderium* are able to delay metamorphosis and successfully recruit after up to 30 days (Sebens 1983). Similarly, larva of the surface brooder *Parerythropodium fulvum*, and of the internal brooders, *Litophyton arboreum*, *Xenia umbellata* and *Heteroxenia fuscescens,* have maximal longevities exceeding 40 days and remain competent to settle throughout this time (Ben-David-Zaslow and Benayahu 1998). Similarly, the occurrence of brooded larvae was not

necessarily related with genetic differentiation among populations of either anemones (Edmands and Potts 1997) or scleractinian corals (Ayre and Hughes 2000).

Also, the degree of genetic differentiation found among populations of *Clavularia koellikeri* was directly related to the geographic distances between them. However, the relation between genetic and geographic distance is weak as sampling was restricted to only two regions and there was considerable variability in genetic differentiation within regions, mainly from the effect of the Britomart population. The marked differences between reefs at small spatial scales while there was little difference between other population pairs at similar distances suggest a more complex pattern. If, with more replication, marked differentiation such as that found for the Britomart population, occurs more commonly between reefs within regions, it is likely that the relationship of isolation by distance would be lost. In Britomart, a mid-shelf reef, reduced genetic diversity, and the genetic distinction from other populations, particularly the relatively closer inshore reefs, suggests restricted recruitment to that reef.

5.3 The timescale for formation of aggregations and local dominance

The demographic study of *Sinularia flexibilis* demonstrates that the formation of aggregations leading to local dominance is not necessarily a rapid process, even for a clonal species. In addition, my results show that although rapid growth and the ability to invade space are characteristic of many clonal organisms, especially plant species (*e.g.* Gray 1986), such life history attributes are not necessarily a consequence of being clonal. Thus, attempts to generalise for all clonal organisms will have poor predictive potential. While it is clear that species that recruit continuously through asexual reproduction and grow rapidly could readily establish aggregations following the opening of space, it is not as clear how species without these life history characteristics accomplish space monopolisation. One possibility is that species with low growth or recruitment rates may have strong competitive abilities that allow them to establish aggregations over longer time frames if disturbances are relatively infrequent.

The demographic modeling study of *Sinularia flexibilis* permits one of the first estimations of the timeframe required for a slow growing species to form aggregations

leading to local dominance. The model predicts that an aggregation 100 m^2 in size with a density of 10 colonies/m^2 (*i.e.* comprising approximately 35% of the total cover) will take up to 43 years to form. Calculations assume maximum growth rates throughout the entire time, and also that only asexual recruitment is occurring following an initial influx of larval recruits onto newly opened substrata. However, given the high genotypic diversity of this species, this scenario is unlikely. Repeating these calculations with the same set of assumptions, but incorporating the observed rate of recruitment as a *per capita* rate (*i.e.* a closed population with constant rate of sexual reproduction of 0.24 recruits/m^2/y, with recruits ranging from >20 to <75cm^2 in size, as observed empirically in this study) yields a similar estimate of 42 years. If the population is assumed to be open, again with a constant recruitment rate, it would take 18 years to achieve the projected cover. Calculations based on the lowest growth rate observed, but with all other assumptions including external recruitment as in the previous case, predict that colony density would still only be 1.5 col/m^2 after 18 years. Even with high recruitment rates (yielding 10 cols/m^2 of < 75cm^2 in size in two years) and with maximum growth rates, the population will still take seven years to reach the target density of 10 cols/m^2 (*i.e.* the population initially declines because of mortality rates at small sizes).

In general, assumptions made to simplify the model mean that the length of time required to generate aggregations has most likely been underestimated rather than overestimated. In particular, assumptions that growth and recruitment rates are constant through time, that the species always wins encounters with competitors, that all available space is suitable for colonisation, and that no major disturbances occur over the period will all lead to underestimates of the time involved in establishing aggregations. *S. flexibilis* has the potential to be a strong competitor (*e.g.* Sammarco *et al.* 1983; van Alstyne *et al.* 1994; Maida *et al.* 1995; but see Dai 1990). However, major disturbances affecting coral reefs such as hurricanes and storms, COTs outbreaks (but not affecting soft corals), and bleaching events do occur at variable frequencies. Disturbances such as storms, with spatial extents of < 100 km, can occur with frequencies ranging from weeks to years (*e.g.* Jackson 1991), and the GBR has been affected by six bleaching events with different intensities, in the last 20 years (reviewed in Berkelmans 2001). On the other hand, highly variable recruitment rates as has been found for fish and hard corals (*e.g.* Sale *et al.* 1984; Fisk and Harriot 1990; Hughes *et*

al. 1999) can shorten those estimates. In particular, even when recruiting larvae are likely to require specific settlement cues (e.g. Morse 1988; Slattery *et al.* 1999), recruitment rates of higher orders of magnitude than the largest used here as a first approximation resembling a 'good' year will shorten these estimates. Besides, this study of three years is relatively short and observed recruitment may has encompassed only bad years. Thus, many factors are likely to extend model estimates of the number of years that it will take to form the hypothetical aggregation and it is expected that *S. flexibilis* will require ecologically long timeframes to attain local aggregations.

