EFFECTS OF ENHANCED CLIMATE CHANGE AND SEA LEVEL RISE ON SHALLOW-WATER REEF CORALS:

An Experimental Analysis of Coral Demographic and Photophysiological Responses to Depth Changes

Thesis submitted by

MARINA J. HUNT B.Sc. Hons. (J.C.U.N.Q.)

September, 1994.

for the Degree of Doctor of Philosophy in the Department of Marine Biology at

James Cook University of North Queensland.

FRONTISPIECE

Acropora millepora Ehrenberg

ABSTRACT

As a result of predicted global climate changes, over the next century eustatic sea level is expected to rise around 5 cm / decade and sea-surface temperatures are expected to increase by 2°C, concurrent with greater seasonal and inter-annual climatic variability. This study assesses the potential consequences of depth changes on three species of common shallow-water reef corals, *Goniastrea retiformis* Lamarck, *Acropora aspera* Dana and A*cropora millepora* Ehrenberg. Field transplant experiments conducted from 1992 to 1994 were used to simulate sea level rises and to determine the effects of depth increases of 25 cm, 50 cm and 1 m on the size-specific demographic and photophysiological responses of the corals. The feasibility of using transplant experiments to simulate predicted sea level rise was assessed, and the long-term effects of depth changes on the demography of the corals was quantified using size-structured population projection models.

The three species responded differently to depth changes because of differences in their morphology and life history traits (*G. retiformis* > *A. aspera* > *A. millepora*). Massive colonies of *G. retiformis,* which had high rates of survival (ca. 84% / year) and slow rates of linear growth (ca. 6 mm / year), exhibited no change in rates of survival in response to a 1 m depth change after 12 months, relative to controls. Of the three species, branching colonies of *A. aspera* which also had high rates of survival (ca. 83% / year) but fast rates of linear growth (ca. 46 mm / year), exhibited a 19%, 40% and 100% decrease in annual rates of survival in response to depth changes of 25 cm, 50 cm and 1 m respectively, relative to controls. Corymbose colonies of *A. millepora* which had low rates of survival (ca. 56% / year) and moderate rates of linear growth (ca. 22 mm / year), exhibited major reductions in annual rates of survival of 34%, 85% and 100% in response to depth changes of 25 cm, 50 cm and 1 m respectively, relative to controls. Rates of linear growth and colony fecundity decreased with increasing depth in all species, but this trend was particularly marked in *A. millepora*, even in response to a depth change of 25 cm. Therefore, rises in sea level of 25 cm, 50 cm or 1 m may significantly affect rates of coral survival, growth and fecundity, particularly for short-lived colonies of *A. millepora*, which are the most vulnerable to changes in environmental conditions.

Because rises in sea level may affect species differently, they have the potential to alter the relative abundance and diversity of species in extant assemblages of shallow-water reef corals.

Colonies of *A. millepora* were more capable of photoadaptation in response to depth-related alterations in light after 10 months, compared to those of *A. aspera*. Photoadaptation by *A. millepora* in response to depth increases of 25 cm and 50 cm was manifested by marked increases in photopigment content per zooxanthellate cell (ca. 65% & 142%, respectively, c.f. the controls). These changes occurred with concurrent reductions in zooxanthellae densities and tissue mass index (estimates of tissue volume). In contrast, the more perforate *A. aspera* (with 24% more endodermal and gastrodermal tissue than *A. millepora*), maintained zooxanthellae densities in response to depth changes of 25 cm and 50 cm, and showed little ability to increase photopigment contents per zooxanthellate cell. Despite the ability of *A. millepora* to photoadapt to depth-related changes in visible light, its survival was significantly lower than *A. aspera*, which showed little ability to photoadapt.

The acclimatization ability of *A. aspera* and *A. millepora* in response to sequential increases in depth was determined, and used to assess the feasibility of using transplant experiments to simulate more gradual rates of sea level rise. Rates of colony survivorship in response to stepwise changes in depth did not differ from those exhibited in response to direct depth changes in either of the two species. This indicates that direct transplantation of these species provides an adequate proxy to determine how corals respond to more gradual changes in sea level.

For the purposes of demographic analyses, the corals on experimental racks at depths of 25 cm, 50 cm and 1 m were considered as separate populations. Their projected demographic fate over 50 years at these depths was assessed. Projection models show that the length of time the populations will persist at different depths is limited, particularly at deeper sites, and depends on their resilience in response to environmental conditions and the proficiency of their reproductive strategies. Without sexual recruitment, populations of *A. millepora* would be the first to disappear from deeper sites as sea level rises 25 cm or 50 cm, within an estimated 6 and 2 years, respectively, from their

initial depth change. In contrast, populations of *A. aspera* could potentially persist indefinitely in response to a 25 cm sea level rise without recruitment, because of their propensity for asexual propagation. However, the difference in environmental conditions between a 25 cm and 50 cm sea level rise would exceed the resilience threshold for populations of *A. aspera*. Without sexual recruitment, they would only persist for 6 years in response to a 50 cm rise in sea level, because gains through asexual propagation would be exceeded by losses through higher rates of mortality. Populations of *G. retiformis* would be the last to disappear from deeper sites as sea level rises, because they could persist for an estimated 22 years without recruitment, even in response to a 1 m rise in sea level. The recruitment rates required for populations to persist indefinitely at deeper sites, were estimated through matrix model simulations. Based on these estimates and previous accounts of net rates of recruitment observed in field populations for these species, it is unlikely that sufficient recruitment would occur at deeper sites, and as a consequence extant populations of these corals would not persist significantly longer than predicted above.

Extant colonies of the three species located in very shallow reef sites may survive a rise in sea level, but survival could depend on colony size. Photophysiological studies show that large colonies of *A. millepora* could photoadapt and increase photopigment contents per unit tissue volume more effectively than smaller ones. Therefore, if small colonies of *A. millepora* cannot rapidly attain a size at which they may photoadapt more effectively, they may not persist even at this depth. Demographic studies also show that mortality patterns in all three species were inversely related to colony size. Therefore, if small colonies cannot rapidly attain a size refuge from mortality, they may not persist despite remaining within the depth confines of the species, particularly those of *G. retiformis* which have slow rates of areal and linear growth. These results indicate that while extant colonies may disappear from deeper sites in response to a sea level rise, they may also disappear from sites where old and new distributions overlap.

The persistence of the three species in response to sea level rise will depend on their ability to colonize presently unsuitable shallow reef sites. *Acropora millepora* and *G. retiformis* are more

reliant on sexual reproduction than *A. aspera*, which may persist through asexual propagation. Based on previous limited accounts of recruitment rates observed in field populations, it is likely that *A. millepora* will colonize new sites at the greatest rate, and *G. retiformis* the lowest. *Acropora aspera,* which showed much lower rates of sexual recruitment than the other species, may colonize new sites through clonal propagation. Alterations in sea state or increases in the frequency and intensity of tropical storms are likely to enhance the dispersal of dislodged branch fragments of *A. aspera* and increase the chances of their establishment in new sites.

The persistence of the species following sea level rise will also depend on the ability of recruits to endure exposure to any physical stresses associated with enhanced climate change. Following a partial bleaching event, coincident with extreme summer temperatures ranging from 18.5 to 33.6°C, all species readily recovered irrespective of their morphology. This indicates that a gradual rise in sea-surface temperatures of 2°C over the next century, which could result in partial bleaching, may have little affect on these shallow reef coral species. A more rapid increase in sea-surface temperatures or greater extremes, may significantly affect recruits, particularly those of *A. millepora*, which are likely to be the most vulnerable to seasonal mortality.

This study indicates that corals will respond differently to rises in sea level and enhanced climate change, because of differences in their morphology, life history traits and reproductive strategies. Short-lived genets, like *A. millepora*, with the least resilience to changes in environmental conditions may be the most useful bioindicators of early responses of coral reef ecosystems to environmental change. Long-lived clones, like *A. aspera*, with much lower rates of sexual recruitment and therefore little ability for genotypic adaptation, may be the most vulnerable to the long-term effects of enhanced climate change and sea level rise.

STATEMENT OF SOURCES

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or 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.

18 August 1997.

MARINA J. HUNT

STATEMENT OF ACCESS

I, the undersigned, the author of this thesis, understand that James Cook University of North Queensland will make it available for use within the University Library, by microfilm or other photographic means and allow access to users in other approved libraries. All users consulting this thesis will have to sign the following statement:

"In consulting this thesis I agree not to copy or closely paraphrase it in whole or in part without the written consent of the author; and to make proper written acknowledgment for any assistance which I have obtained from it."

Beyond this, I do not wish to place any restriction on access to this thesis.

18 August 1997

MARINA J. HUNT

ACKNOWLEDGMENTS

I would like to thank: my supervisor, Dr. T.P. Hughes (J.C.U.N.Q.), for his practical advice and tutelage; my associate supervisor, Associate Professor C.G. Alexander (J.C.U.N.Q.), for his technical advice and unwavering support and encouragement; Professor A.J. Underwood (University of Sydney), for his statistical advice in the design of field experiments; and Vice Chancellor Professor B.G. Thom (University of New England), for his guidance and counsel in addressing broad inter-disciplinary issues.

I would also like to acknowledge D.T. Anderson, R.C. Babcock, J.D. Collins, T.J. Done, P.L. Harrison, J.K. Oliver, D.C. Potts, D.H.R. Spennemann, C.C. Wallace and B.L. Willis not only for their constructive comments but for inspiring my work in the field.

I would also like to express sincere gratitude to: Z. Florian and L. Winsor, for their technical ingenuity and guidance; J.W.P. Larcombe, N.A. Moltschaniwskyj and G. De'ath, for their invaluable advice in the analysis of ecological data sets; the School of Biological Sciences and the Orpheus Island Research Station, for providing research facilities; technical staff for providing equipment; and numerous colleagues and students, for their invaluable field assistance, without which this project could not have been completed.

Finally, I thank my confidante J.W.P. Larcombe, family and friends for their endearing support and belief in everything I do.

This project was funded by the National Greenhouse Advisory Committee (NGAC) as part of a national research commitment to assess potential impacts of enhanced global climate change and sea level rise on coastal environmental conditions. I gratefully acknowledge the NGAC for their firm support and I am pleased to dedicate this work to their national research program.

18 August 1997.

MARINA J. HUNT

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1:

GENERAL INTRODUCTION

CORAL REEF COMMUNITIES AND GLOBAL CLIMATE CHANGE

Coral reefs constitute an immense natural resource, with very high biological diversity, comparable with tropical rainforests (Connell 1978). They support fisheries and tourism and act as barriers providing coastal protection. At present there is widespread debate as to the resilience of coral reef communities (Grigg & Dollar 1990; Done 1991, 1992; Jackson 1992; Smith & Buddemeier 1992), and concern over how they will respond to enhanced climate change and sea level rise (Tegart et al. 1990; D'Elia et al. 1991).

Based on paleoclimatic data, it has been argued that coral reef communities as a whole are robust to perturbations in the physical environment (Mesolella 1967; Newell 1971; Jackson 1992), and are not likely to be affected on a global basis by enhanced climate change and sea level rise (Smith & Buddemeier 1992). This is because there is little sign of elevated tropical sea-surface temperatures during warm periods of earth's history (Ruddiman 1985; MacCracken et al. 1990), and reefs have persisted despite recurrent sea level fluctuations during the Pleistocene (Chappell 1981, 1983), and despite maximum rates of sea level rise in excess of 20 cm / decade during the Holocene (Fairbanks 1989; Bard et al. 1990). There has also been little change in zonation patterns of dominant reef genera throughout the coral fossil record (Mesolella 1967; Jackson 1992). However, these features demonstrating the robustness of reefs over geological timescales have little relevance to the resilience of modern reef communities over ecological timescales.

At present, global mean temperatures are predicted to increase at a rate of 0.3 °C / decade. As a result, global warming is predicted to occur at an unprecedented rate (Houghton et al. 1990, 1992; Wigley & Raper 1992), in terms of coral lifetimes and community turnover (Smith & Buddemeier

1992). Global climatic changes caused by elevated greenhouse gas emissions and other anthropogenically induced alterations, are likely to interact with and enhance impacts of sea level rise (Smith & Buddemeier 1992). Sea level rise, in conjunction with enhanced climate change and anthropogenic activities, may have unprecedented effects on the dynamics and community composition of reefs, world-wide. Widespread observations of coral reef degradation and broad-scale phase-shifts in coral community structure and composition within the last few decades, clearly demonstrate the sensitivity of these systems to current levels of environmental change (D'Elia et al. 1991; Hughes 1989, 1994). Relatively little is known of their responses to climate change. There is, therefore, an obvious need for both long-term monitoring to identify community responses to environmental change, and manipulative research to understand the mechanisms causing the responses.

PREDICTIONS OF ENHANCED CLIMATE CHANGE AND SEA LEVEL RISE

A brief summary of the current status of enhanced climate change and sea level rise predictions for the eastern Australian tropics provides a context for the research discussed here. Exact predictions derived from global circulation models are uncertain, although current consensus predicts that elevated concentrations of radiatively active gases in the atmosphere will enhance the rate of climate change (Houghton et al. 1990, 1992; Pearman & Mitchell 1992; Whetton 1993; Wigley & Raper 1992). In the absence of specific policies for reducing greenhouse gas emissions, levels of atmospheric CO_2 are expected to increase approximately two-fold by 2050 (Houghton et al. 1990, 1992; Whetton 1993), with a concurrent increase in global mean temperatures of around 0.3°C / decade (Houghton et al. 1990, 1992; Wigley & Raper 1992). As a result, eustatic sea level is predicted to rise by around 20 cm by 2030 (range 5-35 cm) and 45 cm by 2070 (range 10-80 cm), an average rise of around 5 cm / decade (Wigley & Raper 1992).

Climate models cannot yet accurately predict regional climate change but research is being

conducted to refine them. In the eastern Australian tropics, the El Niño-Southern Oscillation phenomenon (ENSO) plays a major role in seasonal and inter-annual climatic and oceanic variability (Nicholls, 1988a, 1988b; Pittock 1993). Studies are currently in progress to quantify this variability (eg. Holbrook 1994), and to develop coupled atmospheric-oceanic models to predict how ENSO will behave under enhanced greenhouse conditions (Climate Impact Group CSIRO, pers. comm.; Kleeman 1990; Pittock 1993). Based on current predictions, sea-surface temperatures in the eastern Australian tropics are expected to rise by about 0.8°C by 2030 (range 0-1.5°C) and by 2°C by 2070 (range 0-4°C, Climate Impact Group CSIRO, 1992; Whetton 1993). Each increase in temperature of 1°C is expected to increase levels of evaporation by 2 to 4%.

More vigorous circulation in a warmer atmosphere is expected to cause an increase in the frequency and intensity of extreme climatic events (Climate Impact Group CSIRO 1992; Smith & Tirpak 1989; Houghton et al. 1990; 1992). In eastern Australia, monsoonal westerly winds and south-easterly trade winds are both expected to strengthen, and monsoonal rains and major tropical storms commonly experienced in the north are expected to increase in frequency and intensity and extend further south (Climate Impact Group CSIRO 1992). Apart from these shifts in climatic conditions, enhanced warming is expected to increase the amplitude of extreme temperature events (Houghton et al. 1990, 1992).

While not the result of global climatic changes, current rates of ozone depletion as a result of Chloroflurocarbon halon emissions are expected to increase the intensity of ultraviolet light by 5 to 10% or more over most of Australia by 2002 (WMO/UNEP 1991). Because levels of ultraviolet radiation may be affected by cloud cover, which is one of the most poorly understood and modelled features of the greenhouse climate (Cubasch & Cess 1990), the net increase in ultraviolet light for a given locality is unknown.

SHALLOW-WATER REEF CORALS: BIOINDICATORS OF ENVIRONMENTAL CHANGE

Shallow-water reef-building (Scleractinian) corals may be pre-adapted to a rise in sea level because of the tidal fluctuations they deal with continuously. However, they could also be among the first organisms to be affected by a rise in sea level, because they are sessile and require sunlight, and because many aspects of their biology and physiology are depth-dependent (eg. Baker & Weber 1975; Kojis & Quinn 1984; Chalker et al. 1988). They are often periodically exposed to subaerial stresses (Glynn 1973, 1988), and so may be among the first organisms to respond to enhanced climate change (eg. changes in temperature extremes). Many shallow-water reef corals are long-lived and offer great potential as bioindicators of long-term environmental change. For instance, massive corals such as *Porites* may live for several centuries (Potts et. al. 1985; Potts & Garthwaite 1991), and in branching species such as *Acropora*, that form genetically identical clones, genotypes may persist just as long (Highsmith 1982). Reef corals are also one of the most thoroughly studied organisms of coral reef systems. Much is already known of how they respond to natural variability in their local environment (Connell 1973; Hughes & Jackson 1985; Done 1987, 1988; Knowlton et al. 1990), non-climatic anthropogenic alterations (Brown & Howard 1985; Wells 1988; Grigg & Dollar 1990), and large-scale climatic fluctuations (Glynn 1988; Veron & Kelly 1988; Boekschoten et al. 1989; Paulay 1991; Potts & Garthwaite 1991; Jackson 1992). Because corals are often the most dominant reef organisms, their responses to the environment may be central to the integrity and environmental tolerances of entire reef communities (Johannes 1975).

ASSESSING CORAL RESPONSES TO ENVIRONMENTAL CHANGE

Reef corals have a diverse range of life histories (Hughes et al. 1992), and often exhibit quite different responses to ecological disturbances (Bak & Criens 1981; Knowlton et al. 1981; Woodley et al. 1981; Hughes & Jackson 1985; Potts & Garthwaite 1991). Ephemeral species are often susceptible to physical disturbances, but have high rates of growth and sexual recruitment, and so may

rapidly colonize bare substratum after a disturbance (Loya 1976a 1976b; Hughes & Jackson 1985). Long-lived massive species are inherently less susceptible to physical damage and often have lower rates of growth, sexual recruitment and re-colonization (Babcock 1991; Jackson & Hughes 1985). Some branching species with rapid rates of growth and very low rates of sexual recruitment, may colonize bare substratum through asexual propagation (Highsmith 1982; Rylaarsdam 1983). Most detailed population studies of the life histories and dynamics of reef corals have focussed on subtidal species (Rinkevich & Loya 1979a, 1979b; Bak & Engel 1979; Rylaarsdam 1983; Hughes & Jackson 1985). Most of these studies have also been conducted only within a single depth or reef zone (but see Hughes & Jackson 1985). Consequently, little is known of how a range of shallow water reef coral species with different life histories will respond to changes in sea level (depth).

Based on previous depth-related studies on corals, it seems likely that rates of growth and fecundity will be lower in deeper water (Buddemeier et al. 1974; Baker & Weber 1975; Kojis & Quinn 1984), although these responses may be offset by higher rates of tissue loss and mortality at shallow sites (Hughes & Jackson 1985). Some species can adapt to alterations in light by increasing photopigment contents (Kinzie et al. 1984; Chalker et al. 1988), but they may have limited ability to adapt to additional changes in the physical or biological environment at deeper sites (eg. changes in temperature). Coupled with changes in sea level, elevated sea-surface temperatures in shallow sites may induce bleaching and mortality in corals, resulting in reduced rates of individual and community calcification and a greater net removal of structural material by bioerosion (Smith & Buddemeier 1992; Glynn 1988, 1992). Colony size may also play an important role in determining the responses of corals in their environment. For instance, small colonies typically have high rates of mortality, whereas larger colonies are more often only injured than killed outright (Hughes & Jackson 1985; Babcock 1991). The effects of depth and sea level changes on these demographic and photophysiological responses of corals have traditionally been measured separately (eg. on one variable at a time) so that possible compensatory changes in species-specific responses between depths have been ignored (see below).

Field transplant experiments have been used extensively to evaluate coral responses to changes in environmental conditions (Shinn 1966; Maragos 1974; Neudecker 1977, 1981; Dustan 1979; Hudson 1981; Willis 1985; Yap 1981; Yap et al. 1992). They permit uncontrolled natural fluctuations in all environmental variables except those which are manipulated (such as depth). Therefore, adequate controls for the effects of handling and habitat relocation are essential (eg. Chapman 1986). While transplant experiments offer great potential to assess a broad range of coral responses to environmental change, most experiments have been used to evaluate specific aspects of coral biology or physiology, particularly alterations in survival or growth with depth (eg. Dustan 1979; Willis 1985; Yap et al. 1992). Very few transplant experiments have incorporated a wide range of colony size-classes and species and a large number of replicates.

While it is not possible to simulate exactly the projected sea-level rise, a more thorough understanding of differences among corals species' life history traits and demographic and photophysiological responses to specific depth changes gives a much better basis for predicting possible consequences than currently exists. Transplant experiments have been used in the present study to examine the effects of depth changes of 25 cm, 50 cm and 1 m on a broad range of size-specific demographic and photophysiological responses for a range of shallow-water reef corals with different life histories. An integrative approach has been taken to provide a means of assessing the range of responses likely to be exhibited by coral assemblages following a global change in sea level. Of course, experimentally induced direct depth changes have only a limited ability to simulate field conditions in response to sea level rise. Consequently, this study also examines the ability of corals to acclimatize to more gradual changes in depth (25 cm + 25 cm, over a 12 month period), to assess the feasibility of using transplant experiments to simulate sea level rise.

Many reef corals live much longer than the life-time of a field experiment or research scientist, so that short-term experimental studies provide little direct indication of the long-term effects of depth changes on the demographic fate of reef corals. However, assuming that short-term processes represent long-term processes, size-structured population projection models may be used to predict

long-term changes in plant or animal populations (Hartshorn 1975; Werner & Caswell 1977; Enright & Ogden 1979). They also provide a powerful tool to evaluate the sensitivity of population growth rates to changes in life history parameters (Hughes 1984, 1990; McFadden 1991), and environmental conditions (Hughes 1984; Done 1987, 1988; Gotelli 1991).

As sea level rises, new recruits may colonize presently unsuitable shallow reef sites (Hopley & Kinsey 1988; Smith & Buddemeier 1992), but extant corals will be found in gradually deepening sites where environmental conditions may deteriorate. The resilience of extant coral populations to changes in the physical and biological environment and their ability to replace themselves, either sexually or asexually, will determine their persistence in response to enhanced climate change and sea level rise. Few demographic studies have quantified the relative contributions of asexual and sexual reproduction to the population growth of clonal organisms (Sarukhan & Gadgil 1974; Bierzychudek 1982; McFadden 1991). Most studies using size-structured projection models to evaluate the long-term dynamics or life history strategies of coral populations have also focussed on single species (Hughes 1984; Done 1987, 1988; McFadden 1991), rather than a range of species with different life histories (Caswell 1989; Andres & Rodenhouse 1993).

This study uses a matrix modelling approach to examine the long-term effects of depth changes on the demography of corals and the importance of specific reproductive strategies on rates of population growth. Some reef corals might persist indefinitely at deeper sites by asexual propagation alone, whereas others may face rapid local extinction if unable to reproduce asexually. The matrix models used in this study predict the length of time extant coral populations are likely to persist at specific depths as sea level rises.

This study examines the demography and photophysiology of three shallow-water reef coral species, *Goniastrea retiformis* Lamarck, *Acropora aspera* Dana and *Acropora millepora* Ehrenberg, to changes in environmental conditions within their natural habitat and in response to depth changes. These species have different life histories and are restricted to very shallow depths of less than 1 m below tidal datum on inshore Australian fringing reefs. Data presented here provide information on

the possible causes of coral zonation and the potential resilience of these shallow-water reef corals to environmental change.

CHAPTER 2:

EFFECTS OF DEPTH CHANGES ON THE ECOLOGY OF SHALLOW-WATER REEF CORALS

INTRODUCTION

Sessile reef-building corals with very shallow depth distributions on inshore reefs may be particularly vulnerable to enhanced climate change and sea level rise. While these corals may be pre-adapted to continuous tidal fluctuations, their very narrow depth range may increase their susceptibility to eustatic changes in sea level and to alterations in environmental conditions. Their demographic traits (eg. survival, growth and reproduction) are depth-dependent (eg. Maragos 1972; Baker & Weber 1975; Kojis & Quinn 1984), and readily influence by anthropogenic activities (eg. sediment or nutrient loading from sewage, agricultural practices or land use, Kinsey 1979; Smith et al. 1981; Brown & Howard 1985; Glynn et al. 1989; Grigg & Dollar 1990). Their location in shallow-water with periodic emersion exposes them to any subaerial changes in climate (eg. increases in temperature extremes, Glynn 1973, 1988). Nevertheless, little is known of how shallow-water reef coral assemblages on inshore reefs will respond to enhanced climate change and sea level rise.

Growth forms and life history strategies strongly influence patterns of coral zonation (Loya 1976a; Sheppard 1980; Hughes & Jackson 1985; Jackson & Hughes 1985), and coral responses to ecological disturbances (Veron 1986; Shinn 1972; Loya 1976a; Bak & Criens 1981; Woodley et al. 1981; Knowlton et al. 1981, 1990; Rogers et al. 1982; Hughes 1989; Potts & Garthwaite 1991; Yap et al. 1992). Despite their importance, few quantitative estimates have been made of the life history traits and population dynamics of shallow-water reef corals on inshore reefs (eg. Maragos 1972; Babcock 1991). Most detailed population studies of the life histories and dynamics of reef corals have focussed on subtidal species with relatively broad depth distributions (Loya 1976a, 1976b;

Rinkevich & Loya 1979a, 1979b; Bak & Engel 1979; Rylaarsdam 1983; Hughes & Jackson 1985), or intertidal species restricted to shallow depths on offshore reefs (Connell 1973; Bothwell 1984; Hughes & Connell 1987). Many of these studies have also been conducted only within a single depth or reef zone (but see Hughes & Jackson 1985). Very little is known of the population dynamics of morphologically different shallow-water reef corals on inshore reefs, or how they will respond demographically to sea level changes (depth).

Based on previous depth-related studies on corals it seems likely that rates of growth and fecundity will be lower in deeper water (Buddemeier et al. 1974; Baker & Weber 1975; Kojis & Quinn 1984). In some species, however, these responses may be offset by higher rates of injury and mortality in shallow sites (Hughes & Jackson 1985). Coupled with changes in sea level, elevated sea-surface temperatures may induce bleaching and mortality in corals, resulting in reduced rates of coral calcification and a greater net removal of structural material by bioerosion (Glynn 1988, 1992; Smith & Buddemeier 1992). Colony size may also play an important role in determining the dynamics of corals (Connell 1973; Jackson 1979; Kojis & Quinn 1985; Szmant-Froelich 1985; Soong 1993). For instance, small colonies typically have high rates of mortality, whereas large colonies are often injured and rarely killed outright (Hughes & Jackson 1985; Babcock 1991). Changes in depth and sea level, therefore, have the potential to effect a broad range of size-specific demographic traits (eg. survival, growth, reproduction, tissue loss, and although not demographic, bleaching and bioerosion), in shallow-water reef corals.

Field transplant experiments have been used extensively to assess responses of corals to changes in environmental conditions (Shinn 1966; Maragos 1974; Neudecker 1977, 1981; Dustan 1979; Hudson 1981; Willis 1985; Yap 1981; Yap et al. 1992). They permit natural alterations in all environmental variables, except those variables which are kept constant (such as depth). They offer great potential to assess a broad range of coral responses to environmental change. Most transplant experiments, however, have been used to evaluate specific aspects of coral biology, particularly alterations in survival or growth with depth (eg. Dustan 1979; Willis 1985; Yap et al. 1992). Very few transplant experiments have incorporated a large number of replicates at different depths. As a result, possible compensatory changes in species-specific demographic responses between depths

have been ignored (eg. reduced reproduction rates may occur in deeper water while growth rates increase).

While transplant experiments cannot simulate exactly the projected sea level rise, they can be used to quantify depth-dependent differences in coral life-history traits and to predict the likely impacts of sea level rise on shallow-water reef corals. Transplant experiments have been used in this study to examine the effects of specific depth changes (25 cm, 50 cm and 1 m) on a broad range of size-specific demographic responses for a range of shallow-water reef corals with different morphologies and life histories. Controls for the effects of handling, habitat relocation and depth changes have been incorporated into the experiments to obtain representative estimates of the dynamics of the corals in their natural environment and in response to depth changes. These estimates can be used to identify possible causes of zonation among species and to predict demographic responses of shallow-water coral populations and assemblages to sea level rise. Because sudden experimentally induced direct depth changes may have only a limited ability to simulate gradual sea level rise, this study also examines the ability of corals to acclimatize to more gradual changes in depth (25 cm + 25 cm , over a 12 month period).

The response of corals to sea level rise will be governed to some extent by the impact on their reproductive output. While reef corals may experience a decrease in sexual reproductive output in deeper water (eg. Kojis & Quinn 1984), their ability to propagate clonally by colony fission may be important in determining their persistence among deeper sites. Asexual propagation (cloning) may reduce the risk of genotype mortality, provided the combined survivorship of individual ramets (daughter colonies) formed exceeds that of the original parent or genet (Cook 1979; Babcock 1991; Hughes et al. 1992). Conversely, the process of cloning may reduce the fitness of a genet by increasing mortality and reducing its sexual reproductive output (Babcock 1991). For reef-building corals, cloning is often caused extrinsically through injury or partial mortality (Hughes & Jackson 1985; Babcock 1991). Since fecundity increases with colony size (Kojis & Quinn 1985), daughter colonies often experience an immediate decrease in fecundity (Babcock 1991). However, if colonies have the ability to produce daughter colonies with extremely high rates of survivorship and fast rates of growth, this may compensate for short-term reductions in the fitness of a genet, delay genet

mortality and extend potential longevities in response to sea level rise.

The persistence of individual species in response to sea level rise will also depend partly on the ability of recruits to endure exposure to enhanced physical stresses associated with climate change. Perhaps one of the most thoroughly studied physical-related stress responses of reef corals is bleaching, the loss of normal pigmentation, which is caused as a result of prolonged exposure to temperature or salinity anomalies or excessive solar radiation or shading (Rogers 1979; Glynn 1984; Brown & Howard 1985; Hoegh-Guldberg & Smith 1989; Jokiel & Coles 1990; Brown 1990; Szmant & Gassman 1990). Partially or entirely bleached corals often experience altered physiological functions (Fitt et al. 1993), regenerative abilities (Meesters & Bak 1993), growth (Goreau & MacFarlane 1990) and fecundity (Szmant & Gassman 1990), and survivorship (Meesters & Bak 1993) relative to unbleached corals. The frequency and extent of bleaching among corals is often related to their morphologies and life history traits. For instance, short-lived species which tend to have the highest respiratory rates are often most prone to bleaching (Jokiel & Coles 1974; Coles & Jokiel 1977), and branching species are usually more sensitive than massive species (Jokiel & Coles 1990). Despite this, few quantitative estimates of size-specific bleaching and recovery among morphologically different shallow-water reef corals have been made at different depths through time (De Vantier et al. 1994; Oliver & Berkelmans 1994). This information may provide insight into the resilience of shallow-water coral populations to enhanced physical stresses in their environment.

At present eustatic sea level is predicted to rise around 20 cm by 2030 and by about 45 cm by 2070 (Wigley & Raper 1992). Therefore, this study was designed to determine the effects of specific depth changes (25 cm, 50 cm or 1 m) on the responses of initially four coral species (Anthozoa: Scleractinia), which inhabit very shallow depths (ca. < 1 m below tidal datum) in an inshore environment. The species chosen have different morphologies (digitate, branching, corymbose and massive).

This study has several key objectives: 1. To document the abundance and size-structure of the four species at different depths within their natural environment and gain an understanding of their patterns of reef zonation; 2. to determine the survivorship of the species in response to a 1 m depth change, to identify target species for further investigation; 3. to determine target species responses to

a 25 cm, 50 cm or 1 m depth change, by quantifying their size-specific survivorship, growth (areal and linear), tissue loss, asexual propagation (fission), bleaching and recovery, bioerosion and fecundity; 4. to use this information to determine species-specific life history traits and compensatory responses to depth changes; 5. to determine the acclimatization ability of the target species in response to *stepwise* 25 cm depth changes, as a means of assessing the feasibility of using transplant experiments to simulate predicted sea level rise; and finally 6. to integrate these findings to identify possible cause of zonation among species, and discuss potential impacts of enhanced climate change and sea level rise on shallow-water reef corals.

MATERIALS AND METHODS

STUDY SPECIES

The four species chosen for this study were: *Montipora digitata* Dana (*fat fingers* morph, Stobart 1994), *Acropora aspera* Dana, *Acropora millepora* Ehrenberg (*gracilis* morph, R. Babcock & P. Harrison pers. comm.) and *Goniastrea retiformis* Lamarck (Fig. 2.1). All have very restricted shallow depth distributions, particularly on inshore fringing reefs, and all are common and abundant throughout most of the Indo-Pacific (Birkeland et al. 1979; Bothwell 1984; Veron 1986). They also have moderately long lifespans so extant colonies may in the future be subjected to continual sea level rise.

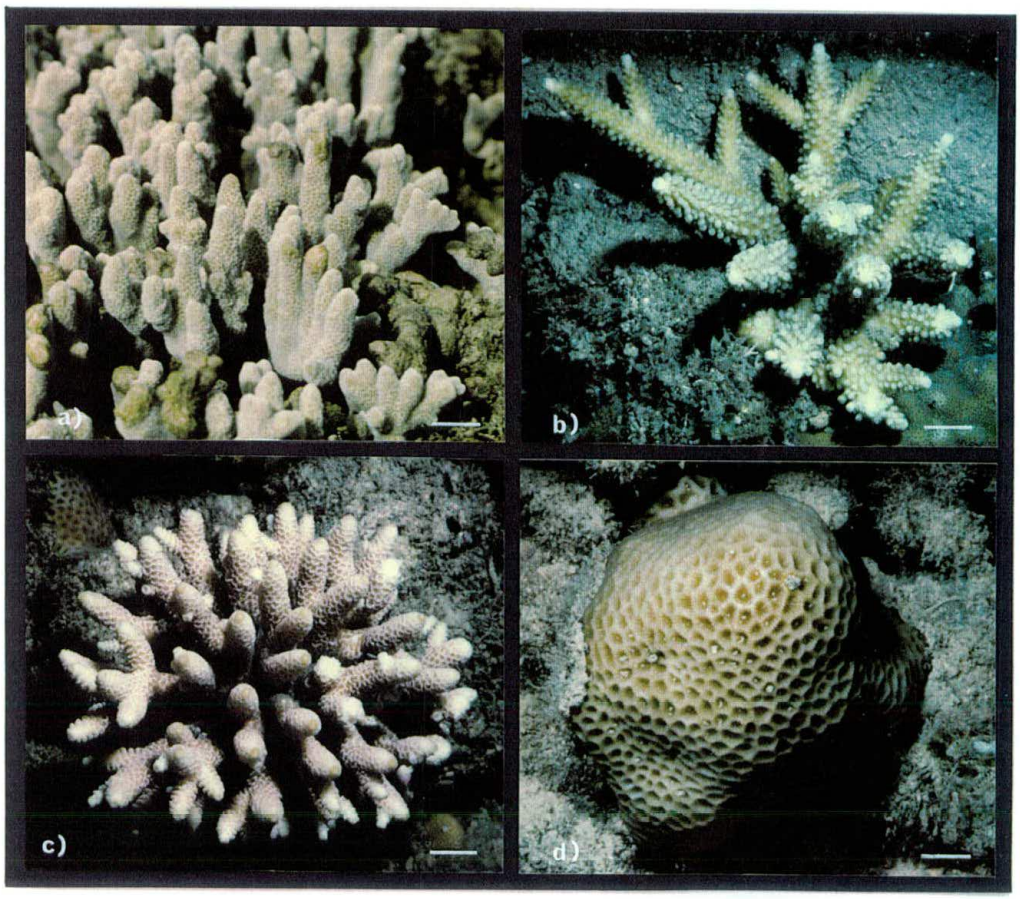

Figure 2.1 Study species: a) *Montipora digitata* Dana 1846, b) *Acropora aspera* Dana 1846, c) *Acropora millepora* Ehrenberg 1834, and d) *Goniastrea retiformis* Lamarck 1816. Scale bars = 2 cm.

RESEARCH AREA

Control and experimental colonies of each species were monitored on a fringing reef within Little Pioneer Bay; an inshore site situated on the western and leeward side of Orpheus Island, Australia (18°35' S & 146°29' E). Orpheus Island is a high continental island located within the Central Section of the Great Barrier Reef Marine Park. The Island is situated 15 km from the mainland coast and the mouth of the Herbert River (Fig. 2.2-a), and has a modified marine tropical climate. Locally generated wave action and occasional high volume outflow from mainland fluvial systems (such as the Herbert River) can strongly affect water turbidity and sediment regimes. Little Pioneer Bay, situated on the leeward side of the island (Fig. 2.2-b), is generally sheltered from prevailing south-easterly trade winds, and the underwater visibility in the bay typically ranges from 3 to 5 meters. Tides exhibit a twice daily cycle with a semi-diurnal inequality, so that extreme low tides occur at night in summer and during the day in winter. Shallow-water reef corals within Little Pioneer Bay experience a broad tidal regime (from 0.2 m on neap tides to 3.5 m on spring tides), and can be exposed for up to several hours during extreme low tides.

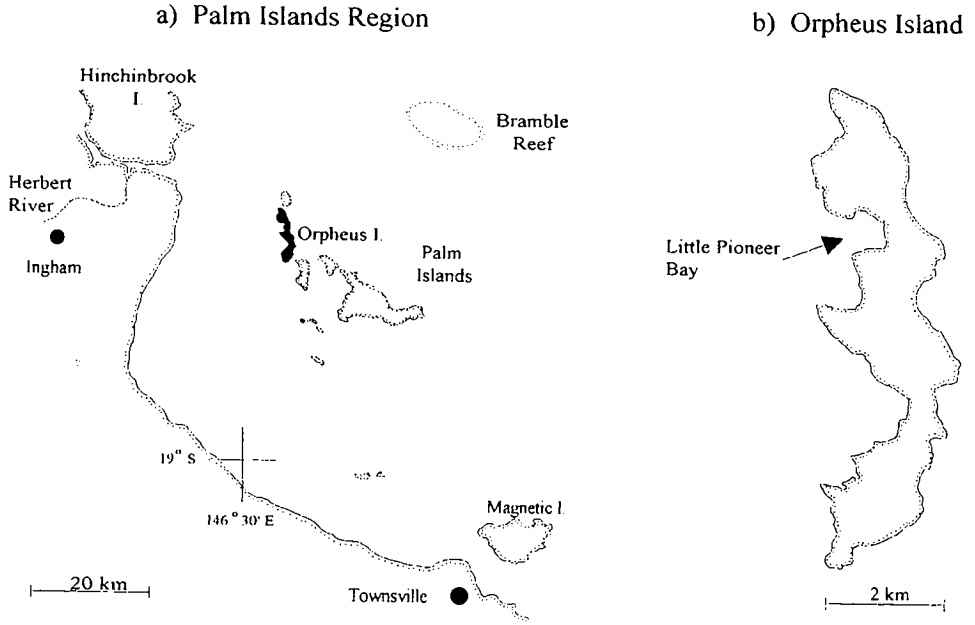

Figure 2.2 Research area: a) indicates the relative position of Orpheus Island and b) Little Pioneer Bay.

ABUNDANCE AND SIZE-STRUCTURE OF CORAL POPULATIONS VS. DEPTH

To measure the abundance and describe the zonation of the study species in Little Pioneer Bay, replicate belt transects were deployed at each of two locations (Fig. 2.3) in December 1991. The sampling design is shown in Figure 2.4. Five depths were identified at each location, representing the: inner flat at 0.02 m below tidal datum, mid flat at 0.05 m, outer flat at 0.20 m, crest at 0.35 m and slope at 1.20 m, and three sampling sites haphazardly selected at each depth per location. At each of the thirty sampling sites, three 10 x 1 m belt transects were laid parallel to the shore. Total counts of all colonies of each species in each transect were recorded. A colony's presence was recorded only when its centre fell entirely within each transect. With the inclusion of species in the design, a four-factor nested analysis of variance was used to test for abundance differences between and among locations, depths, species and sites, and for their interactive effects.

Figure 2.3 Position of study locations, 1 and 2, which were used to examine effects of depth on the abundance and population size-structure of corals within Little Pioneer Bay. Scale bar = 100 m

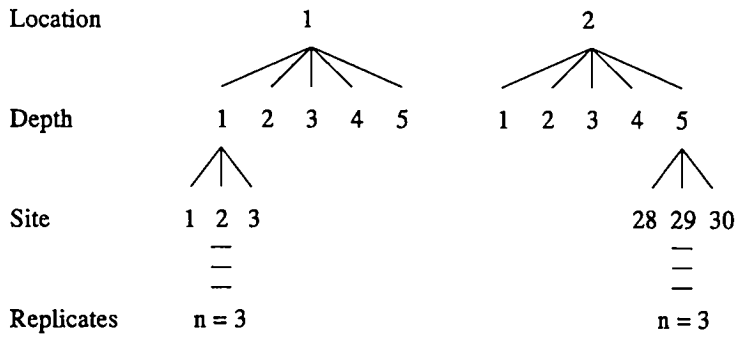

Figure 2.4 Sampling design for quantifying effects of depth on the abundance and population size- structure of corals within Little Pioneer Bay. Depths 1 through to 5 represent the inner flat at 0.02 m below tidal datum, mid flat at 0.05 m, outer flat at 0.20 m, crest at 0.35 m and slope at 1.20 m, respectively.

To determine the population size-structure for each of the study species, the mean diameter of all colonies in each transect was recorded at three depths at each location, the mid flat at 0.05 m, the outer flat at 0.20 m and the crest at 0.35 m (Fig. 2.4). A four-factor nested analysis of variance was used to test for differences in colony size between and among locations, depths, species and sites and for their interactive effects.

All depths were determined using an Aladdin Sports Plus digital depth gauge, accurate to within 2 to 3 centimeters. To confirm depths relative to chart datum, the depth of water over each site was recorded repeatedly during different tidal cycles.

TRANSPLANT EXPERIMENTS

Experiment 1: Effects of a 1 m Depth Change

From January 1992 to January 1993 a pilot study was conducted to determine effects of a 1 m depth change on the survivorship of the species and to identify target species for subsequent demographic and photophysiology studies. The experimental design is shown in Figure 2.5. There

were four different treatments and four species. Initially, 20 small, medium and large colonies of each species (a total of 240 colonies) were tagged *in situ* on the outer flat at 0.20 m, to act as undisturbed control colonies. Small colonies were less than 5 cm in mean diameter, medium ones ranged from 6 to 9 cm in mean diameter and large ones ranged from 10 to 15 cm in mean diameter. Sixty additional small, medium and large colonies of each species (a total of 720 colonies) were also removed from the substratum and assembled onto replicate racks at: the same site at 0.20 m (to control for the effects of handling), 400 m south at 0.20 m (to control for the effects of habitat relocation), and 1 m deeper (these were the depth transplants). For a single species, 10 replicate colonies of each size-class were randomly assigned to each rack (Fig. 2.6), so each rack held a total of 30 colonies (Fig.2.7). All colonies assigned to each rack were separated by a minimum distance of 20 cm. The location of treatments within Little Pioneer Bay is shown in Figure 2.8.

All control and experimental colonies were removed from the substratum from the northern end of the bay adjacent to the *in situ* control treatment at 0.20 m (Fig. 2.8). Within 12 hours of collection, the dead bases of individual colonies were embedded in aluminium containers of quick-setting cement positioned on the intersections of 20 cm mesh steel racks (1.4 x 2.2 m), and left for 24 hours for the cement to cure. At each treatment location, racks were positioned at least 5 m apart parallel to the shore, and secured to the substratum with steel stakes.

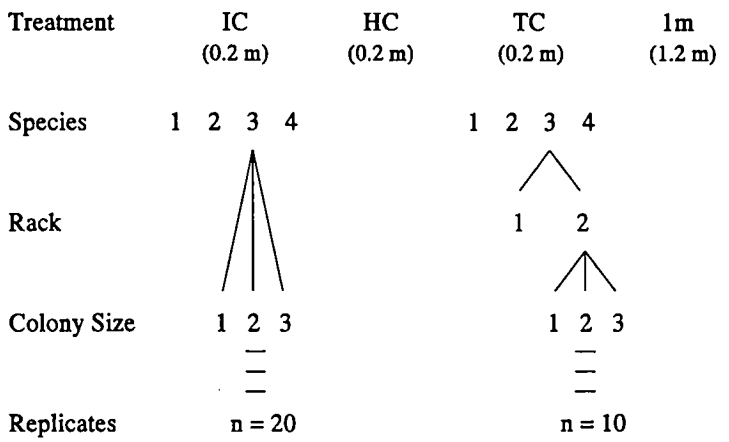

Figure 2.5 Experimental design for determining effects of a 1 m depth change on coral demography. IC, represents the *in situ* controls; HC, the handling controls; TC, the translocated controls, and 1 m, the depth transplants. Treatment depths below tidal datum are shown in parentheses.

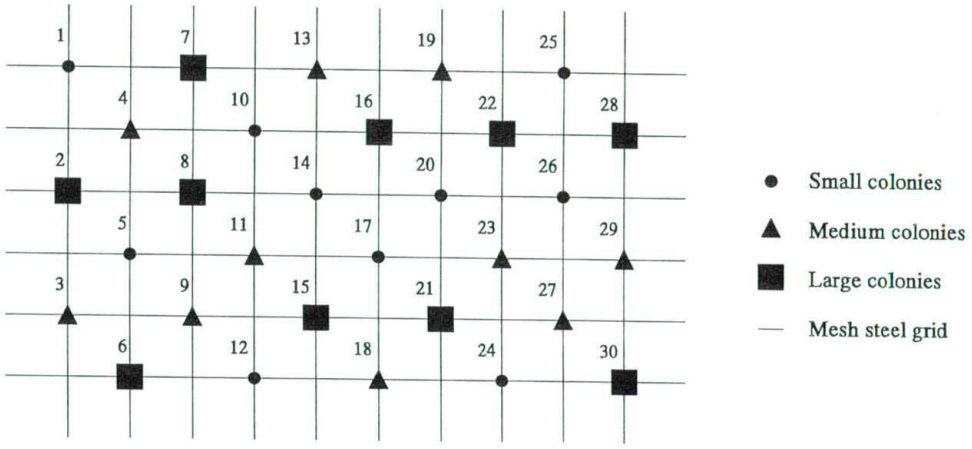

Figure 2.6 Randomized design for the rack allocation of replicate colonies, n = 30. All colonies are separated by a minimum distance of 20 cm.

Figure 2.7 Overall construction of an experimental rack located within the 1 m depth transplant treatment, consisting of small (s), medium (m) and large (l) colonies of *M. digitata*.

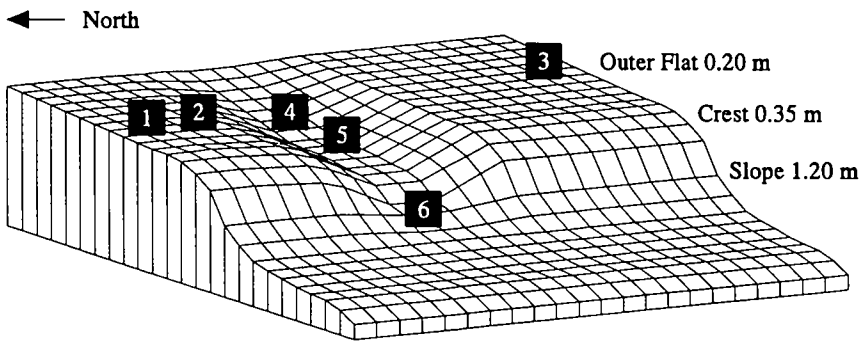

Figure 2.8 Diagrammatic view of the location of treatments within Little Pioneer Bay. 1, shows the location of the *in situ* controls at 0.2 m below tidal datum; 2, the handling controls at 0.2 m; 3, the translocated controls at 0.20 m; 4, the 25 cm transplants at 0.45 m; 5, the 50 cm transplants at 0.70 m; and 6, the 1 m transplants at 1.20 m. The horizontal scale of each grid represents approximately 20 m. The vertical scale is exaggerated.

Experiment 2: Effects of Smaller Depth Changes

From January 1993 to January 1994 a second transplant experiment was conducted to determine demographic and photophysiological effects of 25 cm and 50 cm depth changes on the two most useful depth indicator species, *A. aspera* and *A. millepora* (See Results). The overall design of this experiment was identical to that of the first, except there were five different treatments and only

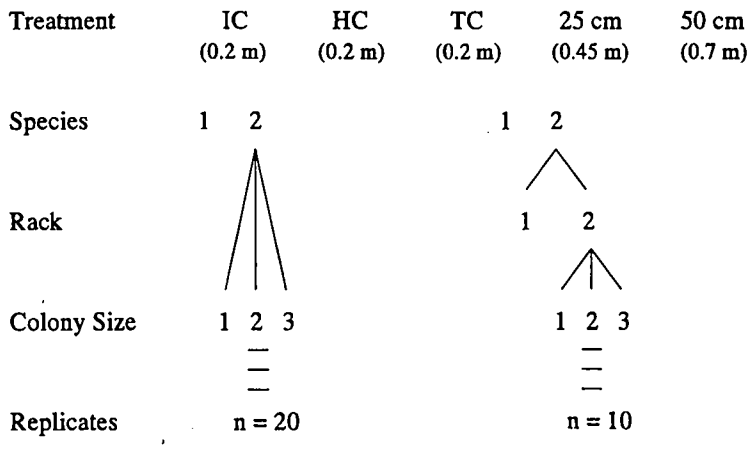

Figure 2.9 Experimental design for determining effects of 25 cm and 50 cm depth changes on coral demography and photophysiology. Treatment abbreviations are identical to those used in Fig. 2.5.

two species (Fig. 2.9). Again, *in situ* controls were tagged and left undisturbed, while the other control and experimental colonies were randomly assembled onto either of two racks within each treatment (Fig. 2.6), in this case, to act as the handling controls, translocated controls and the 25 cm and 50 cm depth transplants. A total of 600 colonies was used. Treatment locations within the bay are indicated in Figure 2.8.

