INJURY AND REGENERATION OF COMMON REEF-CREST CORALS AT LIZARD ISLAND, GREAT BARRIER REEF, AUSTRALIA

Thesis submitted by
Vicki R. Hall

June 1998

in partial fulfilment of the requirements for a Doctor of Philosophy Degree in the Department of Marine Biology of James Cook University.

THESIS DEDICATION

This thesis is dedicated to the loving memory of my father and grandfather.
To my father, thank-you for always believing in my academic abilities and for encouraging me to further my education, I hope I have made you proud.
To my grandfather, my sincere thanks for the financial support that has enabled me to continue my studies and for showing me that quiet achievers can make a difference.

ABSTRACT:

Corals are frequently injured by natural processes and human activities. The response of scleractinian corals to damage is dependent on the nature and extent of damage, the characteristics of the injury, the life-histories of the coral, and the prevailing abiotic and biotic conditions. In this thesis I have examined several aspects of injury including (1) the nature and extent of natural injury, (2) the response of corals to injuries with different characteristics and (3) the influence of morphology and life-history in response to damage.

The spatial and temporal patterns of coral injury were recorded to determine the nature and extent of damage in common reef-crest corals at Lizard Island. The total amount of partial mortality on reef-crest corals was low (<2%) although there was a three-fold difference among sites. Sites with low partial mortality had reef-crest assemblages dominated (both numerically and in cover) by tabular and bushy corals. These corals have low levels of partial mortality, and on average, fewer small colonies with injuries. Conversely, the site where the partial mortality was three times higher had a lower abundance and cover of tabular corals, and an increase in the number and cover of massive and digitate corals. Massive and digitate corals, on average, have a higher amount of partial mortality and more small colonies with injuries.

The amount of injury present on a colony at a particular time is a balance between vulnerability (i.e. frequency of injury and resilience to damage) and recovery rate. An investigation into the patterns of injury over time showed that vulnerability to damage and recovery of injuries was species specific. In general *Goniastrea retiformis* had a high number of old injuries, a slow regeneration rate, and was injured infrequently, suggesting that injuries tended to accumulate on colonies over time. The addition of new injuries was also low for *Acropora gemmifera*, however colonies had few pre-existing injuries and faster recovery rates, reducing the accumulation of injuries on colonies. The injury dynamics for *A. hyacinthus* differed between censuses because of a change in injury regimes from routine to catastrophic, the latter regime caused by an outbreak of *Acanthaster planci*. Under routine conditions, there were few pre-existing injuries on colonies, a moderate addition of new injuries, and rapid regeneration,

suggesting a fast turn-over of injuries. Under catastrophic conditions, there were many more pre-existing injuries, a high number of new injuries, and more injuries increasing in size than recovering, resulting in an accumulation of injuries.

The regeneration of injuries was influenced by the characteristics of the injury including initial size, type, and position within the colony The complete regeneration of an injury was more probable for small injuries (0 - 4 cm^2) than larger injuries. However, recovery rates were also dependent on the type of injury as scraping injuries had a much faster regeneration rate than tissue mortality or breakage. Additionally, recovery was influenced by the position of injuries within colonies for one species *Porites mayeri* where the rate of regeneration of central injuries was greater than edge injuries. Conversely, the recovery of central and edge injuries was similar for *A. robusta, A. hyacinthus, A. palifera, Pocillopora damicornis*, and *Porites lichen*. Variations in levels of partial mortality, zones of tissue from which regeneration can take place, degrees of settlement by other organisms, intensities of damage, and amounts of resources available for regeneration all contributed to the differences in recovery rates found between injuries with varying characteristics.