This conclusion is supported by the relatively minor recovery observed 34 months after the 1998 bleaching for coral communities at two localities on the GBR. Living cover decreased from 63% to 33% on these reefs immediately following the bleaching. Thirty-four months after the disturbance, overall living cover had only increased to 38%. Recovery occurred almost exclusively at 5 m, whereas at 2 m, the community was much the same as in the first census. Therefore depth-related factors will also influence the time required to form aggregations.

In summary, population growth rates estimated from two localities on the GBR and from two year-long intervals indicate that the time scale for the formation of aggregations of *S. flexibilis* is likely to be long in ecological terms. Occurrences of local dominance at scales of 100 m^2 with 35% cover of *S. flexibilis* would require between 7 and 43 years to form in the absence of major disturbances. Major disturbances would substantially increase these time-scale estimates. It is expected that the size of aggregations would be inversely related to the time that has elapsed since the community was affected by local disturbances, when the impact of disturbances are at scales equal to or larger than the aggregation size.

5.4 Relative contribution of demographic processes to population growth

In general, demographic rates of *Sinularia flexibilis* were characteristic of clonal organisms, with colonies having size-dependent growth and mortality rates. Also, fission rates were able to maintain population growth in most circumstances. In contrast to most clonal organisms studied so far, however, elasticity analysis for populations of

S. flexibilis indicated that changes in each of the demographic processes of growth, stasis (staying in the same size class) and shrinkage (i.e. undergoing fission) could have approximately the same contributions to population growth. Of these demographic processes, stasis has commonly been found to make a relatively high contribution to population growth in clonal organisms (Hubbell and Werner 1979; Gotelli 1991; Lasker 1991; Tanner 1997; Mandujano *et al.* 2001), although it has also been reported to contribute to the population growth of some aclonal organisms, particularly for long-lived species (e.g. Sæther and Bakke 2000). Thus, the contribution of stasis to population growth has been associated with long-lived species or with populations having low or declining growth rates (de Kroon *et al.* 2000).

A slower population growth rate, a shorter life span compared with other clonal organisms, and/or an earlier maturity and larger reproductive output (Sæther *et al.* 1996), are among the potential explanations for the relatively lower contribution of stasis to population growth in *Sinularia flexibilis*. In this study, the maximum population growth rate was similar to the maximum estimated in other studies of clonal marine species. The remaining expected life-span of largest colonies of *S. flexibilis* is approximately 10 years, which again compared with other clonal species may not be considered a short longevity (Tanner 2001). *S. flexibilis* has the potential for an early maturity (based on the observation of gonads in a 100 cm^2 colony), and asexually it produces offspring continuously, while it reproduces sexually once a year. If in more favourable years recruitment is larger than the one observed in this study, a comparatively early maturity and large reproductive output could be the most likely explanation for this species having a low contribution of stasis to population growth. However, other factors to consider include that the number of clonal marine species studied in this way is limited for encompassing the range of life histories. Also, the number of size classes used in those studies for large colonies could have been insufficient for this pattern to emerge. This study indicates that the importance of stasis in determining the population growth of marine clonal organisms could be more variable than previously suggested.

5.5 Concluding remarks

This study of two common and abundant soft coral species contributes to our understanding of the mechanisms that sessile organisms use to increase their abundance and attain local dominance. This is the first study of the genetic structure and connectivity for tropical soft coral species in the families Alcyoniidae and Clavulariidae, and it has shown that *Sinularia flexibilis* and *Clavularia koellikeri* reproduce mainly sexually at spatial scales > 5 m, and that populations can differ genetically at spatial scales > 1 km in the GBR. These results suggest that some level of restriction to gene flow, either during fertilisation or dispersion of larvae, of these two species has hampered homogenisation of gene pools among populations on the GBR. Restrictions to gene flow were higher in the brooder *C. koellikeri* than in *S. flexibilis*, which has external fertilisation and a planktonic larval phase, in agreement with expectations of dispersal for these two types of larvae. The demographic study of *Sinularia flexibilis* showed that asexual reproduction could compensate yearly mortality, and could increase population size even in the absence of sexual recruitment. However, a combination of high mortality rate and long time to undergo fission precluded the possibility that asexual reproduction alone could result either in high population growth rate, or in rapid colonisation of newly open space outside the immediate vicinity of parent colonies. Consistent with this result, soft coral cover increased from only 31% immediately after the 1998 bleaching event to 36% after 34 months. Population growth estimates from two localities on the GBR and over two year-long intervals indicate that the time scale for formation of aggregations of *S. flexibilis* is likely to be long in ecological terms. Local dominance at scales of 100 m^2 with 35% cover of *S. flexibilis* would require between 7 and 43 years to form in the absence of disturbances, and much longer in the presence of disturbance. These findings provide a sound basis from which to interpret soft coral abundance in coral reef communities, and from which to understand demographic factors leading to their local dominance.

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