Experiment 3: Effects of *Stepwise* Depth Changes

From January 1994 to May 1994 a third transplant experiment was conducted to examine the acclimatization ability of species to *stepwise* depth changes. The aim of the experiment was to determine if the survivorship of corals moved directly 50 cm deeper differed from those moved in two 25 cm steps over a 12 month period. At the end of experiment 2, all surviving *in situ* controls, handling controls, translocated controls and 25 cm depth transplants formed the basis for the design of this experiment. Consequently, the initializing conditions of this experiment were: 1. The *in situ* controls were left undisturbed, 2. The handling controls were moved 50 cm deeper to 0.70 m (to act as the direct depth transplant controls), 3. The translocated controls were shifted marginally within the same depth to re-initialize the experiment, and 4. the 25 cm depth transplants were moved 25 cm deeper to 0.70 m (to act as the *stepwise* depth transplants). The overall design of this experiment (Fig. 2.10) was thus identical to that of experiment 2, although fewer replicate colonies were alive to be included (a total of 306 colonies), and no colonies were required to control for the effects of handling

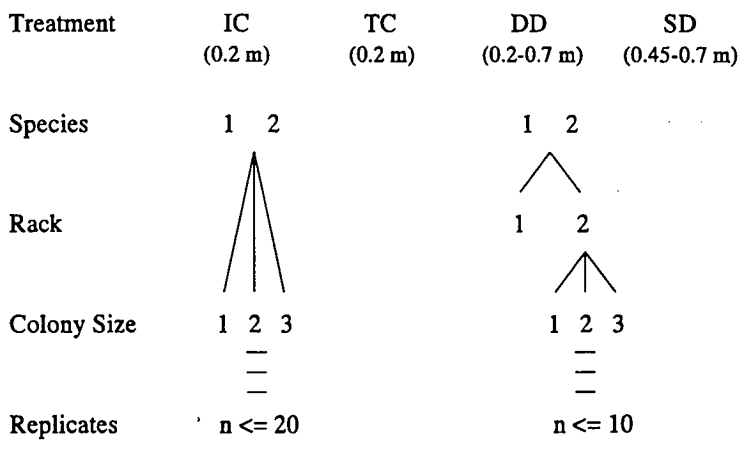

Figure 2.10 Experimental design for examining the acclimatization ability of corals to *stepwise* depth changes. IC, represents the *in situ* controls; TC, the translocated controls; DD, the direct depth transplant controls; and SD, the *stepwise* depth transplants.

CORAL RESPONSES TO DEPTH CHANGES

1. Colony Survivorship

The survivorship of colonies was determined bimonthly for 7 censuses in experiment 1 and 2, and bimonthly for 3 censuses in experiment 3. Log-linear analyses were used to test for survivorship differences between and among treatments, species and colony size- classes.

2. Colony Growth Rates

In experiment 1 and 2, all colonies were photographed bimonthly immediately following transplantation. At each census, colonies were photographed from the same angle and a set perpendicular distance of 23.5 centimeters. A ruler, attached to the outer frame of the camera, provided an accurate scale for each colour slide. After each census, the projected surface area of all individual colonies was traced and digitized, to within ± 3 % of its original size, from the slides. Rates of colony growth and shrinkage were then determined for all colonies, together with rates of colony fission. A colony which underwent fission was defined as one which became divided into two or more live daughter colonies, without breakage of its skeleton. The special case, where a colony fragmented, and formed physically separate daughter colonies due to the breakage of its skeleton, was noted separately. Effects of treatment, species and colony size on rates of colony growth, shrinkage and fission were determined using several repeated measures analyses of variance.

Alizarin-Red vital stain was also used to determine linear growth rates of colonies in experiment 1 and 2. During January 1992, 240 colonies were stained in experiment 1 to determine effects of a 1 m depth change on extension rates. Each colony was incubated for 24 hours in a clear polythene bag containing an Alizarin solution (20 mg / L). Five small, medium, and large colonies of each species were selected haphazardly and stained at each treatment, along with 60 *in situ* control colonies. During January 1993, 150 colonies were also stained in experiment 2 to determine effects of smaller depth changes on extension rates. In this case, 5 small, medium and large colonies of each species were stained at each treatment, along with 30 undisturbed controls. All live colonies stained with Alizarin were collected after 12 months, bleached to remove tissue, and sectioned with a

diamond blade to reveal the stain. Replicate growth measurements were taken from each colony sub-section and recorded to the nearest 0.10 mm with vernier calipers. Differences in annual rates of linear extension between treatments, species and colony size-classes were assessed using several analyses of variance.

3. Colony Tissue Loss, Bleaching and Bioerosion

The projected area of tissue killed between censuses in experiment 1 and 2 was recorded from all photographed colonies to determine rates of colony tissue loss. The percentage of tissue lost from each colony was analyzed using repeated measures analyses.

The projected surface area of bleached coral tissue was also determined in each census for all colonies photographed in experiment 1 and 2 to determine rates of tissue bleaching and recovery. Bleached colonies were defined as those which had lost normal pigmentation to the extent where their live tissue had become translucent and white. Differences in the frequency of bleaching and the percentage of live tissue bleached per colony between treatments, species and colony size-classes were determined using repeated measures analyses. The recovery of bleached colonies after a bleaching event was assessed by their ability to maintain rates of tissue gain and survival equal to that exhibited by unbleached colonies. To do this, the amount of tissue loss among bleached and unbleached colonies and their survivorship 10 months after bleaching was calculated. The magnitude of tissue loss among colonies was scored from zero (no injury) through various amounts of injury (partial mortality or polyp death) to 100% (whole colony mortality), and the fate of bleached and unbleached colonies for each species and treatment was analyzed using log-linear analyses for categorical data.

To determine whether small depth changes influence the extent of bioerosion among species, the total number of boring taxa and the extent of their bioerosion was determined for all stained and living colonies collected at the end of experiment 1 and 2. After colonies were initially sectioned to determined rates of linear extension (by Alizarin-Red staining), the perimeter of each colony sub-section and the extent of its skeletal erosion was traced and digitized from photographs, enlarged to 5 times their original size. All excavation sites were identified and the percentage of bioerosion by

each boring agent was calculated for each colony.

4. Colony Fecundity

Effects of small depth changes on colony fecundity were examined in experiments (1 & 2). During experiment 1, in October 1992 (4 weeks before Spring spawning), 18 surviving colonies of each species within each treatment (a total of 72 colonies, See Results) were subsampled to determine effects of a 1 m depth change on colony fecundity. For each species, three replicate subsamples approximately 2 cm^2 were collected from each of 6 small, medium and large colonies from each treatment. All subsamples were taken only from within the fertile region of each colony (Fig. 2.11). Subsamples were also collected in experiment 2 to determine effects of 25 cm and 50 cm depth changes on colony fecundity. In this case, subsamples of *A. millepora* were collected during October 1993 (4 weeks before Spring spawning), and those of *A. aspera* were collected during January 1994 (4 weeks before Summer spawning). A total of 180 colonies (18 colonies of each of the two species from each of the five treatments) were subsampled in experiment 2, using identical methods.

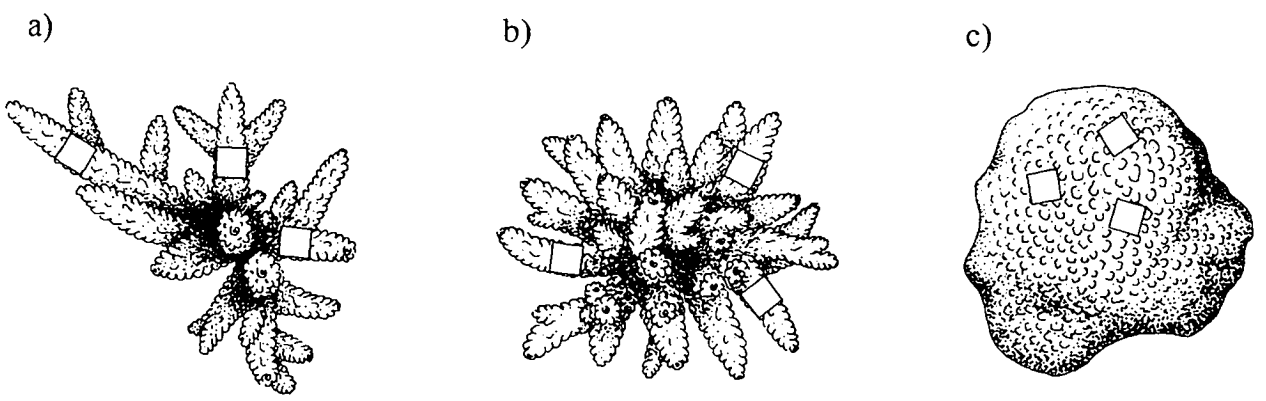

Figure 2.11 Location of fecundity subsamples within the target species: a) *A. aspera*, b) *A. millepora* and c) *G. retiformis*. □, denotes subsamples approximately 2 cm^2.

All subsamples from each experiment were immediately fixed in 10% seawater formalin, decalcified

and dissected under a stereo dissecting microscope fitted with a calibrated micrometer eyepiece. For each of five replicate polyps per subsample, oocyte volume (as calculated by Wolstenhome 1991), and the number of oocytes per polyp were determined. Based on estimates of the average number of polyps per square centimeter of living coral tissue, the mean number of eggs per unit area (colony fecundity) was calculated for each treatment, species and colony size-class. Quantitative estimates of polyp density were obtained from all stained colonies collected at the end of experiment 1 and 2.

CORRELATES OF TEMPERATURE WITH CORAL DEMOGRAPHIC RESPONSES

Seawater temperatures were monitored throughout the study to examine the correlates of a purely physical factor other than depth with coral responses. At the start of each experiment, calibrated maximum and minimum 0-50°C mercury thermometers (accurate to 0.2°C) were tied permanently to the substratum within each treatment. Thermometer readings were taken every two months over the total period and extreme seawater temperatures for each census interval were determined.

STATISTICAL ANALYSES

In all analyses of variance, tests for normality were conducted by examining Wilk-Shapiro rankit plots of analysis residuals (Shapiro & Wilk 1965). Variance homogeneity was also tested using Cochran's C value and, where necessary, data were transformed before analysis to homogenize variances (Winer 1971). *Post hoc* comparisons of means were performed using the methods of Tukey (1953) and Krammer (1956), which accommodate unequal cell sizes. In all analyses, data for the *in situ* controls were analyzed separately from that of all the other treatments, because the *in situ* controls were not placed on experimental racks, as was the case for colonies in all other treatments. Due to the size and complexity of the analysis models used in this study, only relevant statistical tests and ANOVA tables for experimental colonies have been included in the Results. The statistics tables for the *in situ* controls have not been included. Where sources of variation are described as 'non-significant' in the Results Section, they were not statistically significant at $p < 0.05$ or by graphical interpretation. Further details of all statistical analyses are provided in the Results Section.

RESULTS

CORAL ABUNDANCE AND SIZE DISTRIBUTIONS ALONG A DEPTH GRADIENT

The abundance of the selected coral species within Little Pioneer Bay was highly depth-dependent ($p < 0.001$, Tab. 2.1). All four species inhabited shallow depths of less than 1 m, extending from either the inner flat at 0.02 m below tidal datum or the mid flat at 0.05 m to the reef crest at 0.35 m. None were found on the reef slope at 1.20 m. Colony abundance was highest on the outer flat with an average of 29.6 ± 1.6 SE corals per 10 x 1 m transect, and lowest on the inner flat with only 6.4 ± 1.0 per transect. Colonies of *Acropora millepora* were the least abundant (8.3 ± 1.8 / transect), compared to those of *Goniastrea retiformis* (25.7 ± 2.0 / transect), *Montipora digitata* (20.5 ± 2.2 / transect) and *Acropora aspera* (18.5 ± 2.1 / transect). The abundance of species also differed between depths ($p < 0.001$, Tab. 2.1 & 2.2). *Montipora digitata* was most abundant at the shallowest reef zones, while *A. aspera* dominated the outer flat and *A. millepora* the reef crest. In contrast, *Goniastrea retiformis* was found in equal abundance from the mid flat to the reef crest.

Table 2.1 Four-factor nested ANOVA to test for differences in the relative abundance of corals between and among locations, depths, species and sites within Little Pioneer Bay. The analysis was performed on log (x + 1) transformed data. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Location (Lo)	1/2	0.22	$p < 0.01$
Depth (De)	4/2	87.44	$p < 0.001$
Species (Sp)	3/2	6.18	$p < 0.001$
Site	2/318	<0.01	NS
Lo *De	4/2	0.03	NS
Lo*Sp	3/2	0.03	NS
De*Sp	12/2	6.08	$p < 0.001$
Lo*De*Sp	12/2	<0.01	NS
Residual	318		
Total	359		

Colony abundance varied spatially within the bay ($p < 0.01$, Tab. 2.1), and was higher at Location 1 (21.4 ± 1.6 / transect), than at Location 2 situated further south (15.2 ± 1.2 / transect). However, depth-dependent patterns of abundance were identical within the two locations (eg. no location*depth interaction). Given the overall abundance and zonation of corals within the bay (Tab. 2.2), control colonies of each species were established or transplanted to the outer flat at 0.20 m in

all subsequent experiments, because this appeared to be the mid-depth range of the four species' distributions.

Table 2.2 Abundance and zonation of corals with Little Pioneer Bay. Total colony counts were made from within 18 replicate 10 x 1 m belt transects positioned at each depth. Data are means (± SE).

Reef Zone	Depth	Species:			
		M. digitata	*A. aspera*	*A. millepora*	*G. retiformis*
Inner Flat	0.02 m	16.7 (2.0)	0.0 (0.0)	0.0 (0.0)	8.9 (0.9)
Mid Flat	0.05 m	54.8 (4.5)	26.3 (2.3)	6.4 (1.6)	38.8 (1.9)
Outer Flat	0.20 m	22.8 (2.0)	47.4 (3.5)	14.1 (2.1)	41.9 (1.7)
Crest	0.35 m	8.4 (1.0)	18.7 (1.1)	21.2 (2.0)	39.1 (1.8)
Slope	1.20 m	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

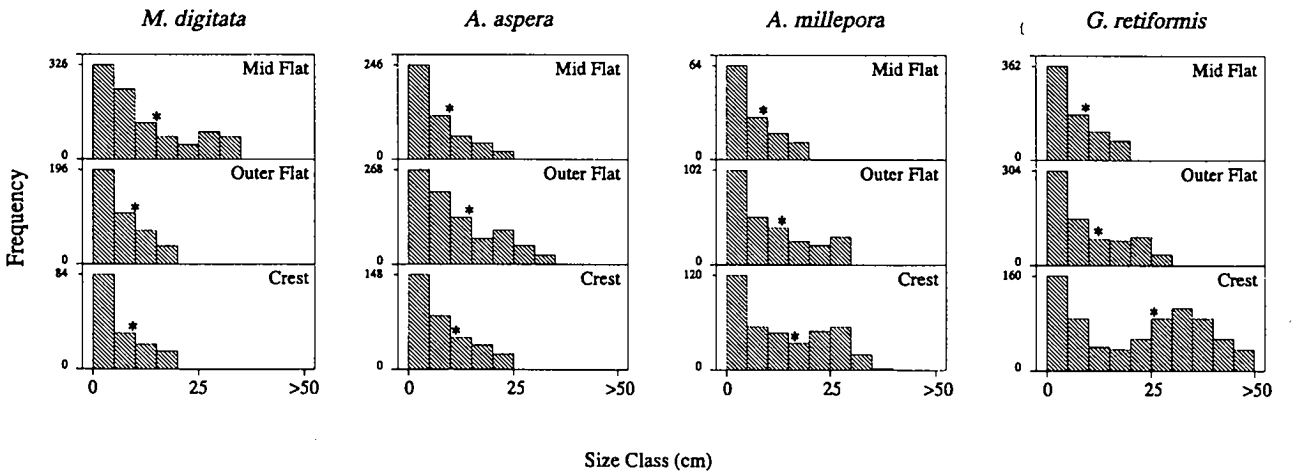

Figure 2.12 Size-frequency distributions for colonies of *M. digitata*, *A. aspera*, *A. millepora* and *G. retiformis*, as a function of reef zone and depth within Little Pioneer Bay. Total colony counts are for populations enclosed within 18, 10 x 1 m belt transects positioned within the inner reef flat at 0.05 m, the outer reef flat at 0.20 m and the crest at 0.35 m. Size-class intervals are based on 5 cm increments in mean diameter (MD), except for the largest size-class which includes all colonies > 50 cm in MD. Mean colony size is shown by * on each graph.

The population size-structure of all species was dominated by small colonies (0-5 cm in mean diameter) at each of the three depths examined (Fig. 2.12). However, there were significant differences in the size-distributions of each species between depths ($p < 0.05$, Fig. 2.12 & Tab. 2.3). Colonies of *M. digitata* had the smallest mean size, with a mean diameter of only 10.9 ± 1.7 cm and never exceeding 35 cm. In contrast, *G. retiformis* colonies were 50% larger (15.7 ± 2.0 cm) and could

exceed 50 cm in size. Species were ranked in mean size as: *G. retiformis* > *A. millepora* > *A. aspera* > *M. digitata*. The largest colonies of *M. digitata* were found at the shallowest reef zones and those of *A. aspera* on the outer flat (Fig. 2.12). Colonies of *A. millepora* and *G. retiformis* exhibited an increase in size with increasing depth, from the mid flat to the reef crest.

Table 2.3 Four-factor nested ANOVA to test for differences in the mean size of colonies between and among locations, depths, species and sites within Little Pioneer Bay. The analysis was performed on log (x + 0.001) transformed data. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Location (Lo)	1/2	0.85	NS
Depth (De)	4/2	43.30	$p < 0.01$
Species (Sp)	3/2	48.35	$p < 0.01$
Site	2/318	0.09	NS
Lo *De	4/2	0.26	NS
Lo*Sp	3/2	0.12	NS
De*Sp	12/2	6.79	$p < 0.05$
Lo*De*Sp	12/2	0.12	NS
Residual	318		
Total	359		

EFFECTS OF DEPTH CHANGES ON THE DYNAMICS OF CORAL POPULATIONS

This section addresses the effects of experimental depth changes on processes that affect colony abundance and colony size within Little Pioneer Bay. These broadly include colony survivorship, areal and linear growth, fission, tissue loss, bleaching and recovery, bioerosion and fecundity. The first part of this section examines survivorship of all four species in response to depth changes, while subsequent parts examine the effects of depth changes on the dynamics of the most useful target species, *A. aspera* and *A. millepora*.

COLONY SURVIVORSHIP

i) Experiment 1: 1 m Transplants of the Four Species

The survivorship of colonies in experiment 1 differed among species ($p < 0.001$) and treatments ($p < 0.001$, Tab. 2.4). Overall, 77% of the *in situ* controls, 49% of the handling controls, and 58% of the translocated controls survived after 1 year, while only 21% of the 1 m transplants were still alive. Most colonies of *G. retiformis* survived 1 year (84%), while less than half of the original

colonies of *M. digitata* were still alive (28%). *Montipora digitata* was the most sensitive species. Only 10% and 33% of the original colonies of this species survived 1 year in response to handling and to habitat relocation, respectively, and all of them died in response to a 1 m depth change (Fig. 2.13). In contrast, *G. retiformis* was the most robust, with all colonies exhibiting very high rates of survivorship (ca. 84%), irrespective of treatment. Colonies of *A. aspera* and *A. millepora*, like those of *M. digitata*, also exhibited 100% mortality in response to a 1 m depth change after 1 year, but they were relatively unaffected by handling and habitat relocation (Fig. 2.13).

Table 2.4 Log-linear analysis to test for survivorship differences between and among treatments, species and colony size-classes through time in experiment 1. The analysis was performed on log (x + 0.001) transformed data and excludes data for the *in situ* controls (the only colonies not placed on experimental racks). Chi-square values are shown for significant factors only. Non-significant factors were excluded from the model. NS = non significant.

Source of Variation	Degrees of Freedom	Chi- Square	Significance
Time (Ti)	6	180.60	$p < 0.001$
Treatment (Tmt)	2	206.42	$p < 0.001$
Ti*Tmt	12	169.22	$p < 0.001$
Species (Sp)	3	210.80	$p < 0.001$
Ti*Sp	18	234.93	$p < 0.001$
Tmt*Sp	6	355.18	$p < 0.001$
Ti*Tmt*Sp	36	-	NS
Size (Si)	2	10.60	$p < 0.01$
Ti*Si	12	-	NS
Tmt*Si	4	-	NS
Ti*Tmt*Si	24	-	NS
Sp*Si	6	-	NS
Ti*Sp*Si	36	-	NS
Tmt*Sp*Si	12	-	NS
Rack	1	-	NS
Likelihood Ratio	0	0.00	$p = 1.000$

Throughout experiment 1, rates of survivorship increased with increasing colony size ($p < 0.01$, Tab. 2.4 & Fig. 2.14). Overall, 38% of small colonies, 51% of medium sized colonies and 65% of large colonies survived after 1 year. This pattern of survivorship among colony size-classes did not differ through time, between species or among treatments (Tab. 2.4).

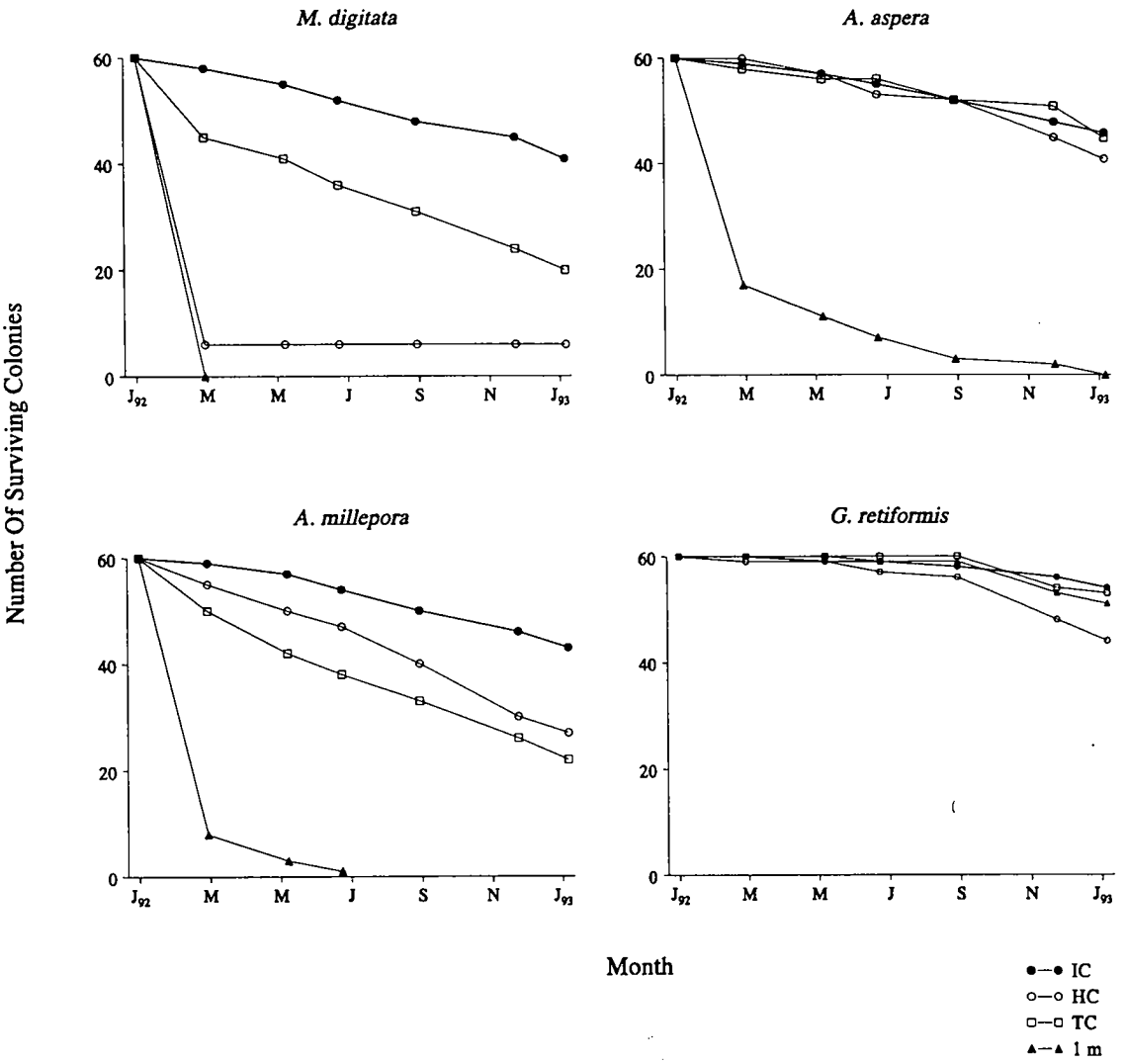

Figure 2.13 Survivorship curves for colonies as a function of treatment during experiment 1, from January 1992 to 1993. IC indicates the *in situ* controls; HC, the handling controls; TC, the translocated controls; and 1 m, the 1 m transplants.

Based on the survivorship of the four species, three target species were identified: *A. aspera*, *A. millepora*, and *G. retiformis*. *Acropora aspera* and *A. millepora* appeared to be the most useful species, because their rates of survivorship decreased significantly in response to the 1 m depth change but they were relatively unaffected by handling and habitat relocation (Fig. 2.13). Thus, they were used to examine of the effects of smaller depth changes of 25 cm and 50 cm on their population dynamics in experiment 2. *Goniastrea retiformis* exhibited no significant change in colony survivorship in response to a 1 m depth change (Fig. 2.13), and was the most robust experimental species. However, this species was not used in experiment 2 because it was unlikely to exhibit

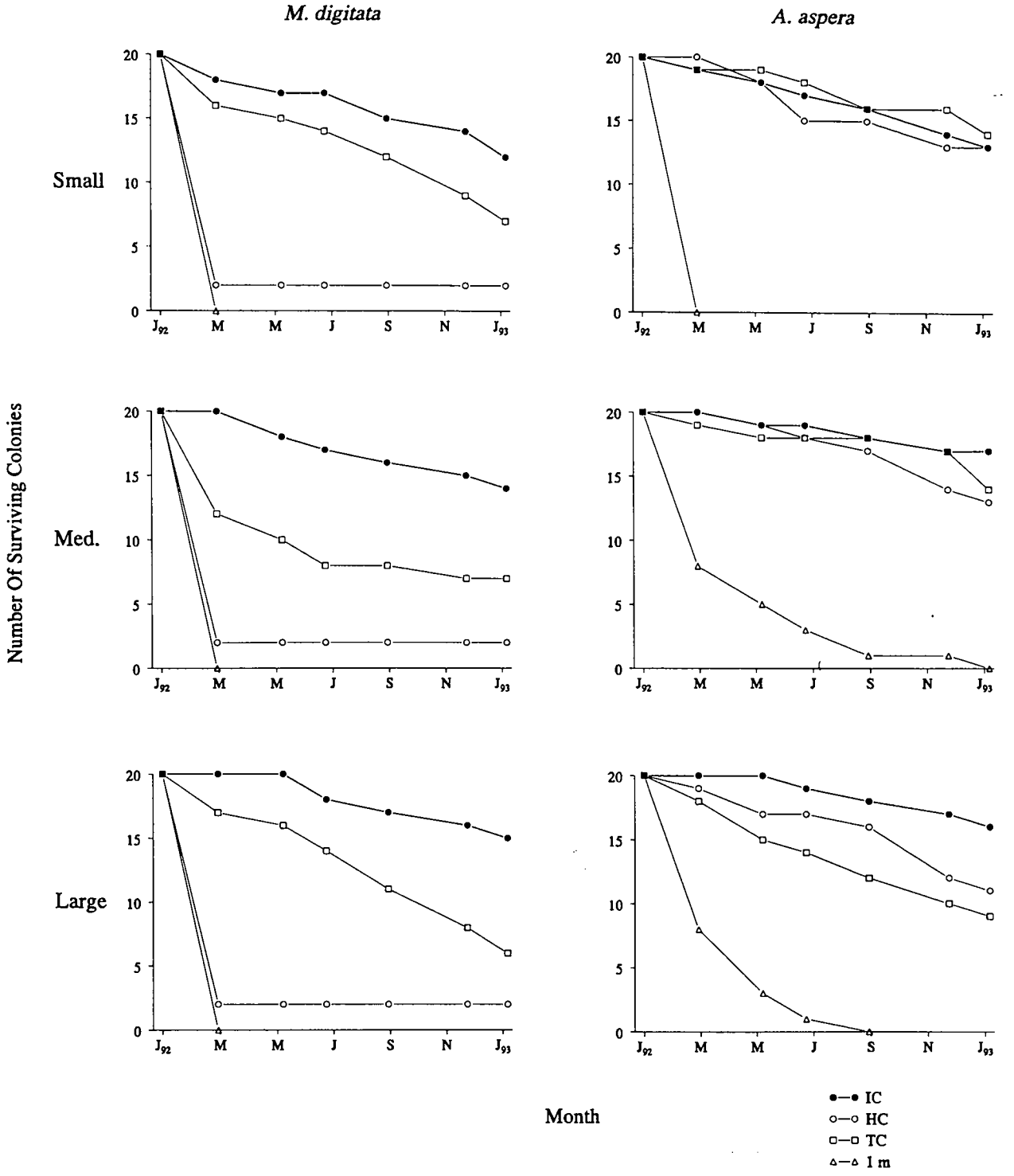

Figure 2.14 Survivorship curves for colonies as a function of treatment and size during experiment 1, from January 1992 to 1993. IC indicates the *in situ* controls; HC, the handling controls; TC, the translocated controls; and 1 m, the 1 m transplants. Colonies were assigned to three broad size classes based on their mean diameter (MD). Small colonies ranged from 2-5 cm in MD, medium ones from 6-8 cm in MD and large ones from 9-14 cm in MD.

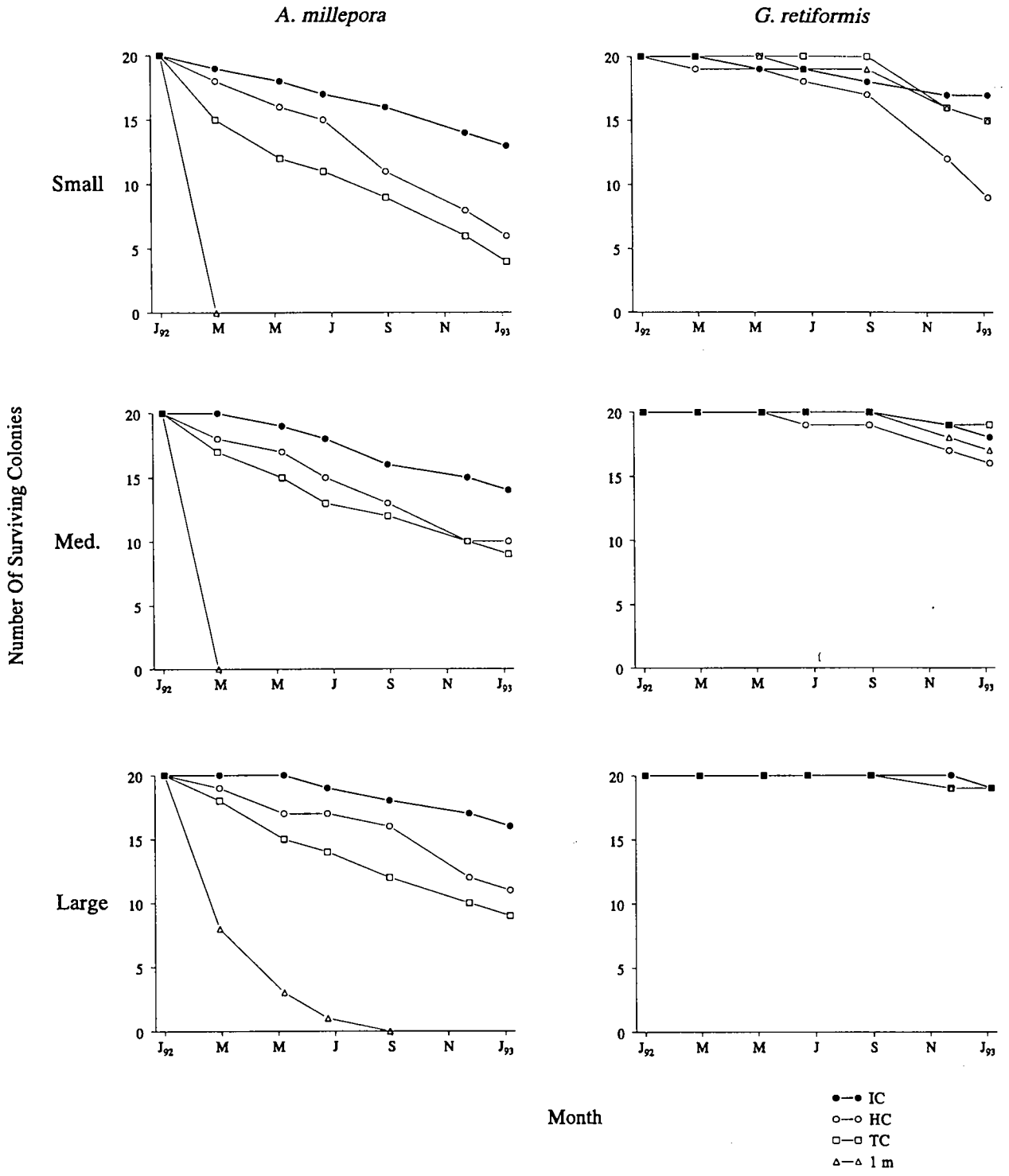

Figure 2.14 cont. Survivorship curves for colonies as a function of treatment and size during experiment 1, from January 1992 to 1993. IC indicates the *in situ* controls; HC, the handling controls; TC, the translocated controls; and 1 m, the 1 m transplants. Colonies were assigned to three broad size classes based on their mean diameter (MD). Small colonies ranged from 2-5 cm in MD, medium ones from 6-8 cm in MD and large ones from 9-14 cm in MD.

detectable responses to depth changes of less than 1 m. Instead, it was identified as a target species to further assess effects of a 1 m depth change on other demographic variables (See subsequent sections). *Montipora digitata* was not selected, as it was too sensitive to manipulation (Fig. 2.13).

ii) Experiment 2: 25 cm and 50 cm Transplants of *A. aspera* and *A. millepora*

Survivorship of *A. aspera* and *A. millepora* colonies in experiment 2 differed between treatments, even in response to very small changes in depth ($p < 0.001$, Tab. 2.5 & Fig. 2.15). The survivorship of colonies after 1 year was highest among the *in situ* controls (75%), handling controls (66%) and translocated controls (64%), slightly lower among the 25 cm transplants (53%), and lowest among the 50 cm transplants (30%). *Acropora millepora* exhibited significantly higher rates of mortality than *A. aspera*. After 2 months, 79% of *A. millepora* colonies survived, while 95% of *A. aspera* colonies were still alive ($p < 0.001$, Tab. 2.5). After 1 year, only 43% of the original colonies of *A. millepora* survived, compared to 73% of *A. aspera* colonies ($p < 0.001$, Tab. 2.5 & Fig. 2.15). For both species, mortality was highest in the deeper transplants. For *A.*

Table 2.5 Log-linear analysis to test for survivorship differences between and among treatments, species and colony size-classes through time in experiment 2. The analysis was performed on log (x + 0.001) transformed data and excludes data for the *in situ* controls. Chi-square values are shown for significant factors only. Non-significant factors were excluded from the model. NS = non significant.

Source of Variation	Degrees of Freedom	Chi- Square	Significance
Time (Ti)	6	22.60	$p < 0.001$
Treatment (Tmt)	3	63.45	$p < 0.001$
Ti*Tmt	18	-	NS
Species (Sp)	1	51.22	$p < 0.001$
Ti*Sp	6	38.68	$p < 0.001$
Tmt*Sp	3	-	NS
Ti*Tmt*Sp	18	-	NS
Size (Si)	2	32.60	$p < 0.001$
Ti*Si	12	23.45	$p < 0.05$
Tmt*Si	6	-	NS
Ti*Tmt*Si	36	-	NS
Sp*Si	2	10.99	$p < 0.01$
Ti*Sp*Si	12	-	NS
Tmt*Sp*Si	6	-	NS
Rack	1	-	NS
Likelihood Ratio	0	0.00	$p = 1.000$

aspera, the percentage survivorship among treatments after 1 year was ranked as: Translocated controls (85%) > *in situ* controls and handling controls (82%) >> 25 cm transplants (67%) >>> 50

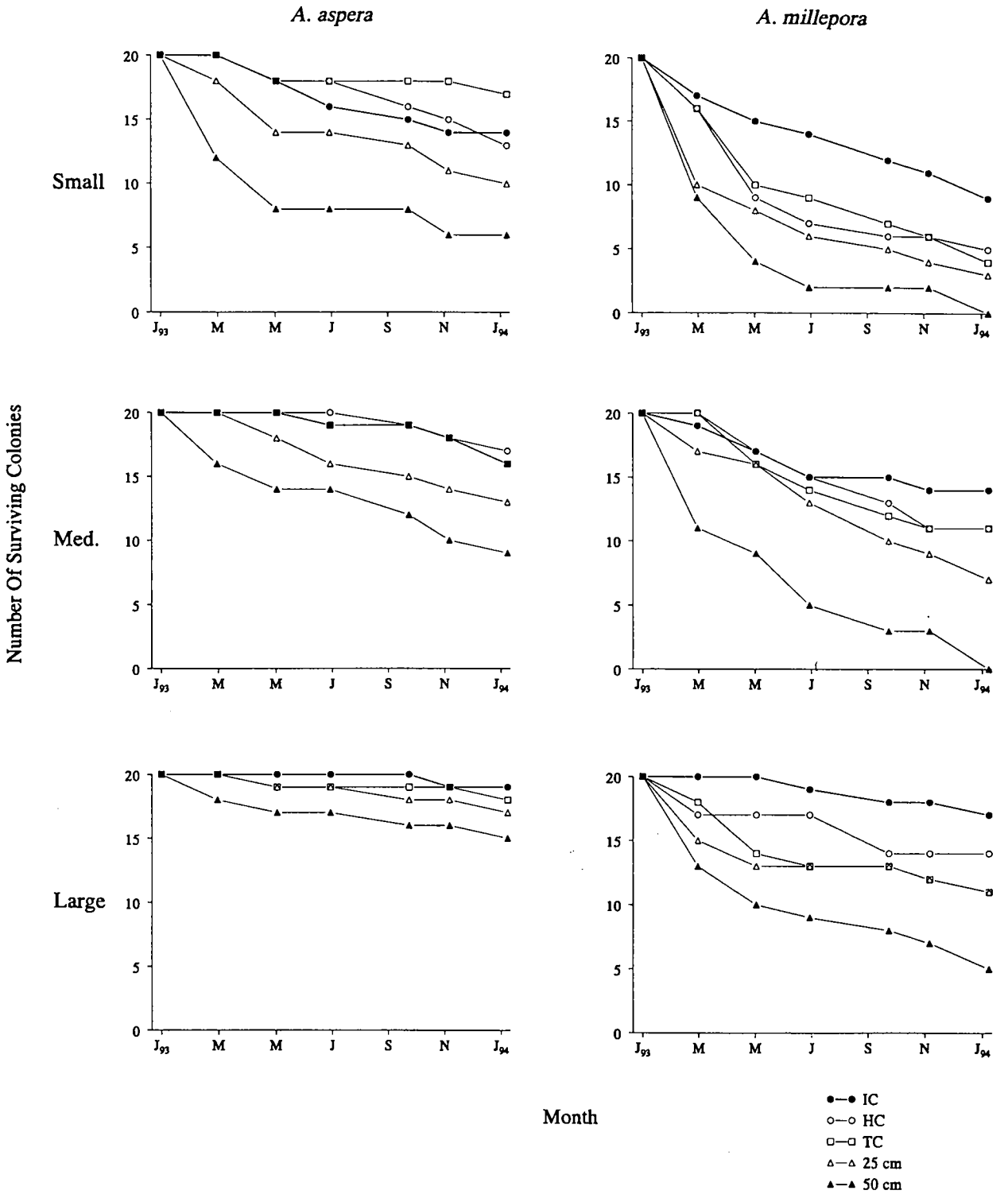

Figure 2.15 Survivorship curves for colonies as a function of treatment and size during experiment 2, from January 1993 to 1994. IC indicates the *in situ* controls; HC, the handling controls; TC, the translocated controls; 25 cm, the 25 cm transplants; and 50 cm, the 50 cm transplants. Colonies were assigned to three broad size classes based on their mean diameter (MD). Small colonies ranged from 2-5 cm in MD, medium ones from 6-8 cm in MD and large ones from 9-14 cm in MD.

cm transplants (52%). For *A. millepora*, the ranking was: *In situ* controls (67%) > handling controls (53%) > translocated controls (48%) >> 25 cm transplants (38%) >>> 50 cm transplants (8%).

Colony survivorship was highly correlated with colony size in experiment 2, with 43% of small colonies, 58% of medium sized colonies and 74% of large colonies left alive after 1 year ($p < 0.001$, Tab. 2.5 & Fig. 2.15). For all size-classes, the survivorship of *A. aspera* exceeded that of *A. millepora* ($p < 0.01$, Tab. 2.5). For *A. aspera*, the percentage survivorship after 1 year was ranked as: Large colonies (88%) > medium colonies (71%) > small colonies (61%). For *A. millepora*, it was: Large colonies (60%) > medium colonies (45%) > small colonies (24%).

iii) Experiment 3: *Stepwise* Depth Transplants of *A. aspera* and *A. millepora*

Survivorship of *A. aspera* and *A. millepora* colonies in experiment 3 was highest in the *in situ* and translocated controls (ca. 85% after 5 months) and significantly lower in deeper sites (ca. 59%, $p < 0.05$, Tab. 2.6 & Fig. 2.16). No significant difference was detected between the survivorship ofthe *stepwise* depth transplants and the direct depth transplant controls. The survivorship of all colonies among treatments after 5 months was ranked as: *In situ* controls (89%) > translocated controls (81%) >> *stepwise* depth transplants (61%) = direct depth transplant controls (58%).

Table 2.6 Log-linear analysis to test for survivorship differences between and among treatments, species and colony size-classes through time in experiment 3. The analysis was performed on log (x + 0.001) transformed data and excludes data for the *in situ* controls. Chi-square values are shown for significant factors only. Non-significant factors were excluded from the model. NS = non significant.

Source of Variation	Degrees of Freedom	Chi- Square	Significance
Time (Ti)	2	19.15	$p < 0.001$
Treatment (Tmt)	2	8.29	$p < 0.05$
Ti*Tmt	4	-	NS
Species (Sp)	1	69.51	$p < 0.001$
Ti*Sp	2	-	NS
Tmt*Sp	2	-	NS
Ti*Tmt*Sp	4	-	NS
Size (Si)	2	40.15	$p < 0.001$
Ti*Si	4	-	NS
Tmt*Si	4	-	NS
Ti*Tmt*Si	8	-	NS
Sp*Si	2	13.86	$p < 0.01$
Ti*Sp*Si	4	-	NS
Tmt*Sp*Si	4	-	NS
Rack	1	-	NS
Likelihood Ratio	0	0.00	$p = 1.000$

Species- and size-specific patterns of colony survivorship in experiment 3 were identical to experiment 2 (Tab. 2.6).

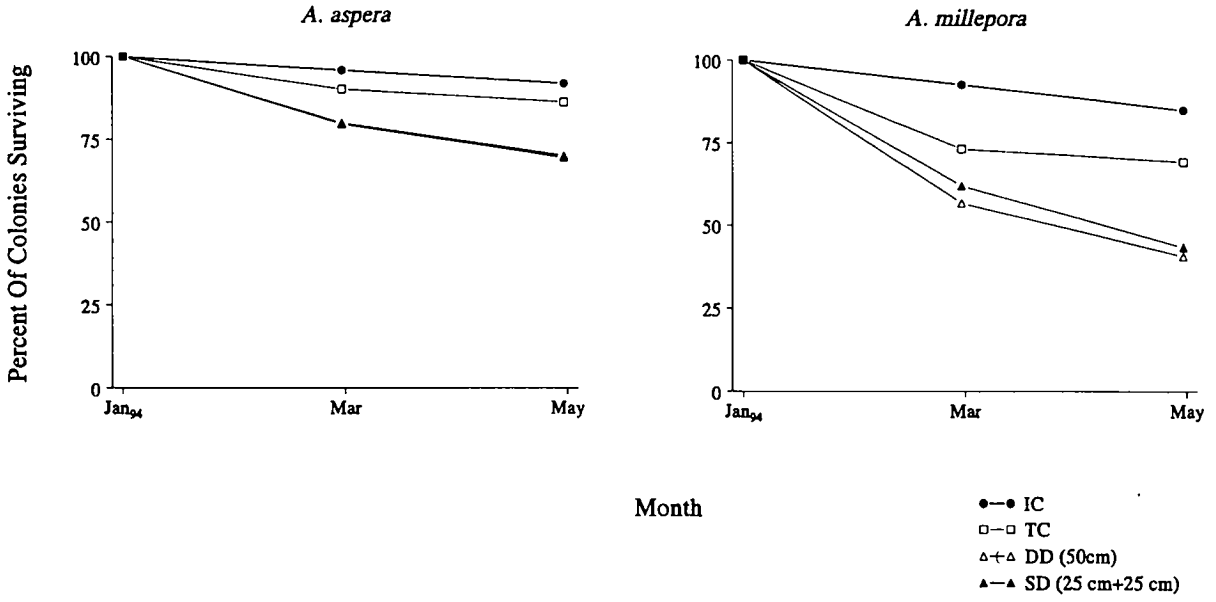

Figure 2.16 Survivorship curves for colonies as a function of treatment during experiment 3, from January 1994 to May 1994. IC, indicates the *in situ* controls; TC, the translocated controls; DD, the direct depth transplant controls; and SD, the *stepwise* depth transplants.

AREAL GROWTH RATES

i) Experiment 1: 1 m Transplants of *G. retiformis*

Although the survivorship of *G. retiformis* colonies did not differ among treatments in experiment 1, their final projected surface area did ($p < 0.001$, Tab. 2.7 & Fig. 2.17). Colonies in the *in situ* and handling controls and the 1 m transplants had shrunk on average by 31% relative to their initial size after 1 year, whereas the translocated controls had grown by 13%. The average shrinkage of colonies relative to their initial size was greatest in the 1 m transplants (ca. 39% after 1 year), lower in the handling controls (ca. 29%), and lowest in the *in situ* controls (ca. 25%). Throughout the experiment, small colonies shrank in area less than larger colonies, relative to their initial size ($p < 0.001$, Tab. 2.7 & Fig. 2.17). After 1 year, medium and large colonies had shrunk around 24%, whereas small colonies had shrunk 17%, and exhibited more variable rates of growth and shrinkage

among treatments. Most surviving medium and large colonies shrank in projected area relative to their initial size after 1 year, whereas the few surviving small colonies grew in area in the *in situ* and handling controls and the 1 m transplants. Throughout the experiment, changes in the surface area of all *G. retiformis* colonies were variable through time ($p < 0.001$, Tab. 2.7 & Fig. 2.17).

Table 2.7 Repeated measures ANOVA to test for differences in the projected surface area of *G. retiformis* colonies between and among treatments and colony size-classes through time in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	Pillai's F Statistic	Significance
Time (Ti)	6/108	12.71	$p < 0.001$
Treatment (Tmt)	2/113	13.30	$p < 0.001$
Rack	3/113	1.54	NS
Size (Si)	2/113	151.09	$p < 0.001$
Si*Rack	6/113	1.12	NS
Tmt*Si	4/113	0.59	NS
Ti *Tmt	12/218	3.91	$p < 0.001$
Ti*Rack	18/330	2.29	$p < 0.01$
Ti *Si	12/218	2.17	$p < 0.05$
Ti*Si*Rack	36/678	1.42	NS
Ti*Tmt*Si	24/444	1.19	NS
Residual	113		
Total	677		

ii) Experiment 2: 25 cm and 50 cm Transplants of *A. aspera* and *A. millepora*

The projected surface area of *A. aspera* and *A. millepora* colonies in experiment 2, did not differ as a result of a 25 cm depth change, relative to all of the controls, but did decrease significantly in response to a 50 cm depth change ($p < 0.001$, Tab. 2.8 & Fig. 2.17). All of the controls and the 25 cm transplants had grown on average by 59% relative to their initial size after 1 year, whereas the 50 cm transplants had shrunk by 18%. After 1 year, small colonies had grown six times more than larger colonies relative to their initial size, except in the 50 cm transplants ($p < 0.05$, Tab. 2.8 & Fig. 2.17). For the controls and the 25 cm transplants, small colonies had grown by 252% after 1 year, while all larger colonies had only grown by 37%. For the 50 cm transplants, small and medium sized colonies had shrunk proportionally more after 1 year (ca. 54%), than large colonies (ca. 30%).

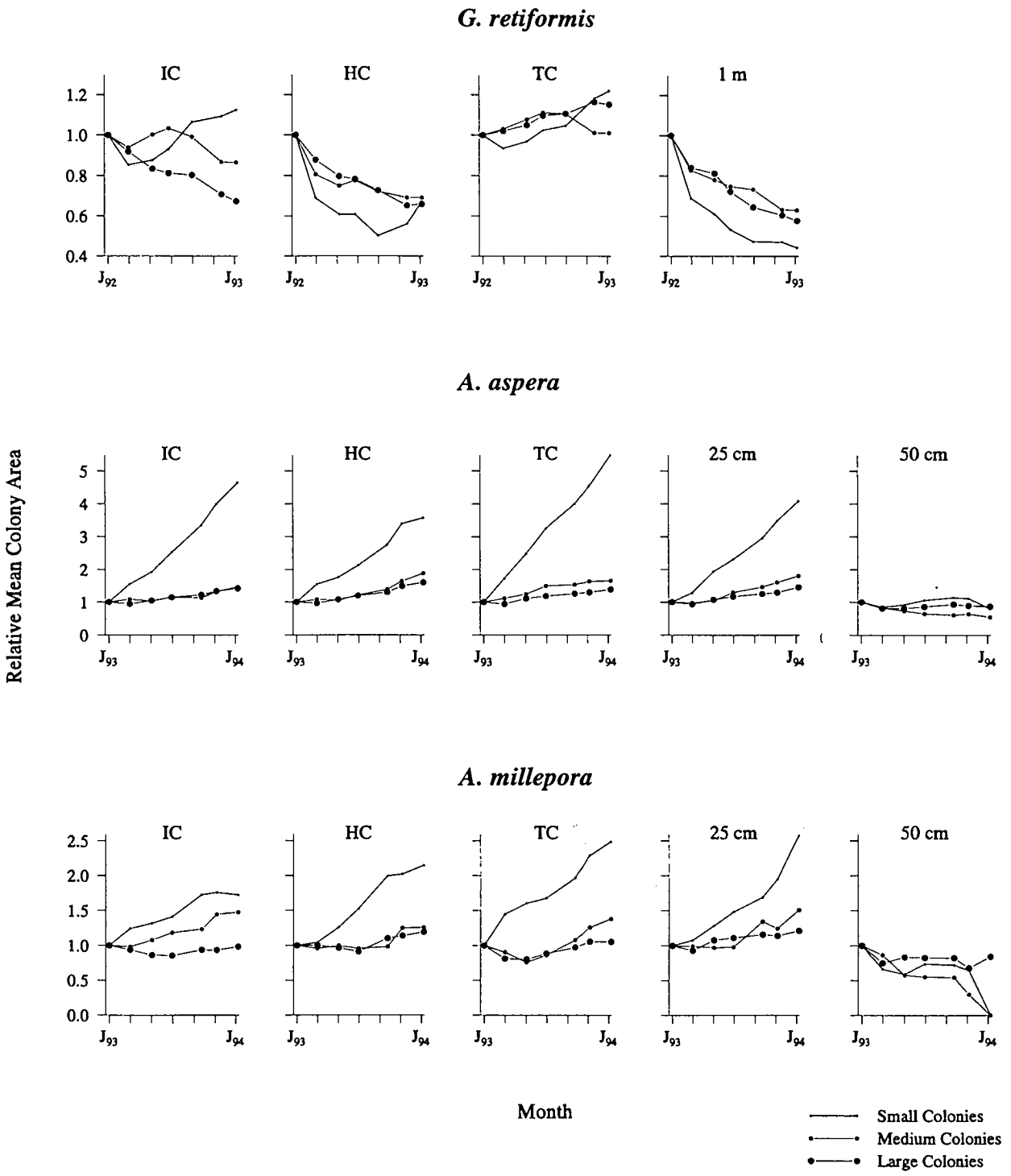

Figure 2.17 Relative mean area of surviving colonies as a function of treatment and size. 1.0 indicates no change in size. Means are expressed relative to the colony's initial size. See Figure 2.13 and 2.15 for treatment abbreviations; size class dimensions and sample sizes. Note differing Y-axes scales.