The regeneration of injuries requires resources that are in limited supply. In this study, there was a marked effect of injury on reproduction for *A. hyacinthus*, *A. gemmifera* and *G. retiformis*, inferring a trade-off between reproduction and regeneration. Presumably the resources usually available for gamete production are being reallocated towards polyp regrowth and defence against fouling organisms. In contrast, injury had no effect on the survival or growth of colonies over nine months for the three species. This result suggests that future reproduction is being preserved through the iteration of new polyps but at the expense of current reproduction. It also suggests that these species are resistant to damage since their survival was unaltered by damage in the short-term.

Species resistant to damage have evolved two alternative, but not mutually exclusive, strategies in response to injury. Corals can invest resources in defensive mechanisms to avoid damage (avoidance strategies) or regrow lost parts after injury has occurred (tolerance strategies). Both strategies were utilised by corals in this study, although the amount of investment in either strategy varied. Generally, the longer-lived species, *G.*

retiformis and *A. gemmifera*, seemed to invest more resources towards defence than the shorter-lived *A. hyacinthus* since the number of new injuries present on colonies was higher for the latter species. Conversely, the shorter-lived coral invested more in tolerance strategies by responding to infrequent damage events or minimal tissue losses with rapid regrowth. The cost of such a strategy is that shorter-lived species are more vulnerable to repetitive injury.

Experimental studies showed that branching species had more regrowth potential than massive and semi-massive species supporting the hypothesis by Jackson (1979) that morphology plays a role in the pattern of investment in regeneration and defence. The morphology of a coral influences its longevity, reproductive output, growth rate, and other life-history processes including regeneration. Consequently, the morphological strategy of an organism has evolved over time in response to a large number of biotic and abiotic processes including partial mortality.

In conclusion, this study on injury and regeneration of scleractinian corals has increased our knowledge of the underlying mechanisms that affect the recovery of corals from damage, and has provided a basis for understanding the consequences of different injury regimes on coral reefs. This is important because injury can adversely affect corals at the individual, population and community level and thus impact on the general ecology of coral reefs.

STATEMENT OF ACCESS

I, the undersigned author of this work, understand that James Cook University will make this thesis available for use within the University Library and, via the Australian Digital Theses network, for use elsewhere.

I understand that, as an unpublished work, a thesis has significant protection under the Copyright Act and;

I do not wish to place any further restriction on access to this work

~~**Or**~~

~~I wish this work to be embargoed until~~

~~**Or**~~

~~I wish the following restrictions to be placed on this work:~~

Signature

Date

ELECTRONIC COPY

I, the undersigned, the author of this work, declare that the electronic copy of this thesis provided to the James Cook University Library, is an accurate copy of the print thesis submitted, within the limits of the technology available.

___________________________________ __________________

Signature Date

DECLARATION

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

W. Hall ------------------------------ (Signature)

5-6-98 ------------------------------ (Date)

ACKNOWLEDGMENTS

Many people have contributed in a variety of ways to this thesis, and to all of you I would like to extend my heart-felt gratitude. Firstly, I would like to thank my closest friends, Jackie, Gilianne, Margaret, Kerri, Judy, Natalie and Alison for their encouragement and support throughout my studies at James Cook University. I would also like to thank Jessie, Ilona, Di, Bronwen, Faye, Lyn, Ian, Dave, Rob, Simon and Kerry for providing me with an endless stream of laugher-filled lunches.

My supervisor, Terry Hughes has provided me with a great deal of editorial support and has taught me an enormous amount about the intricacies of writing scientific papers, presenting seminars, and reviewing manuscripts. He has also assisted in the application of external funding for this PhD and covered the costs of my initial field trips. The use of underwater cameras, some diving gear, and laboratory equipment (e.g. slide-projectors, digitiser, computers and laser printer) were all provided by Terry. I am most grateful for his considerable input towards my PhD.

Jason Tanner has acted as an unofficial supervisor throughout my PhD and has generously given up his time to review many earlier drafts of my data chapters. Chris Alexander and the Coral Reef Discussion Group have also offered comments on some data chapters. Jason Tanner, Chris Alexander and Howard Choat have all been very supportive and encouraging throughout my PhD.