Table 2.8 Repeated measures ANOVA to test for differences in the projected area of *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes through time in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	Pillai's F Statistic	Significance
Time (Ti)	6/225	18.34	$p < 0.001$
Treatment (Tmt)	3/230	7.42	$p < 0.001$
Species (Sp)	1/230	15.00	$p < 0.001$
Tmt*Sp	3/230	1.27	NS
Rack	8/230	1.23	NS
Size (Si)	2/230	219.43	$p < 0.001$
Si*Rack	16/230	0.74	NS
Tmt*Si	6/230	1.73	NS
Sp*Si	2/230	2.46	NS
Tmt*Sp*Si	6/230	0.83	NS
Ti *Tmt	18/681	4.41	$p < 0.001$
Ti*Sp	6/225	7.33	$p < 0.001$
Ti*Tmt*Sp	18/681	2.66	$p < 0.001$
Ti*Rack	48/1380	1.24	NS
Ti *Si	12/452	7.34	$p < 0.001$
Ti*Si*Rack	96/1380	1.14	NS
Ti*Tmt*Si	36/1380	1.56	$p < 0.05$
Ti*Sp*Si	12/452	1.87	$p < 0.05$
Ti*Tmt*Sp*Si	36/1380	1.24	NS
Residual	230		
Total	1379		

Throughout the experiment, areal growth rates were higher in *A. aspera* than in *A. millepora* ($p < 0.001$, Tab. 2.8 & Fig. 2.17). After 1 year, colonies of *A. aspera* had grown by 61% relative to their initial size, whereas those of *A. millepora* had only grown by 33%. For both species, rates of relative growth in area were highly dependent on their initial size ($p < 0.001$, Tab. 2.8 & Fig. 2.17). Overall, small colonies grew six times more than larger colonies relative to their initial size, and rates of areal growth decreased with increasing colony size. After 1 year, small colonies had grown by 226%, whereas medium and large colonies had only grown by 39% and 15%, respectively.

LINEAR GROWTH RATES

i) Experiment 1: 1 m Transplants of *G. retiformis*

Annual rates of linear extension for *G. retiformis* were highly dependent on treatment ($p < 0.01$, Tab. 2.9 & Fig. 2.18). Compared to all of the controls, the 1 m transplants exhibited a 64% decrease in extension rates, and mean annual rates of extension among treatments were ranked as: Translocated controls (7.4 ± 0.2 mm) > *in situ* controls (6.3 ± 0.3 mm) > handling controls (5.3 ± 0.2

mm) >> 1 m transplants (2.3 ± 0.2 mm). Rates of annual linear extension in *G. retiformis* were independent of colony size (ie. within each treatment, all colonies exhibited similar rates of extension, irrespective of their size, p = NS, Tab. 2.9).

Table 2.9 Four-factor nested ANOVA to test for differences in the linear extension rates of *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on log (x + 0.001) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	92.50	$p < 0.01$
Size (Si)	2/2	6.91	NS
Rack	1/2	< 0.01	NS
Colony	2/202	< 0.01	NS
Tmt*Si	4/2	< 0.01	NS
Si*Rack	2/2	0.38	NS
Residual	202		
Total	215		

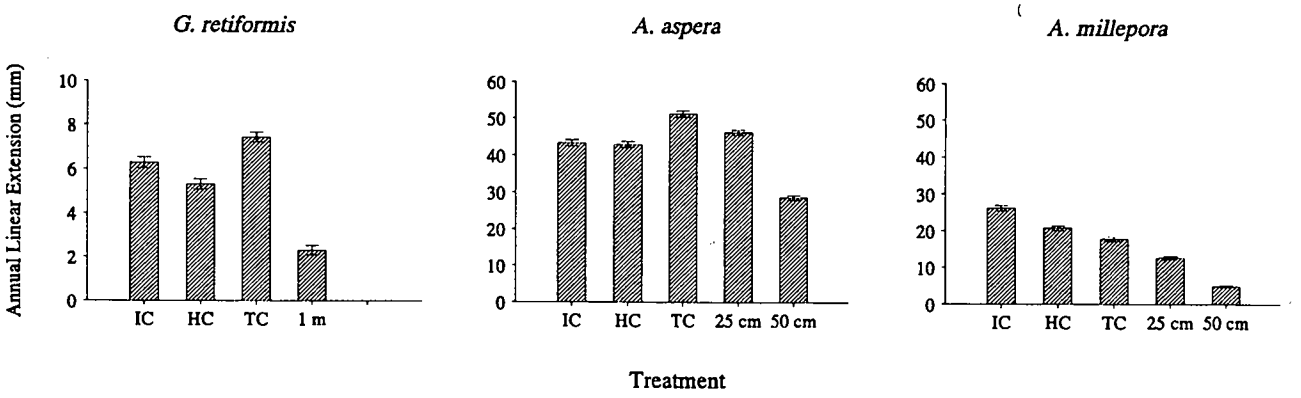

Figure 2.18 Annual linear extension of colonies (mean ± SE), as a function of treatment. Treatment abbreviations defined in Figure 2.14 and 2.15. Sample sizes range from 40 to 72 colonies.

ii) Experiment 2: 25 cm and 50 cm Transplants of *A. aspera* and *A. millepora*

Mean rates of annual linear extension in *A. aspera* (42.5 ± 0.5 mm) were twice that of *A. millepora* (17.6 ± 0.5 mm) ($p < 0.005$, Tab. 2.10 & Fig. 2.18). Rates of extension also differed significantly between treatments ($p < 0.05$, Tab. 2.10). In *A. aspera*, extension rates were highest in the translocated controls and, surprisingly, the 25 cm transplants. In *A. millepora*, they were highest in the *in situ* controls and decreased with increasing levels of manipulation. Rates of extension in both species were significantly lower in the deeper transplants, compared to all of the controls (Fig. 2.18). In *A. aspera*, mean rates of annual linear extension among treatments were ranked as:

Translocated controls (51.2 ± 0.8 mm) > 25 cm transplants (46.2 ± 0.6 mm) > *in situ* controls (43.3 ± 0.9 mm) = handling controls (42.9 ± 0.8 mm) >> 50 cm transplants (28.6 ± 0.6 mm). For *A. millepora*, the order was: *In situ* controls (26.2 ± 0.8 mm) > handling controls (20.8 ± 0.6 mm) > translocated controls (17.8 ± 0.6 mm) > 25 cm transplants (12.7 ± 0.4 mm) >> 50 cm transplants (5.0 ± 0.2 mm). In both species, rates of annual linear extension were independent of colony size, irrespective of treatment (p = NS, Tab. 2.10).

Table 2.10 Five-factor nested ANOVA to test for differences in the linear extension rates of *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 0.001) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/1	10.45	$p < 0.01$
Species (Sp)	1/1	85.21	$p < 0.005$
Size (Si)	2/2	1.44	NS
Rack	1/2	< 0.01	NS
Colony	2/515	0.02	NS
Tmt*Sp	3/1	0.03	$p < 0.05$
Tmt*Si	6/2	0.03	NS
Sp*Si	2/2	0.02	NS
Si*Rack	2/2	0.09	NS
Tmt*Sp*Si	6/2	0.03	NS
Residual	515		
Total	543		

COLONY FISSION

i) Experiment 1: 1 m Transplants of *G. retiformis*

The production of daughter colonies for *G. retiformis* differed significantly among treatments ($p < 0.05$, Tab. 2.11). Per capita rates of fission for *G. retiformis* were highest in the 1 m transplants and the handling controls and significantly lower in the translocated controls. Assuming that rates of fission over a 12 month period, represent the annual proportion of fission for a given species, the annual proportion of fission for parent colonies of *G. retiformis* (pre-fission genets) among treatments was ranked as: 1 m transplants (0.25) > handling controls (0.21) > *in situ* controls (0.15) > translocated controls (0.08). These findings were expected, since high rates of shrinkage in the handling controls and the 1 m transplants of *G. retiformis* (Fig. 2.17) are likely to coincide with high rates of fission and the production of daughter colonies. For *G. retiformis*, rates of fission among

treatments did not differ significantly through time (p = NS, Tab. 2.11). The mean number of daughter colonies (post-fission ramets) produced per fission event was similar among all treatments. Overall, *G. retiformis* produced an average of 2.3 ± 0.2 daughter colonies per fission event, of which 34% survived until the end of the experiment.

Table 2.11 Repeated measures ANOVA to test for differences in the total number of daughter colonies produced by *G. retiformis* between and among treatments and colony size-classes through time in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	Pillai's F Statistic	Significance
Time (Ti)	6/108	2.60	$p < 0.05$
Treatment (Tmt)	2/113	4.71	$p < 0.05$
Rack	3/113	2.35	NS
Size (Si)	2/113	3.18	$p < 0.05$
Si*Rack	6/113	0.47	NS
Tmt*Si	4/113	2.28	NS
Ti *Tmt	12/218	1.58	NS
Ti*Rack	18/330	1.44	NS
Ti *Si	12/218	1.86	$p < 0.05$
Ti*Si*Rack	36/678	0.90	NS
Ti*Tmt*Si	24/444	1.14	NS
Residual	113		
Total	677		

Rates of fission in *G. retiformis* were highest in large colonies and decreased with decreasing colony size ($p < 0.05$, Tab. 2.11 & Tab. 2.12). The mean number of daughter colonies produced per fission event was also greatest in large colonies. However, the daughter colonies produced by medium sized colonies of *G. retiformis* had a higher percentage survival after 12 months (53%), than those produced by small or large colonies (ca. 23%, Tab. 2.12). Throughout the experiment, daughter colony production increased with time, particularly in large colonies ($p < 0.05$, Tab. 2.11)

ii) Experiment 2: 25 cm and 50 cm Transplants of *A. aspera* and *A. millepora*

For *A. aspera* and *A. millepora*, per capita rates of fission appeared lower in the deeper sites, relative to the controls, but this trend was not statistically significant (ie. there were no between treatment effects, p = NS, Tab. 2.13). The mean annual proportion of fission for parent colonies of *A. aspera* among treatments was ranked as: In situ controls (0.47) > handling controls (0.43) > translocated controls (0.41) > 50 cm transplants (0.34) > 25 cm transplants (0.27). For *A. millepora*, it was: Translocated controls (0.17) > *in situ* and handling controls (0.10) > 50 cm transplants (0.07)

> 25 cm transplants (0.00).

Table 2.12 Annual production of daughter colonies (post-fission ramets) by *G. retiformis*, *A. aspera* and *A. millepora*, as a function of their size. The annual proportion of fission was calculated by dividing the number of parent colonies (pre-fission genets) which produced ramets by the total number of parent colonies. The mean number of ramets produced in 1 year (± SE) was determined only from parent colonies which produced ramets, and an estimate of the annual % survival of ramets was calculated by dividing the number of surviving ramets at the last census interval by the total number (N) produced after 12 months. Size-class dimensions are defined in Figure 2.15.

Species	Colony Size:			All Size-Classes
	Small	Medium	Large	
G. retiformis				
Annual Proportion of Fission	0.13	0.18	0.23	0.18
No. Ramets Produced in 1 year	1.20 (0.13)	2.57 (0.39)	2.61 (0.27)	2.26 (0.19)
Annual % Survival of Ramets	25	53	21	34
N =	12	37	33	98
A. aspera				
Annual Proportion of Fission	0.21	0.39	0.42	0.34
No. Ramets Produced in 1 year	2.14 (0.08)	2.34 (0.08)	2.92 (0.09)	2.54 (0.06)
Annual % Survival of Ramets	80	77	84	81
N =	45	91	123	259
A. millepora				
Annual Proportion of Fission	0.02	0.06	0.12	0.07
No. Ramets Produced in 1 year	2.00 (0.00)	2.17 (0.17)	2.17 (0.11)	2.15 (0.08)
Annual % Survival of Ramets	0	15	38	28
N =	4	13	26	43

Overall rates of fission differed significantly between species, with colonies of *A. aspera* being four times more likely to undergo fission than *A. millepora* ($p < 0.01$, Tab. 2.13). For both species, the mean number of daughter colonies produced per fission event was similar (with 2.5 ± 0.1 produced by *A. aspera* and 2.2 ± 0.1 produced by *A. millepora*). However, the estimated annual percentage survival of their daughter colonies differed. Overall, 81% of the daughter colonies produced by *A. aspera* were alive after 1 year, compared with only 28% for *A. millepora* had survived (Tab. 2.12). For *A. aspera*, rates of fission and daughter colony production were relatively similar between treatments. However, for *A. millepora*, no daughter colonies were produced by the 25 cm

transplants and none of those produced by the 50 cm transplants survived after 1 year.

Throughout the experiment, rates of fission in both species were greatest in large colonies, as expected ($p < 0.05$, Tab. 2.13 & Tab. 2.12). However, the size-specific survivorship of daughter colonies differed among species. All daughter colonies produced by small, medium and large colonies of *A. aspera* exhibited high rates of survivorship after 1 year (ca. 83%), while only those produced by medium and large colonies of *A. millepora* survived (Tab. 2.12).

Table 2.13 Repeated measures ANOVA to test for differences in the total number of daughter colonies produced by *A. aspera* and *A. millepora* between and among treatments, species and colony size-classes through time in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	Pillai's F Statistic	Significance
Time (Ti)	6/225	7.43	$p < 0.001$
Treatment (Tmt)	3/230	1.37	NS
Species (Sp)	1/230	9.64	$p < 0.01$
Tmt*Sp	3/230	0.63	NS
Rack	8/230	0.17	NS
Size (Si)	2/230	3.80	$p < 0.05$
Si*Rack	16/230	0.62	NS
Tmt*Si	6/230	0.37	NS
Sp*Si	2/230	1.30	NS
Tmt*Sp*Si	6/230	0.96	NS
Ti *Tmt	18/681	1.25	NS
Ti*Sp	6/225	4.50	$p < 0.001$
Ti*Tmt*Sp	18/681	1.87	$p < 0.05$
Ti*Rack	48/1380	0.59	NS
Ti *Si	12/452	1.27	NS
Ti*Si*Rack	96/1380	0.75	NS
Ti*Tmt*Si	36/1380	0.72	NS
Ti*Sp*Si	12/452	1.77	NS
Ti*Tmt*Sp*Si	36/1380	0.78	NS
Residual	230		
Total	1379		

COLONY TISSUE LOSS

Most colonies of each of the three target species lost live tissue at some time regardless of treatment, even if they had survived throughout the entire study. Because corals are clonal organisms composed of replicated polyps, a proportion of the polyps may die without causing the death of the entire colony.

i) Experiment 1: 1 m Transplants of *G. retiformis*

Total tissue loss in colonies of *G. retiformis* over 1 year was significantly higher in the *in situ* and handling controls and the 1 m transplants, compared to the translocated controls ($p < 0.001$, Tab. 2.14). After 1 year, the percentage of tissue dying among treatments was ranked as: Handling controls (57%) > 1 m transplants (50%) > *in situ* controls (48%) >> translocated controls (24%). The calculated time required for *G. retiformis* colonies to lose an amount of tissue equivalent to their areal cover at the beginning of experiment 1 varied from 1.75 years in the handling controls to 4.17 years in the translocated controls (Tab. 2.15). Net surviving tissue area in all colonies of *G. retiformis* decreased through time ($p < 0.001$, Tab. 2.14), irrespective of their treatment and inspite of some regeneration.

Table 2.14 Repeated measures ANOVA to test for differences in the percentage of tissue lost by *G. retiformis* colonies between and among treatments and colony size-classes through time in experiment 1. The analysis was performed on log (x + 0.01) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	Pillai's F Statistic	Significance
Time (Ti)	6/108	80.06	$p < 0.001$
Treatment (Tmt)	2/113	42.99	$p < 0.001$
Rack	3/113	4.82	$p < 0.01$
Size (Si)	2/113	8.96	$p < 0.001$
Si*Rack	6/113	0.55	NS
Tmt*Si	4/113	2.42	NS
Ti *Tmt	12/218	6.91	$p < 0.001$
Ti*Rack	18/330	2.94	$p < 0.001$
Ti *Si	12/218	2.64	$p < 0.01$
Ti*Si*Rack	36/678	1.12	NS
Ti*Tmt*Si	24/444	1.19	NS
Residual	113		
Total	677		

Throughout the experiment, the proportion of tissue lost in colonies of *G. retiformis* was inversely related to colony size ($p < 0.001$, Tab. 2.14). The time required for total tissue turnover among size-classes of *G. retiformis* varied from 1.85 years in small colonies to 2.44 years in large colonies (Tab. 2.16). Size-specific patterns of tissue loss for *G. retiformis* did not vary significantly among treatments (p = NS, Tab. 2.14).

Table 2.15 Estimates of the number of years required for total tissue turnover (= the death of tissue area equal to 100% of the original live are) among colonies, as a function of treatment. The total area of live tissue present at the beginning of the experiment and the area of tissue dying over 1 year are shown for each species, as a basis for calculating the percentage of tissue dying and tissue turnover times. Treatment abbreviations are defined in Figure 2.13 and 2.15.

Species	Treatment:					
	IC	HC	TC	25 cm	50 cm	1 m
G. retiformis						
Total Area in Jan $_{92}$ (10^3 cm^2)	2.56	2.60	2.61	--	--	2.58
Area of Tissue Dying Jan $_{92\text{-}93}$ (10^3 cm^2)	1.22	1.47	0.62	--	--	1.29
Percent Dying	48	57	24	--	--	50
Turnover Time (yr)	2.08	1.75	4.17	--	--	2.00
A. aspera						
Total Area in Jan $_{93}$ (10^3 cm^2)	2.65	2.63	2.60	2.52	2.56	--
Area of Tissue Dying Jan $_{93\text{-}94}$ (10^3 cm^2)	1.64	1.44	1.75	1.34	1.98	--
Percent Dying	62	55	67	53	77	--
Turnover Time (yr)	1.61	1.82	1.49	1.86	1.30	--
A. millepora						
Total Area in Jan $_{93}$ (10^3 cm^2)	2.72	2.72	2.61	2.61	2.94	--
Area of Tissue Dying Jan $_{93\text{-}94}$ (10^3 cm^2)	1.46	1.54	2.26	1.85	2.67	--
Percent Dying	54	57	87	71	91	--
Turnover Time (yr)	1.85	1.75	1.15	1.41	1.10	--

ii) Experiment 2: 25 cm and 50 cm Transplants of *A. aspera* and *A. millepora*

The amount of tissue lost through whole and partial mortality in colonies of *A. aspera* and *A. millepora* over 1 year varied among treatments ($p < 0.001$, Tab. 2.17). For both species, the percentage of the initial tissue area lost was highest in the translocated controls and the 50 cm transplants (ca. 81% after 1 year) and lowest in the *in situ* and handling controls and the 25 cm transplants (ca. 59%). After 1 year, the *in situ* and handling controls of both species had a similar percentage of tissue loss (ca. 57%), whereas the 25 cm transplants, translocated controls and 50 cm transplants of *A. millepora* exhibited a significantly higher percentage of tissue loss than those of *A. aspera* (Tab. 2.15). This was partly because amounts of tissue loss between species varied through time ($p < 0.05$, Tab. 2.17), with the highest extent of tissue loss evident among colonies of *A.*

millepora, within the first 6 months of the experiment. The time required for total tissue turnover in *A. aspera* ranged from 1.30 years in the 50 cm transplants to 1.89 years in the translocated controls, while in *A. millepora* values ranged from 1.10 years in the 50 cm transplants to 1.85 years in the *in situ* controls. These indicate rapid declines; unsustainable losses.

Table 2.16 Estimates of the number of years required for total tissue turnover (= the death of tissue area equal to 100% of the original live area) among colonies, as a function of their size and for all size-classes combined. Data is presented in the same format as used in Table 2.15. Size-class dimensions are defined in Figure 2.15.

Species	Colony Size:			All Size-Classes
	Small	Medium	Large	
G. retiformis				
Total Area in Jan $_{92}$ (10^3 cm^2)	0.91	3.27	6.16	10.34
Area of Tissue Dying Jan $_{92\text{-}93}$ (10^3 cm^2)	0.49	1.57	2.55	4.60
Percent Dying	54	48	41	44
Turnover Time (yr)	1.85	2.08	2.44	2.27
A. aspera				
Total Area in Jan $_{93}$ (10^3 cm^2)	1.07	4.00	7.90	12.97
Area of Tissue Dying Jan $_{93\text{-}94}$ (10^3 cm^2)	1.28	3.22	3.72	8.22
Percent Dying	120 *	81	47	63
Turnover Time (yr)	0.83	1.23	2.13	1.59
A. millepora				
Total Area in Jan $_{93}$ (10^3 cm^2)	0.99	3.82	8.78	13.60
Area of Tissue Dying Jan $_{93\text{-}94}$ (10^3 cm^2)	1.31	2.88	5.63	9.82
Percent Dying	132 *	75	64	72
Turnover Time (yr)	0.76	1.33	1.56	1.39

* As a result of rapid growth and possibly the regeneration of damaged tissue, the area of tissue death in small colonies of *A. aspera* and *A. millepora* exceeded the original amount present.

The proportion of tissue lost in colonies of *A. aspera* and *A. millepora* over 1 year differed in each of the three size classes ($p < 0.05$, Tab. 2.17). The time required for total tissue turnover in small colonies of both species was less than a year, while total tissue turnover in large colonies of both species required in excess of a year and a half (Tab. 2.16).

Table 2.17 Repeated measures ANOVA to test for differences in the percentage of tissue lost by *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes through time in experiment 2. The analysis was performed on log (x + 0.01) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	Pillai's F Statistic	Significance
Time (Ti)	6/225	152.00	$p < 0.001$
Treatment (Tmt)	3/230	20.70	$p < 0.001$
Species (Sp)	1/230	0.06	NS
Tmt*Sp	3/230	3.60	$p < 0.05$
Rack	8/230	1.78	NS
Size (Si)	2/230	3.27	$p < 0.05$
Si*Rack	16/230	0.60	NS
Tmt*Si	6/230	1.95	NS
Sp*Si	2/230	0.40	NS
Tmt*Sp*Si	6/230	0.83	NS
Ti *Tmt	18/681	5.18	$p < 0.001$
Ti*Sp	6/225	2.51	$p < 0.05$
Ti*Tmt*Sp	18/681	2.20	$p < 0.01$
Ti*Rack	48/1380	1.22	NS
Ti *Si	12/452	1.79	$p < 0.05$
Ti*Si*Rack	96/1380	0.94	NS
Ti*Tmt*Si	36/1380	1.76	$p < 0.01$
Ti*Sp*Si	12/452	1.26	NS
Ti*Tmt*Sp*Si	36/1380	1.57	$p < 0.05$
Residual	230		
Total	1379		

BLEACHING AND RECOVERY

Several colonies of all three species lost normal pigmentation (ie. they bleached) to some extent during summer (between November to March), coincident with extreme seawater temperatures and monsoonal rains. These bleaching events affected both manipulated and *in situ* control colonies.

i) Experiment 1: 1 m Transplants of *G. retiformis*

During experiment 1, 23% of all *G. retiformis* colonies (56 out of a total of 239), bleached between January and March of 1992, coincident with seawater temperatures ranging from 20.4 to 32.4°C (Fig. 2.19). The frequency of bleaching recorded in March differed among treatments ($p < 0.001$, Tab. 2.18). On average, 31% of the controls bleached, while none of the 1 m transplants were affected. The average amount of live tissue bleached per affected colony did not differ among any of the controls (ca. 22%, Tab. 2.19). Bleaching in the reef flat controls was coincident with the seawater temperatures noted above, while for the 1 m transplants, temperatures ranged from 25.6 to 28.3°C (Fig. 2.19).

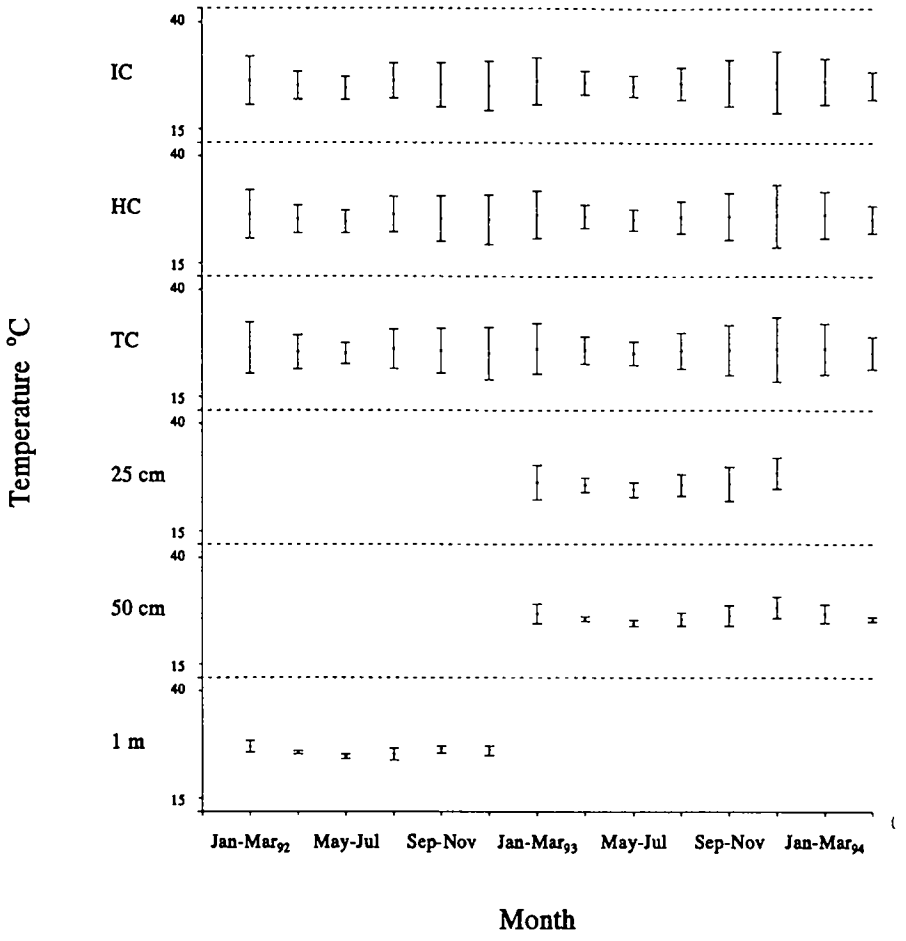

Figure 2.19 Maximum and minimum temperatures of each treatment, for each census interval, from January 1992 to 1993 (the duration of exp. 1), January 1993 to 1994 (exp. 2) and from January 1994 to May 1994 (exp. 3). Treatment abbreviations are defined in Figure 2.13 and 2.15.

Table 2.18 Repeated measures ANOVA to test for differences in the percentage of bleaching in colonies of *G. retiformis* between and among treatments and colony size-classes through time in experiment 1. The analysis was performed on log (x + 0.01) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	Pillai's F Statistic	Significance
Time (Ti)	6/108	36.96	$p < 0.001$
Treatment (Tmt)	2/113	11.75	$p < 0.001$
Rack	3/113	1.23	NS
Size (Si)	2/113	3.06	NS
Si*Rack	6/113	0.86	NS
Tmt*Si	4/113	1.05	NS
Ti *Tmt	12/218	11.75	$p < 0.001$
Ti*Rack	18/330	1.23	NS
Ti *Si	12/218	3.06	NS
Ti*Si*Rack	36/678	0.86	NS
Ti*Tmt*Si	24/444	1.05	NS
Residual	113		
Total	677		

Table 2.19 Bleaching and fate of colonies as a function of treatment. The proportion of colonies bleaching and the percentage of tissue per colony affected by bleaching (bleached colonies only), are shown for each species. Colonies were then assigned to one of two categories, bleached (BC) or unbleached (UC). Ten months after the bleaching event, the percentage tissue loss and percentage survival were quantified for the bleached and unbleached categories. The effect of bleaching on subsequent tissue loss and colony survival was determined with log-linear analyses. Treatment abbreviations are defined in Figure 2.13 and 2.15. Data are means.

Species	Treatment:					
	IC	HC	TC	25 cm	50 cm	1 m
G. retiformis						
Proportion of colonies Bleaching in Mar_{92}	0.35	0.2	0.38	--	--	0.00
% of Live Tissue Bleached / Colony in Mar_{92}	19	23	23	--	--	0
% Tissue Loss for BC Mar_{92} - Jan_{93}	37	39	19	--	--	--
% Tissue Loss for UC Mar_{92} - Jan_{93}	55	62	29	--	--	50
% Survivorship of BC Mar_{92} - Jan_{93}	90	92	100	--	--	--
% Survivorship of UC Mar_{92} - Jan_{93}	90	69	81	--	--	85
A. aspera						
Proportion of colonies Bleaching in Mar_{93}	0.78	0.78	0.83	0.93	0.28	--
% of Live Tissue Bleached / Colony in Mar_{93}	37	31	48	20	17	--
% Tissue Loss for BC Mar_{93} - Jan_{94}	58	49	68	51	59	--
% Tissue Loss for UC Mar_{93} - Jan_{94}	76	74	63	129*	90	--
% Survivorship of BC Mar_{93} - Jan_{94}	79	81	88	68	76	--
% Survivorship of UC Mar_{93} - Jan_{94}	92	85	70	50	40	--
A. millepora						
Proportion of colonies Bleaching in Mar_{93}	0.6	0.57	0.35	0.32	0.02	--
% of Live Tissue Bleached / Colony in Mar_{93}	62	68	42	10	14	--
% Tissue Loss for BC Mar_{93} - Jan_{94}	46	45	80	52	29	--
% Tissue Loss for UC Mar_{93} - Jan_{94}	72	80	90	81	92	--
% Survivorship of BC Mar_{93} - Jan_{94}	75	65	52	63	100	--
% Survivorship of UC Mar_{93} - Jan_{94}	54	31	38	22	7	--

* As a result of rapid growth and possibly the regeneration of damaged tissue, the area of tissue death in unbleached 25 cm transplants of *A. aspera* exceeded the original amount present.

Log-linear analysis of the fate of live colonies subsequent to bleaching, revealed that amounts of tissue loss and colony survivorship after 10 months did not differ significantly among bleached or unbleached colonies (Tab. 2.19 & p = NS, Tab. 2.20). This indicates that colonies of *G. retiformis* may readily recovery from partial bleaching.

The frequency and extent of bleaching in the controls of *G. retiformis* did not differ significantly between size-classes (p = NS, Tab. 2.18). Around 23% of all live colonies in each size-class bleached), and a similar percentage of live tissue bleached per colony, irrespective of their size (ca. 29%). Analysis of the fate of colonies subsequent to bleaching also failed to reveal any size-specific pattern of tissue loss or mortality in bleached and unbleached colonies after a 10 month period (Tab. 2.20).

Table 2.20 Log-linear analysis of the bleaching effects on the fate (tissue loss and survival) of *G. retiformis* colonies, 10 months after bleaching in experiment 1. The variable Bleaching, Bl, represents data for both bleached and unbleached colonies. All other variables are defined in Table 2.18. The percentage of tissue lost in colonies and their percentage survival were both analysed separated and each analysis included data from all treatments. NS = non significant.

Fate	Interactions	Degrees of Freedom	Chi-Square	Significance
% Tissue Lost	Bl	1	0.36	NS
	Tmt*Bl	3	0.17	NS
	Si*Bl	2	0.12	NS
	Tmt*Si*Bl	6	0.07	NS
% Survival	Bl	1	2.45	NS
	Tmt*Bl	3	1.92	NS
	Si*Bl	2	0.45	NS
	Tmt*Si*Bl	6	0.13	NS
	Likelihood Ratio	0	0.00	p = 1.000

ii) Experiment 2: 25 cm and 50 cm Transplants of *A. aspera* and *A. millepora*

During experiment 2, colonies of *A. aspera* and *A. millepora* bleached twice, between January and March of 1993 (coincident with a wide seawater temperature range of 20.3 to 32.2°C), and between November 1993 and January 1994 (with temperatures of 18.5 to 33.6°C, Fig. 2.19). The frequency of bleaching was very similar for both bleaching events. Overall, 63% bleached in the first bleaching event (328 colonies out of a total of 522), and 72% in the second (246 colonies out of 341). Around 30% of live tissue per colony bleached in the first event and 35% in the second. Only data collected from the first bleaching event in March 1993 is presented below and used to assess differences in the fate of bleached and unbleached colonies of *A. aspera* and *A. millepora* through

time.

The frequency of bleaching in both *A. aspera* and *A. millepora* in March differed among treatments ($p < 0.001$, Tab. 2.21). For both species combined, 65% of the *in situ* controls, handling controls, translocated controls and 25 cm transplants bleached, while only 15% of the 50 cm transplants were affected. The percentage of tissue bleached was significantly higher in the controls (ca. 47%) than in the 25 cm and 50 cm transplants (ca. 16%). Bleaching in the controls coincided with seawater temperatures ranging from 20.3 to 32.2°C, while bleaching in the 25 cm and 50 cm transplants occurred with temperatures from 22.4 to 30.4°C and 24.6 to 29.2°C, respectively (Fig. 2.19).

Bleached and unbleached colonies in experiment 2 exhibited striking differences in amounts of tissue loss ($p < 0.001$) and colony survivorship ($p < 0.001$), irrespective of treatment (Tab. 2.22). Typically, colonies which did not bleach at the start of the experiment experienced higher amounts of tissue loss and lower rates of survivorship after 10 months, in contrast to those which bleached (Tab. 2.19). This historical effect of non-bleaching was most evident in the 25 cm and 50 cm transplants ($p < 0.001$, for tissue loss and survivorship data, Tab. 2.22). This suggests that colonies of *A. aspera* and *A. millepora* may do better after recovering from partial bleaching.

Striking differences were also evident in the frequency of bleaching between colonies of *A. aspera* and *A. millepora* ($p < 0.001$, Tab. 2.21). Twice as many colonies of *A. aspera* bleached in March (ca. 72%), compared to those of *A. millepora* (ca. 37%). A similar amount of live tissue per colony was bleached in both species (ca. 30%) during the event. In both species, rates of tissue loss and colony mortality were generally highest among unbleached colonies, particularly among the 25 cm and 50 cm transplants (Tab. 2.19). For all treatments combined, patterns of tissue loss between unbleached and bleached colonies were similar between species (p = NS, Tab. 2.22). Around 85% of tissue died in unbleached colonies of both species after 10 months, while bleached colonies of both species only lost 54% (Tab. 2.19). In contrast, patterns of colony survivorship between unbleached and bleached colonies differed between species ($p < 0.001$, Tab. 2.22). Bleached colonies of both species exhibited similar rates of survivorship (78% for colonies of *A. aspera* and 71% for those of *A. millepora* after 10 months), and unbleached colonies of *A. millepora* exhibited significantly lower

rates of survivorship (30%) than unbleached colonies of *A. aspera* (67%).

Table 2.21 Repeated measures ANOVA to test for differences in the percentage of bleaching in colonies of *A. aspera* and *A. millepora* between and among treatments, species and colony size-classes through time in experiment 2. The analysis was performed on log (x + 0.01) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	Pillai's F Statistic	Significance
Time (Ti)	6/225	214.05	$p < 0.001$
Treatment (Tmt)	3/230	15.00	$p < 0.001$
Species (Sp)	1/230	34.05	$p < 0.001$
Tmt*Sp	3/230	4.01	$p < 0.01$
Rack	8/230	0.43	NS
Size (Si)	2/230	1.24	NS
Si*Rack	16/230	0.40	NS
Tmt*Si	6/230	0.55	NS
Sp*Si	2/230	1.60	NS
Tmt*Sp*Si	6/230	1.14	NS
Ti *Tmt	18/681	4.95	$p < 0.001$
Ti*Sp	6/225	14.18	$p < 0.001$
Ti*Tmt*Sp	18/681	2.06	$p < 0.05$
Ti*Rack	48/1380	0.65	NS
Ti *Si	12/452	0.93	NS
Ti*Si*Rack	96/1380	1.01	NS
Ti*Tmt*Si	36/1380	1.29	NS
Ti*Sp*Si	12/452	1.37	NS
Ti*Tmt*Sp*Si	36/1380	1.79	$p < 0.05$
Residual	230		
Total	1379		

Table 2.22 Log-linear analysis of the bleaching effects on the fate (tissue loss and survival) of *A. aspera* and *A. millepora* colonies, 10 months after bleaching in experiment 2. The variable Bleaching, Bl, represents data for both bleached and unbleached colonies. All other variables are defined in Table 2.21. The percentage of tissue lost in colonies and their percentage survival were both analysed separated and each analysis included data from all treatments. NS = non significant.

Fate	Interactions	Degrees of Freedom	Chi-Square	Significance
% Tissue Lost	Bl	1	35.53	$p < 0.001$
	Tmt*Bl	4	23..2	$p < 0.001$
	Sp*Bl	1	0.06	NS
	Si*Bl	2	0.04	NS
	Tmt*Sp*Bl	4	10.03	$p < 0.05$
	Tmt*Si*Bl	8	0.86	NS
	Sp*Si*Bl	2	0.05	NS
	Tmt*Sp*Si*Bl	8	1.64	NS
% Survival	Bl	1	85.16	$p < 0.001$
	Tmt*Bl	4	47.78	$p < 0.001$
	Sp*Bl	1	33.01	$p < 0.001$
	Si*Bl	2	0.12	NS
	Tmt*Sp*Bl	4	9.54	$p < 0.05$
	Tmt*Si*Bl	8	0.93	NS
	Sp*Si*Bl	2	0.07	NS
	Tmt*Sp*Si*Bl	8	1.88	NS
	Likelihood Ratio	0	0.00	$p = 1.000$

The frequency and extent of bleaching did not differ between size-classes in either species (p = NS, Tab. 2.21). For both species combined, around 55% of colonies in each size-class bleached, and a similar percentage of total tissue (ca. 36%) bleached per colony, irrespective of their size. Size-specific patterns of tissue loss and mortality did not differ among bleached or unbleached colonies, of either species, after 10 months (Tab. 2.22).

BIOEROSION

i) Experiment 1: 1 m Transplants of *G. retiformis*

For all size-classes combined, the total number of boring taxa in live colonies of *G. retiformis* did not differ substantially among treatments ($p < 0.05$, Tab. 2.23). The *in situ* and handling controls had on average 8.3 bioeroders per colony, whereas the translocated controls and the 1 m transplants had only 6.3. In contrast, the percentage of skeletal erosion per colony differed significantly among treatments ($p < 0.01$, Tab. 2.24). Overall, the 1 m transplants exhibited a 92% increase in the total percentage of skeletal erosion per colony, relative to the controls. Around 9% of the skeleton per colony was eroded by boring taxa in the controls, whereas 18% had been lost through bioerosion in the 1 m transplants. This difference in bioerosion in the deeper site, was due to a significant increase in the erosion caused by boring filamentous algae (*Ostreobium* sp., $p < 0.05$, Tab. 2.25) and boring sponges (*Cliona* sp., $p < 0.05$, Tab. 2.26). Polychaetes (*Spirobranchus* sp.), bivalves (*Lithophaga* sp.) and cirriped barnacles were equally prevalent among treatments. For all control colonies of *G. retiformis*, the percentage of skeletal erosion caused by each boring agent was ordered as: Polychaetes > algae > sponges > bivalves > barnacles, whereas in the 1 m transplants it was ranked

Table 2.23 Three-factor nested ANOVA to test for differences in the total number of boring taxa in *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on log (x + 0.001) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	10.36	$p < 0.05$
Size (Si)	2/2	64.74	$p < 0.001$
Rack	1/2	0.89	NS
Tmt*Si	4/2	20.85	$p < 0.001$
Si*Rack	2/42	0.04	NS
Residual	42		
Total	53		

as: Algae > polychaetes > sponges > bivalves > barnacles.

Table 2.24 Three-factor nested ANOVA to test for differences in the percentage of bioerosion in *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	25.59	$p < 0.01$
Size (Si)	2/2	63.60	$p < 0.001$
Rack	1/2	< 0.01	NS
Tmt*Si	4/2	10.11	$p < 0.001$
Si*Rack	2/42	< 0.01	NS
Residual	42		
Total	53		

Table 2.25 Three-factor nested ANOVA to test for differences in the percentage of *Ostreobium* sp. in *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	41.08	$p < 0.05$
Size (Si)	2/2	46.23	$p < 0.001$
Rack	1/2	< 0.01	NS
Tmt*Si	4/2	11.31	$p < 0.001$
Si*Rack	2/42	< 0.01	NS
Residual	42		
Total	53		

Table 2.26 Three-factor nested ANOVA to test for differences in the percentage of *Cliona* sp. in *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	42.56	$p < 0.05$
Size (Si)	2/2	54.22	$p < 0.01$
Rack	1/2	< 0.01	NS
Tmt*Si	4/2	1.89	NS
Si*Rack	2/42	< 0.01	NS
Residual	42		
Total	53		

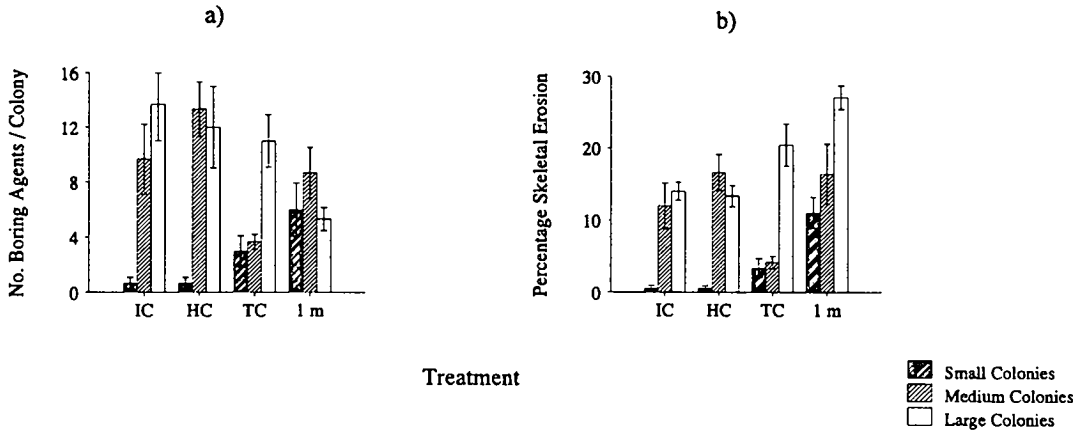

Figure 2.20 Bioerosion of live *G. retiformis* colonies (mean ± SE) as a function of treatment and colony size: a) total boring taxa / colony, b) percentage skeletal erosion / colony. Treatment abbreviations and size-class dimensions are defined in Figure 2.13 and 2.15. Sample sizes range from 4 to 8 replicates / size-class.

For *G. retiformis*, the total number of boring taxa per colony and the percentage of skeletal erosion per colony were both highly influenced by colony size ($p < 0.001$, Tab. 2.23 & 2.24, & Fig. 2.20). Typically, small colonies had the lowest number of bioeroders per colony and the lowest percentage of skeletal erosion. Boring algae ($p < 0.001$, Tab. 2.25), clionid sponges ($p < 0.01$, Tab. 2.26), bivalves ($p < 0.05$, Tab. 2.27) and the polychaete *Spirobranchus* sp. ($p < 0.001$, Tab. 2.28) were uncommon in small colonies but readily abundant in larger colonies. These size-specific trends in the number of bioeroders per colony and the percentage of erosion per colony were evident in most treatments. However, a similar number of bioeroders were found among the 1 m transplants, irrespective of colony size (Fig. 2.20). This result was due to a significant increase in the prevalence of clionid sponges in small live colonies which were transplanted 1 m deeper ($p < 0.05$, Tab. 2.26). Nevertheless, small colonies in the deeper site still had a lower percentage of skeletal erosion than larger colonies (Fig. 2.20).

Table 2.27 Three-factor nested ANOVA to test for differences in the percentage of bivalve excavations in *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	10.70	NS
Size (Si)	2/2	72.15	$p < 0.05$
Rack	1/2	2.24	NS
Tmt*Si	4/2	10.73	NS
Si*Rack	2/42	1.67	NS
Residual	42		
Total	53		

Table 2.28 Three-factor nested ANOVA to test for differences in the percentage of polychaete excavations in *G. retiformis* colonies between and among treatments and colony size-classes, in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	13.06	$p < 0.05$
Size (Si)	2/2	44.93	$p < 0.001$
Rack	1/2	1.03	NS
Tmt*Si	4/2	38.07	$p < 0.001$
Si*Rack	2/42	2.81	NS
Residual	42		
Total	53		

ii) Experiment 2: 25 cm and 50 cm Transplants of *A. aspera* and *A. millepora*

For all treatments combined, colonies of *A. aspera* and *A. millepora* had an average of only 1.03 bioeroders which had eroded an average of only 1.24% of their skeletons prior collection. Consequently, patterns of bioerosion in these species were not assessed any further.

COLONY FECUNDITY

i) Experiment 1: 1 m Transplants of *G. retiformis*

The fecundity (or number of oocytes / cm^2) of *G. retiformis* colonies differed among treatments ($p < 0.001$, Tab. 2.29). Compared to the controls, the 1 m transplants exhibited an 89% decrease in fecundity. Overall, the mean number of eggs per square centimeter among treatments was ranked as follows: *In situ* controls (291.1 ± 15.1) > translocated controls (207.6 ± 15.8) = handling controls (182.1 ± 15.5) >> 1 m transplants (24.9 ± 3.7). This decrease in fecundity in the 1 m transplants of *G. retiformis*, was almost entirely due to a significant decrease in the number of oocytes per polyp, from 45.8 ± 3.1 in the controls to 6.7 ± 1.0 ($p < 0.01$, Tab. 2.30) and to a slight decrease in the number of polyps per unit surface area, from 5.0 ± 0.1 in the controls to 3.7 ± 0.1 ($p < 0.05$, Tab. 2.31). Oocyte volume did not differ among treatments and averaged 0.013 ± 0.001 mm^3 for all colonies of *G. retiformis* (p = NS, Tab. 2.32).

Table 2.29 Four-factor nested ANOVA to test for differences in the number of oocytes / cm^2 in *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	75.41	$p < 0.001$
Size (Si)	2/2	22.02	$p < 0.001$
Rack	1/2	< 0.01	NS
Colony	2/148	< 0.01	NS
Tmt*Si	4/2	1.67	$p < 0.05$
Si*Rack	2/2	< 0.01	NS
Residual	148		
Total	161		

Table 2.30 Four-factor nested ANOVA to test for differences in the number of oocytes / polyp in *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	71.17	$p < 0.01$
Size (Si)	2/2	26.98	$p < 0.001$
Rack	1/2	< 0.01	NS
Colony	2/148	0.44	NS
Tmt*Si	4/2	0.92	$p < 0.01$
Si*Rack	2/2	< 0.01	NS
Residual	148		
Total	161		

Table 2.31 Four-factor nested ANOVA to test for differences in the number of polyps / cm^2 in *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on non-transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	97.00	$p < 0.05$
Size (Si)	2/2	2.53	NS
Rack	1/2	< 0.01	NS
Colony	2/148	< 0.01	NS
Tmt*Si	4/2	0.44	NS
Si*Rack	2/2	< 0.01	NS
Residual	148		
Total	161		

Table 2.32 Four-factor nested ANOVA to test for differences in the oocyte volume of *G. retiformis* colonies between and among treatments and colony size-classes in experiment 1. The analysis was performed on non-transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	2/1	1.27	NS
Size (Si)	2/2	0.21	NS
Rack	1/2	4.20	NS
Colony	2/148	24.12	NS
Tmt*Si	4/2	10.80	NS
Si*Rack	2/2	59.37	NS
Residual	148		
Total	161		

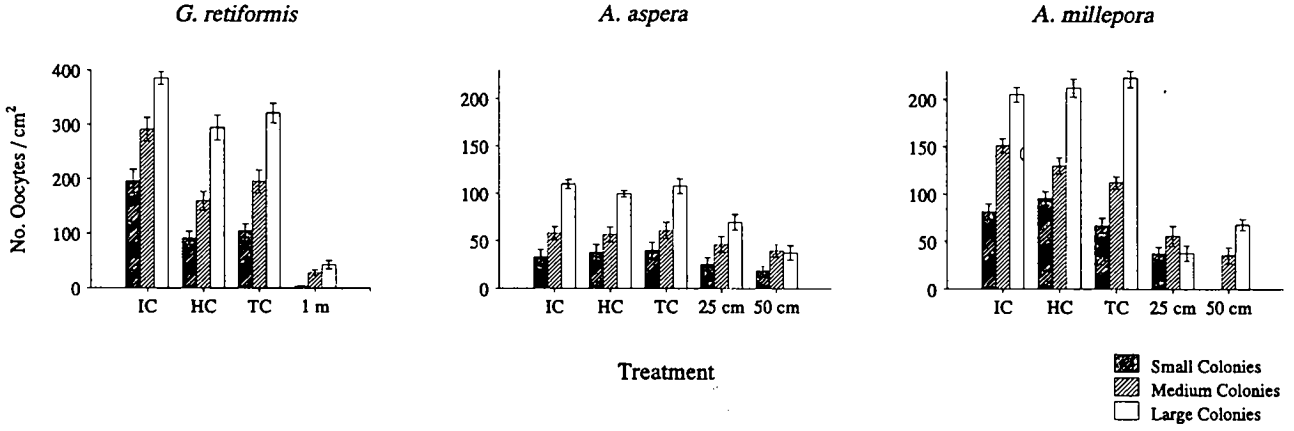

Figure 2.21 Fecundity of colonies (mean ± SE), as a function of size and treatment. Treatment abbreviations and size-class dimensions are defined in Figure 2.13 and 2.15. Sample sizes range from 4 to 8 replicates / size-class.

The fecundity of *G. retiformis* colonies was also strongly dependent on colony size ($p < 0.001$, Tab. 2.29 & Fig. 2.21). Typically, small colonies had the lowest fecundity, and fecundity increased with increasing colony size. The mean number of eggs per square centimeter ranged two-fold among colony size-classes and was ranked as: Small colonies (99.0 ± 10.6) < medium colonies (169.0 ± 14.1) < large colonies (261.4 ± 17.4). Differences in fecundity between colony size-classes of *G. retiformis* differed slightly among treatments ($p < 0.05$, Tab. 2.29 & Fig. 2.21). This was because small colonies transplanted 1 m deeper exhibited a proportionally greater decrease in fecundity than larger colonies subjected to the same treatment, relative to the controls. Regardless, all differences in fecundity among colony size-classes, were due to differences in the number of oocytes per polyp ($p < 0.001$, Tab. 2.30). The number of polyps per unit surface area did not change (p = NS, Tab.

2.31), and oocyte volume was similar in all colonies of *G. retiformis*, irrespective of colony size (p = NS, Tab. 2.32).

ii) Experiment 2: 25 cm and 50 cm Transplants of *A. aspera* and *A. millepora*

The fecundity of *A. aspera* and *A. millepora* differed in response to very small changes in depth ($p < 0.05$, Tab. 2.33). In contrast to the controls (which remained constant), colony fecundity decreased two-fold in the 25 cm and 50 cm transplants. The mean number of eggs per square centimeter among treatments was: *In situ* controls (106.3 ± 6.3) = handling controls (105.3 ± 6.3) = translocated controls (101.8 ± 6.7) >> 25 cm transplants (45.5 ± 3.6) > 50 cm transplants (37.5 ± 3.4). This decrease in fecundity in the 25 cm and 50 cm transplants, was primarily due to a decrease in the number of oocytes per polyp, from 23.4 ± 0.1 in the controls to 19.4 ± 0.1 ($p < 0.05$, Tab. 2.34) as well as a decrease in the number of polyps per unit surface area, from 4.5 ± 0.3 in the controls to 2.1 ± 0.2 ($p < 0.05$, Tab. 2.35). Oocyte volume in colonies of *A. aspera* and *A. millepora* did not differ among treatments (p = NS, Tab. 2.36).

The fecundity of the two *Acropora* species differed significantly ($p < 0.05$, Tab. 2.33). The number of eggs per square centimeter in *A. millepora* (107.0 ± 4.6) was almost double that of *A. aspera* (56.1 ± 2.6). This was due to a difference in the number of oocytes per polyp between species, with 4.7 ± 0.2 in *A. millepora* and 2.5 ± 0.1 in *A. aspera* ($p < 0.05$, Tab. 2.34). The number of polyps per unit surface area did not differ between species and averaged 22.0 ± 0.1 (p = NS, Tab. 2.35). Egg volume did not differ between species either, and for all colonies combined it averaged 0.074 ± 0.004 mm^3 (p = NS, Tab. 2.36). As expected, small colonies of both species were the least fecund, with the lowest number of oocytes per square centimeter ($p < 0.01$, Tab. 2.33 & Fig. 2.21). The mean number of oocytes per square centimeter among size-classes of *A. aspera* was ordered as: Large colonies (85.0 ± 4.3) > medium colonies (52.5 ± 3.5) > small colonies (30.9 ± 3.4). For *A. millepora* it was: Large colonies (149.0 ± 9.2) > medium colonies (101.2 ± 5.9) > small colonies (64.9 ± 4.7).

Table 2.33 Five-factor nested ANOVA to test for differences in the number of oocytes / cm^2 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on non-transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/1	27.25	$p < 0.05$
Species (Sp)	1/1	25.36	$p < 0.05$
Size (Si)	2/2	29.76	$p < 0.01$
Rack	1/2	0.16	NS
Colony	2/385	1.04	NS
Tmt*Sp	3/1	9.42	NS
Tmt*Si	6/2	3.64	$p < 0.05$
Sp*Si	2/2	2.35	$p < 0.05$
Si*Rack	2/2	0.06	NS
Tmt*Sp*Si	6/2	1.65	$p < 0.05$
Residual	385		
Total	413		

Table 2.34 Five-factor nested ANOVA to test for differences in the number of oocytes / polyp in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/1	27.44	$p < 0.05$
Species (Sp)	1/1	19.16	$p < 0.05$
Size (Si)	2/2	39.73	$p < 0.01$
Rack	1/2	0.22	NS
Colony	2/385	0.03	NS
Tmt*Sp	3/1	7.91	NS
Tmt*Si	6/2	1.96	NS
Sp*Si	2/2	0.15	NS
Si*Rack	2/2	0.17	NS
Tmt*Sp*Si	6/2	2.63	$p < 0.05$
Residual	385		
Total	413		

Size-specific differences in fecundity in the *Acropora* species differed slightly among treatments ($p < 0.05$, Tab. 2.33 & Fig. 2.21). This was because large colonies of *A. aspera* transplanted 50 cm deeper exhibited a proportionally larger decrease in fecundity than smaller colonies subjected to the same treatment (c.f. the controls). A similar disproportionate decrease in fecundity was evident in large colonies of *A. millepora* which were transplanted 25 cm deeper. Apart from these two exceptions, large colonies of both species always had the highest fecundity and small colonies, the lowest. This was most evident in the 50 cm transplants, where no egg production per unit area was

detected in small colonies of *A. millepora*. Despite the size-specific differences in colony fecundity, egg volume in both species was unaffected by colony size (p = NS, Tab. 2.36).

Table 2.35 Five-factor nested ANOVA to test for differences in the number of polyps / cm^2 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on non-transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/1	95.00	$p < 0.05$
Species (Sp)	1/1	2.02	NS
Size (Si)	2/2	1.02	NS
Rack	1/2	< 0.01	NS
Colony	2/385	< 0.01	NS
Tmt*Sp	3/1	1.27	NS
Tmt*Si	6/2	0.06	NS
Sp*Si	2/2	0.02	NS
Si*Rack	2/2	< 0.01	NS
Tmt*Sp*Si	6/2	< 0.01	NS
Residual	385		
Total	413		

Table 2.36 Five-factor nested ANOVA to test for differences in oocyte volume in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 0.001) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/1	8.62	NS
Species (Sp)	1/1	11.14	NS
Size (Si)	2/2	0.38	NS
Rack	1/2	5.02	NS
Colony	2/385	26.87	NS
Tmt*Sp	3/1	1.44	NS
Tmt*Si	6/2	2.67	NS
Sp*Si	2/2	0.95	NS
Si*Rack	2/2	34.76	NS
Tmt*Sp*Si	6/2	8.02	NS
Residual	385		
Total	413		

CAUSES OF MORTALITY, SHRINKAGE, TISSUE LOSS AND REDUCED FECUNDITY

The causes of mortality, shrinkage, tissue loss and reduced fecundity could not be identified with complete confidence, and undoubtedly included agents other than those described here. However, there were clear biological interactions and physical factors associated with these changes.

i) Biological Interactions

In all experiments, fewer than 5% of all colonies were affected by competitive interactions with other corals. Several experimental colonies were indirectly affected by dislodged coral fragments. During rough conditions, fragments of the branching species *A. aspera*, *Porites cylindrica* Dana and *Millepora tenella* Linnaeus were occasionally swept onto experimental colonies in shallow sites. In some instances, these fragments became established and hindered the growth of some of the experimental colonies. Most of the colonies examined (ca. 90%) were affected to some extent by other reef biota. Grazing scars inflicted by fishes such as scarids (eg. *Scarus sordidus*), were evident in all treatments, but most pronounced in the deeper transplants. A few corallivorous gastropods (eg. *Drupella rugosa*), were also evident among several colonies of *A. aspera* and *A. millepora* located 50 cm deeper. However, the most striking biological agent of colony tissue loss, shrinkage and mortality in all of the experiments, was colony overgrowth by filamentous algae. Several pomacentrids, most notably *Dischistodus prosopotaenia*, established algal territories over many colonies located in deeper sites. Algae within these territories often grew rapidly and occasionally completely smothered some of the depth transplants. In contrast, only a few minor algal territories were established over control colonies and those that were, were guarded primarily by *Cheiloprion labiatus*, a smaller damsel fish species. Small pockets of sediment often accumulated in algal patches, so it was not always possible to determine whether competition with algae or sedimentation was the source of coral damage. Although competitive interactions with filamentous algae were observed among all treatments during every census, the most prolific algal growth was observed every summer, coincident with extreme high and low seawater temperatures.

ii) Seawater Temperatures

Seawater temperatures differed among depths (t-test statistics: $p < 0.001$ for all temps. recorded in exp.1 and for min. temps. recorded in exp. 2, and $p < 0.05$ for max. temps. recorded in exp. 2 and for all temps. recorded in exp. 3, Fig. 2.19). All of the shallow control colonies were subjected to the greatest fluctuations in temperature, especially during summer, and temperature

fluctuations decreased with increasing depth. Throughout the entire study, the controls experienced temperatures ranging from 18.5 to 33.6°C, the 25 cm and 50 cm transplants experienced temperatures from 22.0 to 32.1°C and 23.9 to 30.8°C, respectively, and the 1 m transplants only experienced temperatures ranging from 23.8 to 28.3°C.

DISCUSSION

CORAL ZONATION

There were striking differences in the distribution and abundance of the target species in Little Pioneer Bay, with *Acropora millepora* most prevalent at the crest, *Acropora aspera* most common on the outer flat, and *Goniastrea retiformis* equally abundant from the mid flat to the reef crest (Tab. 2.2). These distribution patterns have been observed in natural populations in the Indo-Pacific (eg. Morrissey 1980, Bothwell 1984; Brown et al. 1985; Veron 1986; Larcombe 1990). These species are usually found only in shallow reef environments, but in these environments they may dominate specific depth zones.

Mean colony size for each species varied between depths and was not always greatest at deeper sites or where colonies were in the greatest abundance (Fig. 2.12 & Tab. 2.2) Colonies of *A. millepora* increased in size and abundance with increasing depth, from the mid flat to the reef crest, whereas colonies of *A. aspera* were largest and at their greatest abundance on the outer flat. Colonies of *G. retiformis*, like those of *A. millepora*, increased in size with increasing depth, but were found in equal abundance in all shallow reef sites. This difference in the size-distribution of the species, is likely to reflect differences in the species' population size-structure and dynamics.

POPULATION STRUCTURE AND DYNAMICS OF CORALS

Population Structures

Populations of each species were numerically dominated by small colonies (< 5 cm in diameter, Fig. 2.12). This is common in many coral populations throughout the Indo-Pacific (Babcock 1991; Stimson 1985) and the Caribbean (Bak & Engel 1979; Hughes & Jackson 1985; Soong 1993). As shown here (Fig. 2.12) and in other studies (eg. See Sheppard 1980; Hughes & Jackson 1985), the size-structure of a species may also vary with depths. Size frequency distributions of populations merely describe existing patterns (Sebens 1983), and are driven to some extent by episodic and spatially variable rates of recruitment. However, this study showed that the size-structure of each species within each depth zone was relatively constant between the two locations,

despite differences in the relative abundance of corals. Therefore, the size-distributions observed may be largely the result of depth-dependent environmental factors affecting recruitment, growth, shrinkage and mortality and their ultimate expression in colony size. The abundance of corals is obviously dependent on the balance between rates of colony mortality and recruitment and growth.

Growth Constraints

For two of the shallow-water species, *G. retiformis* and *A. millepora*, subaerial stresses in the intertidal outer reef flat appear to pose strict constraints on growth (eg. see Babcock 1991 for other examples). For the third species, *A. aspera*, which dominates this habitat, colony growth appears less constrained by the environment. Of the three species, shrinkage was greatest in small colonies of *G. retiformis*. However, many larger colonies also shrunk considerably after 1 year (Fig. 2.17), and since rates of linear growth were very low (ca. 6 mm / year, Fig. 2.18), compared to the rates of shrinkage (Fig. 2.17), this massive species exhibited negative net growth through the course of a year. In *Acropora millepora*, rates of growth and shrinkage were almost balanced. This species had relatively fast rates of linear growth (ca. 22 mm / year), but as a result of colony injury, it also experienced little net growth over a year (Fig. 2.17). In contrast, the branching species, *A. aspera*, exhibited the greatest positive net growth throughout the year. It rarely shrank as a result of external influences (Fig. 2.17), and had the fastest rates of linear growth (ca. 46 mm / year).

There are notable differences between realized net growth and the potential for individual colony growth which merit mention (Bak 1976; Hughes & Jackson 1985). Extrinsic factors such as algal overgrowth, sedimentation, competition and predation, may enhance colony fission and directly or indirectly affect colony size. While net growth was highest in *A. aspera* and lowest in *G. retiformis* (Fig. 2.17), colonies of both species often underwent fission and produced a similar number of daughter colonies throughout the course of a year (Tab. 2.12). As a result of the differential between rates of growth and shrinkage, daughter colonies produced by the branching species often attained a larger size than those produced by the massive species. Extrinsic constraints on growth, such as these, may be analogous to senescence in aclonal species (eg. see Babcock 1991). All of the corals examined here have indeterminate growth (ie. rates of linear extension independent of colony size),

so are not likely to senesce (Connell 1973; Harper 1980; Hughes & Jackson 1985; Sebens 1987; Babcock 1991). The upper limits to colony size may be set, to some extent, by colony morphology and the environmental constraints of the species (eg. See Hughes & Jackson 1985; Sebens 1987; Babcock 1991).

Colonies of all species were injured at some time throughout the study, but they exhibited marked differences in rates of tissue loss. Rates of tissue loss were lowest in *G. retiformis* (Tab. 2.16), probably because it is inherently less susceptible to physical damage due to its massive morphology and is a relatively good competitor in the natural environment, capable of extra-coelenteric interaction (Loya 1976b). Highest rates of tissue turnover occurred in *A. millepora* (Tab. 2.16), probably because of its relatively high growth rates, more fragile corymbose morphology and, as observed in the field, its poor ability to recover from algal overgrowth. Rates of tissue turnover in *A. aspera* were high, but considerably lower than those in *A. millepora* (Tab. 2.16). *Acropora aspera* often fragments under mechanical stress and daughter colonies are locally dispersed and may, as observed in this study, outcompete other corals entirely. As mentioned previously, several fragments of this species became established in this way among the shallow control sites. Clearly, this would entail some physiological investment (eg. rapid linear extension) to avoid sediment accumulation or algal overgrowth. Recent studies have shown that rates of tissue regeneration in corals may be slowed as a result of sediment-related or thermal stress (Meesters & Bak 1993; Meesters et al. 1992). This may account for higher rates of shrinkage among colonies of *A. millepora* during summer months (Fig. 2.17), coincident with extreme seawater temperatures (Fig. 2.19), and with strong monsoonal westerly winds, which can directly affect turbidity regimes. Rates of tissue turnover for *G. retiformis* are within the range of those found for other similar massive reef flat species (Babcock 1991). Rates of tissue turnover in branching and corymbose corals have not been documented previously. However, as shown here in *A. aspera* and *A. millepora*, they are considerably faster than those known for either massive (Babcock 1991) or foliaceous species (Hughes & Jackson 1985).

Bleaching and Recovery

In summer, the percentage of bleaching in corals was highest in branching colonies of *A. aspera* (0.80), lower in corymbose colonies of *A. millepora* (0.51) and lowest in massive colonies of *G. retiformis* (0.31, Tab. 2.19 with all controls combined). This ranking is similar to that found when species with different growth morphologies are ranked in terms of their thermal tolerances and respiratory rates (Jokiel & Coles 1974, 1977). However all species, irrespective of their size or morphology, lost normal pigmentation to a similar extent during each mass bleaching event, (on average < 40% of live tissue bleached per colony). Partial bleaching did not leave individuals more susceptible to injury or mortality (c.f. Goreau & MacFarlane 1990; Meesters & Bak 1993). All species examined appeared to be tolerant to periodic exposure to the air, and to partial bleaching, which is often induced by temperature and salinity extremes, excessive solar radiation or shading (Rogers 1979; Egana & DiSalvo 1982; Brown & Howard 1985; Hoegh-Guldberg & Smith 1989; Jokiel & Coles 1990; Szmant & Gassman 1990). Interestingly, rates of tissue loss and mortality subsequent to partial bleaching in *A. aspera* and *A. millepora* were often higher in colonies which had not bleached during summer, in contrast to those which had (Tab. 2.19). This indicates that partial bleaching may be an adaptive mechanism for shallow-water reef corals. This finding may support the hypothesis proposed by Buddemeier & Fatten (1993) that partial bleaching may act as a normal regulatory process to maintain stable symbiotic algal populations in host species. It also has implications for current evaluation measures used to assess impacts of bleaching on reef corals.

Mortality Patterns

Growth form and dynamics probably influence not only a coral's recovery from injuries but may also affect survival. Rates of colony survivorship were highest in *G. retiformis*, moderately high in *A. aspera* and lowest in *A. millepora* which appeared the least able to recover from physical or biological damage (Fig. 2.13, Fig. 2.15). The survivorship of all species was size-dependent, with highest mortalities among small colonies (eg. Fig. 2.15). These mortality patterns represent Type III survivorship curves (Begon & Mortimer 1986) and are similar to those found in other coral species (Connell 1973; Loya 1976a; Bak & Engel 1979; Harriott 1985; Hughes & Jackson 1985; Babcock

1991). Small colonies may have a poor ability to recover from injuries (Connell 1973), and may be more susceptible to algal overgrowth or sediment accumulation. Based on probabilities alone, Jackson (1979) noted that the chance of any event killing a small colony outright is greater than that for a large colony. Hughes and Jackson (1980, 1985) and Babcock (1991), demonstrated that although large colonies are rarely killed outright, they experience a higher incidence of injury. This may also explain the observed higher frequency of tissue fission among larger size-classes (Tab. 2.12).

Fission

The frequency of fission differed between species (Tab. 2.12). The annual probability of fission in *A. millepora* was relatively low (0.12), but comparable to highest values found in foliaceous species, such as *Leptoseris cucullata* Ellis & Solander and *Agaricia lamarcki* Milne Edwards & Haime (Hughes & Jackson 1985). In contrast, the annual probability of fission in *G. retiformis* was slightly higher (0.15), and far exceeds that recorded for massive reef flat corals (ca. 0.03, Babcock 1991), possibly because annual monitoring (eg. Babcock 1991), rather than bimonthly, is likely to underestimate actual rates of fission within coral populations. No previous studies have documented rates of fission for branching corals, although Hughes and Connell (1987) suggested that rates of fission are likely to be greater in branching corals than those with other growth morphologies. This suggestion has been supported, as the annual proportion of fission in *A. aspera* over 1 year was extremely high at 0.44; a rate twice that exhibited by *G. retiformis* and three-times that exhibited by *A. millepora.*

Reproduction

There is speculation on whether daughter colonies formed as a result of injury or breakage, rather than those formed by intrinsic means, are adaptive (eg. Hughes et al. 1992). This is because few studies have measured the combined survivorship of daughter colonies formed, together with the total sexual reproductive output of the genet (Tab. 2.12 & Fig. 2.21). Because all colonies remaining after fission are smaller in size than before, and fecundity is often directly related to colony size (Kojis

& Quinn 1985; Szmant-Froelich 1985; Babcock 1991; Fig. 2.21), the process of tissue fission may cause a temporary decrease in total fecundity. Fission appears to form an integral part of the life history of *A. aspera,* but an incidental set back in the life histories of *G. retiformis* and *A. millepora.* Colonies of *A. aspera* were the least fecund, but often produced daughter colonies by fission, with high rates of survival (ca. 90% after 1 year). In contrast, although colonies of *G. retiformis* and *A. millepora* were highly fecund, they rarely produced daughter colonies and few of these survived (ca. 33% compared to 90% in *A. aspera*). Like some other branching species, the asexual propagation of daughter colonies by *A. aspera* may provide a means of mobility for the genet, to ensure more rapid occupation of space, and is likely to spread the risk of genet mortality (Shinn 1976; Stimson 1978; Bak & Engel 1979; Birkeland et al. 1979; Highsmith 1982; Rylaarsdam 1983). Like other massive or more laminar species, fission is perhaps best considered a more costly investment in *G. retiformis* and *A. millepora* (Hughes & Jackson 1985; Babcock 1991). These issues are explored further using projection matrices of colony size-class transitions and sensitivity analyses (See Chapter 4).

Findings from this study, indicate that colonies of *G. retiformis* and *A. millepora* may invest more heavily in the production of sexually derived recruits, than those of *A. aspera.* Several compensatory changes are made to optimize reproductive output. *Goniastrea retiformis*, was the most fecund and had the smallest eggs. *Acropora millepora* and *A. aspera* had larger eggs, but produced them in lower numbers (Fig. 2.21). Lower fecundity for *A. millepora* and *A. aspera* may be offset by faster growth rates, to ensure colonies rapidly attain a size refuge from mortality. However, even small colonies of the slow growing *G. retiformis* were more fecund than most colonies of *A. millepora* and *A. aspera. Acropora millepora* was twice as fecund as *A. aspera* despite having eggs equivalent in size, and it produced a greater volume of eggs per unit area than *G. retiformis.* Several aspects of the gametogenic cycle in *A. aspera* have been assessed previously (Bothwell 1984), but not its fecundity. Fecundity values for *G. retiformis* and *A. millepora,* are comparable with those found in other massive reef flat corals (Babcock 1984, 1991) and corymbose or laminar *Acropora* species (Wallace 1985).

Longevity

Massive species with some propensity for asexual propagation, like *G. retiformis*, tend to have low rates of sexual recruitment (around 0.2 visible recruits / m^2 / year), but extremely high rates of adult survivorship, so may persist for many decades, with their reproductive output spread over many years (Babcock 1991; Fig. 2.13). Corymbose colonies of *A. millepora*, appear to have high rates of sexual recruitment, around 0.8 recruits / m^2 / year (Connell 1973; Bothwell 1984), but low rates of adult survivorship (Fig. 2.15), so may persist for much shorter periods of time. Branching colonies of *A. aspera* with an extreme propensity for asexual propagation tend to have extremely low rates of sexual recruitment, often less than 0.2 recruits / m^2 / year, but high rates of adult survivorship and relatively long lifespans (Connell 1973; Birkeland et al. 1976; Highsmith 1982; Bothwell 1984; Fig. 2.15). Overall, the three species examined had very different population dynamics.

POPULATION RESPONSES TO DEPTH CHANGES

The responses of the species to depth changes were associated with their morphologies and life history traits. Of the three species, *G. retiformis* was the least affected by a change in depth and *A. millepora*, the most (Tab. 2.6). Nevertheless all species, even *G. retiformis*, experienced a marked decrease in linear growth and fecundity in response to depth changes (Tab. 2.37). This confirms previous studies which show that depth increases often slow rates of coral growth (Buddemeier et al. 1974; Baker & Weber 1975; Bak 1976; Buddemeier & Kinzie 1976; Dustan 1979; Highsmith 1979; Tunnicliffe 1980), and reduces colony fecundity (Kojis & Quinn 1984). In addition, damage by grazing herbivores and predators (Hay 1981, 1984, Hay et al. 1983), overgrowth by filamentous algae (within damsel fish territories) and choking by sediment trapped in algal mats (Potts 1977) are often higher at sites below reef margins. Therefore, the allocation of energy resources to repair injuries or to deter algal overgrowth, is likely to restrict energy use for physiological functions, such as growth and reproduction and in extreme cases, survival.

Table 2.37 A summary of the life history traits of *G. retiformis*, *A. aspera* and *A. millepora* and their responses to 25 cm, 50 cm or 1 m depth changes. A significant increase or decrease in a trait, as a result of transplantation into deeper water, is shown by the direction of each arrow, the magnitude of a response is shown by the number of arrows, and --, indicates that no significant change occurred as a result of transplantation.

Trait	*G. retiformis*		*A. aspera*			*A. millepora*		
	Controls	1 m	Controls	25 cm	50 cm	Controls	25 cm	50 cm
Adult Survival	high	--	mod.	↓	↓↓	low	↓↓	↓↓↓
Areal Growth	slow	--	V. fast	--	↓	fast	--	↓
Linear Growth	slow	↓↓↓	V. fast	--	↓	fast	↓	↓↓
Bioerosion	high	↑↑↑	V. low	--	--	V. low	--	--
Tissue Loss	mod.	--	high	--	↑	V. high	↑	↑↑
Rates of Fission	mod.	--	V. high	--	--	mod.	↓↓↓	--
Daughter Colony	poor	--	V. high	--	--	poor	↓↓↓	↓↓↓
Fecundity	high	↓↓↓	low	↓	↓↓	mod.	↓	↓↓
Egg Volume	low	--	high	--	--	high	--	--

Colonies of *G. retiformis* exhibited no significant change in rates of tissue loss, fission or survival, in response to a 1 m depth change (Tab. 2.37). When transplanted 1 m deeper, these massive colonies exhibited a large decrease in linear growth and fecundity and a large increase in skeletal erosion by filamentous algae and clionid sponges (Tab. 2.37). The latter observation supports previous accounts that these boring agents and consequent rates of bioerosion are often higher in sites below reef margins (Davies & Hutchings 1983; Wilkinson 1983; Wilkinson & Evans 1988), in heavily grazed areas (Ogden 1977; Sammarco et al. 1986), and in established damsel fish territories (Sammarco et al. 1987). *Goniastrea retiformis* was the only species to exhibit marked skeletal erosion, irrespective of depth (Tab. 2.37). This difference in rates of bioerosion between the species, is consistent with that found by Musso (1992) for morphologically different *Acropora* species, with branching and laminar corals exhibiting lower rates of bioerosion than mound shaped species. Colonies of *G. retiformis*, with high rates of survival, are likely to persist the longest in response to a 1 m depth change. They may grow large over long periods of time. In some instances, the action of bioerosion may limit longevity. Those colonies that persist will contribute little to the total sexual reproductive output of the population.

Colonies of *A. millepora* appeared to be the most sensitive to depth-related changes in the physical and biological environment. They not only exhibited considerable reductions in linear growth and fecundity in response to small depth changes, but had very high rates of tissue loss and very low rates of asexual propagation and survival (Tab. 2.37). Rates of mortality in *A. millepora* were highest in summer, with the greatest extremes in temperature (Fig. 2.15 & Fig. 2.19). This finding could support similar observations that short-lived species, such as *A. hyacinthus* and *Pocillopora damicornis* Linnaeus may be prone to temperature-dependent mortality (Yap et al. 1992). Given the overall sensitivity of *A. millepora* to depth-related changes in environmental conditions, colonies of this short-lived species may be the first of the three species to disappear in response to small depth changes. Some colonies may survive for a relatively short time in response to a sudden 25 cm or a 50 cm depth change, but their potential fecundity could decrease considerably and any daughter colonies formed by fission are not likely to survive.

Colonies of *A. aspera* exhibited fewer detrimental responses to depth changes than those of *A. millepora* (Tab. 2.37). Interestingly, colonies of *A. aspera* transplanted 25 cm deeper than the controls maintained very fast rates of linear growth and very high rates of asexual propagation, despite experiencing slightly higher rates of adult mortality and producing fewer eggs per unit area (Tab. 2.37). The production of daughter colonies with high rates of survival and fast growth rates may offset higher rates of adult mortality in response to a 25 cm depth change (Tab. 2.37), and extant colonies of *A. aspera* could therefore persist for quite some time at this depth. Colonies of *A. aspera* transplanted 50 cm deeper, exhibited a greater amount of tissue loss and some reduction in rates of linear growth, which resulted in a larger amount of colony shrinkage (Tab. 2.37). They also had higher rates of adult mortality and were considerably less fecund than those transplanted 25 cm deeper (Tab. 2.6). Despite these changes in response to a 50 cm depth change, colonies of *A. aspera* maintained high rates of fission, and most daughter colonies survived (Tab. 2.37). Thus, even in response to a 50 cm depth change, extant colonies of *A. aspera* may persist for some time, as a result of their effective ability for asexual propagation.

LIFE HISTORY TRAITS AND CAUSES OF ZONATION

This study provides new insights into the relationship between life history traits and patterns of coral zonation. The zonation of species appears to be highly related to their different morphologies, life history traits and responses to depth changes. Seawater temperature fluctuations (physical changes) were most extreme at control sites on the outer flat (Fig. 2.19), while the chances of biological damage were higher at deeper sites below the reef crest (eg. Hay 1981, 1984, Hay et al. 1983). *Acropora millepora* appeared most sensitive to changes in all these environmental conditions. Consequently, it is not surprising that this short-lived species is most abundant at the reef crest (Fig. 2.12), possibly the less stressful because even at low tide it is often wet by the breaking of waves. Branching colonies of *A. aspera* have weak basal attachment plates and therefore little ability to secure themselves to the substratum in exposed reef crest environments (Bothwell 1984), but they appear to be relatively unaffected by physical or biological changes in environmental conditions, compared to colonies of *A. millepora*. Branching species, which may rely heavily on asexual propagation and on the passive dispersal of daughter colonies by currents (c.f. sexual recruitment), have elsewhere been shown to dominate slightly calmer waters on outer reef flats (eg. *A. aspera*, Bothwell 1984; Fig. 2.12), and just below reef crests (eg. *A. palmata*, Adey 1978).

All of these reef zones are prone to damage by storms (Adey 1978). Massive colonies, like *G. retiformis*, are inherently less susceptible to storms than branching or corymbose species (Veron 1986; Woodley et al. 1981; Rogers et al. 1982; Hughes 1989). However, their low rates of sexual recruitment and slow growth rates (Babcock 1991; Fig. 2.18), are likely to delay re-colonization of disturbed sites and prevent their domination where disturbance is frequent (Jackson & Hughes 1985). In contrast, short-lived species, like *A. millepora*, often have high rates of sexual recruitment and fast growth rates (Connell 1973; Bothwell 1984; Fig. 2.18), so are likely to be the first to invade bare space and re-populate sites following a severe disturbance (Loya 1976a, 1976b; Hughes & Jackson 1985; Endean & Cameron 1990). Fragmenting species, like *A. aspera*, may have very low rates of sexual recruitment (Bak & Engel 1979; Rylaarsdam 1983; Bothwell 1984), but produce individual daughter colonies with high rates of survival and fast growth rates (Birkeland et al. 1979; Tab. 2.12, Fig. 2.18). Consequently, they are likely to re-establish disturbed sites rapidly through the persistence

of dispersed or dislodged fragments (Gilmore & Hall 1976; Birkeland et al. 1979; Tunnicliffe 1981; Highsmith 1982). However, in some cases, severe storms may slow or even prevent their re-establishment (Knowlton et al. 1981).

The persistence of transplanted species (even only for a very short period), supports the hypothesis suggested by Pielou (1977), that as a result of competition and predation, the realized zone of a species may be a significant contraction of the fundamental zone. As evidenced here and in other ecological studies, species-specific patterns of zonation and community structure may not be solely governed by their physiological tolerances and preferences, since they are often regulated to some extent by biological interactions (Dayton 1971; Porter 1974; Connell 1975, 1976; Jackson 1977; Underwood 1979; Menge & Farrell 1989; Underwood & Barrett 1990). Consequently, the absence of *G. retiformis*, *A. aspera* and *A. millepora* from deeper sites (Tab. 2.2), may reflect their poor ability to recover from damage caused by competitive interactions and predation. The role of physiological tolerances in determining the zonation of the species examined, is assessed further in Chapter 3.

ASSESSMENT OF TRANSPLANT EXPERIMENTS:

Field transplant experiments permit uncontrolled natural fluctuations in all environmental variables except those which are manipulated, such as depth. Extrapolation of the effects of direct depth changes on the responses of corals to potential impacts of sea level rise requires some knowledge of the acclimatization ability of corals to the predicted, slow, changes in sea level. Logistical constraints prevent direct simulation of the effects of predicted sea level rise on corals within their natural environment, so the effects of *stepwise* depth changes were examined to ascertain the acclimatization ability of corals to more gradual changes in depth. As demonstrated, two stepwise changes in depth had the same effect on the survivorship of the experimental corals as the direct changes in depth (Fig. 2.16). Thus, direct transplantation, as performed here, appears to provide a useful proxy to determine how corals respond to more gradual changes in sea level. Clearly, other species may have quite different acclimatization abilities and may be less suitable for direct depth transplant experiments.

POTENTIAL IMPACTS OF ENHANCED CLIMATE CHANGE AND SEA LEVEL RISE

Shallow-water reef-building corals with different morphologies and life history traits are likely to respond differently to predicted sea level rise. As sea level rises, corals will be located in gradually deepening sites and possibly in suboptimal environmental conditions. Those species which can allocate sufficient energy resources to growth may persist. However, changes in the physical and biological environment could limit their ability to grow, recover from injuries, optimize reproductive output (sexual or asexual), and survive. From findings presented here, it seems likely that extant colonies of *A. millepora* will be the first of the species to disappear from deeper sites, while those of *G. retiformis* will be the last. Because patterns of mortality in all three species were size-dependent (eg. Fig. 2.15), small colonies of each species may be the most vulnerable to sea level rise.

Coupled with these findings, recruits are likely to keep pace with predicted sea level rise, by colonizing presently unsuitable shallow reef sites. Even in species with very low rates of sexual recruitment, increases in the intensity and frequency of tropical storms predicted as a result of enhanced global warming (Climate Impact Group 1992; Mitchell et al. 1990), may provide a means for the asexual propagation of daughter colonies into these shallow reef sites. If sea-surface temperatures rise gradually at the rates currently predicted, around 2°C by 2070 in the eastern Australian tropics (Climate Impact Group CSIRO 1992; Whetton 1993) recruits of *G. retiformis*, *A. aspera* and *A. millepora* may be little affected, because of their ability to recover rapidly from partial bleaching events (Tab. 2.19). More rapid changes in temperatures or greater extremes than currently predicted may severely affect recruits, particularly those of *A. millepora*, which appear most prone to seasonal mortality (Fig. 2.15, Fig. 2.19). Thus, short-lived shallow-water reef corals, like *A. millepora*, are likely to be the most vulnerable to changes in local environmental conditions and may be the most useful bioindicators of early responses of coral reef ecosystems to enhanced climate change and sea level rise.

CHAPTER 3:

EFFECTS OF DEPTH CHANGES ON ASPECTS OF THE PHOTOPHYSIOLOGY OF SHALLOW-WATER REEF CORALS

INTRODUCTION

The ability of reef-building corals to adapt physiologically to alterations in light intensity and spectral composition is considered by some to be an important determinant governing their depth distributions (Roos 1967; Dustan 1979; Gattuso 1985; Chalker et al. 1988). However, few quantitative accounts of the photoadaptive abilities of reef corals have been documented, and these understandably focus primarily on subtidal species with broad depth distributions or on species located at depths of at least 3 m below tidal datum (Maragos 1972; Dustan 1982; Chalker et al. 1984; McCloskey & Muscatine 1984; Porter et al. 1984). Detailed accounts of the photo-responses of corals restricted to very shallow depths have been relatively neglected. Quantitative estimates of the photoadaptive abilities of shallow-water reef corals are presently limited to a single bushy intertidal species, *Pocillopora damicornis* Linnaeus (Houck 1978; Kinzie et al. 1984; Jokiel & Morrissey 1986).

Barnes & Chalker (1990) provide a detailed review of the photoadaptive mechanisms of reef corals. Based on their findings and other photophysiological studies of corals, it seems likely that shallow-water reef corals would exhibit a wide range of photo-responses to optimize light acquisition in response to depth changes. The corals may exhibit more planar growth, with fewer polyps per unit surface area in deeper water (Dustan 1979), which may reduce rates of colony respiration (Chalker et al. 1988). They may exhibit increased skeletal density in deeper water (eg. Bak & Weber 1975; Hughes 1987) and reduced vertical skeletal extension (eg. Buddemeier et al. 1974; Bak 1976; Chapter

2), which may result in a concurrent decrease in the amount of tissue within the coral skeleton. They may also darken in colour in deeper water as increased concentrations of zooxanthallate photosynthetic pigments, chlorophyll a, chlorophyll c_2 and carotenoids, are produced in the coral tissue (Kinzie et al. 1984; Barnes & Chalker 1990; Falkowski et al. 1990). Increased concentrations of these pigments are likely to increase the photosynthetic capacity of reef corals in deeper water (eg. Kinzie et al. 1984; Chalker et al . 1988). High concentrations of carotenoids may also act to reduce the possibility of photoinhibition (Barnes & Chalker 1990). The size of photosynthetic units and photopigment contents per algal cell may also increase in response to an increase in depth, while zooxanthellae numbers within the coral tissue may increase (eg. Titlyanov 1981; Titlyanov et al. 1980) or decrease (eg. Dustan 1979), depending on the species (Kinzie et al. 1984).

Increases in photosynthetic pigments in coral tissue in response to depth-related changes in light enhance light harvesting capabilities (Kinzie et al. 1984; Chalker et al. 1988). To date, increases in photopigment contents have been attributed primarily to alterations in the size of photosynthetic units and photopigment contents per algal cell (eg. Dustan 1979, 1982; Falkowski & Dubinsky 1981; Chalker et al. 1988), rather than to alterations in zooxanthellae numbers per unit tissue volume or their spatial arrangement within the tissue. Many studies have neglected to consider the effects of coral tissue volume on species-specific photo-responses to depth changes. The tissues of all reef-building corals overlay outer skeletal surfaces and, in perforate species, lie within the periphery of skeletal structures (Barnes & Lough 1992). Changes in the amount of skeletal cavities occupied by tissue may play an important role in determining zooxanthellae densities in reef corals (Houck 1978; Kinzie & Hunter 1987; Kinzie et al. 1984), yet no photophysiological studies have quantified tissue volume together with the photo-responses of corals (eg. see Titlyanov 1981; Titlyanov et al. 1980). Variations in tissue volume may exist in both perforate and imperforate species, because of the geometrically complex surface and peripheral structures of coral skeletons.

This study was designed to determine the photo-responses (eg. changes in tissue volume, zooxanthellae densities and photopigment contents) of two morphologically different perforate shallow-water reef corals, as a result of small depth changes below their current depth range. Quantitative estimates of the photophysiological traits of the corals in their natural environment and

in response to depth changes, provide information on two matters: the role of visible light in the zonation of species; and the likely photoadaptive responses of shallow-water reef coral populations to enhanced climate change and sea level rise.

Photophysiological responses of corals to changes in light are analogous to those exhibited by the leaves of terrestrial plants, for ensuring optimal light acquisition irrespective of their position in the plant canopy (Chow et al. 1988; Vogelmann 1993). Studies on the effects of leaf tissue volume and anatomy on the photoadaptive responses of leaves, show that the internal light environment of a leaf may be highly affected by the light reflected from lower leaf surfaces, tissue refraction and cell shading by other chloroplasts (Gates et al. 1965; Terashima & Saeki 1983; Vogelmann et al. 1989; Cui et al. 1991). Photosynthetic pigment concentrations may also be maximal in the upper portion of low-light adapted leaves and in the middle portion of high-light adapted leaves (Nishio et al. 1993). These studies demonstrate that leaf tissue volume and structure are extremely important in determining photoadaptive responses. Analogous anatomical alterations in light fields and pigment gradients may also occur in the tissues of reef-building corals. Symbiotic zooxanthellae are located within the tissues of reef-building corals, which overlay and often permeate highly reflective white aragonitic skeletons; just as chloroplasts are located within the tissues of leaves, which often have highly reflective white lower leaf surfaces (Vogelmann 1993).

Species-specific photo-responses to depth changes may also be governed by changes in tissue volume during colony development. In reef-building corals, skeletal growth accommodates tissue growth (Barnes 1971, 1973, Darke 1991). Vertical skeletal extension is often continuous throughout colony development (eg. Gladfelter 1985; Babcock 1991; Chapter 2), but recent evidence based on several massive species of *Porites* suggests that tissue thickness may be dependent on colony size (Barnes & Lough 1992). Few studies have examined the influence of colony size on the photophysiological traits of corals (eg. their zooxanthellae densities or photopigment contents). Those that have, report different findings. Smith & Hoegh-Guldberg (1987) found that rates of zooxanthellae population growth differed little between small and large colonies of *Stylophora pistillata* Esper and *Goniastrea edwardsi* Chevalier. Yet, Jokiel & Morrissey (1986) demonstrated that the relationship between photosynthesis and irradiance (P-I curve) in *P. damicornis* was inversely

related to colony size. In some species, colony morphology may also change with increasing size (Barnes 1973). This is important, because morphologically different colonies, either within or between species, may receive different amounts of incident light (Titlyanov 1991), and as a result may have different mechanisms of photoadaptation. Colony size and morphology may therefore play a role in determining species-specific responses to depth-related changes in light.

Current predictions suggest, eustatic sea level is predicted to rise around 20 cm by 2030 and by about 45 cm by 2070 (Wigley & Raper 1992). Increased water depth over currently established corals may expose them to suboptimal light regimes. Those species which can photoadapt to depth-related changes in light may persist the longest. Thus, this study was designed to determine the effects of 25 cm and 50 cm depth changes on the size-specific photophysiological responses of two common perforate reef corals, *Acropora aspera* Dana and *Acropora millepora* Ehrenberg, which are restricted to very shallow depths of less than 1 m in an inshore environment. Average instantaneous measurements of the quantum planar irradiance (μ mol photons / m^2 / sec) in the photosynthetic active range (PAR), recorded at the study sites at five minute intervals for 6 hours during November 1993, show that: 1. The 25 cm and 50 cm transplants receive a lower percentage of the surface irradiance (61.3 ± 0.6 and 59.0 ± 0.5, respectively), compared to all of the controls (ca. 70.0 ± 0.6); and 2. the percentage of the surface irradiance decreased with increasing depth (unpublished data).

The two *Acropora* species have different morphologies (branching and corymbose, ~~respectively~~), and so may photo-respond differently to the depth changes and to the associated changes in visible light. This study has several key objectives: 1. To determine the size-specific photophysiological traits of species in their natural environment; 2. to determine their photo-responses to 25 cm and 50 cm depth changes when transplanted below their current depth range, by quantifying their tissue volume, zooxanthellae densities and spatial arrangement, and photopigment contents; 3. to determine whether photoadaptive responses to depth changes differ among species or colony size-classes; and finally 4. to integrate these findings to examine the role of physiological responses to light in the zonation of species, and to discuss potential impacts of enhanced climate change and sea level rise on the photo-responses of shallow-water reef corals.

MATERIALS AND METHODS

COLLECTION OF CORAL SAMPLES

Control and experimental colonies of *Acropora aspera* and *Acropora millepora* were sampled during 1993 as part of experiment 2 (See Materials & Methods Chapter 2). Half of the subsamples were used to determine zooxanthellae densities and tissue mass index (an estimate of tissue volume), and the remainder were used to determine photopigment concentrations. To avoid confounding historical effects of partial bleaching (See Results Chapter 2) with species-specific photophysiological responses, colonies were sampled between October and November, 10 months after they had partially bleached. The corals had regained normal pigmentation and had recovered their zooxanthellae densities, as much as possible, within this period. Previous studies have also shown that zooxanthellae densities are often re-established within this time interval after partial bleaching (Szmant & Gassman 1990; Fitt et al. 1993). In the experiment, all corals were anaesthetised with 1% sea water formalin, before sampling. Then, 6 replicate subsamples (2 x 1 cm in size and devoid of bioeroders) were collected from 6 small, medium and large colonies of each species from within each of the five treatments (the *in situ* controls, the handling controls, the translocated controls, and the 25 cm and 50 cm transplants).

ZOOXANTHELLAE DENSITIES AND TISSUE MASS INDEX

To determine the density of zooxanthellae and index of tissue mass, subsamples were immediately fixed in 10% seawater formalin for at least 24 hours, then decalcified in 3% formalin and 3% hydrochloric acid solution. They were divided longitudinally through the center and a single portion of each was embedded in paraffin wax, using standard histological procedures, while the other was placed in 70% v/v ethanol. Shrinkage of decalcified tissue was measured by dividing the diameter of each histological sample by the diameter of its counterpart stored in ethanol. Histological procedures caused a 25% reduction in tissue volume in all subsamples processed, irrespective of treatment, species or colony size. As a result, it was possible to standardize all photophysiological measurements per unit coral tissue volume.

Histological samples were sectioned, serially, to a thickness of 8 μm to encompass the maximum diameter of zooxanthellae within both species (unpublished data). In each of 6 randomly chosen sections per subsample, counts of zooxanthellae were taken from two tissue locations: the outer gastrodermal coenosarc (which includes the mesentarial filaments, oral disc and coenchyme between polyps) and the inner basal endoderm (Fig. 3.1). To obtain representative estimates of zooxanthellae numbers in each tissue location, a calibrated Weibel graticule eyepiece was positioned randomly over four independent sampling sites. Numbers of zooxanthellae within each field of view, a sampling unit volume of 6×10^{-5} cm^3, were counted. The sampling protocol used is illustrated in Figure 3.2.

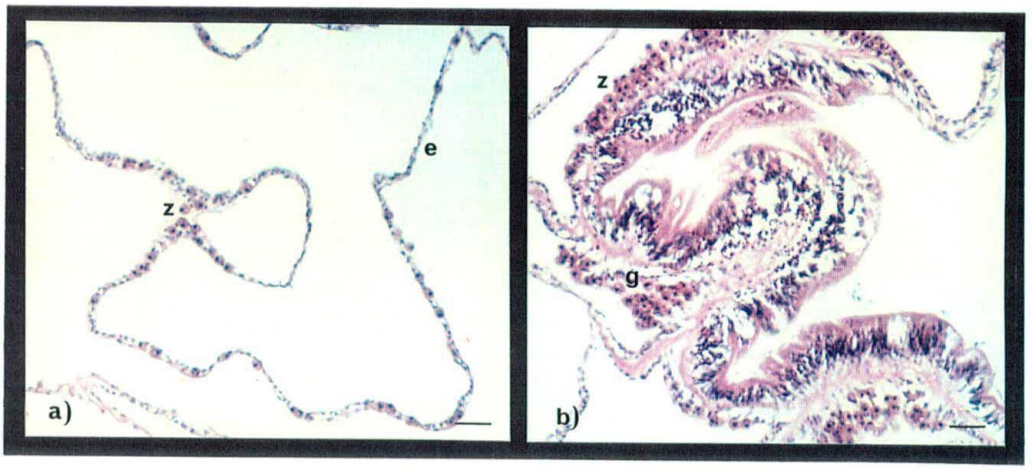

Figure 3.1 Longitudinal 8 μm sections of the a) inner basal endoderm and b) outer gastrodermal coenosarc of *A. aspera*. Sections are stained with Mayer's Haematoxylin and Eosin. e, represents endodermal tissue; g, gastrodermis of the coenosarc; and z, zooxanthellae. Scale bars = 25 μm.

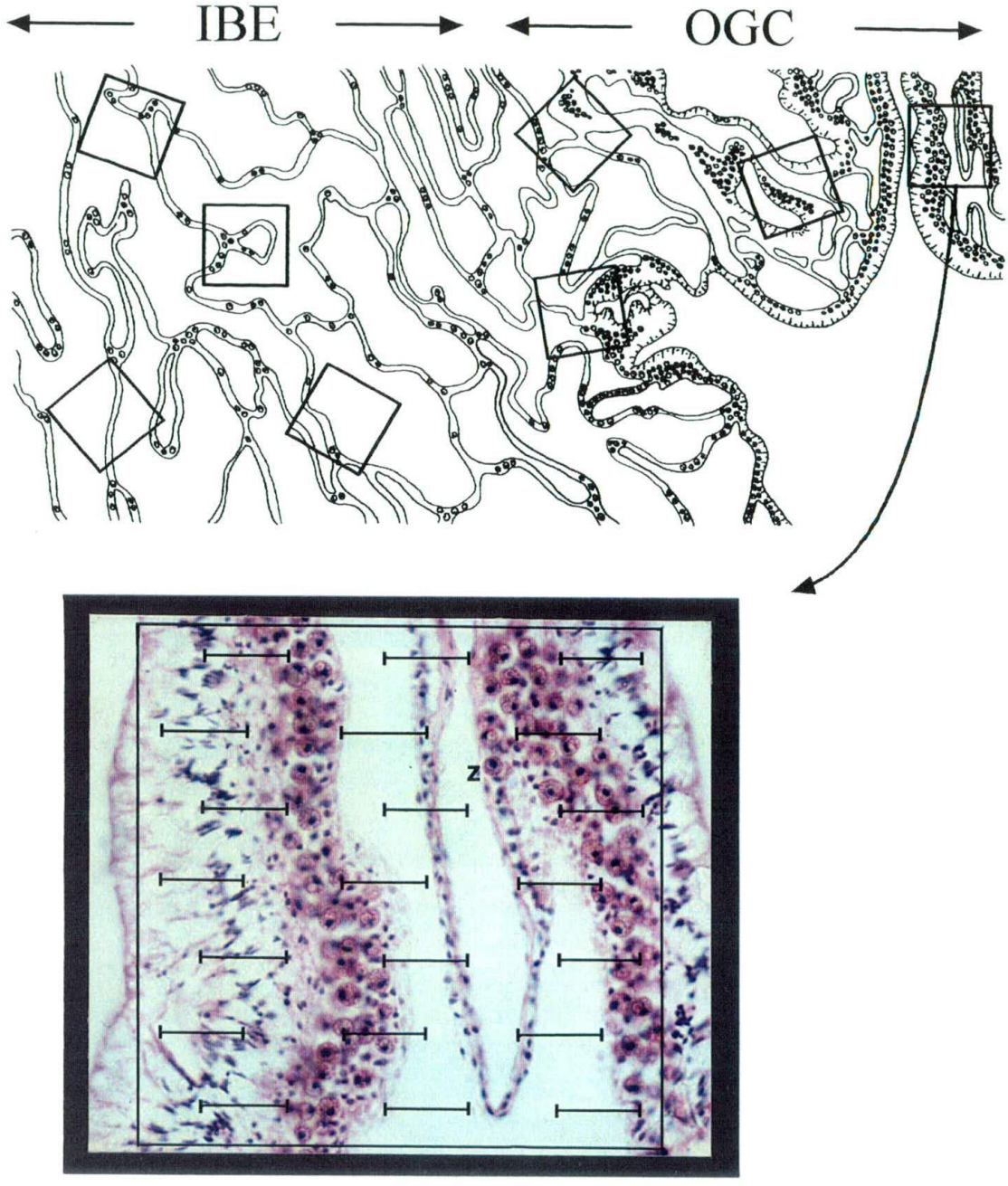

Figure 3.2 Diagrammatic longitudinal section of *A. aspera*, showing the sampling protocol used to quantify zooxanthellae densities in the inner basal endoderm (IBE) and outer gastrodermal coenosarc (OGC). □, denotes sampling sites 6 x 10^{-5} cm^3. Insert shows actual sampling site in the outer gastrodermal coenosarc with a Weibel graticule superimposed. The 8 µm section is stained with Mayer's Haematoxylin and Eosin. z, represents zooxanthellae. Magnification x 400

At all histological sampling sites, tissue volume was estimated by calculating the proportion of coral tissue to non-tissue within each field of view using standard stereological procedures for the Weibel graticule eyepiece (eg. Gander 1970). For each sampling site, the total number of end points of each of the 21 test lines overlying coral tissue was calculated, and divided by the total number of end points (42) present on the eyepiece (Fig. 3.2). The resultant proportion of coral tissue to non-tissue (hereafter referred to as the 'tissue mass index') was then multiplied by the sampling unit volume, 6×10^{-5} cm^3, to provide an estimate of tissue volume for each field of view (eg. Gander 1970). All zooxanthellae counts were then standardized per cubic centimetre of coral tissue. Differences in tissue mass index and zooxanthellae densities between treatments, species, colony size-classes and tissue locations were then assessed using several analyses of variance.

PHOTOPIGMENT CONCENTRATIONS

To determine photopigment concentrations, subsamples were measured immediately after collection and their volume was calculated to the nearest 0.10 mm^3 (using the equation for a cylinder). To obtain adequate coral tissue for extraction, three of the replicate subsamples collected per colony were pooled. They were then rinsed briefly in distilled water, placed into 8 ml of 100% acetone and transferred to a freezer at -18°C for 24 hours. Solvent fractions were collected, and using the same procedure, three additional extractions were conducted every 2 hours. Solvent fractions were then pooled for each sample. As shown by repeated measurement of the photopigment content of each sample, this process extracted in excess of 85% of the photopigments from each sample (unpublished data). Extracts were centrifuged for 5 minutes at 3000 rpm, and 3.5 mls of each was placed into a 1 cm path cell length quartz cuvette. Absorption readings, individually referenced against a quartz cuvette filled with 100% acetone, were then determined for each extract at wavelengths of 750, 663, 645, 630, 510 and 480 nm, using a LKB Biochrom Ultraspec III UV/Visible spectrophotometer. This entire operation was carried out in dim light to avoid photodestruction of the pigments.

The equations derived by Jeffrey & Humphrey (1975) were used to convert absorption readings to total chlorophyll a and total chlorophyll c_2 concentrations (µg / ml of solvent). Total carotenoid concentrations were determined crudely using the equation in Strickland and Parsons

(1972) derived for extractions in 90% acetone. Absorption readings taken at 645 nm were used to check for the presence of endolithic algae in the sample and to ensure that chlorophyll a concentrations were calculated accurately and without bias (eg. see Kleppel et al. 1989). Readings taken at 750 nm were used to calibrate turbidity blanks (eg. see Strickland & Parsons 1972) and to standardize all of the photopigment measurements. All photopigment concentrations were then quantified:

$$\text{per unit coral tissue volume} = \left(\mu g \,/\, (cm^3 \text{ of subsample x mean tissue mass index}) \right) \text{ and}$$

$$\text{per algal cell} = \left((\mu g \,/\, cm^3 \text{ of coral tissue}) \,/\, (\text{mean \# zooxanthellae} \,/\, cm^3 \text{ of coral tissue}) \right).$$

Differences in photopigment content per unit coral tissue volume and per algal cell between treatments, species and colony size-classes were then assessed with analyses of variance.

STATISTICAL ANALYSES

In all analyses of variance, tests for normality were conducted by examining Wilk-Shapiro rankit plots of analysis residuals (Shapiro & Wilk 1965). Variance homogeneity was also tested using Cochran's C value and, where necessary, data were transformed before analysis to homogenize variances (Winer 1971). *Post hoc* comparisons of means were performed using the methods of Tukey (1953) and Krammer (1956), which accommodate unequal cell sizes. In all analyses, data for the *in situ* controls were analyzed separately from that of all the other treatments, because the *in situ* controls were not placed on experimental racks, as was the case for colonies in all other treatments. Due to the size and complexity of the analysis models used in this study, only relevant statistical tests and ANOVA tables for experimental colonies have been included in the Results Section. The statistics tables for the *in situ* controls have not been included. Where sources of variation are described as 'non-significant', they were not statistically significant at $p < 0.05$ or by graphical interpretation. Further details of the statistical analyses are provided in the Results Section.

RESULTS

EFFECTS OF DEPTH CHANGES ON ASPECTS OF THE PHOTOPHYSIOLOGY OF CORALS

TISSUE MASS INDEX

The tissue mass index was on average 24% higher in *Acropora aspera* (0.33 ± 0.01 SE), than in *Acropora millepora* (0.27 ± 0.01, $p < 0.001$, Tab. 3.1 & Fig. 3.3-a). This difference between the species, was evident at each of the two tissue locations, the outer gastrodermal coenosarc and the inner basal endoderm (Fig. 3.3-b,c), and indicates that *A. aspera* is a more perforate species. Tissue mass index in both species were higher (on average by 15%) in the outer gastrodermal coenosarc (0.31 ± 0.01), than in the inner basal endoderm (0.27 ± 0.01, $p < 0.01$, Tab. 3.1 & Fig. 3.3-b,c). Obviously, the outer gastrodermal coenosarc, which includes the mesentarial filaments, oral disc and coenchyme is more likely to constitute a greater tissue mass index than the inner basal endoderm.

Table 3.1 Mixed model ANOVA to test for differences in tissue mass index of *A. aspera* and *A. millepora* colonies between and among treatments, species, colony size-classes and tissue locations in experiment 2. The analysis was performed on non-transformed data and excludes data for the *in situ* controls (the only colonies not placed onto experimental racks). NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/15	14.95	$p < 0.01$
Species (Sp)	1/15	37.32	$p < 0.001$
Tissue Location (Tl)	1/15	14.61	$p < 0.01$
Tmt*Sp	3/15	11.36	$p < 0.01$
Tmt*Tl	3/15	2.70	$p < 0.05$
Sp*Tl	1/15	0.02	NS
Tmt*Sp*Tl	3/15	2.41	$p < 0.01$
Rack	15/30	0.05	NS
Size (Si)	2/30	0.34	NS
Tmt*Si	6/30	3.07	$p < 0.05$
Sp*Si	2/30	0.39	NS
Tl*Si	2/30	2.08	$p < 0.05$
Tmt*Sp*Si	6/30	4.54	$p < 0.05$
Tmt*Tl*Si	6/30	2.21	$p < 0.05$
Sp*Tl*Si	2/30	1.46	NS
Tmt*Sp*Tl*Si	6/30	1.67	$p < 0.05$
Si*Rack	30/4104	0.08	NS
Colony	12/36	0.57	NS
Subsample	36/4104	< 0.01	NS
Residual	4104		
Total	4247		

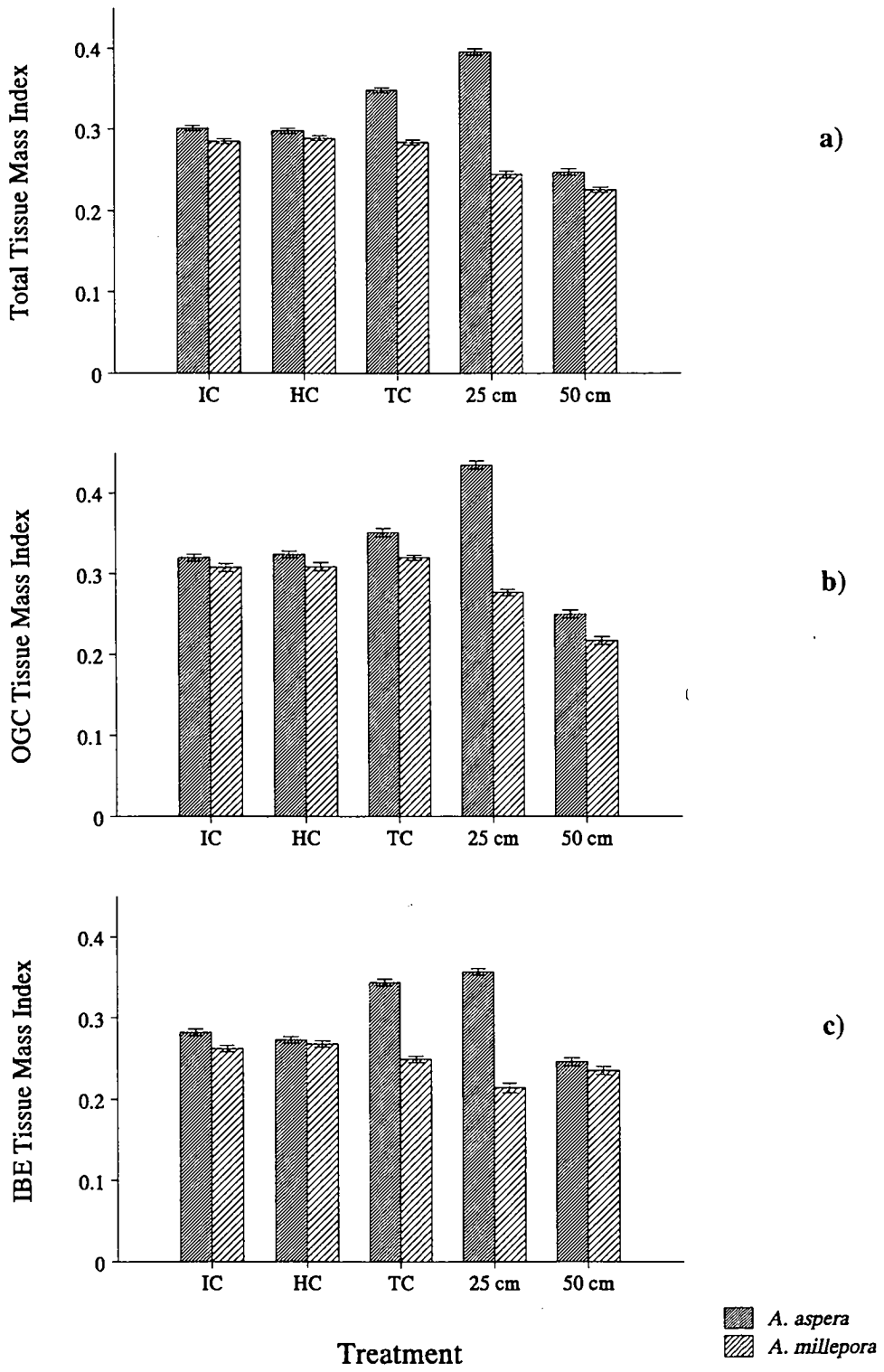

Figure 3.3 Tissue mass index of *A. aspera* and *A. millepora* (mean ± SE), as a function of treatment, for: a) both tissue locations combined (total), b) the outer gastrodermal coenosarc (OGC), and c) the inner basal endoderm (IBE). IC represents the *in situ* controls; HC, the handling controls; TC, the translocated controls; 25 cm, the 25 cm transplants; and 50 cm, the 50 cm transplants. Data are from 6 readings, taken in 4 sites at each of 2 tissue locations, from the sections of 3 subsamples / colony for each of 6 small , medium and large colonies / treatment. Sample sizes range from 180 to 648 histological readings.

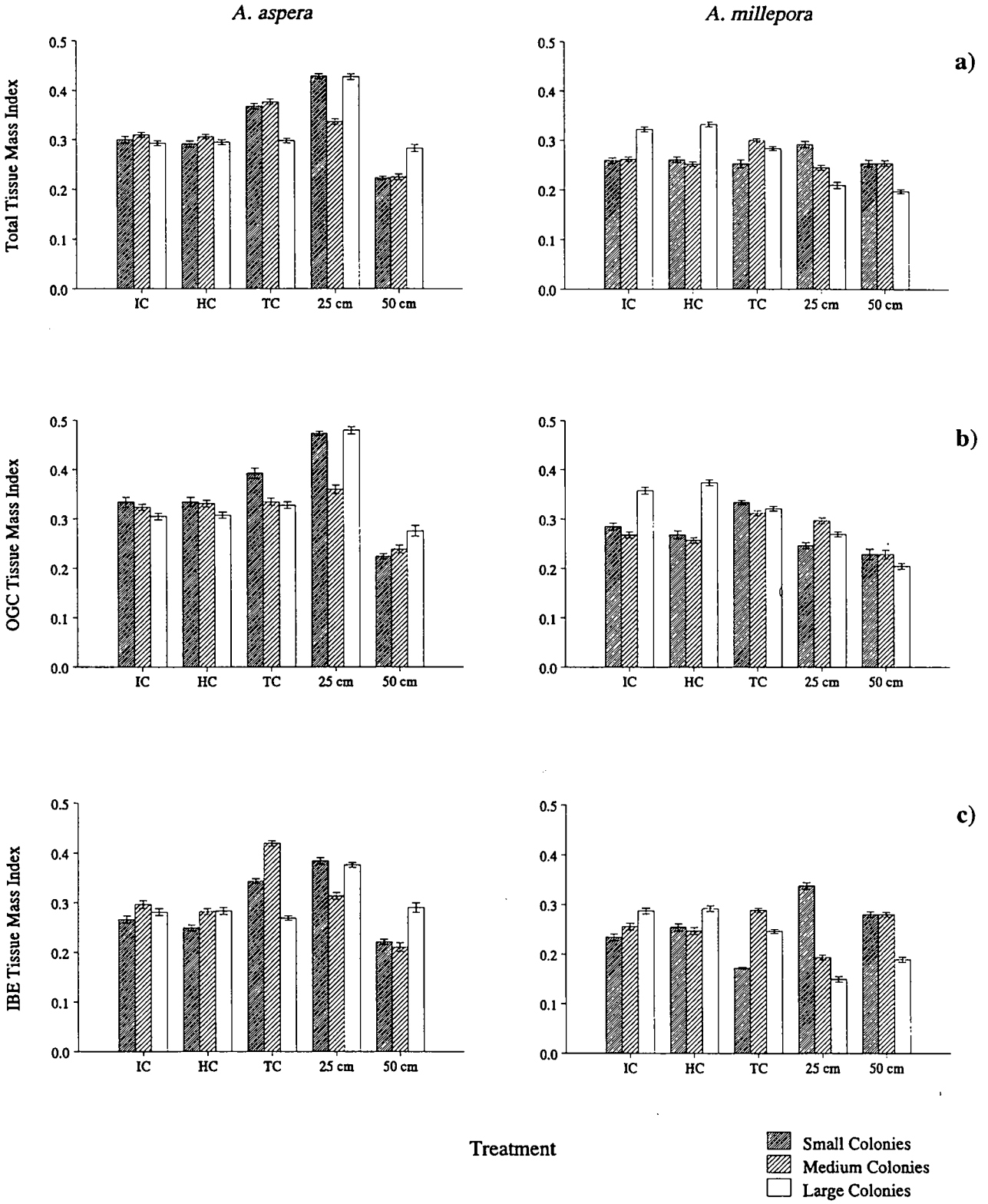

Figure 3.4 Tissue mass index of *A. aspera* and *A. millepora* (mean ± SE), as a function of their size and treatment, for: a) both tissue locations combined (total), b) the outer gastrodermal coenosarc (OGC), and c) the inner basal endoderm (IBE). Abbreviations are defined in Figure 3.3. Sample sizes range from 36 to 216 histological readings / size-class.

The responses of transplantation differed between the two species ($p < 0.01$, Tab. 3.1 & Fig. 3.3-a). In *A. millepora*, tissue mass index was highest among all of the shallowest controls and decreased with increasing depth. Colonies exhibited a 14% decrease in tissue mass index in response to a 25 cm depth change, and a 21% decrease in response to a 50 cm depth change, relative to the controls. In contrast, tissue mass index in *A. aspera* was highest in the translocated controls and the 25 cm transplants compared with the other controls and 17% lower in the deeper 50 cm transplants. In both species, the decrease in tissue mass index in the 50 cm transplants was most pronounced in the outer gastrodermal coenosarc (Fig. 3.3-b). In *A. aspera*, the increase in tissue mass index in the translocated controls and the 25 cm transplants occurred in both tissue locations (Fig. 3.3-b,c).

Tissue mass index in the three size-classes of each species also responded differently among treatments, particularly in response to habitat relocation and depth changes ($p < 0.05$, Tab. 3.1 & Fig. 3.4-a). For *A. aspera*, tissue mass index did not differ between size-classes in the *in situ* or handling controls, but was highly variable between size-classes in the translocated controls and the 25 cm transplants, and 21% higher in large colonies than in smaller ones in the deeper transplants. In contrast in the *in situ* and handling controls of *A. millepora,* tissue mass index was 27% higher in large colonies than in smaller ones. These size-specific trends for *A. millepora* also altered in response to habitat relocation and reversed in response to both depth changes, where tissue mass index was on average 24% higher in small and medium sized colonies than in large ones. Size-specific changes in tissue mass index among treatments, for *A. millepora*, were most pronounced in the inner basal endoderm (Fig. 3.4-c), and for *A. aspera*, in both tissue locations (Fig. 3.4-b,c). Overall, reductions in tissue mass index in response to depth changes were most pronounced in small and medium sized colonies of *A. aspera* and in large colonies of *A. millepora.*

ZOOXANTHELLAE NUMBERS / cm^3

There were marked differences in zooxanthellae densities between the species ($p < 0.01$, Tab. 3.2 & Fig. 3.5-a). On average, densities were 25% higher in *A. aspera* ($1.5 \pm 0.01 \times 10^6$ / cm^3) than in *A. millepora* ($1.2 \pm 0.02 \times 10^6$ / cm^3). This trend was evident at both tissue locations, but most pronounced in the inner basal endoderm, where zooxanthellae densities were 56% higher in *A. aspera*

than in *A. millepora* (Fig. 3.5-b,c). Zooxanthellae densities were greater in the more perforate species. In both species, zooxanthellae densities in the outer gastrodermal coenosarc ($1.9 \pm 0.02 \times 10^6$) were double those in the inner basal endoderm ($0.9 \pm 0.01 \times 10^6$, $p < 0.001$, Tab. 3.2 & Fig. 3.5-b,c). They were around 79% and 151% higher in the outer gastrodermal coenosarc for *A. aspera* and *A. millepora*, respectively.

Table 3.2 Mixed model ANOVA to test for differences in the number of zooxanthellae / cm^3 of coral tissue x 10^6 in *A. aspera* and *A. millepora* colonies between and among treatments, species, colony size-classes and tissue locations in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/15	2.15	$p < 0.05$
Species (Sp)	1/15	12.38	$p < 0.01$
Tissue Location (Tl)	1/15	76.56	$p < 0.001$
Tmt*Sp	3/15	1.11	$p < 0.05$
Tmt*Tl	3/15	1.56	$p < 0.05$
Sp*Tl	1/15	0.42	NS
Tmt*Sp*Tl	3/15	0.98	$p < 0.05$
Rack	15/30	0.04	NS
Size (Si)	2/30	0.19	NS
Tmt*Si	6/30	1.28	$p < 0.05$
Sp*Si	2/30	0.65	NS
Tl*Si	2/30	0.94	$p < 0.05$
Tmt*Sp*Si	6/30	0.98	$p < 0.05$
Tmt*Tl*Si	6/30	0.31	NS
Sp*Tl*Si	2/30	0.04	NS
Tmt*Sp*Tl*Si	6/30	0.30	NS
Si*Rack	30/4104	0.02	NS
Colony	12/36	0.09	NS
Subsample	36/4104	< 0.01	NS
Residual	4104		
Total	4247		

Zooxanthellae for the two species responded differently between treatments ($p < 0.05$, Tab. 3.3 & Fig. 3.5-a). In *A. millepora*, zooxanthellae densities were highest in the *in situ* and handling controls and they decreased with increasing depth. Zooxanthellae densities in the translocated controls, 25 cm transplants and 50 cm transplants of *A. millepora* were 19%, 24% and 32% lower, respectively, relative to the *in situ* and handling controls. The lower densities occurred in the outer gastrodermal coenosarc (Fig. 3.5-b), and not in the inner basal endoderm (Fig. 3.5-c). For *A. aspera*, zooxanthellae densities were much more variable among treatments, they and did not differ significantly in response to depth changes, relative to the *in situ*, handling and translocated controls

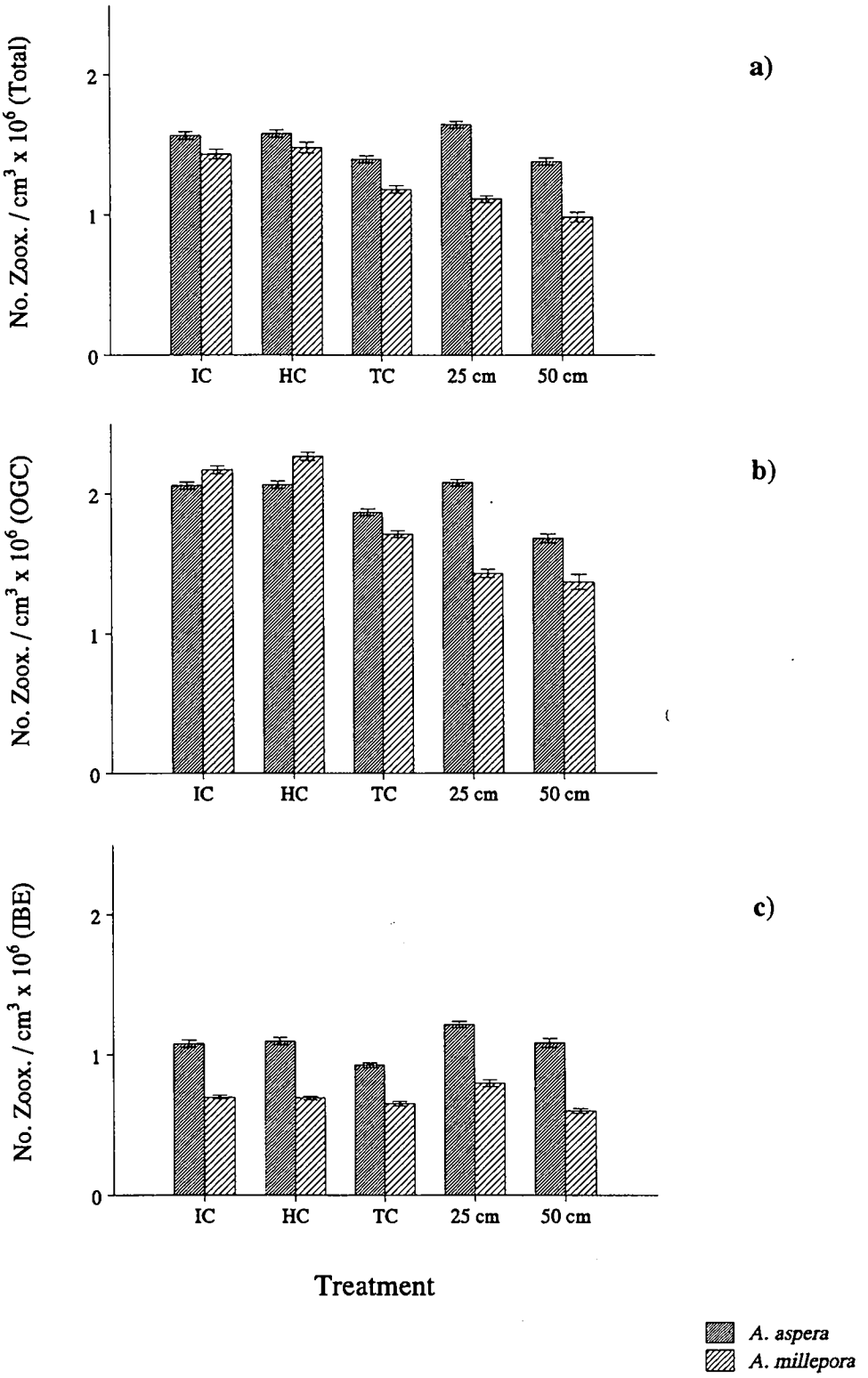

Figure 3.5 Zooxanthellae numbers per unit tissue volume in *A.aspera* and *A. millepora* (mean ± SE), as a function of their treatment, for: a) both tissue locations combined (total), b) the outer gastrodermal coenosarc (OGC), and c) the inner basal endoderm (IBE). Abbreviations are defined in Figure 3.3. Sample sizes raange from 180 to 648 histolological readings / species.

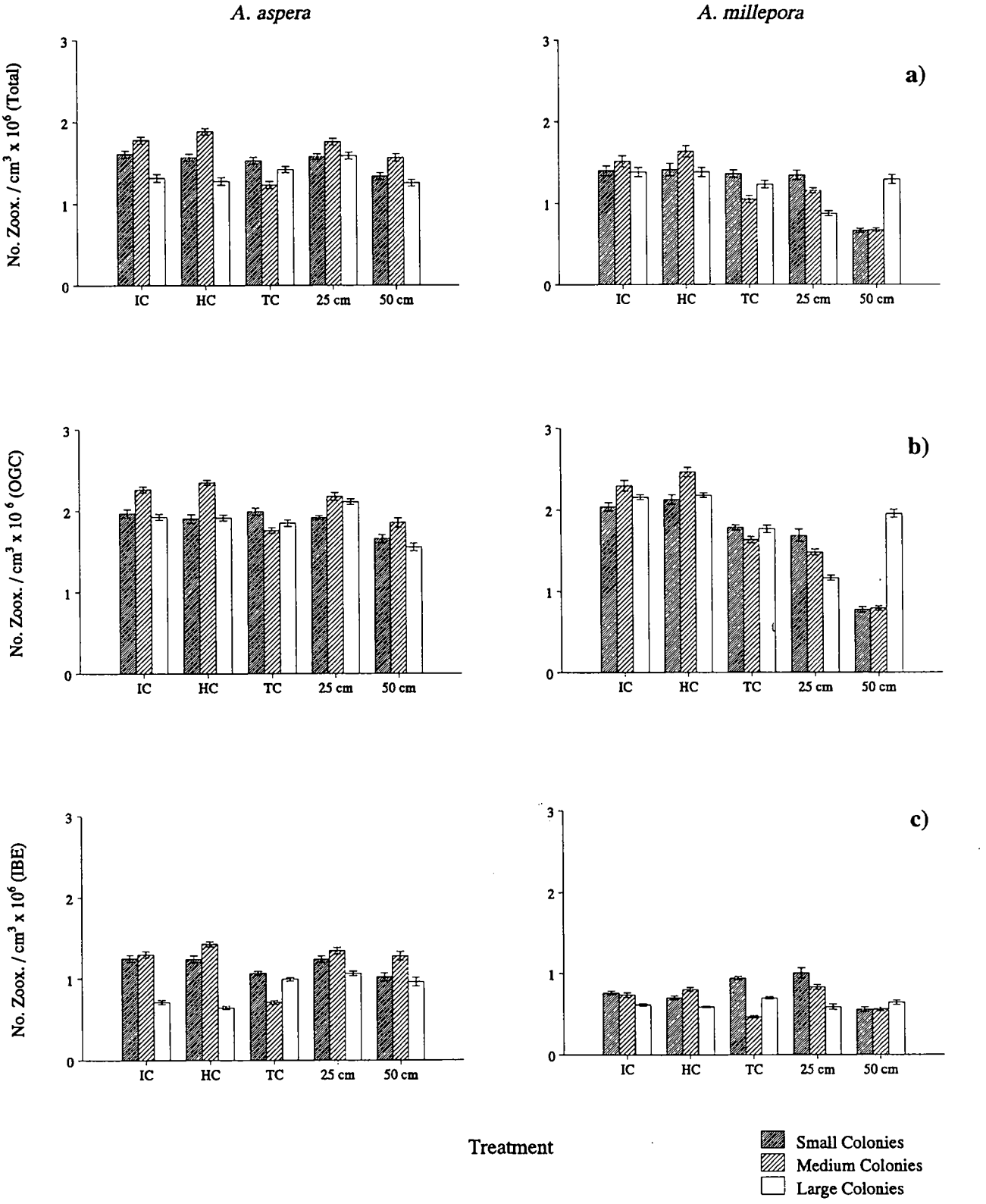

Figure 3.6 Zooxanthellae numbers per unit tissue volume in *A.aspera* and *A. millepora* (mean ± SE), as a function of their size and treatment, for: a) both tissue locations combined (total), b) the outer gastrodermal coenosarc (OGC), and c) the inner basal endoderm (IBE). Abbreviations are defined in Figure 3.3. Sample sizes range from 36 to 216 histological readings / size-class.

(Fig. 3.5-a). This indicates that the more perforate of the two species, has a greater ability to maintain zooxanthellae densities in response to small depth changes.

Size-specific zooxanthellae densities for the two species varied between treatments ($p < 0.05$, Tab. 3.3 & Fig. 3.6-a). In the *in situ* and handling controls of both species, zooxanthellae densities were around 18% higher in medium sized colonies than in small and large colonies combined. This trend in *A. aspera* was unaffected by depth changes and altered only slightly in response to habitat relocation. For *A. millepora,* size-specific zooxanthellae densities altered slightly in response to habitat relocation and to a greater extent with increasing depth. In the 50 cm transplants of *A. millepora*, the density of zooxanthellae in large colonies was similar to the controls, but in small and medium sized colonies were 50% lower. This response was particularly evident in the outer gastrodermal coenosarc (Fig. 3.6-b). Reductions in zooxanthellae densities in response to depth changes for *A. millepora* were most pronounced in small and medium sized colonies. However, all colonies of *A. aspera*, irrespective of their size, maintained zooxanthellae densities in response to depth changes, relative to the controls.

PHOTOPIGMENT CONCENTRATIONS

Pigment / Algal Cell

The two species showed marked differences in concentrations of chlorophyll a, chlorophyll c_2 and total carotenoids per algal cell ($p < 0.001$, Tab. 3.3, 3.4, 3.5 & Fig. 3.7-a,b,c). Concentrations of chlorophyll a, chlorophyll c_2 and total carotenoids per cell were 85%, 88% and 63%, respectively, higher in *A. millepora* than in *A. aspera*. However, in both species concentrations of pigments per cell were ranked as: Total carotenoids > chlorophyll c_2 > chlorophyll a.

Table 3.3 Five-factor nested ANOVA to test for differences in the content of Chl a / algal cell x 10^6 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/7	13.84	$p < 0.001$
Species (Sp)	1/7	72.91	$p < 0.001$
Tmt*Sp	3/7	6.73	$p < 0.001$
Rack	7/14	0.39	NS
Size (Si)	2/14	0.02	NS
Tmt*Si	6/14	2.29	$p < 0.01$
Sp*Si	2/14	0.66	NS
Tmt*Sp*Si	6/14	1.53	$p < 0.05$
Si*Rack	14/58	0.35	NS
Colony	12/58	0.75	NS
Residual	58		
Total	117		

Table 3.4 Five-factor nested ANOVA to test for differences in the content of Chl c_2 / algal cell x 10^6 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/7	15.01	$p < 0.001$
Species (Sp)	1/7	71.15	$p < 0.001$
Tmt*Sp	3/7	5.94	$p < 0.001$
Rack	7/14	0.23	NS
Size (Si)	2/14	0.40	NS
Tmt*Si	6/14	1.60	$p < 0.05$
Sp*Si	2/14	1.83	$p < 0.05$
Tmt*Sp*Si	6/14	1.91	$p < 0.01$
Si*Rack	14/58	0.47	NS
Colony	12/58	0.91	NS
Residual	58		
Total	117		

Table 3.5 Five-factor nested ANOVA to test for differences in the content of Carotenoids / algal cell x 10^6 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/7	18.25	$p < 0.001$
Species (Sp)	1/7	56.58	$p < 0.001$
Tmt*Sp	3/7	13.84	$p < 0.001$
Rack	7/14	0.92	NS
Size (Si)	2/14	0.09	NS
Tmt*Si	6/14	5.30	$p < 0.001$
Sp*Si	2/14	0.26	NS
Tmt*Sp*Si	6/14	2.08	$p < 0.05$
Si*Rack	14/58	0.99	NS
Colony	12/58	0.95	NS
Residual	58		
Total	117		

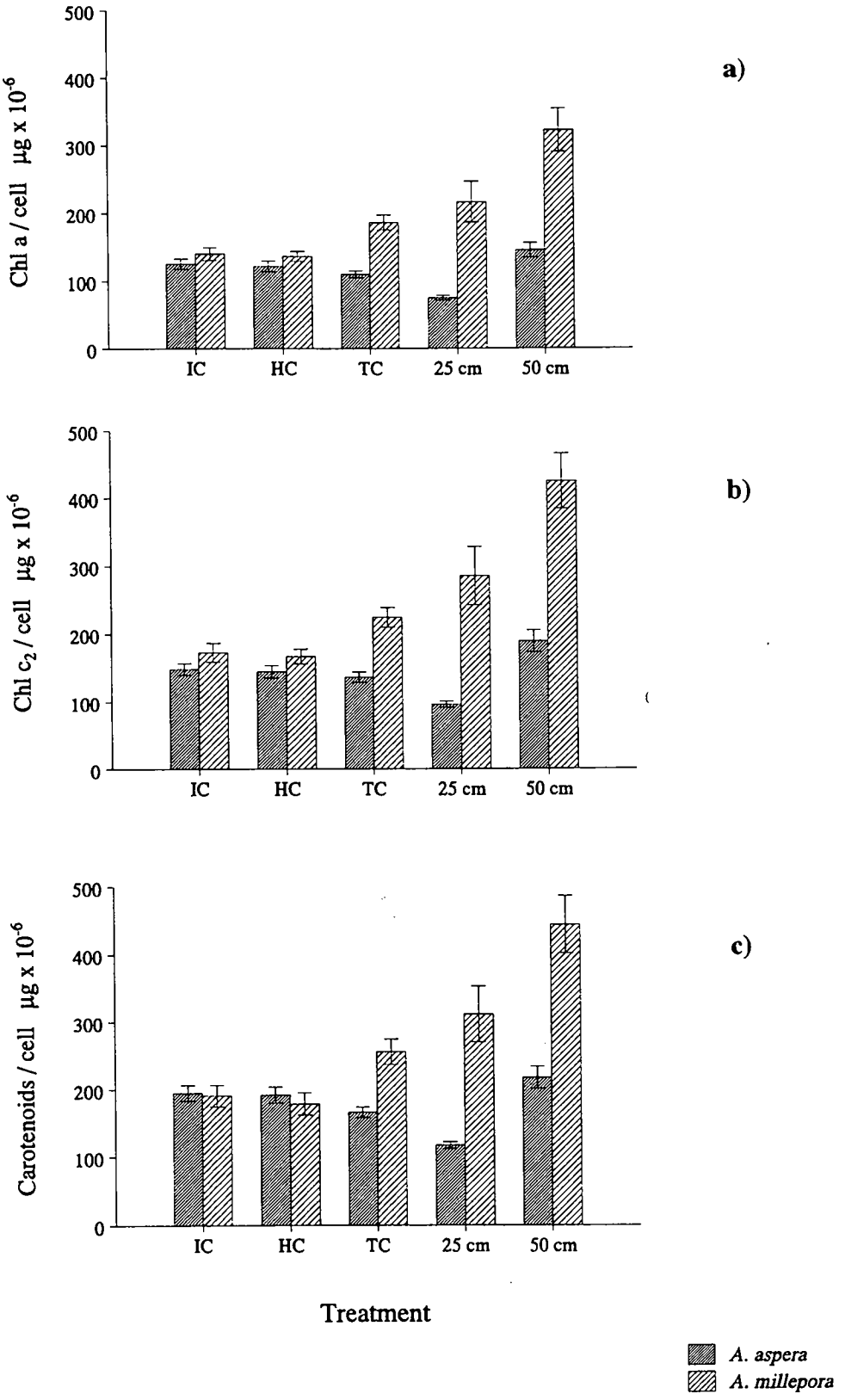

Figure 3.7 Photopigment content per algal cell in *A. aspera* and *A. millepora* (mean ± SE), as a function of their treatment, for: a) chlorophyll a, b) chlorophyll c_2 and c) total carotenoids. Abbreviations are defined in Figure 3.3. Sample sizes range from 10 to 18 coral samples / species.

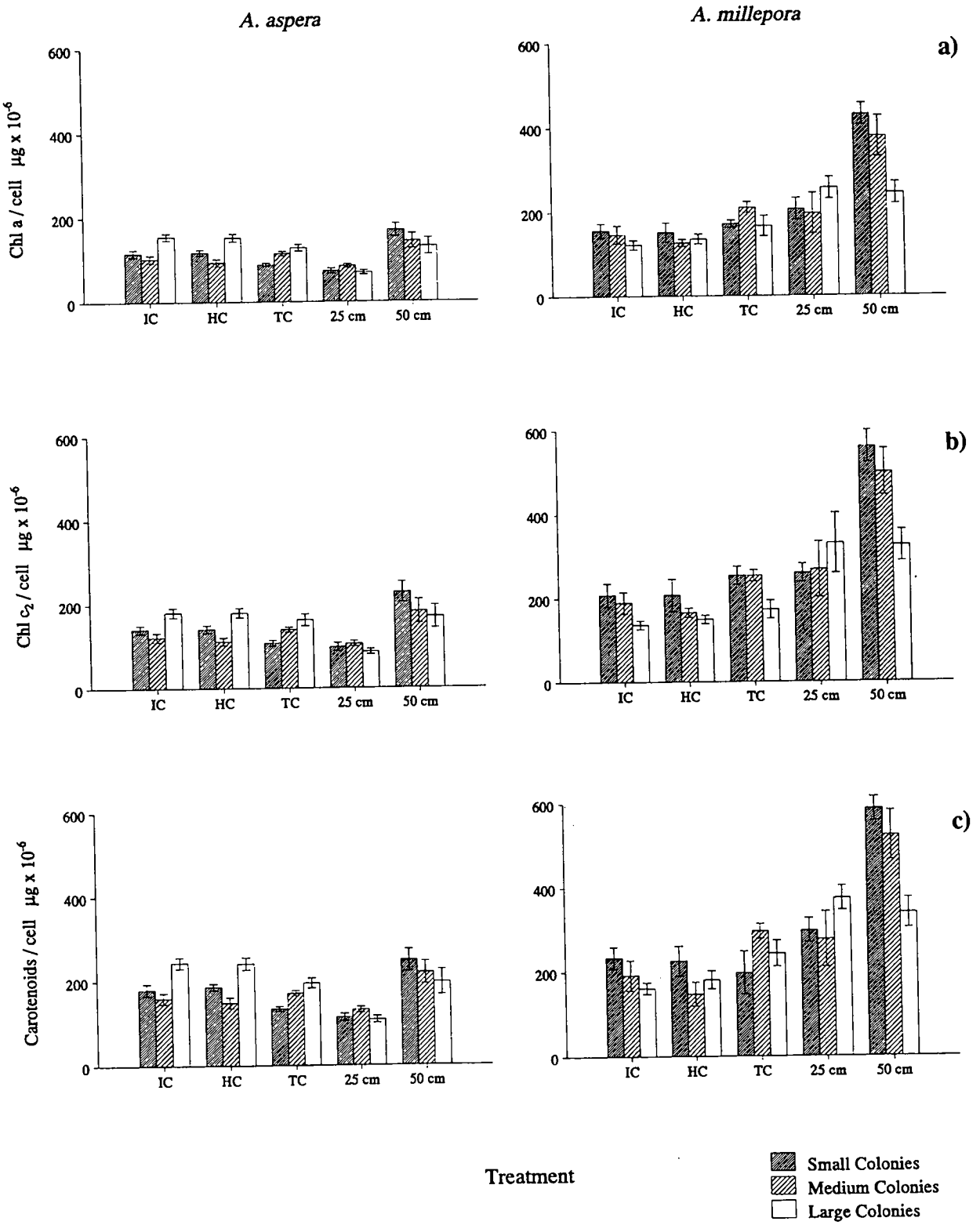

Figure 3.8 Photopigment content per algal cell in *A. aspera* and *A. millepora* (mean ± SE), as a function of their size and treatment, for a) chlorophyll a, b) chlorophyll c_2, and c) total carotenoids. Abbreviations are defined in Figure 3.3. Sample sizes range from 4 to 8 replicates / size-class.

Species-specific changes in photopigment contents per cell differed among treatments ($p < 0.001$, Tab. 3.3, 3.4, 3.5 & Fig. 3.7-a,b,c). In both species, however, concentrations of chlorophyll a, chlorophyll c_2 and total carotenoids responded similarly to the treatments. In *A. millepora*, concentrations were lowest in the *in situ* and handling controls, increased by 35% in response to habitat relocation and by 65% and 142%, respectively, in response to the 25 cm and 50 cm depth changes. Increases in pigments per cell were most pronounced for chlorophyll c_2 (Fig. 3.7-b). These findings show that colonies of *A. millepora* increased photopigments per algal cell in response to small depth changes, despite a reduction in zooxanthellae densities. In contrast, colonies of *A. aspera* appear to have little ability to increase algal pigment content in response to depth changes (Fig. 3.7-a,b,c). All pigments per cell in *A. aspera* decreased on average by 51% in response to the 25 cm depth change, relative to all of the controls. These decreases were most pronounced for chlorophyll a and total carotenoids (Fig. 3.7-a,c). Chlorophyll c_2 actually increased by 32% per cell (c.f. all of the controls) in response to the 50 cm depth change, but this is a minor increase compared with the changes in the depth transplants of *A. millepora* (Fig. 3.7-b).

For the two species, size-specific algal pigment content differed among treatments ($p < 0.01$ for Tab. 3.3 & 3.5, $p < 0.05$ for Tab. 3.4 & Fig. 3.8-a,b,c). In all *A. aspera* controls, pigment concentrations per cell were around 39% higher in large colonies than in smaller ones, but they did not differ between size-classes at 25 cm and 50 cm. In *A. millepora*, algal pigment contents did not differ between size-classes in any of the controls or in the 25 cm transplants. However, in the deeper transplants, pigment contents per cell were around 64% higher in small and medium sized colonies combined compared to large ones. In other words, the most marked increase in pigment contents per algal cell in *A. millepora* occurred in small and medium sized colonies in response to the 50 cm depth change. This contrasts with *A. aspera*, where all colonies, irrespective of their size, increased their chlorophyll c_2 content per cell in response to this depth change.

Pigment / cm^3

Most trends in concentrations of pigments per unit tissue volume (Fig. 3.9-a,b,c) were identical to those established for pigment contents per algal cell (Fig. 3.7-a,b,c), but increases in

pigments per unit tissue volume in response to depth changes were less pronounced for both species ($p < 0.001$, Tab. 3.6, 3.7, 3.8 & Fig. 3.9-a,b,c). There were two notable exceptions to the similarity between the pigment per unit tissue volume and pigment per cell data. Increases in pigment contents per cell in response to the 50 cm depth change were most pronounced in small and medium sized colonies of *A. millepora* (Fig. 3.8-a,b,c), but large colonies exhibited the greatest increase in pigment contents per unit tissue volume (Fig. 3.10-a,b,c). Similarly, increases in chlorophyll c_2 contents per cell in response to the 50 cm depth change did not differ between size-classes in *A. aspera* (Fig. 3.8-b), but chlorophyll c_2 contents per unit tissue volume did (Fig. 3.10-b). Typically, small and medium sized colonies of *A. aspera* located 50 cm deeper exhibited higher chlorophyll c_2 contents per unit tissue volume than large colonies (Fig. 3.10-b). Consequently, large colonies of *A. millepora* and small and medium sized colonies of *A. aspera* were the most effective at increasing pigment contents per unit tissue volume in response to the larger depth change.

Table 3.6 Five-factor nested ANOVA to test for differences in the content of Chl a / cm^3 of coral tissue x 10^6 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/7	10.17	$p < 0.001$
Species (Sp)	1/7	74.84	$p < 0.001$
Tmt*Sp	3/7	4.81	$p < 0.01$
Rack	7/14	1.09	NS
Size (Si)	2/14	0.05	NS
Tmt*Si	6/14	1.31	NS
Sp*Si	2/14	0.81	NS
Tmt*Sp*Si	6/14	3.32	$p < 0.05$
Si*Rack	14/58	1.12	NS
Colony	12/58	1.39	NS
Residual	58		
Total	117		

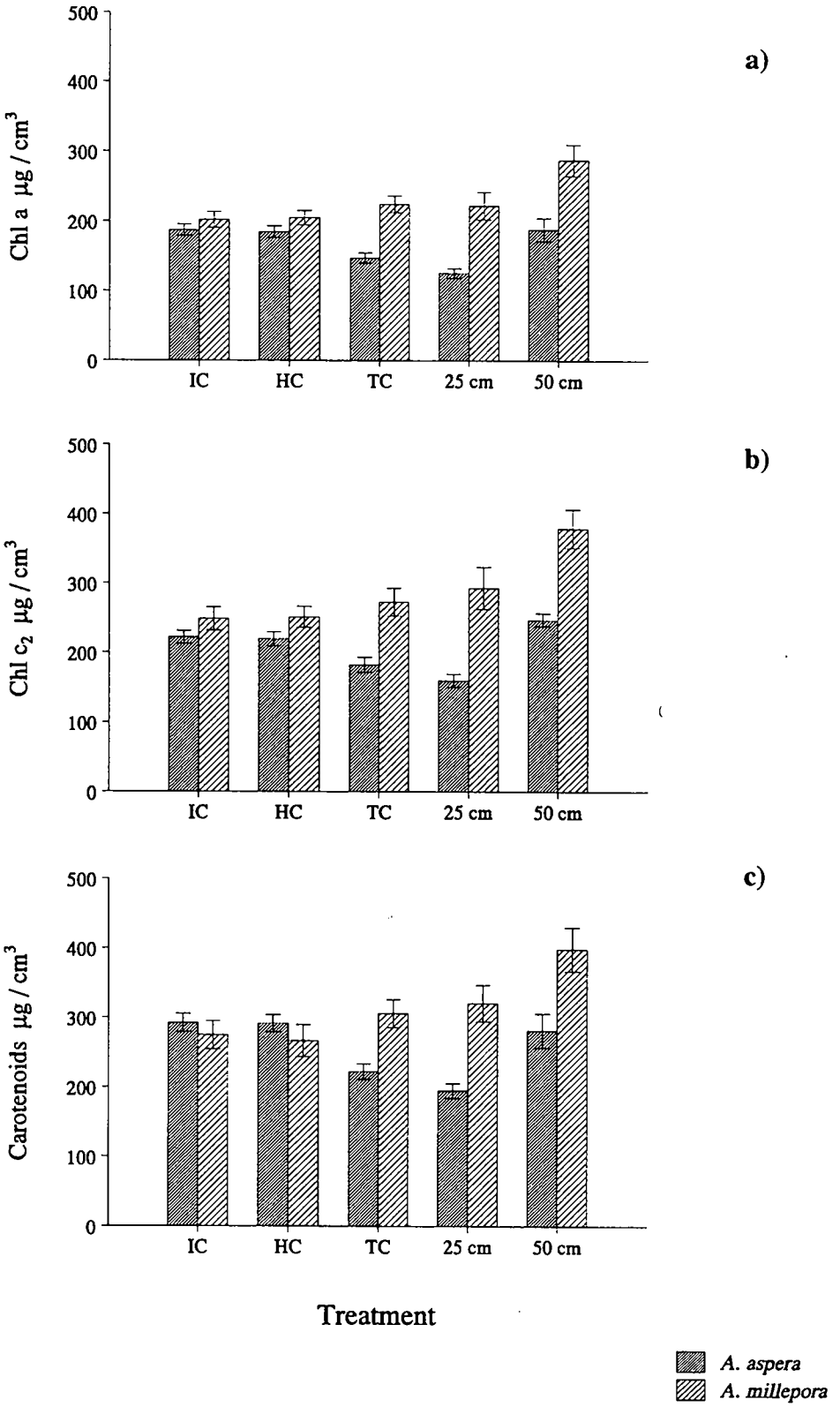

Figure 3.9 Photopigment content per unit tissue volume in *A. aspera* and *A. millepora* (mean ± SE), as a function of their treatment, for a) chlorophyll a, b) chlorophyll c_2, and c) total carotenoids. Abbreviations are defined in Figure 3.3. Sample sizes range from 10 to 18 replicates / species.

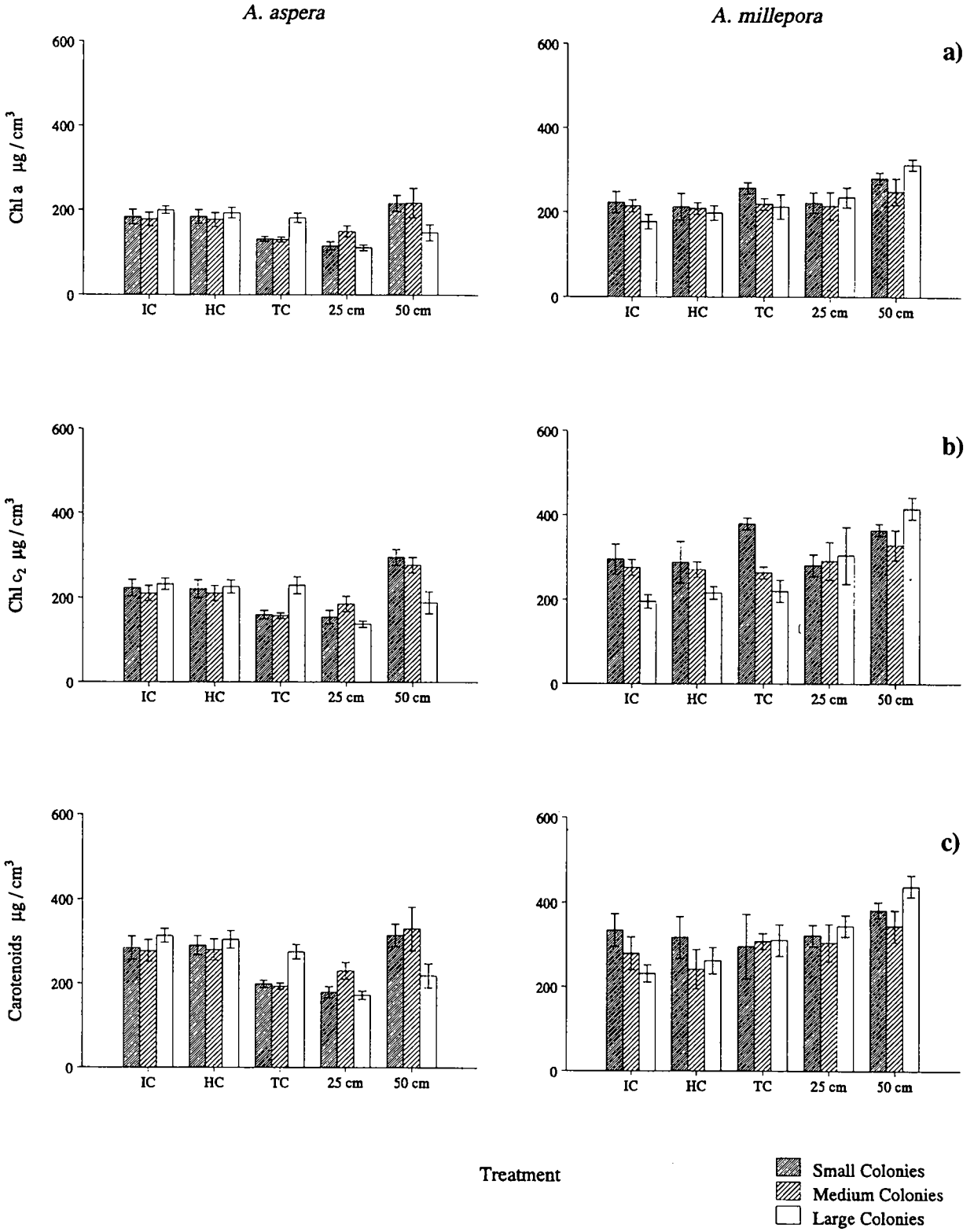

Figure 3.10 Photopigment content per unit tissue volume in *A. aspera* and *A. millepora* (mean ± SE), as a function of their size and treatment, for a) chlorophyll a, b) chlorophyll c_2 and c) total carotenoids. Abbreviations are defined in Figure 3.3. Sample sizes range from 4 to 8 replicates / size-class.

Table 3.7 Five-factor nested ANOVA to test for differences in the content of Chl c_2 / cm^3 of coral tissue x 10^6 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/7	10.87	$p < 0.001$
Species (Sp)	1/7	72.67	$p < 0.001$
Tmt*Sp	3/7	3.51	$p < 0.05$
Rack	7/14	0.95	NS
Size (Si)	2/14	1.08	NS
Tmt*Si	6/14	1.08	NS
Sp*Si	2/14	0.32	NS
Tmt*Sp*Si	6/14	5.21	$p < 0.001$
Si*Rack	14/58	1.36	NS
Colony	12/58	1.80	NS
Residual	58		
Total	117		

Table 3.8 Five-factor nested ANOVA to test for differences in the content of Carotenoids / cm^3 of coral tissue x 10^6 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on log (x + 1) transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/7	14.84	$p < 0.001$
Species (Sp)	1/7	44.67	$p < 0.001$
Tmt*Sp	3/7	16.80	$p < 0.001$
Rack	7/14	3.60	NS
Size (Si)	2/14	0.34	NS
Tmt*Si	6/14	4.74	$p < 0.001$
Sp*Si	2/14	3.41	NS
Tmt*Sp*Si	6/14	4.82	$p < 0.05$
Si*Rack	14/58	2.81	NS
Colony	12/58	2.07	NS
Residual	58		
Total	117		

Pigment Ratios

Chlorophyll a to chlorophyll c_2 ratios were identical in both species (0.81 ± 0.01 for both), irrespective of treatment (p = NS, Tab. 3.9). However in both species, the ratio of chlorophyll a to chlorophyll c_2 decreased by 7% in deeper sites, relative to the controls ($p < 0.05$, Tab. 3.9). Across all treatments, the ratio was ordered as: In situ and handling controls (0.84 ± 0.02) = translocated controls (0.83 ± 0.01) > 25 cm transplants (0.78 ± 0.01) = 50 cm transplants (0.77 ± 0.02). Colony size did not influence the ratio of chlorophyll a to chlorophyll c_2 in *A. aspera* colonies, but it did in colonies of *A. millepora* ($p < 0.01$, Tab. 3.9). For all size-classes of *A. aspera*, the ratio averaged 0.81 ± 0.02. For *A. millepora*, it was: Large colonies (0.87 ± 0.03) > medium sized ones (0.78 ± 0.02) =

small colonies (0.75 ± 0.03).

Table 3.9 Five-factor nested ANOVA to test for differences in the ratio of Chl a to Chl c_2 in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on non-transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/7	17.04	$p < 0.05$
Species (Sp)	1/7	2.91	NS
Tmt*Sp	3/7	2.85	NS
Rack	7/14	6.52	NS
Size (Si)	2/14	22.83	$p < 0.01$
Tmt*Si	6/14	6.44	NS
Sp*Si	2/14	25.78	$p < 0.01$
Tmt*Sp*Si	6/14	6.32	NS
Si*Rack	14/58	3.94	NS
Colony	12/58	4.43	NS
Residual	58		
Total	117		

Acropora aspera had a significantly higher proportion of total carotenoids relative to chlorophyll a than *A. millepora* ($p < 0.001$, Tab. 3.10). The ratio of chlorophyll a to carotenoids in *A. aspera* (0.65 ± 0.01) was 16% lower than that evident in *A. millepora* (0.77 ± 0.01). Despite this difference, ratios of chlorophyll a to carotenoids did not differ among treatments for either species (p = NS, Tab. 3.10), and were not significantly influenced by colony size (p = NS, Tab. 3.10).

Table 3.10 Five-factor nested ANOVA to test for differences in the ratio of Chl a to Carotenoids in *A. aspera* and *A. millepora* colonies between and among treatments, species and colony size-classes in experiment 2. The analysis was performed on non-transformed data and excludes data for the *in situ* controls. NS = non significant.

Source of Variation	Degrees of Freedom	% Mean Square	Significance
Treatment (Tmt)	3/7	2.11	NS
Species (Sp)	1/7	68.23	$p < 0.001$
Tmt*Sp	3/7	11.79	$p < 0.001$
Rack	7/14	3.67	NS
Size (Si)	2/14	1.96	NS
Tmt*Si	6/14	2.63	NS
Sp*Si	2/14	1.94	NS
Tmt*Sp*Si	6/14	2.82	NS
Si*Rack	14/58	3.01	NS
Colony	12/58		NS
Residual	58		
Total	117		

DISCUSSION

PHOTOPHYSIOLOGICAL TRAITS OF THE SPECIES

In perforate species, like *Acropora aspera* and *Acropora millepora*, tissues are not solely organized into polyps (outer gastrodermal coenosarc), but may also form intricate and extensive networks (inner basal endoderm) through the surface of skeletal structures (Barnes & Lough 1992; Fig. 3.3). As shown here, differences in tissue mass index occur among two perforate species of the same genus (Fig. 3.3), and between size-classes within a species, such as *A. millepora* (Fig. 3.4). Differences in tissue mass index (Fig. 3.3), reflect differences in tissue volume and skeletal porosity, which are influenced by rates of vertical skeletal extension and thickening (Barnes 1971, 1973; Darke 1991; Fig. 2.18 Chapter 2). The two species also differ in morphology. Branching colonies of *A. aspera* generally have faster rates of linear extension, more porous branch tips and much weaker observed basal attachment plates, compared to corymbose colonies of *A. millepora* (Bothwell 1984; Chapter 2; pers. obs.). The early development of strong basal attachment plates in colonies of *A. millepora*, may also account for lower tissue mass index in small and medium sized colonies, than in large colonies of this species (i.e. tissue may grow in the plate rather than the branches, Fig. 3.4). Tissue mass index for reef corals have not been measured previously, but Barnes & Lough (1992) have shown that tissue thickness in a range of massive *Porites* species, is greatest in large colonies; a pattern comparable with the differences in tissue mass index found between size-classes of *A. millepora*. However, tissue mass index in *A. aspera* were independent of colony size (Fig. 3.4), and this could suggest that a combination of colony growth rates and morphology may influence tissue mass index in perforate reef corals.

Zooxanthellae densities and photopigment contents also differed between the two species; *A. aspera* had the higher zooxanthellae densities (Fig. 3.5), but the lower photopigment content per algal cell or per unit tissue volume (Fig. 3.7, Fig. 3.9). This lends some support to the hypothesis that the amount of skeleton occupied by tissue may be related to zooxanthellae densities in reef corals (Houck 1978; Kinzie et al. 1984; Kinzie & Hunter 1987). It can be speculated that these differences between the species may also be governed by the spatial and physical constraints dictated by colony

morphology. Unlike arborescent colonies of *A. aspera*, corymbose colonies of *A. millepora* have short, compact branches, and may receive a lower total amount of incident light, because of shading between adjacent branches (eg. Titlyanov 1991). For *A. millepora*, effects of shading due to branch compaction may be offset by higher photopigment contents in the coral tissue, to ensure a greater acquisition of light. These photophysiological differences between the two species are comparable with those found by Houck (1978) and Kinzie et al. (1984) between *P. damicornis* an imperforate, compact branching species and *Montipora verrucosa* Lamarck a perforate and more laminar species, with the former exhibiting the lowest zooxanthellae densities and the highest photopigment contents. For perforate corals, like *A. aspera* and *A. millepora*, zooxanthellae densities and photopigment concentrations may be influenced by their tissue volume and morphology. For both species, medium sized colonies had the highest zooxanthellae densities compared to small and large colonies combined (Fig. 3.6). Despite this unusual trend, concentrations of all photopigments per unit tissue volume did not differ between colony size-classes for either species (Fig. 3.10).

PHOTO-RESPONSES TO DEPTH CHANGES

The responses of the species to depth changes were different and related to their morphologies and photophysiological traits. Overall, photo-responses to depth changes were more pronounced in corymbose colonies of *A. millepora* than in branching colonies of *A. aspera* (Tab. 3.11). Nevertheless, both exhibited marked alterations in tissue mass index in response to depth changes (Tab. 3.11), which directly reflect alterations in their rates of vertical skeletal extension (see Chapter 2). With the exception of the 25 cm transplants of *A. aspera*, which exhibited a 24% increase in tissue mass index with an increase in skeletal extension, tissue mass index decreased by 14 to 21% in all other depth transplant colonies of the two species coincident with similar reductions in skeletal extension (Fig. 2.18, Chapter 2; Fig. 3.3). This indicates to some extent that increasing depth may ultimately reduce

Table 3.1 A summary of the photophysiological traits of *A. aspera* and *A. millepora*, and their responses to 25 cm and 50 cm depth changes. An increase or decrease in a trait, as a result of transplantation into deeper water, is shown by the direction of each arrow and the magnitude of a response is shown by the number of arrows. The tissue location or pigment contributing the most pronounced effect on the direction of arrows is shown and colony size-class trends for each trait are listed in decreasing order of magnitude. --, indicates no significant change occurred as a result of transplantation; OGC, outer gastrodermal coenosarc; IBE, inner basal endoderm; S, small colonies; M, medium sized colonies; and L, large colonies; /, shows no significant difference between size-classes; Chl a, chlorophyll a; Chl c_2, chlorophyll c_2; and Car, total carotenoids.

Trait	*A. aspera*			*A. millepora*		
	Controls	25 cm	50 cm	Controls	25 cm	50 cm
Tissue Mass Index	high	↑↑	↓	low	↓	↓↓
Tissue Location		OGC>IBE	OGC		IBE>OGC	OGC
Colony Size-Class Trends	S/M/L	S/L>M	L>S/M	L>S/M	S>M>L	S/M>L
No. Zooxanthellae / cm^3	high	--	--	low	↓	↓↓
Tissue Location					OGC	OGC
Colony Size-Class Trends	M>S/L	--	--	M>S/L	S>M>L	L>S/M
Photopigments / cell	low	↓	↑	high	↑↑	↑↑↑
Pigment		Chl a / Car	Chl c_2		Chl c_2	Chl c_2
Colony Size-Class Trends	L>M/S	S/M/L	S/M/L	S/M/L	S/M/L	S/M/L
Photopigments / cm^3	low	↓	↑	high	↑	↑↑
Pigment		Chl a / Car	Chl c_2		Chl c_2	Chl c_2
Colony Size-Class Trends	S/M/L	S/M/L	S/M>L	S/M/L	S/M/L	L>S/M

tissue mass index in reef corals. In addition to these physical factors, changes in the nutritional status of the environment may have occurred with increasing depth. As noted by Barnes & Lough (1992), a well-fed colony may have a thicker tissue layer than a starved colony having the same size and skeletal growth rate. Colony size-classes exhibiting a reduction in tissue mass index with increasing depth differed between species. Large colonies of *A. millepora* and small and medium sized colonies of *A. aspera* exhibited the most marked reductions in tissue mass index in response to the 50 cm depth change (Fig. 3.4, Tab. 3.11).

The 50 cm transplants of *A. aspera* and all depth transplants of *A. millepora* showed an increased photopigment content per unit tissue volume, relative to the controls (Fig. 3.9, Tab. 3.11).

Increases in photopigment content may enhance light harvesting ability and are comparable with those found for reef corals in response to a decrease in light intensity and a concurrent decrease in the proportion of red light (Kinzie et al. 1984; Chalker et al. 1988; Falkowski et al. 1990). Studies which have documented similar responses of reef corals to depth related changes in light have used species which inhabit broad depth ranges, often in excess of 10 m (eg. *Porites lobata* Dana, Maragos 1972; *Montastrea annularis* Ellis and Solander, Dustan 1979, 1982, Wyman et al. 1987, *Stylophora pistillata* Esper, McCloskey & Muscatine 1984; Porter et al. 1984; Gattuso et al. 1991). This study found marked increases in photopigment content among shallow reef flat corals in response to depth changes of less than 50 cm. Most studies tend to attribute increases in photopigment content to alterations in the size of photosynthetic units and photopigment contents per algal cell (Dustan 1979, 1982; Falkowski & Dubinsky 1981; Barnes & Chalker 1990), rather than to alterations in zooxanthellae numbers per unit tissue volume or their spatial arrangement. As shown here, alterations in zooxanthellae numbers (Fig. 3.5) and changes in tissue mass index (Fig. 3.3) probably play an important role in determining photopigment concentrations and species-specific responses to depth changes.

The more perforate species, *A. aspera*, maintained zooxanthellae densities more readily than *A. millepora*, which tended to alter its pigment content per algal cell (Tab. 3.11). Photopigment contents per algal cell within colonies of *A. millepora* increased by 65% and 142%, respectively, in response to a 25 cm and 50 cm depth change, despite concurrent reductions in zooxanthellae densities and tissue mass index (Fig. 3.3, Fig. 3.5, Fig. 3.7). It is proposed that decreases in zooxanthellae densities and tissue mass index may minimize the effects of cell shading, enhance skeletal reflection of light within the coral tissue and influence increases in algal pigment content by providing a larger surface area for the acquisition of light by photosynthetic units (eg. See also Dustan 1982; McCloskey & Muscatine 1984). This would also account for the small increase (ca. 36%) in chlorophyll c_2 content per cell exhibited by the 50 cm transplant colonies of *A. aspera*, since they only exhibited minor reductions in zooxanthellae densities and tissue mass index, compared to *A. millepora* (Fig. 3.3, Fig. 3.5, Fig. 3.7). Greater reductions in zooxanthellae densities may not result in greater increases in photopigment content per algal cell, as shown by Dustan (1979) in transplant colonies

of *M. annularis* in response to a depth change from 10 to 15 m. However, for *A. millepora* and *A. aspera*, slight reductions in zooxanthellae densities and tissue mass index in combination with increases in photopigment contents per cell, may occur in response to small depth changes.

The photophysiological responses of corals to depth-related changes in light are analogous to those which occur in the chloroplasts and leaves of terrestrial plants to optimize light acquisition (Boardman 1977; Chow et al. 1988; Vogelmann 1993). Nishio et al. (1993) recently demonstrated that photosynthetic pigments and CO_2 fixation gradients were highest just below the upper leaf surface in low-light adapted leaves and in the middle of high-light adapted leaves. Similar photopigment gradients may be evident in the tissues of reef-building corals, with the upper section of a leaf equivalent to the outer gastrodermal coenosarc and the middle of section of a leaf equivalent to the inner basal endoderm. Reductions in tissue mass index and zooxanthellae densities per unit tissue volume were most pronounced in the outer gastrodermal coenosarc, rather than in the inner basal endoderm (Fig. 3.3-b,c, 3.5-b,c, Tab. 3.11). If these reductions facilitate increases in photopigments per cell and per tissue mass, photopigment concentrations are likely to be higher in the outer gastrodermal coenosarc, than in the inner basal endoderm. Testing this hypothesis awaits development of paradermal sectioning techniques for the tissues of reef-building corals.

This study also demonstrates that photopigment content per unit tissue volume varied among colony size-classes of both species. Photopigment contents within the tissue were generally highest in small and medium sized colonies of *A. aspera* and in large colonies of *A. millepora* (Fig. 3.10, Tab. 3.11). Most photophysiological studies on corals have assumed equivalent photo-responses among colony size-classes of the same species and do not mention the size of the corals studied (Maragos 1972; Dustan 1979, 1982; Titlyanov et al. 1980; Chang et al. 1983; Porter et al. 1984; Gattuso et al. 1991). A unique study by Jokiel and Morrissey (1986) revealed that the relationship between photosynthesis and irradiance (P-I curve) in *P. damicornis* collected at depths of 50 cm, was inversely related to colony size. This response is comparable with the changes exhibited by *A. millepora* (Fig. 3.10). Jokiel & Morrissey (1986) stressed that colony size was an important determinant of photo-responses. The present study also demonstrates that photo-responses may differ among species.

Colonies of *A. aspera,* when transplanted 25 cm deeper than the controls, had responses that

appeared to reduce light harvesting abilities (Tab. 3.11). While these colonies maintained zooxanthellae densities at levels equivalent to the controls (Fig. 3.5), they exhibited marked reductions (ca. 51%) in pigment content per algal cell and per unit tissue volume (Fig. 3.7 & 3.9). Several factors may have contributed to these changes. For example, fast rates of skeletal extension (Fig. 2.18, Chapter 2) and high tissue mass index (Fig. 3.3, Tab. 3.11), may have influenced the rate at which colonies respond to changes in light regimes.

Large colonies of *A. millepora* and small and medium sized colonies of *A. aspera* are best able to maximize light acquisition in response to a 50 cm change in depth. Of the two species, *A. millepora* is the most effective at rapidly responding to depth-related changes in light by increasing its photopigment contents, even in response to very small changes in depth.

Extant colonies of *A. millepora*, particularly large colonies, are likely to acclimatize to changes in light attenuation and spectral composition in response to small changes in sea level, whereas extant colonies of *A. aspera*, even small and medium sized ones, appear to have little ability to photoadapt.

THE ROLE OF PHYSIOLOGICAL RESPONSES TO LIGHT IN CORAL ZONATION

The zonation of species is only partly related to their photophysiological traits and photo-responses to depth changes. Colonies of *A. millepora*, with observed strong basal attachment plates (Bothwell 1984), are usually common at reef crests, coincident with the strongest wave energy regimes, whereas colonies of *A. aspera*, which were observed to have little ability to attach firmly to the substratum in the field, are more common in calmer and shallower outer reef flat sites (Chapter 2). Findings presented here show that *A. millepora* is the more physiologically tolerant of deeper water than *A. aspera*. High relative levels of accessory carotenoids in *A. aspera* also indicate that this species should be more common at shallow sites, because carotenoids such as β-carotene and yellow xanthophylls are often high in corals in high light regimes, to minimize the possibility of photoinhibition (Titlyanov et al. 1980; Barnes & Chalker 1990; Gattuso et al. 1991). However, the ability of *A. aspera* and *A. millepora* to survive and photoadapt (even to a small extent) at transplant depths below their current depth range, demonstrates that additional factors, other than physiological responses to light, affect the zonation of species. Depth changes are not associated with changes in

the physical environment, such as light, temperature, salinity, turbidity and sedimentation (Buddemeier & Kinzie 1976), they also correspond with changes in competitive interactions, herbivorous grazing, predation and bioerosion (MacIntyre & Glynn 1976; Hay 1981, 1984, Davies & Hutchings 1983; Wilkinson & Evans 1988; Chapter 2). Consequently, coral responses to depth changes are likely to be multiplicative or synergistic responses to concurrent changes in several environmental variables (eg. light, temperature and salinity, Coles & Jokiel 1978), or are indirect responses to sequential changes in several environmental variables (eg. light and temperature followed by predation, Chapter 2), rather than a simple response to changes in light.

The observation that large colonies of *A. millepora* and small and medium sized colonies of *A. aspera* are most effective in surviving at deeper sites (Chapter 2) is also relevant to zonation. Small colonies of *A. millepora,* and other species like *P. damicornis* and *Goniastrea retiformis* Lamarck are usually abundant at shallow sites, and colony size increases with increasing depth (Jokiel & Morrissey 1986; Chapter 2). In contrast, large colonies of *A. aspera* are often common on outer reef flats, and smaller colonies are equally abundant from inner reef flats to reef crests (Chapter 2). This pattern of zonation is likely to occur because *A. aspera* often propagates clonally in response to mechanical stresses by fragmentation (eg. see Chapter 2). The ability of small and medium sized colonies of *A. aspera* to respond to alterations in depth, by increasing concentrations of chlorophyll c_2 within the tissue, indicates that branch fragments may readily photoadapt in response to dispersal throughout shallow reef flat zones. Despite this relationship between the photo-responses of both species and their size-specific patterns of reef zonation, population size-structures in the field are also governed to a large extent by colony age, time of recruitment, skeletal growth rates, competition for resources among size-classes, selective grazing or predation and microhabitat differences (Hughes & Jackson 1980; Sheppard 1980; Sebens 1983; Chapter 2). Severe disturbances or high wave energy regimes in unpredictable environments can also rapidly restrict the development of large size-classes across reef zones (Jokiel & Morrissey 1986).

POTENTIAL IMPACTS OF ENHANCED CLIMATE CHANGE AND SEA LEVEL RISE

Shallow-water reef corals with different morphologies and photophysiological traits are likely

to photo-respond quite differently to predicted sea level rise. As sea level rises, increased water depth over extant corals may expose them to suboptimal light regimes. Those species which can photoadapt may persist. However, changes in the physical and biological environment could limit their ability to optimize light acquisition, grow, reproduce and survive. The rate of sea level rise associated with global warming will also be important in determining the long-term fate of the corals (see Chapter 4). From findings presented here, it seems likely that extant colonies of *A. millepora*, particularly large colonies, may be most capable of photoadapting to alterations in light following sea level rise, while large colonies of *A. aspera* may be the least capable. While levels of peak clear day visible irradiance are not expected to be modified by enhanced climate change, alterations in cloud cover, sea state and water turbidity are expected to affect light attenuation in tropical waters (Smith & Buddemeier 1992). Strengthening of monsoonal westerly winds in the eastern Australian tropics, expected as a result of enhanced global warming (Climate Impact Group CSIRO 1992), may drastically affect the extent of outflow from mainland fluvial systems and subject turbid inshore fringing reefs to higher sediment or nutrient loads. As a result, increased levels of water turbidity may have profound affects on the depth range of photoadaptation for reef corals. Photoadaptive responses to small changes in sea level, in themselves, provide no indication of the ability of species to persist at deeper sites from other physical or biological agents of mortality. Even if a species can photoadapt to alterations in light, sea level rise may provide new sites for predators and competitors (eg. see Chapter 2), so that only the coral species which can recovery from injuries, outcompete new recruits and survive will remain the longest.

CHAPTER 4:

MODELS OF THE LONG-TERM EFFECTS OF DEPTH CHANGES ON THE DEMOGRAPHY OF SHALLOW-WATER REEF CORALS

INTRODUCTION

Sessile reef corals restricted to shallow depths on inshore reefs may be particularly vulnerable to enhanced global climate change and sea level rise, despite being well adapted to the broad tidal changes they deal with continuously. They are often periodically exposed to the air and subaerial stresses (Glynn 1973, 1988), and their demographic traits (eg. survival, growth and reproduction), are depth-dependent (eg. Maragos 1972; Baker & Weber 1975; Kojis & Quinn 1984). While there is an obvious need for long-term monitoring to identify coral population and community responses to environmental change, manipulative studies are also essential to understand the underlying mechanisms causing those responses. Detailed examination of species-specific demographic and physiological responses to experimentally induced small changes in depth may provide the basis for understanding future responses of coral populations and assemblages to enhanced climate change and sea level rise (Chapter 2 & 3). However, many corals live much longer than the average life-time of a field experiment or research scientist, and eustatic sea level is predicted to rise slowly at around 5 cm / decade up to 2070 (Wigley & Raper 1992). While it is not possible to simulate exactly the projected se level rise, matrix projection models can be used to predict the long-term dynamics of coral populations in response to short-term perturbations in their environment (Hughes 1984; Done 1987, 1988; Gotelli 1991), and hence can be used to assess the long-term fate of reef corals in response to specific changes in sea level.

Size-structured matrix projection models have been used to quantify long-term rates of population growth and the transient behaviour of plant and animal populations (Hartshorn 1975;

Werner & Caswell 1978; Enright & Ogden 1979). They also provide a powerful tool to evaluate the influence of life history parameters on population growth rates (Caswell & Werner 1977; Bierzychudek 1982; Hughes 1984, 1990; McFadden 1991). These models, initially developed for populations of aclonal organisms (Bernardelli 1941; Lewis 1942; Leslie 1945, 1948), may be applied to demographic data for clonal organisms with indeterminate growth (Hughes 1984; Caswell 1985, 1989), and can be used to evaluate the long-term effects of experimentally induced depth changes on the demography of shallow-water reef corals.

Given current predictions, eustatic sea level is predicted to rise around 20 cm by 2030 and by about 45 cm by 2070 (Wigley & Raper 1992). As sea level rises, new recruits may colonize presently unsuitable shallow reef sites, but extant corals will be located in gradually deepening sites and may be exposed to suboptimal environmental conditions. As a consequence, the resilience of these corals to changes in the physical and biological environment and their ability to replace themselves either sexually or asexually is likely to play an important role in determining their persistence among deeper sites. Reef corals have a diverse range of life histories (Hughes et al. 1992), and so often exhibit different responses to ecological disturbances (Bak & Criens 1981; Knowlton et al. 1981; Woodley et al. 1981; Hughes & Jackson 1985; Potts & Garthwaite 1991). Like other clonal and aclonal organisms, their reproductive strategies may also differ. Reef corals may reproduce sexually by brooding planulae or releasing gametes, or asexually by colony fission, fragmentation or intrinsic means (Harrison & Wallace 1990). However, few demographic studies have quantified the relative contributions of asexual and sexual reproduction to the population growth of clonal organisms which incorporate both modes of reproduction into their life cycle (eg. Sarukhan & Gadgil 1974; Bierzychudek 1982; McFadden 1991). In addition, most studies using size-structured projection models to evaluate the long-term dynamics or life history strategies of coral populations have focused on single species (Hughes 1984; Done 1987, 1988; McFadden 1991), rather than a range of species with different life histories (eg. see Caswell 1989; Andres and Rodenhouse 1993). This study was designed to examine the long-term effects of experimentally induced depth changes on the demography of three shallow-water reef corals with different life history traits, and to evaluate the relative importance of reproductive strategies to their rates of population growth.

Colonies of *Goniastrea retiformis* Lamarck, *Acropora millepora* Ehrenberg and *Acropora aspera* Dana were subjected to small depth changes of 25 cm, 50 cm and 1 m in controlled field experiments and their demographic responses including survival, growth, shrinkage, asexual propagation and fecundity, were monitored for a 12 month period (Chapter 2). While these species spawn gametes en mass (sexually reproduce) once per annum (Bothwell 1984; Babcock et al. 1986), and can propagate asexually by colony fission (Chapter 2), their life history traits differed considerably throughout the course of a year (Chapter 2). These species are therefore likely to exhibit quite different long-term demographic responses to depth changes.

This study uses an integrative approach to quantifying the likely fate of the species in response to specific changes in sea level. It has six objectives: 1. To construct size-class transition matrices describing the annual demographic responses of the *in situ*, handling and translocated controls and depth transplants of these species; 2. to determine the persistence of the coral populations from their measured rates of colony fission (asexual propagation), growth, shrinkage and survival. These projections assume that sexual recruitment does not occur in the field populations. They are used to quantify the contributions of asexual reproduction to rates of population growth; 3. to determine the amount of 'self-seeding' (ie. larval recruitment from within the site) required for each population to persist in a stable state. These projections assume that the planula derived from colonies within the study area are the only source of sexual recruits for each population. They are used to quantify the contributions of sexual reproduction to rates of population growth. In reality however, there is potentially a much larger source of external recruits (including all those outside the study area). Changes in local water currents may influence the distribution and settlement of coral larvae in the field (eg. Willis & Oliver 1990), and they could prevent 'self-seeding'; 4. to determine, bearing these factors in mind, the number of external recruits per annum required to maintain populations at their original size. These simulations assume that the populations derive their sexual recruits purely from external sources and do not 'self-seed'. They are used to quantify effects of externally sourced recruits on rates of population growth; 5. to a) quantify the dynamics of each population with both modes of reproduction incorporated into their life cycle, by determining their stable size-structures, transient behaviour and reproductive values, and b) quantify the demography of the species, by determining

the sensitivity of population growth rates to proportional changes in individual size-class transitions; and finally 6. to integrate these findings to speculate on the long-term effects of depth changes on the demography of these shallow-water reef corals.

MATERIALS AND METHODS

SIZE-CLASS TRANSITION MATRICES

The annual size-specific survivorship, fecundity and growth transitions of individual colonies of *Goniastrea retiformis*, *Acropora aspera* and *Acropora millepora* exhibited *in situ* and as a result of handling, habitat relocation and depth changes (See Results Chapter 2), were used to construct size-class transition matrices. Initially, 4 x 4 matrices describing the annual demographic responses of each group of treatment colonies (*G. retiformis* from experiment 1 and of *A. aspera* and *A. millepora* from experiment 2) were constructed; a total of 14 separate matrices (Tab. 4.1). The columns of each matrix represent transitions from initial size-classes, while the rows give transitions to final size-classes after a 12 month period. Adult size-categories used in each matrix represent: I, colonies 0.5 to < 25 cm^2; II, 25 to < 60 cm^2; and III, 60 to < 120 cm^2. These categories were chosen to encompass the range of colony areas in experiment 1 and 2, while maintaining at least 19 to 20 corals within each of the three size-classes (See Materials & Methods Chapter 2). Colonies of *G. retiformis* typically grow at much slower rates than those of *A. aspera* and *A. millepora* (see Results Chapter 2). Using a greater number of size-categories with much smaller size limits than those used here, could accommodate these growth differences between the species. However, dividing each group of treatment colonies into more than three size-classes would have reduced sample sizes and increased the sampling error around matrix probabilities. Choosing different adult size-categories for each species would also prevent direct comparison of the demographic responses of the three species, so the same categories were used for all three species.

The form of each matrix (Tab. 4.1), is identical to those conventionally used for populations whose structure is described by size rather than age classes (Werner & Caswell 1978; Hughes 1984; Caswell 1986, 1989; McFadden 1991). In the matrices, probabilities below the diagonal represent

Table 4.1 Annual size-class transition matrices and initial column vectors, $n_{(t)}$, for colonies of *G. retiformis*, *A. aspera* and *A. millepora*, as a function of their treatment. IC represents data for *in situ* controls; HC, the handling controls; TC, the translocated controls; 25 cm, 50 cm and 1 m, the depth transplants; E, eggs; I, colonies 0.5 to 25 cm^2; II, colonies 25 to 60 cm^2; III, colonies 60 to 120 cm^2; $\sum$, sum of transition probabilities excluding fecundities; and d_x, size specific mortality provided colonies do not undergo fission (ie. when the sum of transition probabilities in each column, excluding those at the top, does not exceed 1).

IC

G. retiformis

	E	I	II	III	$n_{(t)}$
E	0	2452	12385	34727	0
I	0	0.85	0.55	0.25	20
II	0	0.05	0.50	0.30	20
III	0	0.00	0.05	0.40	20
$\sum$	0	0.9	1.1	0.95	60
d_x	0	0.1	0	0.05	

A. aspera

	E	I	II	III	$n_{(t)}$
E	0	410	2469	9887	0
I	0	0.4	0.6	0.6	20
II	0	0.45	0.25	0.5	20
III	0	0.15	0.3	0.7	20
$\sum$	0	1	1.15	1.8	60
d_x	0	0	0	0	

A. millepora

	E	I	II	III	$n_{(t)}$
E	0	1017	6414	18424	0
I	0	0.25	0.05	0.4	20
II	0	0.2	0.2	0.05	20
III	0	0	0.45	0.55	20
$\sum$	0	0.45	0.7	1	60
d_x	0	0.55	0.3	0	

HC

G. retiformis

	E	I	II	III	$n_{(t)}$
E	0	1144	6804	26536	0
I	0	0.5	0.65	0.35	20
II	0	0	0.4	0.25	20
III	0	0	0.05	0.4	20
$\sum$	0	0.5	1.1	1	60
d_x	0	0.5	0	0	

A. aspera

	E	I	II	III	$n_{(t)}$
E	0	473	2414	8975	0
I	0	0.6	0.45	0.45	20
II	0	0.3	0.1	0.15	20
III	0	0.05	0.65	0.85	20
$\sum$	0	0.95	1.2	1.45	60
d_x	0	0.05	0	0	

A. millepora

	E	I	II	III	$n_{(t)}$
E	0	1192	5517	19072	0
I	0	0.15	0.1	0.2	20
II	0	0.1	0.2	0.05	20
III	0	0	0.25	0.5	20
$\sum$	0	0.25	0.55	0.75	60
d_x	0	0.75	0.45	0.25	

TC

G. retiformis

	E	I	II	III	$n_{(t)}$
E	0	1313	8330	28969	0
I	0	0.74	0.14	0.05	19
II	0	0.05	0.71	0.15	21
III	0	0	0.09	0.75	20
$\sum$	0	0.79	0.95	0.95	60
d_x	0	0.21	0.05	0.05	

A. aspera

	E	I	II	III	$n_{(t)}$
E	0	499	2604	9708	0
I	0	0.3	0.7	0.45	20
II	0	0.5	0.4	0.6	20
III	0	0.3	0.35	0.6	20
$\sum$	0	1.1	1.45	1.65	60
d_x	0	0	0	0	

A. millepora

	E	I	II	III	$n_{(t)}$
E	0	837	4762	20051	0
I	0	0.14	0.16	0.2	21
II	0	0.05	0.21	0.05	19
III	0	0	0.27	0.4	20
$\sum$	0	0.19	0.63	0.65	60
d_x	0	0.81	0.37	0.35	

25 cm

A. aspera

	E	I	II	III	$n_{(t)}$
E	0	320	1977	6279	0
I	0	0.2	0.35	0.6	20
II	0	0.25	0.15	0.15	20
III	0	0.1	0.5	0.75	20
$\sum$	0	0.55	1	1.5	60
d_x	0	0.45	0	0	

A. millepora

	E	I	II	III	$n_{(t)}$
E	0	471	2375	3388	0
I	0	0.1	0	0.05	20
II	0	0.5	0.24	0	21
III	0	0	0.09	0.53	19
$\sum$	0	0.6	0.33	0.58	60
d_x	0	0.4	0.67	0.42	

50 cm

A. aspera

	E	I	II	III	$n_{(t)}$
E	0	229	1690	3395	0
I	0	0.3	0.6	0.8	20
II	0	0.05	0.1	0.45	20
III	0	0	0.05	0.2	20
$\sum$	0	0.35	0.75	1.45	60
d_x	0	0.65	0.25	0	

A. millepora

	E	I	II	III	$n_{(t)}$
E	0	0	1506	6114	0
I	0	0	0	0	20
II	0	0	0	0.05	20
III	0	0	0	0.2	20
$\sum$	0	0	0	0.25	60
d_x	0	1	1	0.75	

1 m

G. retiformis

	E	I	II	III	$n_{(t)}$
E	0	41	1209	3858	0
I	0	0.8	0.75	0.65	20
II	0	0	0.5	0.35	20
III	0	0	0	0.35	20
$\sum$	0	0.8	1.25	1.35	60
d_x	0	0.2	0	0	

net growth in area into a larger size-class after a 12 month period. The diagonal describes the likelihood of an individual remaining within the same size-class after this time as a result of stasis or a balance between rates of growth and shrinkage, and probabilities above the diagonal represent contributions to a smaller size-class after this time, either through shrinkage, sexual reproduction or asexual propagation (fission). In contrast to traditional age-based matrices (eg. Leslie 1945), the sum of transition probabilities within each column (excluding those at the top), may exceed 1 as a result of colony fission. Assuming that no colonies undergo fission, size-specific mortality rates, d_x, are equal to 1 minus the sum of transition probabilities within each column (Hughes 1984; McFadden 1991).

Entries in the top row of each matrix (Tab. 4.1), denote the number of eggs, E, produced by each of the three adult size-classes after a 12 month period. These later values were determined by calculating the mean number of eggs produced per unit surface area per colony size-class of each species per annum (Fig. 2.21, Chapter 2), and multiplying these size-specific fecundities by the mean digitized surface area of colonies within each size-class.

Bold values within the first column of each matrix (Tab. 4.1), denote the probability of self-seeding, ie. eggs growing to a size I adult, a_{EI}, after a 12 month period. In the modified projection models used here, estimates of self-seeding and recruitment from external sources are simulated separately, to examine the importance of asexual propagation, sexual reproduction and recruitment, on the fate of colonies within each treatment.

POPULATION PROJECTION MODELS

Each size-class transition matrix, $\bar{A}$, was used to model population growth and size-structure over time, using standard population projection models of the form: $\bar{A} * n_{(t)} = n_{(t+1)}$, where $n_{(t)}$ is a column vector describing the size-structure of each group of treatment colonies at time t (Tab. 4.1). For the purpose of this study, each group of treatment colonies is hereafter referred to as a population. Although demographic data for each population was available for bimonthly intervals, a time interval of one year was used to model population growth within each treatment, since all species spawn en mass (sexually reproduce) only once per annum. To determine the long-term effects of depth changes

on the demography of the species, five different methods were used to quantify the relative contributions of asexual propagation, sexual reproduction and recruitment to rates of population growth, and the long-term dynamics of colonies within each treatment.

1. Persistence without Sexual Reproduction or External Recruits

Initially, the demographic traits of each population were projected through time without any sexual reproductive contributions towards population growth or any external recruits. This was achieved simply by omitting size-specific fecundity estimates within the top row of each matrix (Tab. 4.1). These modified matrices incorporating the asexual propagation of daughter colonies by fission were classified as the *fission replacement models*, since they were used to quantify the basic demographic behaviour of each population: λ_{fr}, *fission replacement model* population growth rate, given by the dominant eigenvalue of each matrix (Caswell 1986, 1989).

2. Effects of Asexual Propagation on Persistence

To assess the importance of asexual propagation to the persistence of each population, effects of fission were temporarily removed from each matrix (Tab. 4.1), while the transition probability from eggs to size I adults, a_{EI}, was calculated so that each matrix would yield a stable population over time (where $\lambda = 1$), then effects of fission were replaced. Temporary removal of the effects of fission from each matrix was achieved by removing transition probabilities derived from the asexual production of daughter colonies, leaving only those derived from the original parent colonies. These modified matrices were classified as the *fission models* and were projected through time to assess the relative contribution of asexual propagation to the growth rate of each population (eg. whether or not *fission model* population growth rates, $\lambda_f > 1$).

3. Effects of Sexual Reproduction on Persistence

To assess the importance of sexual reproduction to the persistence of each population, an estimate of each growth transition probability from eggs to size I adults, (a_{EI}, Tab. 4.1) was made so that each matrix would yield a stable population over time (where $\lambda = 1$), without any other

modifications. Values of a_{EI} for each matrix were compared to assess the importance of self-seeding to the persistence of each population. These modified matrices were classified as the *complete models*, since they included both asexual and sexual reproductive contributions to population growth.

4. Effects of External Recruits on Persistence

All *fission replacement models*, with asexual propagation as the only mode of reproduction, were used to quantify the number of external recruits required to maintain populations at their original size (where n = 60). This was achieved by adding a recruitment vector, $R_{(t)}$, describing the net number of recruits per annum, to population projection models, in the form of: $\bar{A} * n_{(t)} + R_{(t)} = n_{(t+1)}$, and solving for the number of recruits to size I adults per annum, *R*, required to yield n = 60 after 50 iterations (eg. See Hughes 1984, 1990). Differences in these simulated values between populations were also examined and compared to documented accounts of net rates of recruitment observed in the field.

5. Population Dynamics

Using standard analytical procedures for matrix projection models (eg. See Caswell 1986, 1989; de Kroon et al. 1986; Van Groenendael et al. 1988), the *complete models* incorporating both reproductive modes were used to quantify in detail the long-term dynamics of each population:

w, stable size-structure, given by the dominant vector of each matrix,

ρ, damping ratio, a measure of the rate of convergence to a stable size-structure,

v, reproductive value, the relative contribution of each size-class to population growth rate, λ , and

e, growth rate elasticity, the relative contribution of individual entries in each matrix to population growth rate, λ.

BASIC DEMOGRAPHIC ASSUMPTIONS

The simple population projection models used here, assume that transition probabilities are constant and ignore changes in demographic performance (eg. increased mortality coupled with

decreased recruitment and growth) likely to result due to crowding. Analytical procedures can be used to incorporate density-dependent effects into population projection models (eg. see Hughes 1984, 1990). However, the aim of this study is to determine the fate of treatment populations, if their measured size-class transition probabilities (from Chapter 2) were to continue indefinitely as they did in the first 12 month period. The results which follow are, therefore, based on the assumption that the transitions measured in 1992 to 1993 (for *G. retiformis*) and in 1993 to 1994 for (*A. aspera* and *A. millepora*) are the same for the 50 subsequent years.

RESULTS

LONG-TERM EFFECTS OF DEPTH CHANGES ON THE PERSISTENCE OF CORALS

PERSISTENCE WITHOUT SEXUAL RECRUITMENT

The projected fate of species differed among treatments, even without sexual reproductive contributions to population growth or any external recruits (Fig. 4.1). All treatment and control colonies of *G. retiformis* and *A. millepora* and the 50 cm transplants of *A. aspera* would eventually decline in number. Of these, all colonies of *A. millepora* and the 50 cm transplants of *A. aspera* would exhibit the most rapid population decline, with local extinction (defined arbitrarily as the time required to reach 2% of their original population size), in less than 14 years, compared to those of *G. retiformis* with extinction in 9 to 55 years. In contrast, the controls and the 25 cm transplants of *A. aspera* would persist through time and grow in number, as a result of asexual propagation

These differences in the persistence of species are shown by the projected *fission replacement model* rates of population growth, λ_{fr} (Tab. 4.2). Interestingly, rates of population growth ($\lambda_{fr} > 1$) or decline ($\lambda_{fr} < 1$) were not always depth-dependent. For *G. retiformis*, the 1 m transplants would exhibit relatively similar rates of population decline as the translocated and *in situ* controls, with local extinction in 22, 34 and 55 years, respectively, while the handling controls would become locally extinct in less than half the time (9 years, Fig. 4.1). For *A. millepora*, however, the 50 cm transplants would exhibit the fastest rates of population decline, with local extinction in only 2 years, compared

to the controls and the 25 cm transplants, with extinction in 13, 7, 5 and 6 years, respectively. The controls and the 25 cm transplants of *A. aspera* would persist and grow in number, but the 50 cm transplants would become locally extinct in only 6 years (Fig. 4.1)..

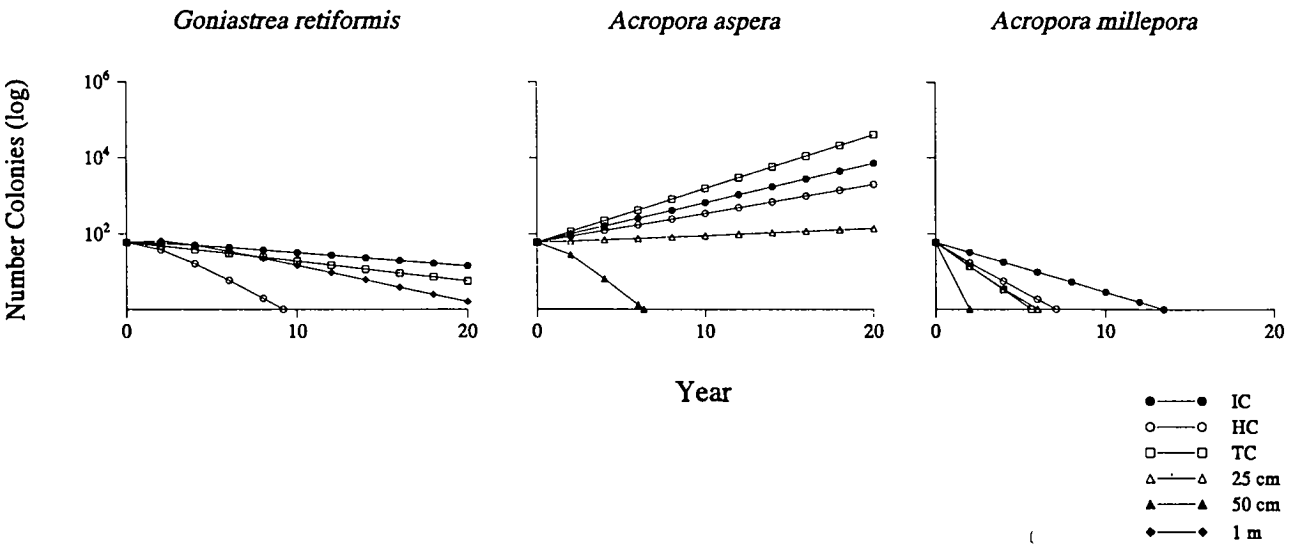

Figure 4.1 Projected fate of *G. retiformis*, *A. aspera* and *A. millepora* colonies over 20 years, as a function of their treatment, without sexual reproductive contributions or external recruits (*fission replacement model* projections). Treatment abbreviations are defined in Table 4.1.

The effects of fission on the persistence of populations is shown by species-specific differences in projected *fission model* rates of population growth, λ_f (with sexual reproductive contributions set to yield stable populations, Tab. 4.2). Overall, asexual propagation by fission contributes to the population growth of each species (where $\lambda_f > 1$) as expected, except the translocated controls of *G. retiformis* and the 25 cm transplants of *A. millepora* (where $\lambda_f = 1$). Despite this, the controls and 25 cm transplants of *A. aspera* are the only populations in which gains through asexual propagation exceed losses through mortality (where λ_f and $\lambda_{fr} > 1$). Interestingly, contributions from fission ($\lambda_f > 1$), do not necessarily delay local extinction (increase *fission replacement model* rates of population growth, λ_{fr}), in declining populations. This is demonstrated by the handling controls of *G. retiformis* which grew in number through asexual propagation ($\lambda_f > 1$), but exhibited faster rates of extinction (lower *fission replacement model* rates of population growth, $\lambda_{fr} = 0.517$), than the translocated controls with no asexually assisted growth ($\lambda_f = 1$, $\lambda_{fr} = 0.884$). Similar mortality in the translocated controls of *A. millepora* also far exceeded gains through

asexual propagation (c.f. the 25 cm transplants).

Table 4.2 Projected demographic traits for colonies of *G. retiformis*, *A. aspera* and *A. millepora* as a function of their treatment. λ_{fr}, *fission replacement model* projected rates of population growth; λ_f, *fission model* projected rates of population growth; a_{EI}, growth transition probabilities from eggs to size I adults for *complete model* projection matrices; and *R*, the number of recruits required per annum to maintain the original size of each population (N = 60). Treatment abbreviations are defined in Table 4.1.

Species	Treatment:					
	IC	HC	TC	25 cm	50 cm	1 m
G. retiformis						
λ_{fr}	0.923	0.517	0.884	--	--	0.800
λ_f	1.050	1.033	1.000	--	--	1.040
a_{EI}	2.2×10^{-5}	4.4×10^{-4}	3.9×10^{-5}	--	--	4.9×10^{-3}
R	5	30	10	--	--	12
A. aspera						
λ_{fr}	1.268	1.190	1.386	1.045	0.448	--
λ_f	1.329	1.241	1.442	1.146	1.008	--
a_{EI}	0	0	0	0	2.0×10^{-3}	--
R	0	0	0	0	38	--
A. millepora						
λ_{fr}	0.737	0.570	0.482	0.545	0.200	--
λ_f	1.010	1.001	1.002	1.000	N/A	--
a_{EI}	8.2×10^{-5}	2.6×10^{-4}	5.0×10^{-4}	3.6×10^{-4}	N/A	--
R	25	41	46	30	60	--

N/A As a result of 100% mortality among size I adults of *A. millepora*, no growth transitions probabilities of eggs to size I adults, a_{EI}, could be simulated to ensure the stability of the 50 cm transplant population.

Unfortunately, as a result of 100% mortality among size I adults of the 50 cm transplants of *A. millepora* (Tab. 4.1), it was not possible to simulate growth transition probabilities from eggs to size I adults, a_{EI}, to yield a stable population, because they face inevitable extinction. Consequently, self-seeding and fission would have no effect on the persistence of the 50 cm transplants of *A. millepora.*

EFFECTS OF SELF-SEEDING AND EXTERNALLY SOURCED RECRUITS

Apart from the controls and the 25 cm transplants of *A. aspera*, all other declining populations

would have to self-seed or gain externally sourced recruits to persist.

The value of transition probabilities from eggs to size I adults, a_{EI}, required for populations to retain a stable state, varied little in most declining populations, and ranged from 2.2×10^{-5} to 5.0×10^{-4} (Tab. 4.2). For *A. millepora*, they did not differ in response to a 25 cm depth change, relative to the controls. However, very high growth transition probabilities from eggs to size I adults were essential to maintain stability in the 50 cm transplants of *A. aspera* ($a_{EI} = 2.0 \times 10^{-3}$) and the 1 m transplants of *G. retiformis* ($a_{EI} = 4.9 \times 10^{-3}$). Consequently, self-seeding (even to a small extent) may considerably affect the persistence of species with little propensity for asexual propagation, and without recruitment it would be essential to ensure the persistence of populations located in deeper sites.

Declining populations may persist with the addition of recruits from external sources. The importance of these recruits on the persistence of populations is accentuated by the number of recruits growing to size I adults, *R*, required per annum to maintain populations at their original size (Tab. 4.2). As expected the number of recruits required was highest among populations with the fastest rates of decline (Tab. 4.2). Overall, all treatment colonies of *A. millepora* would require the greatest number of external recruits, ranging from 25 to 60 per annum, compared to *G. retiformis* and *A. aspera* with 5 to 30 and 0 to 38, respectively.

The annual recruitment required to maintain populations at their original size was not always depth-dependent (Tab. 4.2). In *G. retiformis*, for example, the handling controls required 30 recruits per year, compared to the 1 m transplants and the *in situ* and translocated controls with 12, 5 and 10 per year, respectively. This difference occurred because the handling controls exhibited 50% mortality in all size I adults, within a year and none of them grew to size II (Tab. 4.1). For *A. millepora*, the 25 cm transplants required a similar amount of annual recruitment as the controls to maintain their original population size (30, 25, 41 and 46 recruits per year, respectively), while the 50 cm transplants require 60 per year. The 50 cm transplants of *A. aspera* would require 38 recruits per year to maintain their population size, whereas all of the controls and the 25 cm transplants would persist and grow in number without any external recruits.

LONG-TERM EFFECTS OF DEPTH CHANGES ON THE DYNAMICS OF CORALS

STABLE SIZE-STRUCTURES

A property of all projection models based on fixed size-class transition probabilities (Tab. 4.1), is that populations will eventually achieve a stable size-structure, irrespective of initial size-distributions. *Complete model* projections with asexual and sexual contributions set to yield stable populations (Tab. 4.1, with the inclusion of a_{EI} in Tab. 4.2), were used to assess differences between projected population size-structures (Fig. 4.2). Assuming annual transition probabilities were to remain constant, striking differences would be evident in the projected size-structure, w, of each population (Fig. 4.2). For *A. aspera*, all of the controls and the 25 cm transplants would have a similar and stable proportion of size I, II and III adults after 50 years. All of the other populations, would be dominated by size I adults, immediately preceding local extinction. Most of the *A. aspera* populations, in contrast to the others, rely on frequent fission to attain a stable size-structure, after only 1 year (Fig. 4.2).

Differences between populations in rates of convergence to a stable size-distribution are shown by the damping ratios, ρ (Tab. 4.3). Populations of *A. aspera*, with high damping ratios would attain stable size-structures faster than *G. retiformis* and *A. millepora*. Rates of convergence to stable size-distributions would be relatively unaffected by depth changes. For *G. retiformis*, for example, the 1 m transplants would attain a stable size-structure at the same rate as the *in situ* and handling controls, but at a rate faster than the translocated controls. Similarly, for *A. aspera*, the 50 cm transplants would attain a stable size-structure at the same rate as the controls, but the 25 cm transplants would exhibit the most rapid rate of convergence. For *A. millepora*, stable size-structures would be attained more rapidly by the *in situ* and handling controls, than by the translocated controls and the 25 cm transplants. Of course, the 50 cm transplants of *A. millepora* would face only immediate extinction. Although asexual propagation appears to promote rates of convergence to stable size-distributions (eg. in populations of *A. aspera*), depth changes appear to have little effect on these rates of convergence.

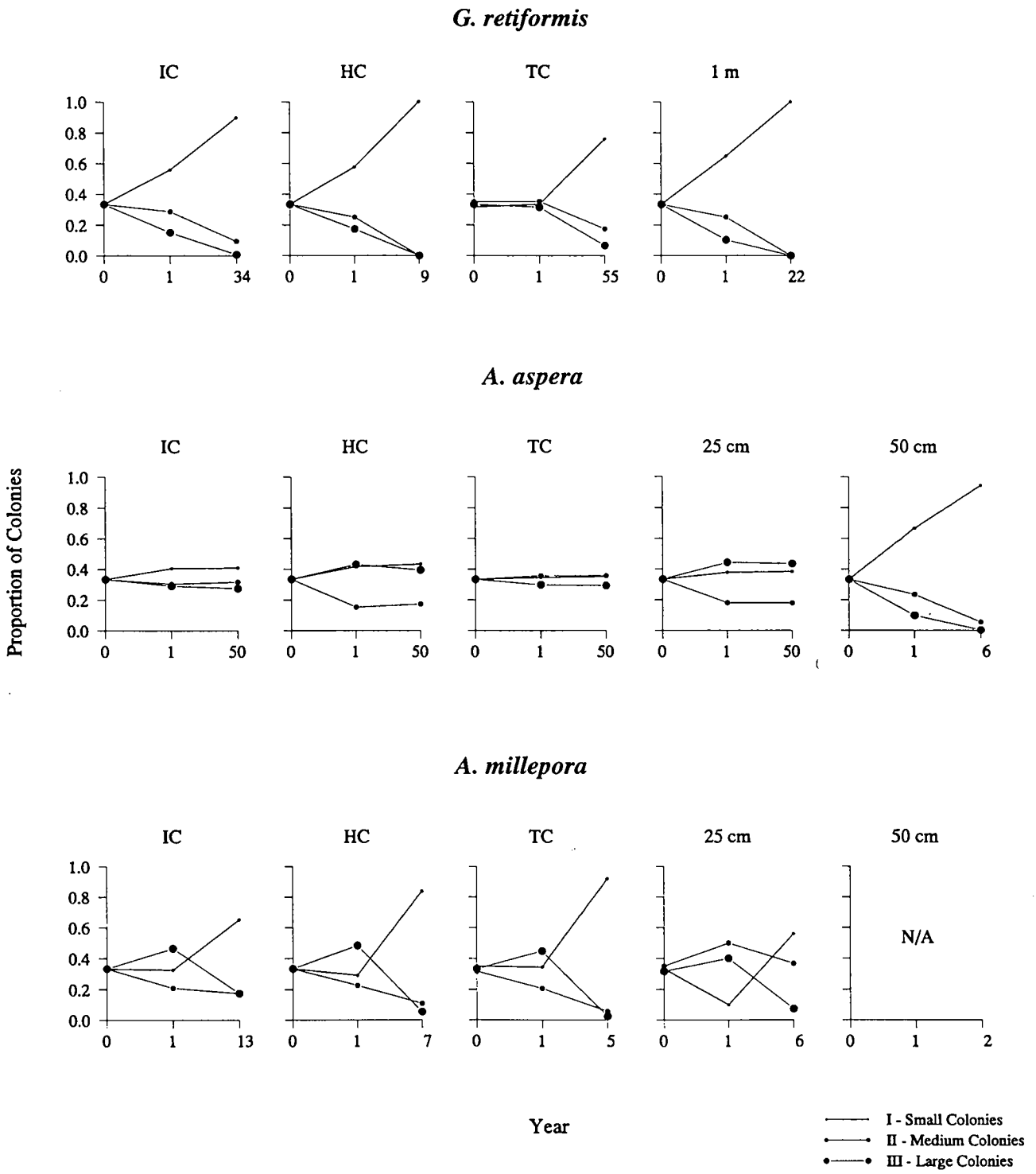

Figure 4.2 Projected size-structure, *w*, for colonies of *G. retiformis*, *A. aspera* and *A. millepora*, as a function of their treatment. The initial and year one size-distributions are shown, with the stable size-structures evident a) immediately preceding local extinction, after x years (for declining populations), or b) after 50 years (for growing populations). All size-structures are based on *complete model* projections (asexual and sexual reproductive contributions set to yield stable populations). Treatment abbreviations and adult size class dimensions are defined in Table 4.1.

Table 4.3 Damping ratio, *p*, for colonies of *G. retiformis*, *A. aspera* and *A. millepora* as a function of their treatment. *Complete model* matrices (asexual and sexual contributions set to yield stable populations) were used for calculating *p*. High values indicate rapid convergence to a stable size-structure following perturbation. Treatment abbreviations are defined in Table 4.1.

Species	Treatment:					
	IC	HC	TC	25 cm	50 cm	1 m
G. retiformis	2.14	1.95	1.58	--	--	2.00
A. aspera	4.39	2.80	5.82	9.33	3.09	--
A. millepora	1.90	2.12	1.68	1.64	N/A	--

SIZE-SPECIFIC REPRODUCTIVE CONTRIBUTIONS TO POPULATION GROWTH

Size-specific reproductive values, *v*, among populations were also assessed using *complete model* projections (Fig. 4.3). For all populations, size III adults would contribute the most to population growth, and size-specific contributions would decrease with decreasing colony size. However, size I adults would make a greater relative contribution to future generations in the *in situ* controls of *G. retiformis*, the 25 cm transplants of *A. millepora* and most populations of *A. aspera* than they would in any of the other populations. Species-specific reproductive values could also differ with depth changes (Fig. 4.3). For *A. aspera*, size I 50 cm transplants would contribute proportionally less to population growth, compared to the size I controls and 25 cm transplants. Conversely, for *A. millepora*, size I 25 cm transplants would contribute proportionally more to population growth, compared to the controls. For *G. retiformis*, size I 1 m transplants would contribute a similar amount to population growth as the size I handling and translocated controls, and proportionally less than the size I *in situ* controls.

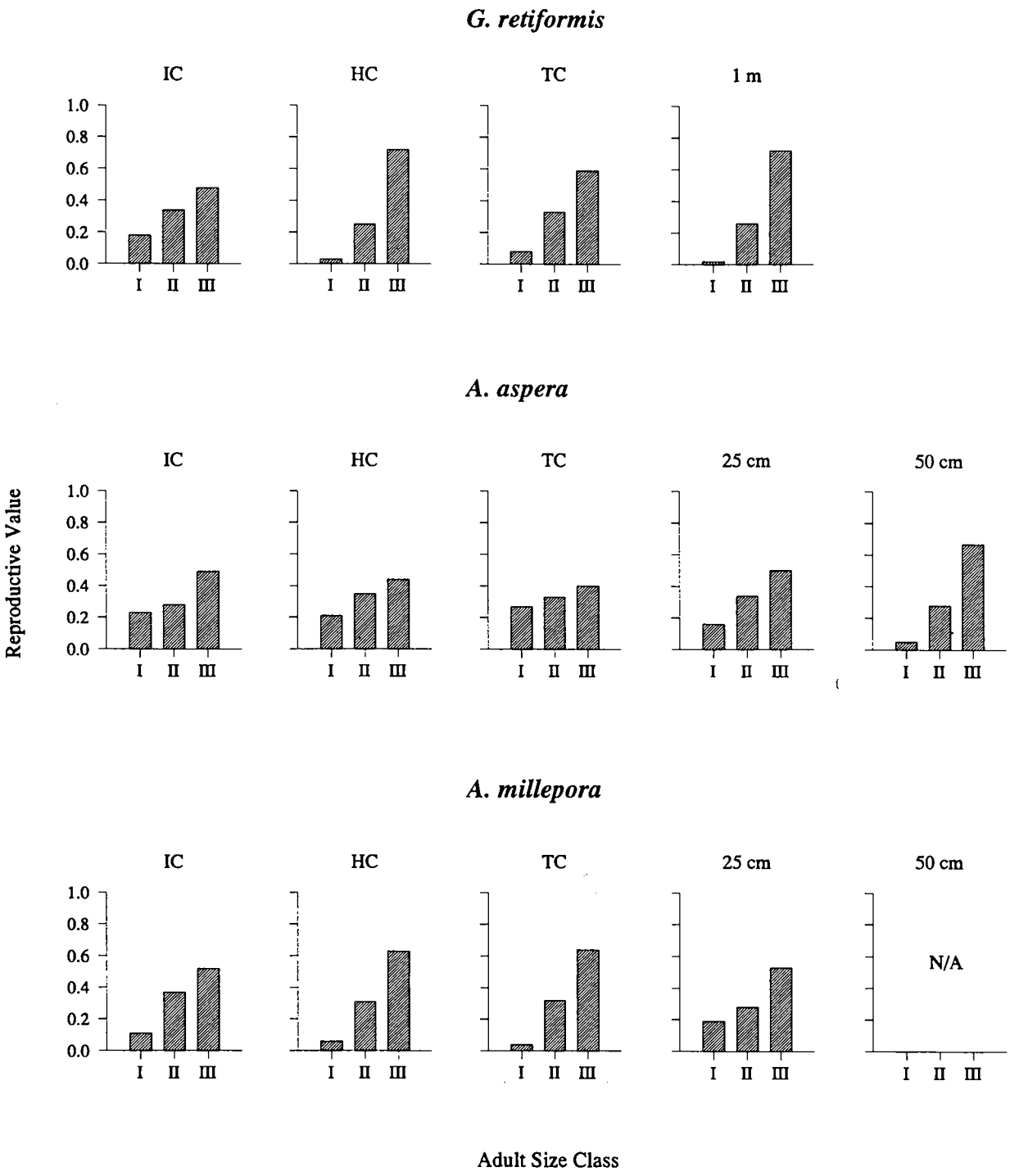

Figure 4.3 Projected reproductive values, *v*, for live colonies of *G. retiformis*, *A. aspera* and *A. millepora* as a function of their size and treatment. Reproductive values are based on *complete model* projections (asexual and sexual reproductive contributions set to yield stable populations). Treatment abbreviations and adult size class dimensions are defined in Table 4.1.

Table 4.4 Elasticity matrices for colonies of *G. retiformis*, *A. aspera* and *A. millepora*, as a function of their treatment. All elasticity values are based on *complete model* matrices (Table 4.1 with the inclusion of a_{EI} in Table 4.2). Size-class transitions that contribute more than 10% to λ are shown in bold type. Treatment abbreviations and adult size-class dimensions are defined in Table 4.1. With the exception of rounding error, elasticity values within each matrix sum to 1.

	G. retiformis				*A. aspera*				*A. millepora*			
IC	E	I	II	III	E	I	II	III	E	I	II	III
E	0	0.041	0.022	0.005	0	0	0	0	0	0.022	0.037	**0.110**
I	0.068	**0.650**	0.044	0.002	0	0.094	**0.110**	0.094	**0.17**	0.067	0.004	0.029
II	0	0.073	0.077	0.004	0	**0.130**	0.055	0.096	0	**0.180**	0.047	0.012
III	0	0	0.011	0.007	0	0.075	**0.120**	**0.230**	0	0	**0.150**	**0.180**
HC	E	I	II	III	E	I	II	III	E	I	II	III
E	0	**0.330**	0	0	0	0	0	0	0	0.097	0.058	**0.100**
I	**0.330**	**0.330**	0	0	0	**0.140**	0.043	0.098	**0.260**	0.047	0.004	0.004
II	0	0	0	0	0	**0.120**	0.016	0.053	0	**0.170**	0.043	0.005
III	0	0	0	0	0	0.024	**0.130**	**0.380**	0	0	**0.110**	**0.110**
TC	E	I	II	III	E	I	II	III	E	I	II	III
E	0	0.018	0.027	0.036	0	0	0	0	0	**0.140**	0.051	0.095
I	0.001	**0.270**	0.012	0.002	0	0.061	**0.140**	0.076	**0.290**	0.049	0.003	0.002
II	0	0.076	**0.240**	0.019	0	**0.130**	**0.100**	**0.130**	0	**0.150**	0.041	0.004
III	0	0	0.056	0.002	0	0.093	**0.110**	**0.160**	0	0	**0.100**	0.067
25 cm					E	I	II	III	E	I	II	III
					E	0	0	0	0	0.053	**0.180**	0.050
					I	0	0.035	0.028	**0.120**	**0.280**	0.031	0	0.002
					II	0	0.092	0.026	0.063	0	**0.230**	0.071	0
					III	0	0.054	0.013	**0.460**	0	0	0.052	0.058
50 cm					E	I	II	III	E	I	II	III
					E	0	**0.230**	0.095	0.012				
					I	**0.330**	**0.150**	0.017	0.001		N/A		
					II	0	**0.130**	0.014	0.004				
					III	0	0	0.017	0.004				
1 m	E	I	II	III								
E	0	**0.170**	0	0								
I	**0.170**	**0.670**	0	0								
II	0	0	0	0								
III	0	0	0	0								

GROWTH RATE ELASTICITIES

Elasticity values for the *complete model* projection matrices (Tab. 4.1, with the inclusion of a_{EI} in Tab. 4.2), showed striking differences in the relative sensitivity of population growth rates, λ, to each transition (Tab. 4.4). Projected growth rates of the controls and the 25 cm transplants of *A. aspera* were most sensitive to proportional changes in transitions that occur by growth, shrinkage or fission. In contrast, the growth rates of all declining populations were generally most sensitive to proportional changes in sexual reproductive parameters (estimates of fecundity and self-seeding, a_{EI},

Tab. 4.4). The sensitivity of population growth rates to proportional changes in individual size-class transitions also differed between species and depth changes.

Projected growth rates for the controls and the 25 cm transplants of *A. aspera* were very insensitive to proportional changes in sexual reproductive parameters (Tab. 4.4). Overall, they were most sensitive to proportional changes in the probability of size III adults remaining within the same size-class after a 12 month period. This is not unexpected, because size III adults of *A. aspera* often exhibit the highest rates of asexual propagation (c.f. smaller colonies, Chapter 2), so a slight change in the number of size III adults remaining within the same size-class, would yield a considerable change in the number of daughter colonies generated through fission. In contrast, the projected growth rate of the 50 cm transplants of *A. aspera* was very sensitive to proportional changes in sexual reproductive parameters (c.f. all other transition probabilities, Tab. 4.4). Overall, it was most sensitive to proportional changes in self-seeding and to the fecundity and growth transitions of size I adults. Thus, populations of *A. aspera* would be relatively unaffected by a 25 cm depth change and could persist through asexual propagation, but their growth rates in response to a 50 cm depth change would be most sensitive to sexual recruitment and to the survival, growth and fecundity of size I adults.

Projected growth rates of the *in situ* and translocated controls of *G. retiformis* were relatively insensitive to sexual reproductive parameters, compared to size-class transitions which occur through growth, shrinkage and fission (Tab. 4.4). Overall, they were most sensitive to proportional changes in the probability of size I adults remaining within the same size-class after a 12 month period. This is not surprising, since size I adults of *G. retiformis* often exhibit very slow rates of relative growth (c.f. larger colonies, Chapter 2), so a slight change in the number of size I adults remaining within the same size-class would yield a considerable change the number of daughter colonies generated through fission among larger size-classes. In contrast, projected growth rates of the handling controls and the 1 m transplants of *G. retiformis* were sensitive to proportional changes in both sexual reproductive parameters and to size-class transitions which occur through growth, shrinkage or fission (Tab. 4.4). Nevertheless, the growth rates of these populations were most sensitive to proportional changes in self-seeding, to the fecundity of size I adults and to the probability of size I adults remaining within

the same size-class. Thus, the growth rates of *G. retiformis* populations at shallow sites and in response to a 1 m depth change, would be equally sensitive to sexual recruitment and to the growth transitions exhibited by size I adults.

In *A. millepora*, projected growth rates for the controls and the 25 cm transplants were sensitive to both sexual reproductive parameters and size-class transitions (Tab. 4.4). They were also very sensitive to self-seeding and to the probability of size I growing to size II. Apart from these two factors, growth rate elasticities differed only slightly between the controls and the 25 cm transplants. Projected growth rates of the controls were more sensitive, than the 25 cm transplants, to proportional changes in the growth and fecundity of size III adults. The 25 cm transplants were more sensitive to proportional changes in the growth and fecundity of size II adults. These differences reflect size-specific differences in mortality, growth and fecundity between the controls and the 25 cm transplants (Tab. 4.1). Thus, the growth rates of *A. millepora* populations in response to a 25 cm depth change would be most sensitive to sexual recruitment and to the growth and fecundity of size II adults, while the growth rates of those located at shallow sites may be more sensitive to sexual recruitment and to the growth and fecundity of size III adults.

DISCUSSION

ADEQUACY OF PROJECTION MODELS

The projection models used here are site-specific and assume temporal constancy in size-class transitions, no density-dependent alterations in demographic traits, and that individuals within each size-class will exhibit identical size-specific patterns of mortality, growth and fecundity, regardless of their history (eg. See Hughes 1984, 1990; Caswell, 1986, 1989; Tanner et al. 1996). Nevertheless, inspite of these constraints, the projection models provide a means for evaluating the long-term effects of sea level changes on the demography of shallow-water reef corals. The stable size-structures of the controls of each species, obtained through *complete model* projections (Fig. 4.2), match the size-distributions of the species on the outer reef flat, where the controls were located (Fig. 2.12, Chapter 2). This indicates that the annual size-class transition matrices and projection models appear to

represent accurately the demography of these corals at this site. However, the same species located, for example, in less turbid water on offshore reefs may exhibit quite different demographic responses to identical changes in depth.

POTENTIAL POPULATION RESPONSES TO SEA LEVEL RISE

The simulations performed here demonstrate striking differences between the species in their long-term demographic responses to depth changes.

Responses of *Acropora aspera* Colonies: Long-Lived Clones

The simulations suggest that colonies of *A. aspera* located at shallow sites could persist indefinitely without sexual recruitment, provided gains through asexual propagation exceed losses through mortality (Fig. 4.1, Tab. 4.2). Some fragmenting corals, like *A. aspera*, have relatively low fecundities (Chapter 2; Tab. 4.1), and very low rates of sexual recruitment, often less than 0.2 recruits / m^2 / year (Connell 1973; Birkeland et al. 1979; Highsmith 1982; Rylaarsdam 1983; Bothwell 1984). However, high rates of adult survival and fast rates of growth (Chapter 2; Tab. 4.1), make it possible for colonies of *A. aspera* to rapidly attain a size where they may contribute asexually to future generations (eg. size III adults, Fig. 4.3). Unlike sexually derived recruits which are produced only once per annum (Bothwell 1984), daughter colonies of *A. aspera* can be produced at any time through extrinsic means and may themselves be capable of dividing, because they retain high rates of growth and survival (Chapter 2). As a consequence, even size I adults (be they genets or clones) may propagate clonally and hence contribute substantially to rates of population growth (Fig. 4.3).

Cloning also appears to promote the rapid convergence to a stable size-structure composed of a similar proportion of adult size-classes (Tab. 4.3, Fig. 4.2). This results because, daughter colonies are distributed among all adult size-classes, in contrast to sexual recruitment which manifests itself in the smallest size-class. These life history traits of *A. aspera* colonies in shallow sites directly parallel those of *Alcyonium* soft corals with a high propensity for asexual propagation (McFadden 1991). Population growth rates of *A. aspera*, like *Alcyonium* soft corals, are most sensitive to colony growth, shrinkage and fission, and very insensitive to changes in sexual reproductive parameters

(estimates of self-seeding and fecundity, McFadden 1991; Tab. 4.4).

The long-term demographic responses of *A. aspera* colonies located 25 cm deeper are not likely to differ considerably from those located at shallow sites. They too may persist indefinitely through asexual propagation alone (Fig. 4.1, Tab. 4.2), with all size-classes contributing to population growth (Fig. 4.3). Even with a sudden change in size-class transitions they would converge rapidly to a new stable size-structure, at transition rates equivalent to their counterparts at shallow sites (Tab. 4.3 & Fig. 4.2). Of course, a small increase in rates of colony fission may reduce the number of size III adults remaining within the same size-class after a 12 month period, and yield an increase in their rates of population growth (Tab. 4.4). Based on previous studies (Bell 1982; Cook 1985; Jackson 1986; McFadden 1991; Hughes et al. 1992), populations reliant on asexual propagation for replication and dispersal (like the shallow-water populations of *A. aspera)*, may exhibit lower genetic diversity than those reliant on sexual reproduction.

Under adverse conditions, sexual reproduction may be essential for colonies of *A. aspera* to persist. As demonstrated here, the difference in the physical and biological environment between a 25 cm and a 50 cm depth change may be sufficient to exceed the resilience threshold for populations of *A. aspera* (Fig. 4.1 & Tab. 4.2). Unlike colonies at shallower sites, the growth rate of those located 50 cm deeper was most sensitive to proportional changes in sexual reproductive parameters (Tab. 4.4), and without sexually derived recruits they would decline to local extinction in only 6 years (Fig. 4.1, Tab. 4.2). If they relied solely on self-seeding, they would require an very high growth transition probability from eggs to size I adults, 2.0×10^{-3}, to support a stable state (Tab. 4.2). This value, encompassing larval release, dispersal, settlement and juvenile survival, far exceeds similar estimates calculated by Babcock (1991) for several massive reef flat corals which range from only 1.9×10^{-6} to 2.2×10^{-5}. Thus, even if colonies of *A. aspera* located 50 cm deeper can self-seed, it is unlikely that rates of larval recruitment and juvenile survival would be high enough to ensure their persistence.

In field populations, larval spawn slicks of reef corals may extend for tens of kilometers in calm conditions and further in stronger trade winds (Willis & Oliver 1990), so it would be incorrect to assume that the source of settling larvae always originates from the same local population. Consequently, sexual replication in *A. aspera*, like *Alcyonium* soft corals, may be retained as a result

of selection for greater dispersal (McFadden 1991). Nevertheless, colonies of *A. aspera* located 50 cm deeper would require 38 externally sourced recruits for every 60 adults growing to size I per annum to maintain their population at its original size (n = 60, Tab. 4.2). Given field densities from the mid flat to the reef crest (Chapter 2), 60 colonies of *A. aspera* would inhabit an area approximately 20 m^2. Even with maximum rates of larval recruitment observed for this species at shallow sites (0.2 recruits / m^2 / year, Connell 1973; Bothwell 1984), only 4 recruits per annum are likely to enter the entire area. Thus, it is extremely unlikely that colonies of *A. aspera* would persist for any great length of time in response to a 50 cm depth change.

If the colonies managed to persist (even for a short period) by self seeding or through the addition of external recruits, their demography would alter considerably. Size I adults would exhibit higher rates of mortality and lower rates of growth than their shallow counterparts (Tab. 4.1, Chapter 2), and would thus contribute proportionally less to population growth (Fig. 4.3). In addition, reduced rates of growth in sizes I and II, coincident with little change in rates of fission in size III (Tab. 4.1), would yield a 100% dominance by size I adults (Fig. 4.2). In this state, the growth rate of the population would be totally subject to the sexual recruitment, survival, growth and fecundity of the size I adults (Tab. 4.4). Asexual propagation is not an option.

Responses of *Goniastrea retiformis* Colonies: Long-Lived Genets

Colonies of *G. retiformis* located at shallow sites could persist for decades (range 9 to 55 years), without sexual recruitment (Fig. 4.1). Compared to colonies of *A. aspera*, fission appears to be a more costly investment for colonies of *G. retiformis*, because gains through asexual propagation appear to contribute little to their population growth and dynamics and may be exceeded by losses through mortality (Tab. 4.2, Fig. 4.1, 4.2 & 4.3). Massive corals, like *G. retiformis*, have very slow rates of linear and areal growth (Babcock 1991; Chapter 2; Tab. 4.1), which may partly explain why populations are often dominated by small colonies (Babcock 1991; Chapter 2; Fig. 4.2). They also tend to produce a large number of small eggs and exhibit high rates of adult survival (Babcock 1984, 1991; Chapter 2; Tab. 4.1). In most reef corals, fecundity increases with colony size (Kojis & Quinn 1985; Szmant-Froelich 1985, Tab 4.1), and mortality decreases (Hughes & Jackson 1985, Babcock

1991; Tab 4.1). As a result sexual reproductive contributions to future generations are often highest among large colonies (Babcock 1984, 1991; Hughes et al. 1992), as is the case for those of *G. retiformis* (Fig. 4.3). Asexually produced daughter colonies of this species have high rates of mortality, compared to those of *A. aspera* (Chapter 2), so are likely to contribute very little to the total reproductive output of the population.

For slow growing, long-lived colonies of *G. retiformis*, a small increase in colony growth or survival, particularly among size I adults (Tab. 4.4), would considerably enhance the reproductive output of the entire population. The growth rates of *G. retiformis* populations located at shallow sites were most sensitive to changes in the survival and growth of the size I adults, rather than to changes in estimates of self-seeding and fecundity (Tab. 4.4). This is not unexpected, because population growth rates of perennial organisms with indeterminate growth, such as gorgonians (Grigg 1977; Gotelli 1991), and forest trees (Enright & Ogden 1979; See also Gotelli 1991 for review), are often insensitive to proportional changes in sexual reproductive parameters. However, populations of *G. retiformis* located at shallow sites must gain sexually produced recruits to persist (Fig. 4.1, Tab. 4.2), and in some instances their growth rates are most sensitive to proportional changes in sexual reproductive parameters (Tab. 4.4).

For colonies of *G. retiformis* located at shallow sites, relatively low transition probabilities from eggs to size I adults are required to support a stable population (2.2×10^{-5} to 4.4×10^{-4}, Tab. 4.2). These values are very similar to those calculated from rates of larval survival in the field for two massive reef flat species of the same genus (Babcock 1991). Assuming that self-seeding was the only source of sexual recruitment, colonies of *G. retiformis* located at shallow sites would therefore persist in a relatively stable state, given present estimates of larval survival. This conclusion is also supported to some extent through the simulation of externally sourced recruits. Colonies of *G. retiformis* located at shallow sites require 5 to 30 recruits growing to size I per annum to maintain their original population size (n = 60, Tab. 4.2). Field densities from the mid flat to the reef crest (Chapter 2), indicate that 60 colonies of *G. retiformis* inhabit an area of approximately 15 m^2, so with maximal rates of larval recruitment observed for species of *Goniastrea* (0.8 recruits / m^2 / year, Babcock 1991), 12 recruits per annum may enter the area. Consequently, all colonies of *G. retiformis*

at shallow sites (excluding the handling controls), might well persist indefinitely. The 12 recruits per annum would be insufficient for the handling controls to maintain their original population size (Tab. 4.2), but this is because size I adults of the handling controls experienced marked mortality and no growth within a 12 month period (Chapter 2; Tab. 4.1).

While colonies of *G. retiformis* at shallow sites are likely to persist through sexual recruitment, those located 1 m deeper will only persist providing recruitment occurs at deeper sites. Estimates of self-seeding, a_{EI}, required to maintain deeper populations of *G. retiformis* in a stable state, 4.9×10^{-3} (Tab. 4.2), exceed by two orders of magnitude the values documented by Babcock (1991) for *Goniastrea* species at shallow sites. This occurs partly because colony fecundity decreases with increasing depth (Kojis & Quinn 1984; Tab. 4.1). Colonies of *G. retiformis* located 1 m deeper would require 12 recruits out of 60 adults growing to size I per annum to maintain their original population size (Tab. 4.2). While this rate of recruitment is possible at shallow sites, it may not be achieved 1 m deeper, because colonies of *G. retiformis* have not been observed at this depth in the field (Chapter 2). Environmental factors at this depth, such as increased filamentous algal growth or sediment accumulation (Chapter 2), may hinder larval settlement, recruitment and rates of juvenile survival (Potts 1977; Te 1992). If however, recruitment did occur 1 m deeper, the long-term dynamics of *G. retiformis* populations at this depth would not differ considerably from their counterparts located at shallow sites (Fig. 4.1, 4.2, 4.3, Tab. 4.2, 4.3 & 4.4).

Responses of *Acropora millepora* Colonies: Short-Lived Genets

Acropora millepora appears to be the most ephemeral, the least reliant on asexual propagation, and the most sensitive to changes in sexual reproductive parameters (Fig. 4.1, Tab. 4.2, 4.4). Without sexual recruitment, shallow populations would decline to local extinction in only 5 to 13 years (Fig. 4.1, Tab. 4.2). However, colonies of *A. millepora* often have high rates of sexual recruitment (on average, 0.8 recruits / m^2 / year, Connell 1973; Bothwell 1984). Consequently, their low rates of adult survival (Chapter 2; Tab. 4.1), may be offset by their propensity for high recruitment rates. To self-seed and persist in a stable state, populations of *A. millepora* in shallow sites would require similar transition probabilities from eggs to size I adults as those of *G. retiformis* at the same depth (Tab.

4.2); which appear biologically realistic given present estimates of their rates of sexual recruitment at shallow sites (Connell 1973; Bothwell 1984). In addition, shallow colonies of *A. millepora* are likely to gain sufficient external recruits to maintain their original population size. Given their field densities from the mid flat to the crest, 60 colonies would inhabit an area approximately 43 m^2. With average rates of recruitment observed for this species at shallow sites (ca. 0.8 recruits / m^2 / year), 34 recruits per annum may enter the area, a number which could maintain populations close to their original size (Tab. 4.2). Therefore, it is likely that short-lived colonies of *A. millepora* would persist at shallow sites through episodic recruitment.

Populations of *G. retiformis* appear to be less reliant on sexual recruitment than those of *A. millepora* (Tab. 4.2, 4.4), but both have stable size-structures dominated by small colonies, which they attain at a similar rate (Chapter 2; Fig. 4.2, Tab. 4.3), and identical size-specific reproductive values (Fig. 4.3). This is likely to result because neither species relies heavily on asexual propagation (c.f. *A. aspera*, Chapter 2; Tab. 4.2), which may promote the convergence to a stable size-structure composed of a similar proportion of adult size-classes and the reproductive contributions to future generations made by small colonies (McFadden 1991; Tab. 4.3, Fig. 4.2, 4.3). For shallow populations of *A. millepora*, recurrent sexual recruitment coupled with low rates of adult survival may also partly explain why their populations are often dominated by size I adults (Chapter 2; Fig. 4.2). Many coral populations, like those of *A. millepora* and *G. retiformis*, are numerically dominated by small colonies (Hughes & Jackson 1985; Babcock 1991; Soong 1992). Large colonies, however, contribute the greatest reproductive output to future generations (Fig. 4.3). A small change in the reproductive output of size III adults, for instance, through an increase in colony growth rates, would yield a considerable change in the reproductive output of the entire population (Tab. 4.4). However, the population growth rate of *A. millepora* was most sensitive to changes in estimates of self-seeding and fecundity (Tab. 4.4). These findings are comparable to those of clonal ascidians in a seasonal environment (Gotelli et al. unpublished manuscript), and annual or short-lived plants (Law et al. 1977; Werner & Caswell 1977; Schmidt & Levin 1985), which are also most sensitive to proportional changes in sexual reproductive parameters. The local population size of marine organisms is often influenced by recruitment, post-recruitment interactions and mortality from disturbances (Underwood

& Denley 1984; Hughes 1984, 1990). The demographic analyses performed here suggest that the local population of short-lived colonies of *A. millepora*, may be strongly affected by rates of sexual recruitment.

Populations of *A. millepora* also appear to be the most sensitive even to very small changes in depth. Without sexual recruitment, populations of *A. millepora* located 25 cm deeper would decline to local extinction in only 6 years (Fig. 4.1, Tab. 4.2). However, if they gained externally derived recruits to the same extent as their counterparts at shallow sites (Tab. 4.2), they would persist 25 cm deeper, where size I adults exhibited slightly higher rates of growth and survival (Tab. 4.1) and contributed proportionally more to future generations than equivalent sized colonies at shallow sites (Fig. 4.3). Size II adults would have higher mortality and slower transitions to size III adults (Tab. 4.1). The population would be more sensitive to changes in the fecundity of size II adults, in contrast to changes in the fecundity of the largest colonies which readily influence the shallow populations (Tab. 4.4).

The most striking long-term demographic response in this study is that populations of *A. millepora* located 50 cm deeper than the controls would, without further recruitment, decline to local extinction in only 2 years (Fig. 4.1, Tab. 4.2). At this depth, populations would require 60 recruits growing to size I per annum to maintain their original size (n = 60, Tab. 4.2). Based on their possible rates of recruitment at shallow sites (eg. 34 recruits per 60 adults per annum, see above), and their absence from deeper sites in the field (Chapter 2), this is highly unlikely, and populations of *A. millepora* located 50 cm deeper will face inevitable and rapid local extinction.

POTENTIAL RESPONSES OF CORAL ASSEMBLAGES TO SEA LEVEL RISE

The projection models used here indicate that the persistence of the corals following a rise in sea level rise will depend on the demographic responses of the species to changes in the physical and biological environment, and on their potential to recruit to deeper sites. The ecological basis of this prediction is not new, as demographic factors (eg. mortality and growth) and recruitment have been previously ascribed as important determinants of community composition (Connell & Slatyer 1977; Sale 1978; Hughes 1984; Hughes & Jackson 1985; Jackson & Hughes 1985). As demonstrated here,

a sea level rise of 50 cm may be sufficient to initiate considerable shifts in community composition for extant corals in deeper sites (eg. with the local extinction of *A. millepora*, Fig. 4.1), assuming deviations from demographic transitions estimated here are minor.

Of course, if sea level rise and enhanced climate change create more adverse conditions than those induced experimentally over the 12 months of demographic monitoring, these corals may be less tolerant of small changes in depth. For example, an expected strengthening of monsoonal westerly winds in the eastern Australian tropics (Climate Impact Group CSIRO 1992), may significantly increase the outflow from mainland rivers subject inshore environments to higher sediment and nutrient loads, with profound affects on rates of larval settlement and recruitment (Te 1992). If recruitment decreases, it would have significant affects on rates of population decline and the persistence of corals, particularly at deeper sites. An increase in the frequency and intensity of tropical storms (Mitchell et al. 1990; Climate Impact Group CSIRO 1992), may also considerably affect community composition (Connell 1973; Connell & Slatyer 1977; Woodley et al. 1981), over much broader spatial scales. If, however, an intertidal species is unable to maintain its local population size in response to a rise in sea level, space may be available for the recruitment of subtidal species, and as a result, the diversity of coral communities could be maintained.

The models used here demonstrate firstly, that shallow-water reef corals can have quite different life histories. The reproductive strategies of the species examined range from a reliance on asexual propagation (long-lived clones) to episodic recruitment (short-lived genets). Secondly, reproductive strategies may significantly affect the long-term dynamics of corals in response to depth changes. Extant long-lived clones or genets, may be best adapted to persist at deeper sites, as they appear to be the least reliant on episodic recruitment. Finally, very little is known of the determinants of larval dispersal, habitat selection, recruitment and early survival of corals (eg. Hughes 1984; Fisk & Harriott 1990; Babcock 1991), yet, this area of research will be important to establish the likely fate of other reef corals in response to sea level rise.

CHAPTER 5:

CONCLUDING DISCUSSION

POTENTIAL IMPACTS OF ENHANCED CLIMATE CHANGE AND SEA LEVEL RISE ON SHALLOW-WATER REEF CORALS

As a result of enhanced global warming, eustatic sea level is currently predicted to rise around 5 cm / decade over the next century (Wigley & Raper 1992). Because eustatic sea level in the past several thousand years has remained relatively constant around present levels (Davies & Hopley 1983), many reefs have grown to an elevation where further upward growth is constrained by sea level. Rises in sea level are expected to remove this constraint (Smith & Buddemeier 1992), and result in increased coral recruitment and greater longevity on tidal and subtidal reef flats (Hopley & Kinsey 1988). As a consequence, coral communities are expected to extend in range into presently unsuitable environments, initiating shifts in current patterns of reef zonation (Smith & Buddemeier 1992). Expected shifts in zonation for colonies of *Acropora aspera*, *Goniastrea retiformis* and *Acropora millepora* as a result of eustatic sea level rise may be broadly categorized into three concurrent phases: 1. Extant corals may be left as relict populations at deeper sites;
2. new recruits and extant corals may overlap in present shallow reef sites; and 3. upward expansion may be facilitated through sexual or asexual recruitment (Figure 5.1). Apart from these broad shifts, sea level rise coupled with enhanced climate change, may drastically modify the dynamics and composition of these shallow-water reef corals, as suggested here.

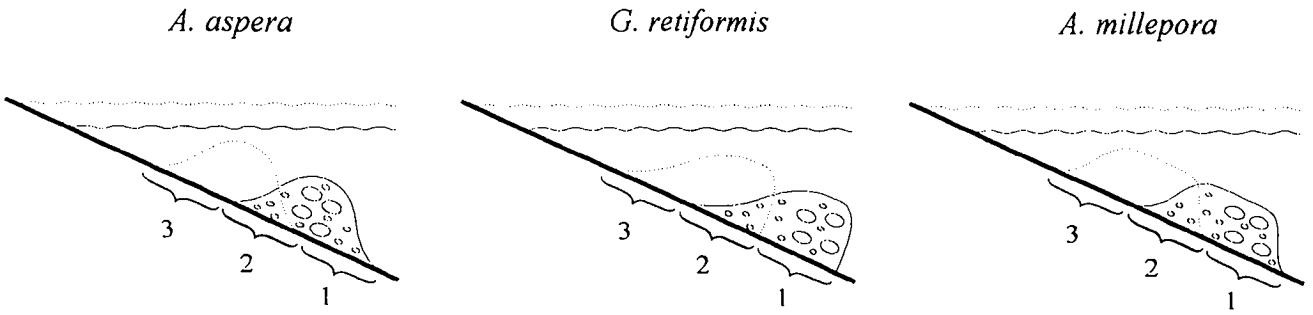

Figure 5.1 Projected sea level rise scenario for colonies of *A. aspera*, *A. millepora* and *G. retiformis* given their present size-frequency distributions within Little Pioneer Bay. Dashed lines represent sea level and coral distributions in the future, and the size-distribution of ellipses denotes the distribution of colony size-classes within the population. 1, represents relict populations of extant corals; 2, overlap between extant corals and new recruits; and 3, upward expansion through sexual or asexual recruitment.

RESPONSES OF EXTANT CORALS AND CORAL ASSEMBLAGES

The responses of extant corals to changes in depth (Fig. 5.1-1), are likely to differ considerably as a result of differences in their life histories. Short-lived corymbose colonies of *A. millepora* appear the most able to photoadapt to alterations in light with a 25 cm or 50 cm depth change (c.f. those of *A. aspera*), by increasing photopigment contents per algal cell and per unit tissue volume (Fig. 3.7 & 3.9); a response which typically enhances light harvesting abilities (Kinzie et al. 1984; Chalker et al. 1988). However, they are likely to be the first to disappear from deeper sites, through excessive tissue loss (Tab. 2.15), colony shrinkage (Fig. 2.17), and mortality (Fig. 2.15). The chances of damage caused by grazing herbivores or predators (Hay 1981, 1984, Hay et al. 1983), or overgrowth by filamentous algae within established damsel fish territories (Potts 1977), are often highest at deeper sites below reef margins, as was the case in this study. Colonies of *A. millepora*, appeared to be the most sensitive of the three species to these external influences which may reduce rates of coral growth

(Knowlton et al. 1990; Fig. 2.17, Fig. 2.18), and survival in corals (Potts 1977, Fig. 2.13, 2.15). Of course, additional and less obvious environmental factors other than these biological interactions may have also contributed as mortality agents. Nevertheless, without new recruits, extant colonies of *A. millepora* (Fig. 5.1-1), may experience local extinction in an estimated 6 years in response to a 25 cm rise in sea level, and in only 2 years in response to a 50 cm sea level rise, because losses through mortality (Fig. 2.15) are likely to exceed gains through asexual propagation (Fig. 4.1).

Long-lived branching colonies of *A. aspera* showed little ability to photoadapt to alterations in light with small changes in depth (Fig. 3.7, Fig. 3.9), but unlike colonies of *A. millepora*, they may persist despite changes in the local environment in response to a 25 cm depth change. Their rapid rates of areal and linear growth (Fig. 2.17, 2.18), high rates of survival (Fig. 2.15) and extreme propensity for asexual propagation (Tab. 2.12), are likely to promote population growth (Fig. 4.1). Consequently, even at depths of 25 cm their rapid rates of linear extension may contribute substantially to rates of reef vertical accretion (eg. MacIntyre & Glynn 1976; Adey 1978). However, for colonies of *A. aspera*, environmental differences between a 25 cm and a 50 cm depth change may be sufficient for losses through colony shrinkage (Fig. 2.17) and mortality (Fig. 2.15) to exceed gains through asexual propagation (Fig. 4.1). Consequently, without new recruits, extant colonies of *A. aspera* (Fig. 5.1-1) may experience local extinction in only 6 years in response to a 50 cm rise in sea level (Fig. 4.1), and would probably be the second of the three species to disappear from deeper sites.

Long-lived massive colonies of *G. retiformis* were the most robust of the three species to depth-related changes in the physical and biological environment and are likely to be the last to disappear from deeper sites. However, in response to a 1 m depth change they may experience a 2-fold decrease in rates of linear extension (Fig. 2.18), and as a result, they may contribute very little to rates of reef vertical accretion (eg. Focke 1978; Hopley et al. 1983; Smith 1983). They may also experience a 2-fold increase in rates of skeletal erosion by filamentous algae and clionid sponges when located 1 m deeper (Fig. 2.20). These boring agents are often more prevalent at sites below reef margins (Davies & Hutchings 1983; Wilkinson 1983; Wilkinson & Evans 1988), in heavily grazed areas (eg. Ogden 1977; Sammarco et al. 1986), and in established damsel fish territories (Sammarco

et al. 1987). Once established within coral skeletons, they may also facilitate bioerosion by other agents (eg. Hutchings et al. 1992). Colonies of *G. retiformis* may persist for a much longer period than those of *A. millepora* and *A. aspera* at deeper sites, but their mortality (Fig. 2.13) may exceed gains through asexual propagation (Fig. 4.1). Consequently, without new recruits, 60 extant colonies of *G. retiformis* (Fig. 5.1-1) may persist for an estimated 22 years before experiencing local extinction in response to a 1 m rise in sea level (Fig. 4.1). In some cases, high rates of bioerosion may facilitate colony dislodgment from the substratum and reduce potential longevity.

Extant colonies of *A. millepora*, *A. aspera* and *G. retiformis* that are presently located at shallow reef sites may remain within the confines of their depth range following a rise in sea level (Fig. 5.1-2). Within the depth range of each species, colonies may be distributed across a size gradient (Fig. 2.12 & 5.1). Findings here and those reported by Jokiel & Morrissey (1986) suggest that size may be an important factor determining the ability of a colony to photoadapt to depth-related alterations in light (Tab. 3.11). A colony with little ability to photoadapt may die following a sea level rise, despite remaining within the depth confines of the species. For instance, large colonies of *A. millepora* had a greater ability to photoadapt by increasing photopigment contents per unit tissue volume, than smaller ones (Fig. 3.10). Therefore, if small colonies of *A. millepora* cannot rapidly attain a large size at which they may photoadapt more effectively, they may not persist even at this depth. This study, like many others, also demonstrated that coral mortality patterns were inversely related to colony size (eg. Connell 1973; Jackson 1979; Hughes & Jackson 1985; Babcock 1991). Therefore, if small colonies of each species cannot rapidly attain a size refuge from mortality, they may not persist at this depth, particularly those of *G. retiformis*, which have very slow rates of areal and linear growth (Fig. 2.17, 2.18). Thus, extant colonies may not only disappear from deeper sites in response to a sea level rise but may also disappear from sites where old and new distributions overlap (Fig. 5.1-2).

Of course, if enhanced climate change creates more adverse conditions than those experienced during the monitored period, the length of time extant corals persist may be considerably lowered. Levels of peak clear day visible irradiance are not expected to increase as a result of climate change

(Climate Impact Group CSIRO 1992), and changes in cloud cover are uncertain (Cubasch & Cess 1990), but changes in sea state and water turbidity may significantly affect the fate of the corals. For instance, a strengthening of monsoonal westerly winds in the eastern Australian tropics coupled with an increase in monsoonal rains during heavy storms (Climate Impact Group CSIRO 1992), could increase the outflow from mainland rivers and subject the corals to higher sediment or nutrient loads. An increase in water turbidity from planktonic primary production stimulated by nutrient loading, or from increased levels of suspended sediments may affect the maximum depth range of photoadaptation for shallow-water reef corals, and result in suboptimal growth and mortality (Maragos 1972; Dodge & Vaisnys 1977; Bak 1978; Kinsey 1979, 1988; Smith et al. 1981; Brown & Howard 1985). In high nutrient regimes, competitively advantaged benthic algae may outcompete reef corals, initiating phase shifts in reef community structure and dynamics (Banner 1975; Smith et al. 1981; Birkeland 1988). High nutrient or sediment loads may also generate sulfide or other forms of toxicity and facilitate bacterial infections (Brown & Howard 1985; Grigg & Dollar 1990). Even if these factors do not affect extant colonies of *A. millepora*, *A. aspera* and *G. retiformis* in the near future as a result of sea level rise, they may all experience a considerable decrease in fecundity at deeper sites (Fig. 2.21).

PERSISTENCE AND DIVERSITY OF REEF CORALS: THE ROLE OF RECRUITMENT

Although fecundity may not limit or regulate local population size or structure when larvae are dispersed away from the site, recruitment to the site may do so (eg. Hughes 1984, 1990; Underwood & Denley 1984; Gaines & Roughgarden 1985). As demonstrated here, sexual and asexual recruitment will play an important role in determining the population structure (Fig. 4.2) and persistence (Fig. 4.1, Tab. 4.2 & 4.4) of shallow-water reef corals in response to sea level rise. Small changes in sexual recruitment could significantly affect the persistence of *A. millepora* populations, and to a lesser extent those of *G. retiformis* (Tab. 4.2 & 4.4). In contrast, small changes in factors which promote asexual propagation (eg. colony growth and survival), would significantly affect the

persistence of *A. aspera* populations (Tab. 4.2 & 4.4). Despite this difference between the species, the simulations show that all of these populations would require sexual recruitment at rates greater than those present at shallow sites, to persist when located at depths of 50 cm or more (Tab.4.2). Based on net rates of sexual recruitment observed in field populations of these species (Connell 1973, Bothwell 1984; Babcock 1991), it is unlikely that greater recruitment will occur at deeper sites (See Discussion Chapter 4). This is further supported by the observation that none of the three species inhabit these depths in their inshore environment (Fig. 2.12). Therefore, extant colonies of *A. aspera*, *A. millepora* and *G. retiformis* are likely to decline in number with sea level rise and form relic populations.

The upward expansion of corals into presently unsuitable environments coincident with a rise in sea level will depend on their ability to recruit, either sexually or asexually, into new shallow reef sites (Fig. 5.1-3). While short-lived colonies of *A. millepora* may be the first to disappear from deeper sites, they are likely to be the first to colonize new sites, because of their high rates of sexual recruitment (ca. 0.8 recruits / m^2 / year, Connell 1973, Bothwell 1984). Massive reef flat colonies of *Goniastrea* species have lower rates of sexual recruitment (ca. 0.2 recruits / m^2 / year, Babcock 1991), and so may colonize these sites at a slower rate. Branching corals, like *A. aspera*, can have very low rates of sexual recruitment, often less than 0.2 recruits / m^2 / year (Connell 1973, Bothwell 1984), but because of their high propensity for asexual propagation, they may rapidly colonize shallow reef sites through the persistence of dispersed or dislodged fragments (eg. Birkeland et al. 1979; Highsmith 1982).

To date, it has been tacitly assumed that local populations of reef corals which release positively buoyant gametes once per annum rarely self-seed, because larval spawn slicks may travel for tens of kilometers in ocean currents (Willis & Oliver 1990). However, very little is known of the determinants of larval dispersal, habitat selection, recruitment and early survival for reef corals (eg. Hughes 1984; Sammarco & Andrews 1988; Fisk & Harriott 1990; Babcock 1991). This information will be important to predict the persistence of extant shallow-water reef corals reliant on sexual recruitment, like short-lived colonies of *A. millepora* (Tab. 4.4). If some reefs are sources for sexual

recruitment and others sinks (eg. Hughes et al. 1992), local and regional changes in water currents associated with a rise in sea level may significantly affect current patterns of larval dispersal and recruitment. As demonstrated here, without self-seeding or the addition of externally derived recruits, short-lived populations of *A. millepora* may face rapid local extinction (Fig. 4.1, Tab. 4.2). As a consequence, hydrographic changes associated with sea level rise may significantly alter the relative abundance and the diversity corals on presently established reefs.

Similarly, very little is known of the rates or determinants of asexual propagation for reef corals (Highsmith 1982; Hughes & Jackson 1985; Babcock 1991; Tab. 2.12), or of the survival of daughter colonies produced by branching species (Knowlton et al. 1981, 1990; Tab. 2.12). Unlike populations reliant on sexual recruitment, fragmenting species, like *A. aspera* (Tab. 4.2 & 4.4), can potentially escape larval and juvenile agents of mortality, and may benefit from hydrographic changes due to enhanced climate change. For instance, changes in local currents and waves as a result of a rise in sea level could promote the passive dispersal of asexual propagules into new reef sites. An increase in the frequency and intensity of tropical storms (Mitchell et al. 1990), may also promote asexual dispersal over broader spatial scales (eg. Gilmore & Hall 1976; Tunnicliffe 1981; Highsmith 1982). However, in some cases, severe storms may increase mortality and as a result, slow or even prevent the re-establishment of coral fragments (Knowlton et al. 1981).

The persistence of sexually or asexually derived recruits in new reef sites may depend on alterations in present environmental conditions associated with enhanced global climate change. If sea-surface temperatures rise gradually at rates currently predicted (around 2°C by 2070 in the eastern Australian tropics, Climate Impact Group CSIRO 1992; Whetton 1993), populations of *A. aspera*, *A. millepora* and *G. retiformis* may be little affected. As demonstrated in this study, they may readily recover from periodic partial bleaching events coincident with extremes in summer temperatures ranging from 18.5 to 33.6°C (Tab. 2.19). More rapid changes in sea-surface temperatures or greater extremes may severely affect recruits, particularly those of *A. millepora* that are likely to be the most prone to seasonal mortality (Fig. 2.15 & 2.19). Of course, bleaching may be induced by other

physical factors such as extremes in salinity, excessive solar radiation and shading (Rogers 1979; Egana & DiSalvo 1982; Hoegh-Guldberg & Smith 1989; Jokiel & Coles 1990), and cannot be solely ascribed to temperature. Seasonal mortality can also reflect changes in the temporal abundance of filamentous algae which may indirectly affect coral growth and mortality (Potts 1977). These additional determinants of coral bleaching and mortality could also alter as a result of enhanced climate change. For instance, an increase in the frequency and intensity of monsoonal rains associated with tropical storms (Climate Impact Group CSIRO 1992), may considerably affect rates of bleaching and recovery for these shallow-water reef corals. The predicted enhanced algal growth due to elevated levels of CO_2 (Smith & Roth 1979) in tropical waters (Smith & Buddemeier 1992), may also drastically affect rates of seasonal mortality for reef corals.

Acropora millepora may be the first to be affected by changes in the physical environment in new reef sites, but they may be most capable of adapting in the long-term. The potential for genetic adaptation to changes in environmental conditions is likely to be higher among corals populations reliant on sexual recruitment, rather than those reliant on asexual propagation (eg. Potts & Garthwaite 1991). Sexually derived recruits of *A. millepora* or *G. retiformis* in this inshore environment may, through selection of adaptive genotypes, survive recurrent exposure to elevated sea-surface temperatures or a 5 to 10% increase in levels of ultraviolet radiation expected by 2002 (WMO/UNEP 1991). Conversely, asexually derived recruits of *A. aspera* and other branching species, with a high propensity for asexual propagation and very low rates of sexual recruitment, may be the most genetically vulnerable in the long-term to alterations in the physical environment.

CONCLUSIONS AND RECOMMENDATIONS

1. Coral responses to depth changes may be multiplicative or synergistic responses to concurrent changes in several environmental variables (Coles & Jokiel 1978; Hoegh-Guldberg & Smith 1989), or indirect responses to sequential changes in several environmental variables, rather than a direct response to a change in depth. However, field transplant experiments provide a valuable tool for understanding coral responses to depth-related alterations in their environment. While this study is site specific and it examines extreme scenarios of sea level rise, it provides the basis for understanding future responses of the corals in their inshore environment to enhanced environmental change, and has identified several key issues for future research.

2. Short-lived corals reliant on sexual recruitment, such as *A. millepora*, may be the most useful as bioindicators of early responses of coral reef ecosystems to enhanced environmental change, because they may be among the first organisms to shift vertically upward in distribution and to respond negatively to alterations in the physical and biological environment.

3. There is an obvious need to quantify current patterns of larval dispersal, habitat selection, recruitment and early survival for a range of shallow-water reef corals with different life histories and reproductive strategies. Although this information is difficult to quantify, it will be important to determine the likely persistence of different coral species reliant on sexual recruitment.

4. Long-lived corals reliant on asexual propagation, such as *A. aspera*, may be the most genetically vulnerable to the long-term effects of enhanced global climate change and sea level rise, because of their limited ability for sexual recruitment.

5. Estimates of the rates and determinants of asexual propagation and the relative contribution of this reproductive mode to rates of population growth will be necessary to identify species reliant on asexual propagation, and those most prone to the long-term effects of enhanced environmental change.

6. To determine the evolutionary consequences of enhanced climate change and sea level rise on shallow-water reef corals, it will be necessary to quantify the genetic diversity of local populations and their rates of gene flow over a variety of spatial scales, particularly for those most reliant on asexual propagation. This research will be important in establishing the vulnerability of long-lived clones to environmental change.

7. Finally, potential impacts of enhanced climate change or sea level rise on shallow-water reef corals should not be considered in isolation. Current and widespread reef degradation from anthropogenic activities pose a much greater immediate threat and can reinforce negative impacts of global climatic and hydrographic changes (eg. Smith & Buddemeier 1992). Shallow-water reef corals on inshore reefs could be most vulnerable to enhanced climate change and sea level rise, because their demographic responses to changes in physical and biological factors may be readily exacerbated by anthropogenic impacts, such as increased nutrient and sediment loads due to deforestation, agricultural practices, mining, dredging and coastal developments (Brown & Howard 1985; Wells 1988; Grigg & Dollar 1990; Smith & Buddemeier 1992; Hughes 1994). Detailed scientific studies of species-specific responses to environmental change and the comprehensive monitoring of local inshore reef responses, will be necessary for the long-term management and conservation of these diverse assemblages.

REFERENCES

ADEY, W.H. 1978. Coral reef morphogenesis: a multidimensional model. Science **202**:831-837.

ANDRES, N.G. & N.L. RODENHOUSE. 1993. Resilience of corals to hurricanes: a simulation model. Coral Reefs **12**:167-175.

BABCOCK, R.C. 1984. Reproduction and distribution of two species of *Goniastrea* (Scleractinia) from the Great Barrier Reef Province. Coral Reefs **2**:187-195.

BABCOCK, R.C. 1991. Comparative demography of three species of Scleractinian corals using age- and size-dependent classifications. Ecological Monographs **61(3)**:225-244.

BABCOCK, R.C., G.D. BULL, P.L. HARRISON, A.J. HEYWARD, J.K. OLIVER, C.C. WALLACE & B.L. WILLIS. 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Marine Biology **90**:379-394.

BAK, R.P.M. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Netherlands Journal of Sea Research **10(3)**:285-337.

BAK, R.P.M. 1978. Lethal and sublethal effects of dredging on coral reefs. Marine Pollution Bulletin **23**:14-16.

BAK, R.P.M. & S.R. CRIENS. 1981. Survival after fragmentation of colonies of *Madracis mirabilis*, *A. palmata* and *A. cervicornis* (Scleractinia) and the subsequent impact of coral disease. Proceedings of the 4th International Coral Reef Symposium, Manila **2**: 221-227.

BAK, R.P.M. & M.S. ENGEL. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Marine Biology **54**:341-352.

BAKER, P.A. & J.N. WEBER. 1975. Coral growth rate: variation with depth. Earth and Planetary Sciences Letters **27**:57-61.

BANNER, A.H. 1975. Kaneohe Bay, Hawaii: Urban pollution in a coral reef ecosystem. Proceedings of the 2nd International Symposium of Coral Reefs **2**:685-702.

BARD, E., B. HAMELIN, R.G. FAIRBANKS & G. ZINDLER. 1990. Calibration of the ^{14}C timescale over the past 30,000 years using mass spectrometic U-Th ages from Barbados corals. Nature **345**:405-410.

BARNES, D.J. 1971. A study of growth, structure and form in modern coral skeletons. Ph.D Dissertation. University of Newcastle-upon-Tyne, UK. 180p.

BARNES, D.J. 1973. Growth in colonial scleractinians. Bulletin of Marine Science **23**:280-298.

BARNES, D.J. & B.E. CHALKER. 1990. Calcification and photosynthesis in reef-building corals and algae. **In** DUBINSKY, Z. (Ed.) Coral Reefs: Ecosystems of the world **25**:109-132. New York, Elsevier.

BARNES, D.J. & J.M. LOUGH. 1992. Systematic variations in the depth of skeleton occupied by coral tissue in massive colonies of *Porites* from the Great Barrier Reef. Journal Experimental Marine Biology and Ecology **159**:113-128.

BEGON, M. & M. MORTIMER. 1986. Population Ecology: a unified study of animals and plants. Blackwell Scientific Publications, Oxford. 220p.

BELL, G. 1982. The masterpiece of nature: the evolution and genetics of sexuality. Croom Helm, London, England.

BERNARDELLI, H. 1941. Population waves. Journal of the Burma Research Society **31**:1-18.

BIERZYCHUDEK, P. 1982. The demography of Jack-in-the-Pulpit, a forest perennial that changes sex. Ecological Monographs **52**:335-351.

BIRKELAND, C. 1988. Geographic comparisons of coral-reef community processes. Proceedings of the 6th International Coral Reef Symposium, Townsville **1**:211-220.

BIRKELAND, C., G. GRIMM, & R.H. RANDALL. 1979. Separation of age and colony size as factors influencing the growth rates of corals. **In** KRASNOV, E.V. (Ed.) Use and Preservation of Coral Reef Resources. XIV Pacific Science Congress, Khabarovsk. Abstract p. 18.

BIRKELAND, C., A.A. REIMER. & J.R. YOUNG. 1976. Survey of marine communities in Panama and experiments with oil. EPA Ecological Research Series. 176 p.

BOARDMAN, N.K. 1977. Comparative photosynthesis of sun and shade plants. Annual Review of Plant Physiology **28**:355-377.

BOEKSCHOTEN, G.J., M.B. BEST, A. OOSTERBANN & F.M. MOLENKAMP. 1989. Past corals and recent reefs in Indonesia. Netherlands Journal of Sea Research **23(2)**:117-122.

BOTHWELL, A.M. 1984. Community organization and biology of Scleractinian corals on the reef crest at Heron Island, G.B.R. Ph.D Dissertation, University of Queensland, Australia. 400p.

BROWN, B.E. 1990. Coral bleaching: special issue. Coral Reefs **8**:153-232.

BROWN, B.E. & L.S. HOWARD. 1985. Assessing the effects of 'stress' on reef corals. Advances in Marine Biology **22**:1-63.

BROWN, B.E., L. SYA'RANI & M. Le TISSIER. 1985. Skeletal form and growth in *Acropora aspera* (Dana) from the Palau Seribu, Indonesia. Journal of Experimental Marine Biology and Ecology **86**:139-150.

BUDDEMEIER, R.W. & D.G. FAUTIN. 1993. Coral bleaching as an adaptive mechanism: a testable hypothesis. BioScience **43**:320-326.

BUDDEMEIER, R.W. & R.A. KINZIE. 1976. Coral growth. Oceanography and Marine Biology Annual Review **14**:183-225.

BUDDEMEIER, R.W., J.E. MARAGOS & D. W.KNUTSON. 1974. Radiographic studies of reef coral exoskeletons: Rates and patterns of coral growth. Journal of Experimental Marine Biology and Ecology **14**:179-200.

CASWELL, H. 1985. The evolutionary demography of clonal reproduction. **In** JACKSON, J.B.C., L.W. BUSS & R.E. COOK (Eds.) Population Biology and Evolution of Clonal Organisms. Yale University Press, New Haven, USA. pp. 187-224.

CASWELL, H. 1986. Life cycle models for plants. Lectures on Mathematics in the Life Sciences **18**:171-233.

CASWELL, H. 1989. Matrix population models. Chapter **3**: Stage-classified life cycles. pp. 27-44. Sinauer, Sunderland, Massachusettes, USA.

CASWELL, H & P.A WERNER. 1978. Transient behaviour and life history analysis of teasel (*Dipsacus sylvestris* Huds.). Ecology **59**:53-66.

CHALKER, B.E., D.J. BARNES, W.C. DUNLAP & P.L. JOKIEL. 1988. Light and reef-building corals. Interdisciplinary Science Reviews **13(3)**:222-237.

CHALKER, B.E., T. COX & W.C. DUNLAP. 1984. Seasonal changes in primary production and photoadaptation by the reef-building coral *Acropora granulosa* on the Great Barrier Reef. **In** HOLM-HANSEN, O., L. BOLIS & R. GILLES (Eds.) Marine Phytoplankton and Productivity. pp. 73-87. Springer-Verlag, Berlin. pp. 73-87. (Lecture Notes on Coastal and Estuarine Studies, Volume **8**).

CHANG, S.S., B.B. PREZELIN & R.K. TRENCH. 1983. Mechanisms of photoadaptation in three strains of the symbiotic dinoflagellate *symbiodinium microadriaticum.* Marine Biology **76**:219-229.

CHAPMAN, M.G. 1986. Assessment of some controls in experimental transplants of intertidal gastropods. Journal of Experimental Marine Biology and Ecology **103**:181-201.

CHAPPELL, J. 1981. Relative average sea level changes, and endo-, epi-, an dexogenic processes on the earth. **In** Sea level, Ice and Climatic Change International Association of Hydrological Science Publication 131:411-430.

CHAPPELL, J. 1983. Sea level changes and coral reef growth. **In** BARNES, D.J. (Ed.) Perspectives on Coral Reefs. Australian Institute of Marine Science Publication, Australia. pp. 46-55.

CHOW, W.S., L. QIAN, D.J. GOODCHILD & J.M. ANDERSON. 1988. Photosynthetic acclimation of *Alocasia macrorrhiza* (L.) G. Don to growth irradiance: structure, function and composition of chloroplasts. Australian Journal of Plant Physiology **15**:107-122.

CLIMATE IMPACT GROUP, CSIRO. 1992. Climate change scenarios for the Australian region. CSIRO Division of Atmospheric Research Publication. pp. 1-6.

COLES, S.L. & P.L. JOKIEL. 1977. Effects of temperature on photosynthesis and respiration in hermatypic corals. Marine Biology **43**:209-216

COLES, S.L. & P.L. JOKIEL. 1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. Marine Biology **49**:187-195.

CONNELL, J.H. 1973. Population ecology of reef-building corals. **In** JONES, O.A. & R. ENDEAN (Eds.) Biology and Geology of Coral Reefs, **2**. Academic Press, New York. pp. 205-245.

CONNELL, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. **In** CODY, M.L. & J.M. DIAMOND (Eds.) Ecology and Evolution of Communities. Belknap Press, Cambridge. pp. 460-490.

CONNELL, J.H. 1976. Competitive interactions and species diversity of corals. **In** MACKIE. G.O. (Ed.) Coelentrate Ecology and Behaviour. Plenum Press, New York. pp. 51-58.

CONNELL, J. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302-1310.

CONNELL, J.H. & R.O. SLATYER. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **111**:1119-1144.

COOK, R.E. 1979. Asexual reproduction: a further consideration. American Naturalist **113**:769-772.

COOK, R.E. 1985. Growth and development in clonal plant populations. **In** JACKSON, J.B.C., L.W. BUSS & R.E. COOK (Eds.) Population Biology and Evolution of Clonal Organisms. Yale University Press, New Haven Connecticut, USA. pp. 259-296.

CUBASCH, U. & R.D. CESS. 1990. Processes and modeling. **In** HOUGHTON, J.T., G.J. JENKINS & J.J. EPHRAUMS. (Eds.) Climate change: The IPCC Scientific Assessment. Cambridge, Cambridge University Press, pp. 69-92.

CUI, M., W.K. SMITH & T.C. VOGELMANN. 1991. Chlorophyll and light gradients in sun and shade leaves of *Spinacia oleracea*. Plant Cell Environment 14:493-500.

DARKE, W. 1991. Growth and growth form of the massive coral *Porites*. Ph.D. Dissertation. James Cook University of North Queensland, Townsville. 161p.

DAVIES, P.J. & D. HOPLEY. 1983. Growth facies and growth rates of Holocene reefs in the

Great Barrier Reef. Bureau of Mineral Resources Journal of Australian Geology and Geophysics **8**:237-251.

DAVIES, P.J. & P.A. HUTCHINGS. 1983. Initial colonization, erosion and accretion on coral substrate, experimental results, Lizard Island, Great Barrier Reef. Coral Reefs **2**:27-35.

DAYTON, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**:351-389.

De KROON, H., A. PLAISIER, J. VAN GROENENDAEL & H. CASWELL. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology **67**:1427-1431.

D'ELIA, C.F., R.W. BUDDEMEIER & S.V. SMITH. 1991. Workshop on coral bleaching, coral reef ecosystems and global change: Report of Proceedings. Maryland Sea Grant College Publ. No. UM-SG-TS-91-03. University of Maryland; College Park.

De VANTIER, L.M., E. TURAK, T.J. DONE & J. DAVIDSON. 1994. Bleaching of reef-building corals on nearshore reefs of the central Great Barrier Reef in summer-autumn 1994. Australian Coral Reef Society, Australian Marine Sciences Association and International Society for Reef Studies Conference Abstracts, Townsville, Australia. Abstract. p.16.

DODGE, R.E. & J.R. VAISNYS. 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. Journal of Marine Research **35**:715-730.

DONE, T.J. 1987. Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus Porites: evidence of population resilience? Coral Reefs **6**:75-90.

DONE, T.J. 1988. Simulation of recovery of pre-disturbance size structure in populations of *Porites* sp. damaged by the crown of thorns starfish *Acanthaster planci*. Marine biology **100**:51-61.

DONE, T.J. 1991. The debate continues--robust versus fragile reefs. Reef Encounter **9**:5-7.

DONE, T.J. 1992. Phase changes in coral reefs. Hydrobiologia (In press).

DUSTAN, P. 1979. Distribution of zooxanthallae and photosynthetic chloroplast pigments of the reef-building coral *Montastrea annularis* Ellis and Solander in relation to depth on a West Indian coral reef. Bulletin of Marine Science **29(1)**:79-95.

DUSTAN, P. 1982. Depth-dependent photoadaptation by zooxanthallae of the reef coral *Montastrea annularis*. Marine Biology **68**:253-264.

EGANA, A.C. & L.H. DiSALVO. 1982. Mass expulsion of zooxanthellae by Easter Island corals. Pacific Science **36**:61-63.

ENDEAN, R. & A.M. CAMERON. 1990. Trends and new perspectives in coral-reef ecology. **In** DUBINSKY, Z. (Ed.) Coral Reefs: Ecosystems of the World **25**:469-492. New York, Elsevier.

ENRIGHT, N. & J. OGDEN. 1979. Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. Australian Journal of Ecology **4**:3-23.

FAIRBANKS, R.G. 1989. A 17,000 year glacio-eustatic sea level record. Nature **342**:637-642.

FALKOWSKI, P.G. & Z. DUBINSKY. 1981. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Elat. Nature **289**:172-174.

FALKOWSKI, P.G., P.L. JOKIEL & R.A. KINZIE.III. 1990. Irradiance and corals. **In** DUBINSKY, Z. (Ed.) Coral Reefs: Ecosystems of the world **25**:89-108. New York, Elsevier.

FISK, D.A. & V.J. HARRIOTT. 1990. Spatial and temporal variation in coral recruitment on the Great Barrier Reef: implications for dispersal hypotheses. Marine Biology **107**:485-490.

FITT, W.K., H.J. SPERO, J. HALAS, M.W. WHITE & J.W. PORTER. 1993. Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 Caribbean "bleaching event". Coral Reefs **12**:57-64.

FOCKE, J.W. 1978. Holocene development of coral fringing reefs, leeward off Curacao and Bonair (Netherlands Antilles). Marine Geology **28**:31-34.

GAINES, S. & J. ROUGHGARDEN. 1985. Larval settlement rate: a leading determinant of structure in and ecological community of the marine intertidal zone. Proceedings of the National Academy of Sciences (USA) **82**:3707-3711.

GANDER, R. 1970. Micro-stereology: practical examples. **In** Microskopion 18 + 19: New Developments and Techniques, Wild Heerbrugg Ltd. Publishers. pp. 14-16.

GATES, D.M., H.J. KEEGAN, J.C. SCHLETER & V.R. WEIDNER. 1965. Spectral properties of plants. Applied Optics **4**:86-101.

GATTUSO, J.P. 1985. Features of depth effects on *Stylophora pistillata*, an hermatypic coral in the Gulf of Aqaba (Jordan, Red Sea). Proceedings of the 5th International Coral Reef Congress **6**:95-100.

GATTUSO, J.P., M. PICHON & J. JAUBERT. 1991. Physiology and taxonomy of Scleractinian corals: a case study in the genus Stylophora. Coral Reefs **9**:173-182.

GILMORE, M.D. & B.R. HALL. 1976. Life-history, growth habits, and constructional roles of *Acropora cervicornis* in the patch reef environment. Journal of Sedimentary Petrology **46**:519-522.

GLADFELTER, E.H. 1985. Metabolism, calcification and carbon production. II. Organisms-level

studies. Proceedings of the 5th International Coral Reef Congress, Tahiti **4**:527-539.

GLYNN, P.W. 1973. Aspects of the ecology of coral reefs in the western Atlantic region. **In** JONES, O.A. & R. ENDEAN (Eds.) Biology and Geology of Coral Reefs, **2**, Biology 1, Academic Press, New York, pp. 271-324.
GLYNN, P.W. 1984. Widespread coral mortality and the 1982/1983 El Niño warming event. Environmental Conservation **11**:133-146.

GLYNN, P.W. 1988. El Niño-southern oscillation 1982-83: Nearshore population, community and ecosystem responses. Annual Review of Ecology and Systematics **19**:309-345.

GLYNN, P.W. 1992. Coral reef bleaching: ecological perspectives. Coral Reefs (Submitted).

GLYNN, P.W., A.M. SZMANT, E.F. CORCORAN & S.V. COFER-SHABICA. 1989. Condition of coral reef cnidarians from the northern Florida reef tract: Pesticides, heavy metals, and histopathological examination. Marine Pollution Bulletin **20**:568-576.

GOREAU, T.J. & A.H. MACFARLANE. 1990. Reduced growth rate of *Montastrea annularis* following the 1987-1988 coral-bleaching event. Coral Reefs **8**:211-215.

GOTELLI, N.J. 1991. Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. Ecology **72(2)**:457-467.

GOTELLI, N.J., A.R. DAVIS & H. CASWELL. Size-structured demography of the colonial ascidian *Clavelina moluccensis* in a seasonal environment (unpublished manuscript).

GRIGG, R.W. 1977. Population dynamics of two gorgonian corals. Ecology **58**:278-290.

GRIGG, R.W. & S.J. DOLLAR. 1990. Natural and anthropogenic disturbance on coral reefs. **In** DUBINSKY, Z. (Ed.) Coral Reefs: Ecosystems of the world **25**:439-452. New York, Elsevier.

HARPER, J.L. 1980. Plant demography and ecological theory. Oikos 35:244-253.

HARRIOTT, V.J. 1985. Recruitment patterns of scleractinian corals at Lizard Island, Great Barrier Reef. Proceedings of the 5th International Coral Reef Symposium **4**:367-372.

HARRISON, P.L. & C.C. WALLACE. 1990. Reproduction, dispersal and recruitment of scleractinian corals. **In** DUBINSKY, Z. (Ed.) Coral Reefs: Ecosystems of the world **25**:133-208. New York, Elsevier.

HARTSHORN, G. 1975. A matrix model of tree population dynamics. **In** GOLLEY, F.B. & E. MEDINA (Eds.) Tropical Ecological Systems. Springer-Verlag, New York. pp. 41-52.

HAY, M.E. 1981. Spatial patterns of grazing intensity on a Caribbean Barrier Reef: herbivory and algal distribution. Aquatic botany **11**:97-109.

HAY, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous

results typical? Ecology **65**:446-454.

HAY, M.E., T. COLBURN & D. .DOWNING. 1983. Spatial and temporal patterns in herbivory on a Caribbean fringing reef: The effects on plant distribution. Oecologia (Berlin) **58**:299-308.

HIGHSMITH, R.C. 1979. Coral growth rates and environmental control of density banding. Journal of Experimental Marine Biology and Ecology **37**:105-125.

HIGHSMITH, R.C. 1982. Reproduction by fragmentation in corals. Marine Ecology Progress Series **7**:207-226.

HOEGH-GULDBERG, O. & G.J. SMITH. 1989. Light, salinity, and temperature and the population density, metabolism, and export of zooxanthellae from *Stylophora pistillata* and *Seriatopora hystrix*. Journal of Experimental Marine Biology and Ecology **129**:279-303.

HOLBROOK, J. 1994. Temperature variability in the southwest Pacific Ocean between 1955 and 1988. Ph.D Dissertation, The University of Sydney, Australia.

HOPLEY, D. & D.W. KINSEY. 1988. The effects of rapid short term sea level rise on the Great Barrier Reef. **In** PEARMAN, G.I. (Ed.) Greenhouse: Planning for Climate Change. Brill, New York. pp. 189-201.

HOPLEY, D., A.M. SLOCOMBE, F. MUIR & C. GRANT. 1983. Nearshore fringing reefs in North Queensland. Coral Reefs **1**:151-160.

HOUCK, J.E. 1978. The potential utilization of scleractinian corals in the study of marine environments. Ph.D. Dissertation. University of Hawäii. 199p.

HOUGHTON, J.T., G.J. JENKINS, & J.J. EPHRAUMS (Eds.) 1990. Climate change: The IPCC Scientific Assessment. Cambridge University Press: Cambridge.

HOUGHTON, J.T., G.J. JENKINS & J.J. EPHRAUMS. (Eds.) 1992. Climate Change: The Supplementary Report to the IPCC Scientific Assessment. Cambridge University Press, Cambridge.

HUDSON, J.H. 1981. Response of *Montastrea annularis* to environmental change in the Florida Keys. Proceedings of the 4th International Coral Reef Symposium **2**:233-240.

HUGHES, T.P. 1984. Population dynamics based on size rather than age: A general model with a reef coral example. American Naturalist **123**:778-795.

HUGHES, T.P. 1987. Skeletal density and growth form of corals. Marine Ecology Progress Series **35**:259-266.

HUGHES, T.P. 1989. Community structure and diversity of coral reefs: the role of history. Ecology **70**:275-279.

HUGHES, T.P. 1990. Recruitment limitation, mortality and population regulation in open systems: a case study. Ecology **71**:12-20.

HUGHES, T.P. 1994. Catastrophes, phase-shifts and large-scale degradation of a Caribbean coral reef. Science **265**(5178).

HUGHES, T.P, D. AYRE & J.H. CONNELL. 1992. The evolutionary ecology of corals. Trends in Ecology and Evolution **7**:292-295.

HUGHES, T.P. & J.H. CONNELL. 1987. Population dynamics based on size or age? A reef coral analysis. American Naturalist **129**:818-829.

HUGHES, T.P. & J.B.C. JACKSON. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. Science **209**:713-715.

HUGHES, T.P. & J.B.C. JACKSON. 1985. Population dynamics and life histories of foliaceous corals. Ecological Monographs **55**:141-166.

HUTCHINGS, P.A., W.E. KIENE, R.B. CUNNINGHAM & C. DONNELLY. 1992. Spatial and temporal patterns of non-colonial boring organisms (polychaetes, sipunculans and bivalve molluscs) in *Porites* at Lizard Island, Great Barrier Reef. Coral Reefs **11**:23-31.

JACKSON, J.B.C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. American Naturalist **111**:743-767.

JACKSON, J.B.C. 1979. Morphological strategies of sessile animals. **In** LARWOOD, G. & B.R. ROSEN Biology and Systematics of Colonial Organisms, **11**. Academic Press, New York. pp. 499-555.

JACKSON, J.B.C. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species distributions and genetic structure of local populations. Bulletin of Marine Science **39**:588-606.

JACKSON, J.B.C. 1992. Pleistocene perspectives on coral reef community structure. American Zoologist **32**:719-731.

JACKSON, J.B.C, & T.P. HUGHES, 1985. Adaptive strategies of coral-reef invertebrates. American Scientist **73**:265-274.

JEFFERY, S.W. & G.F. HUMPHREY. 1975. New spectrophotometric equations for determining chlorophylls a, b, c_1 and c_2 in higher plants, algae and natural phytoplankton. Biochemical Physiology **167**:191-194.

JOHANNES, R.E. 1975. Pollution and degradation of coral reef communities. **In** FERGUSON-WOOD, E.J. & R.E. JOHANNES (Eds.) Tropical Marine Pollution, Elsevier Oceanography Series No. 12. Elsevier Scientific Publication, New York. pp. 13-51.

JOKIEL, P.L. & S.L. COLES 1974. Effects of heated effluent on hermatypic corals at Kahe Point, Oahu. Pacific Science **28**:1-18.

JOKIEL, P.L. & S.L. COLES. 1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. Marine Biology **43**:201-208.

JOKIEL, P.L. & S.J. COLES. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs **8**:155-162.

JOKIEL, P.L & J.I. MORRISSEY. 1986. Influence of size on primary production in the reef coral *Pocillopora damicornis* and the macroalga *Acanthophora spicifera*. Marine Biology **91**:15-26.

KINSEY, D.W. 1979. Carbon turnover and accumulation by coral reefs. Ph.D. Dissertation. University of Hawaii. 284 p.

KINSEY, D.W. 1988. Coral reef system responses to some natural and anthropogenic stresses. Galaxea **7**:113-128.

KINZIE, R.A.III. & T. HUNTER. 1987. Effect of light quality on photosynthesis of the reef coral *Montipora verrucosa*. Marine Biology **94**:95-109.

KINZIE, R.A.III., P.L. JOKIEL & R. YORK. 1984. Effects of light of altered spectral composition on coral zooxanthellae associations and on zooxanthellae *in vitro*. Marine Biology **78**:239-248.

KLEEMAN, R. 1990. A simple model of the atmospheric response to ENSO sea surface temperature anamolies. Journal of Atmospheric Science **48**:13-18.

KLEPPEL, G.S., R.E. DODGE & C.J. REESE 1989 Changes in pigmentation associated with the bleaching of stony corals. Journal of Limnology and Oceanography **34**:1331-1335.

KNOWLTON, N., J.C. LANG & B.D. KELLER. 1990. Case study of natural population collapse: Post-hurricane predation on Jamaican staghorn corals. Smithsonian contributions to the Marine Sciences **31**:1-25. Smithsonian institution press, Washington, D.C.

KNOWLTON, N., J.C. LANG, M.C. ROONEY & P. CLIFFORD. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature **294**:251-252.

KOJIS, B.L & N.J. QUINN. 1984. Seasonal and depth variation in fecundity of *Acropora palifera* at two reefs in Papua New Guinea. Coral Reefs **3**:165-172.

KOJIS, B.L. & N.J. QUINN. 1985. Puberty in *Goniastrea favulus*: age or size limited? Proceedings of the 5th International Coral Reef Congress, Tahiti **4**:289-293.

KRAMMER, C.Y. 1956. Extension of multiple range tests to group means with unequal numbers of replications. Biometrics **12**:307-310.

LARCOMBE, J.W.P. 1990. A comparison of the coral communities of Pioneer Bay and North East Reef, Orpheus Island. B.Sc. Hons. Thesis. James Cook University of North Queensland, Townsville, Australia. 71p.

LAW, R., A.D. BRADSHAW & P.D. PUTWAIN. 1977. Life history variation in *Poa annua*. Evolution **31**:233-246.

LESLIE, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika **33**:183-212.

LESLIE, P.H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika **35**:213-245.

LEWIS, E.G. 1942. On the generation and growth of a population. Sankhya: The Indian Journal of Statistics **6**:93-96.

LOYA, Y. 1976a. Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. Ecology **57**:278-289.

LOYA, Y. 1976b. The Red Sea coral *Stylophora pistillata* is an r strategist. Nature **259**:478-480.

MacCRACKEN, M.C., M.I. DUDYKO, A.D. HECHT & Y.A. IZRAEL (Eds.). 1990. Prospects for future climate: A special US/USSR report on climate and climate change. Lewis Publishers: Chelsea, Michigan. 270 p.

MacINTYRE, I.G. & P.W. GLYNN. 1976. Evolution of modern Caribbean fringing reef, Galeta Point, Panama. Amer. Assoc. Petrol. Geology Bulletin **60**:1054-1071.

MARAGOS, J.E. 1972. A study of the ecology of Hawaii reef corals. Ph.D Dissertation. University of Hawaii. 290 p.

MARAGOS, J.E. 1974. Coral transplantation: a method to create, preserve and manage coral reefs. Seagrant Advisory Report No. UNIHI-SEAGRANT-AR-74-03 CORMAR-14, University of Hawaii Seagrant Program, Honolulu, 30p.

McCLOSKEY, L.E & L. MUSCATINE. 1984. Production and respiration in the Red Sea coral *Stylophora pistillata* as a function of depth. Proceedings of the Royal Society of London, B, **222**:215-230.

McFADDEN, C.S. 1991. A comparative demographic analysis of clonal reproduction in a temperate soft coral. Ecology **72**:1849-1866.

MEESTERS, E.H. & R.P.M. BAK. 1993. Effects of coral bleaching on tissue regeneration potential and colony survival. Marine Ecology Progress Series **96**:189-198.

MEESTERS, E.H., A. BOS & G.J. GUST. 1992. Effects of sedimentation and lesion position on coral tissue regeneration. Proceedings of the 7th International Coral Reef Symposium **2**:671-678.

MENGE, B.A. & T.M. FARRELL. 1989. Community structure and interaction webs in shallow marine hard-bottom communities: Tests of an environmental stress model. Advances in Ecological Research **19**:189-262.

MESOLELLA, K.J. 1967. Zonation and uplifted Pleistocene coral reefs on Barbados, West Indies. Science **156**:638-640.

MITCHELL, J.F.B., S. MANABE, V. MELESHKO & T. TOKIOKA. 1990. Equilibrium climate change-and its implication for the future. **In** HOUGHTON, J.T., G.J. JENKINS & J.J. EPHRAUMS (Eds.) Climate Change: The IPCC Scientific Assessment. Cambridge University Press, Cambridge. pp. 131-164.

MORRISSEY, J. 1980. Community structure and zonation of macroalgae and hermatypic corals on a g
fringing reef flat of Magnetic Island (Queensland, Australia). Aquatic Botany **8**:91-139.

MUSSO, B.M. 1992. Rates of skeletal degradation following death in three species of *Acropora*. Proceedings of the 7th International Coral Reef Symposium **1**:413-418.

NEUDECKER, S. 1977. Transplant experiments to test the effect of fish grazing on coral distribution. Proceedings of the 3rd International Coral Reef Symposium **1**:317-323.

NEUDECKER, S. 1981. Effects of substratum orientation, depth, and time of coral recruitment at Guam. Proceedings of the 4th International Coral Reef Symposium **2**:376.

NEWELL, N.D. 1971. The evolution of reefs. Scientific American **226**:54-65.

NICHOLLS, N. 1988a. El Nino-Southern Oscillation impact prediction. Bulletin of American Meteorological Society **69**: 173-176.

NICHOLLS, N. 1988b. ENSO and rainfall variability. Journal of Climate **1**: 418-421.

NISHIO, J.N., J. SUN & T.C. VOGELMANN. 1993. Carbon fixation gradients across spinach leaves do not follow internal light gradients. The Plant Cell **5**:953-961.

OGDEN, J.C. 1977. Carbonate sediment production by parrotfish and sea urchin on Caribbean reefs. **In** FROST, S.H., M. WEISS & J.B. SAUNDERS (Eds.) Reefs and Related Carbonates-Ecology and Sedimentology, Am. Assoc. Petrol. Geol. Studies in Geology **4**:281-288.

OLIVER, J.K. & R. BERKELMANS. 1994. Coral bleaching on the Great Barrier Reef over the last decade. Australian Coral Reef Society, Australian Marine Sciences Association and International Society for Reef Studies Conference Abstracts, Townsville, Australia. Abstract. p.58.

PAULAY, G. 1991. Late Cenozoic sea level fluctuations and the diversity and species composition of insular shallow water marine faunas. **In** DUDLEY, E.C. (Ed.) The Unity of Evolutionary Biology: Proceedings of the 4th International Congress of Systematic and

Evolutionary Biology. Portland, Dioscorides Press.

PEARMAN, G.I. & C.D. MITCHELL. (Eds.) 1992. CSIRO Climate change research program annual report 1991-1992. CSIRO Institute of Natural Resources and Environment, Melbourne.

PIELOU, E.C. 1977. Mathematical Ecology. John Wiley & Sons, New York.

PITTOCK, A.B. 1993. Developing regional climate change scenarios: their reliability and seriousness. **In** BURGIN. S. (Ed.) Climate change, Implications for Natural Resource Conservation. University of Western Sydney, Hawkesbury. Occasional Papers in Biological Sciences **1**:3-28.

PORTER, J.M. 1974. Community structure of coral reefs on opposite sides of the Isthmus of Panama. Sciences **183**:543-545.

PORTER, J.W., L. MUSCATINE, Z. DUBINSKY & P.G. FALKOWSKI. 1984. Primary production and photoadaptation on light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. Proceedings of the Royal Society of London B, **222**:161-180.

POTTS, D.C. 1977. Suppression of coral populations by filamentous algae within damselfish territories. Journal of Experimental Marine Biology and Ecology **28**:207-216.

POTTS, D.C., T.J. DONE, P.J. ISDALE & D.A. FISK. 1985. Dominance of a coral community by the genus *Porites* (Scleractinia). Marine Ecology Progress Series **23**:79-84.

POTTS, D.C. & R.L. GARTHWAITE. 1991. Evolution of reef-building corals during periods of rapid global change. **In** DUDLEY, C. (Ed.) The Unity of Evolutionary Biology, Proceedings of the 4th International Congress of Systematic and Evolutionary Biology. Dioscorides Press, Oregon. pp. 170-178.

RINKEVICH, B. & Y. LOYA. 1979a. The reproduction of the Red Sea coral *Stylophora pistillata*. I. Gonads and planulae. Marine Ecology Progress Series **1**:133-144.

RINKEVICH, B. & Y. LOYA. 1979b. The reproduction of the Red Sea coral *Stylophora pistillata*. II. Synchronization in breeding and seasonality of planulae shedding. Marine Ecology Progress Series **1**:145-152.

ROGERS, C.S. 1979. The effect of shading on coral reef structure and function. Journal of Experimental Marine Biology and Ecology **41**:269-288.

ROGERS, C.S., T.H. SUCHANEK & F.A. PECORA. 1982. Effects of hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. Bulletin of Marine Science **32**:532-548.

ROOS, P.J. 1967. Growth and occurrence of the reef coral *Porites astreoides* Lamarck in relation to submarine radiance distribution. Ph.D. Dissertation, Univ. of Amsterdam, Utrecht. 72 p.

RUDDIMAN, W.F. 1985. Climate studies in ocean cores. **In** HECHT, A.D. (Ed.) Paleoclimate Analysis and Modeling. New York, John Wiley & Sons. pp. 197-257.

RYLAARSDAM, K.W. 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. Marine Ecology Progress Series **13**:249-260.

SALE, P.F. 1978. Chance patterns of demographic change in populations of territorial fish in coral rubble patches at Heron Reef. Journal of Experimental Marine Biology and Ecology **34**:387-395.

SAMMARCO, P.W. & J.C. ANDREWS. 1988. Localized dispersal and recruitment in Great Barrier Reef corals: the Helix experiment. Science **239**:1422-1424.

SAMMARCO, P.W., J.H. CARLETON & M.J. RISK. 1986. Effects of grazing and damselfish territoriality on bioerosion of dead corals: direct effects. Journal of Experimental Marine Biology and Ecology **98**:1-19.

SAMMARCO, P.W., M.J. RISK & C. ROSE. 1987. Effects of grazing and damselfish territoriality on internal bioerosion of dead corals: indirect effects. Journal of Experimental Marine Biology and Ecology **112**:185-199.

SARUKHAN, J. & M. GADGIL. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. Journal of Ecology **62**:921-936.

SCHMIDT, K.P. & D.A. LEVIN. 1985. The comparative demography of reciprocally sown populations of *Phlox drummondii* Hook. I. Survivorships, fecundites and finite rates of increase. Evolution **39**:396-404.

SEBENS, K.P. 1983. Size structure and growth rates in populations of colonial solitary invertebrates. **In** REAKA, L. (Ed.) Symposia Series for Undersea Research: NOAA'S Undersea Research Program: The Ecology of Deep and Shallow Coral Reefs. Department of Commerce, U.S.

SEBENS, K.P. 1987. The ecology of indeterminate growth in animals. Annual Review of Ecological Systematics **18**:371-407.

SHAPIRO, S.S. & M.B. WILK. 1965. An analysis of variance test form normality (complete samples). Biometrika **52**:591-611.

SHEPPARD, C.R.C. 1980. Coral cover, zonation and diversity on reef slopes of Chagos Atolls, and population structures of the major species. Marine Science Progress Series **2**:193-205.

SHINN, E.A. 1966. Coral growth-rate, an environmental indicator. Journal of Palaeontology **40**:233-241.

SHINN, E.A. 1972. Coral reef recovery in Florida and in the Persian Gulf. Environmental Conservation Department, Shell Oil Company, Houston, Texas, USA.

SHINN, E.A. 1976. Coral reef recovery in Florida and the Persian Gulf. Environmental Geology **1**:241-254.

SMITH, A.D. & A.A. ROTH. 1979. Effect of carbon dioxide concentration on calcification in the red coralline alga *Bossiella orbigniana*. Marine Biology **52**:217-225.

SMITH, G.J. & O. HOEGH-GULDBERG. 1987. Variation in the growth rates of zooxanthellae with coral host colony size and ontogenetic stage is not controlled by changes in the duration of cytokinesis. Eos **68**:1724.

SMITH, J.B. & D. TIRPAK. 1989. The potential effects of global climate change on the United States. Policy, Planning, and Evaluation (PM-221), EPA-230-05-89-050. United States Environment Protection Agency. 412 p.

SMITH, S.V. 1983. Coral reef calcification. **In** BARNES, D.G. (Ed.) Perspectives on Coral Reefs. Manuka, Australia, Brian Clouston. pp. 240-247.

SMITH, S.V. & R.W. BUDDEMEIER. 1992. Global change and coral reef ecosystems. Annual Review of Ecology and Systematics **23**:89-118.

SMITH, S.V., W.J. KIMMERER, E.A. LAWS, R.E. BROCK & T.W. WALSH. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. Pacific Science **35**:279-395.

SOONG, K. 1992. Reproduction and colony size of reef coral species. Proceedings of the 7th International Coral Reef Symposium, Guam (In Press).

SOONG, K. 1993. Colony size as a species character in massive reef corals. Coral Reefs **12**:77-83.

STIMSON, J.S. 1978. Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. Marine Biology **48**:173-184.

STIMSON, J. 1985. The effect of shading by the table coral *Acropora hyacinthus* on understory corals. Ecology **66(1)**:40-53.

STOBART, B. 1994. Allyzome electrophoresis demonstrates that the scleractinian coral *Montipora digitata* (Dana 1846) is two species. Marine Biology (Submitted).

STRICKLAND, J.D.H. & T.R. PARSONS. 1972. A practical handbook of seawater analysis. 2nd Edition, Bulletin of Fisheries Research Board Canada **167**:1-310.

SZMANT, A.M. & M.P. GASSMAN. 1990. The effects of prolonged 'bleaching' on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. Coral Reefs **8**:217-224.

SZMANT-FROELICH, A. 1985. The effect of colony size on the reproduction ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). Proceedings of the 5th International

Coral Reef Congress, Tahiti **4**:295-300.

TANNER, J.E., T.P.HUGHES & J.H.CONNELL. 1996. The role of history in community dynamics: A modelling approach. Ecology **77**: 108-117.

TE, F.T. 1992. Response to higher sediment loads by *Pocillopora damicornis* planulae. Coral Reefs **11**:131-134.

TEGART, W.J. McG., G.W. SHELDON & D.C. GRIFFITHS (Eds.). 1990. Climate Change: The IPCC Impacts Assessment. Australian Government publishing Service, Canberra.
TERASHIMA, I. & T. SAEKI. 1983. Light environment within a leaf. I. Optical properties of paradermal sections of *Camellia* leaves with special reference to differences in the optical properties of palisade and spongy tissues. Plant and Cell Physiology **24**:1493-1501.

TITLYANOV, E.A. 1981. Adaptation of reef-building corals to low light intensity. Proceedings of the 4th International Coral Reef Symposium **2**:39-43.

TITLYANOV, E.A. 1991. Light adaptation and production characteristics of branches differing by age an illumination of the hermatypic coral *Pocillopora verrucosa*. Symbiosis **10**:249-260.

TITLYANOV, E.A., M.G. SHAPOSHNIKOVA & V.I. ZVALINSKII. 1980. Photosynthesis and adaptation of corals to irradiance. I. Contents and native state of photosynthetic pigments in symbiotic microalga. Photsynthetica **14**:413-421.

TUKEY, J.W. 1953. The problem of multiple comparisons. Department of Statistics, Princetown University. (unpublished)

TUNNICLIFFE, V.J. 1980. Biological and physical processes affecting the survival of a stony coral, *Acropora cervicornis*. Ph.D. Dissertation. Yale University, New haven, Connecticut, USA.

TUNNICLIFFE, V. 1981. Breakage and propagation of the stony coral *Acropora cervicornis*. Proceedings of the National Academy of Science (USA) **76**:2427-2431.

UNDERWOOD, A.J. 1979. The ecology of intertidal gastropods. Advances in Marine Biology **16**:111-210.

UNDERWOOD, A.J. & G. BARRETT. 1990. Experiments on the influence of oysters on the distribution, abundance and sizes of the gastropod *Bembicium auratum* in a mangrove swamp in New South Wales, Australia. Journal of Experimental Marine Biology and Ecology **137**:25-45.

UNDERWOOD, A.J. & E.J. DENLEY 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. **In** STRONG, D.R., D. SIMBERLOFF, L.G. ABELE & A.B. THISTLE (Eds.) Ecological Communities. Princetown University Press, Princetown, New Jersey, USA. pp. 151-180.

VAN GROENENDAEL, J., H. DE KROON & H. CASWELL. 1988. Projection matrices in population biology. Trends in Ecology and Evolution **3(10)**:264-269.

VERON, J.E.N. 1986. Corals of Australia and the Indo-Pacific. Angus & Robertson Publishers, Australia. 644p.

VERON, J.E.N. & R. KELLEY. 1988. Species stability in reef corals of Papua New Guinea and the Indo-Pacific. Memoirs of the Australian Paleontologists **6**:1-69.

VOGELMANN, T.C. 1993. Plant tissue optics. Annual Review of Plant Physiology and Plant Molecular Biology **44**:231-51.

VOGELMANN, T.C., J.F. BORNMAN & S. JOSSERAND. 1989. Photosynthetic light gradients and spectral regime within leaves of *Medicago sativa*. Philosophical Transactions of the Royal Society of London B, **323**:411-421.

WALLACE, C.C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. Marine Biology **88**:217-233.

WELLS, S.M. 1988. Coral reefs of the world. Vol **1-3**. IUCN: Cambridge.

WERNER, P.A. & H. CASWELL. 1977. Population growth rates and age vs. stage distribution models for teasel (*Dipsacus sylvestris* Huds.). Ecology **58**:1103-1111.

WHETTON, P. 1993. New Climate change scenarios. Climate Change Newsletter **5**:7-8.

WIGLEY, T.M.L. & S.C.B. RAPER. 1992. Implications for climate and sea level of revised IPCC emissions scenarios. Nature **357**:293-300.

WILKINSON, C.R. 1983. Role of sponges in coral reef structural processes. **In** BARNES, D.J. (Ed.) Perspectives on coral reefs. Australian Institute of Marine Science Publication, Australia. pp. 263-274.

WILKINSON, C.R. & E. EVANS 1988. Sponge distribution across Davies Reef, GBR, relative to location, depth and water movement. Coral Reefs (Submitted).

WMO/UNEP. 1991. Scientific assessment of ozone depletion. WMO Global Ozone Research and Monitoring Project, Report No. 25, NASA; NOAA; VKDOE; UNEP; WMO.

WILLIS, B.L. 1985. Phenotypic plasticity verus phenotypic stability in the reef corals *Turbinaria mesenterina* and *Pavona cactus*. Proceedings of the 5th International Coral Reef Congress **4**:107-112.

WILLIS, B.L. & J.K. OLIVER. 1990. Direct tracking of coral larvae: Implications for dispersal studies of planktonic larvae in topographically complex environments. Ophelia **32(1-2)**:145-162.

WINER, B.J. 1971. Statistical principles in experimental design. 2nd Edition. McGraw-Hill, Kogakusha, Tokyo.

WOLSTENHOME, J.K. 1991. An investigation of the reproductive biology and early stages of

the life history of the scleractinian coral *Tubastrea faulkneri* (Wells 1892). B.Sc.Hons. Thesis. James Cook University of North Queensland, Townsville.

WOODLEY, J.D., E.A. CHORNESKY, P.A. CLIFFORD, J.B.C. JACKSON, L.S. KAUFMAN, N. KNOWLTON, J.C. LANG, M.P. PEARSON, J.W. PORTER, M.C. ROONEY, K.W. RYLAARSDAM, V.T. TUNNICLIFFE, C.M. WAHLE, J.L. WULFF, A.S.G. CURTIS, M.D. DALLMEYER, B.P. JUPP, M.A.R. KOEHL, J. NEIGEL & E.M. SIDES. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science **214**:749-755.

WYMAN, K.D., Z. DUBINSKY, J.W. PORTER & P.G. FALKOWSKI. 1987. Light absorption and utilization among hermatypic corals: A study in Jamaica, West Indies. Marine Biology **96**:283-292.

YAP, H.T. 1981. Studies on the growth, regeneration and transplantation of *Acropora pulchra* (Brook) (Coelenterata: Anthozoa) at Santiago Island, Bolinao, Pangasinan. M.Sc. Thesis. Marine Sciences Center, University of the Philippines, Quezon City.

YAP, H.T., P.M. ALIÑO & E.D. GOMEZ. 1992. Trends in growth and mortality of three coral species (Anthozoa: Scleractinia), including effects of transplantation. Marine Ecology Progress Series **83**:91-101.