This study was field intensive and I spent much of my time at Lizard Island with a whole sweep of field assistants. I would like to thank Luke Smith, Andrew Baird, Sheryl Fitz-Patrick, Francis Pantus, Annabel Miles, Robyn Cumming, Patrick Sutton, Lachie Maclay, Larnie Linton, Jo Sadler and Jackie Wolstenholme for being very patient and enthusiastic field assistants. I would also like to extend my gratitude to the staff at the Lizard Island Research Station, Anne, Lyle, Mari-anne and Lance for all their help and the use of their excellent facilities. I really miss the BBQs, halloween parties and game nights held at Lizard Island. Dive gear for the field trips was provided by Phil Osmond, and Jo Gaudie and Paul Givney from Geology kindly lent me their compressor.

There was quite a large laboratory component to this study which was made possible by the assistance of several people. Zollie Florian offered help with microscopy, Francis Pantus very kindly allowed me the use of his image analysis program, Image-it, Gordon Bailey and Vince Pullella provided computer support, Larnie Linton and Jo Sadler helped with coral polyp dissections, Rachael Groves and Leigh Winsor assisted with histology, Jackie Wolstenholme offered her expertise in coral taxonomy, and Bette Willis supplied laboratory space and some technical equipment as did the School of Earth Sciences.

The statistical analysis of my data was very challenging. I would like to thank Natalie Moltschaniwskyj, Jason Tanner and particularly Glen De'ath for providing me with statistical advice. Additionally, discussions about damage in coral with many colleagues has been very rewarding. I would like to thank Buki Rinkevich, Joe Connell, Uri Oren, Esther Kramarsky-Winter, Erik Meesters, Robyn Cumming, Paul Marshall, Vicki Nelson, Tony Rauphael, Vicki Harriett and Katharina Fabricius for their stimulating conversations about coral damage. Kerry Neil and Rowan Pratt took the time to read the final draft of my thesis, for this special effort I am most appreciative.

This project would not have been possible without funding. I would like to thank the following granting bodies for their financial support: Lizard Island Research Station Fellowship (Australian Museum), Australian Federation of University Women, Australian Coral Reef Society, CRC Reef, Department of Marine Biology, and the Great Barrier Reef Marine Park Authority.

An initial investigation into the biochemical and histological aspects of this project was carried out. I would like to thank David Yellowlees, Bill Folley and Brett Moloney for their assistance with the biochemistry and Buki Rinkevich for providing a very detailed description of the histology of regenerative processes in corals. Your help was most appreciated and I hope to continue this work in the future.

Finally, I would like to thank my family for their continued support and love. I know that you have found it hard to accept my ambition of spending many years at university studying in a field very distant from my rural background, but I sincerely hope that one day you will realise just what it is that I have achieved.

TABLE OF CONTENTS **Page**

Title Page ………… i
Thesis Dedication ………… ii
Abstract ………… iii
Statement of Access ………… vi
Declaration ………… vii
Acknowledgments ………… viii
Table of Contents ………… x
List of Tables ………… xiv
List of Figures ………… xvii

Chapter 1 General Introduction ………… 1

1.1. Introduction ………… 1
1.1.1. Nature and extent of damage ………… 2
1.1.2. Characteristics of injuries ………… 2
1.1.3. Life-histories of corals ………… 3
1.1.4. Pre-existing biotic and abiotic conditions ………… 3
1.2. General Aims and Significance ………… 4

Chapter 2 The nature and extent of natural injury on reef-crest corals at Lizard Island ………… 6

2.1. Abstract ………… 6
2.2. Introduction ………… 8
2.3. Materials and Methods ………… 9
2.3.1. Description of study sites ………… 10
2.3.2. Spatial patterns of injury ………… 10
2.3.2.1. Patterns of tissue loss among sites ………… 12
2.3.2.2. The effect of morphology and colony size on injury patterns ………… 12

2.3.2.3. Coral community composition and size-
structure within sites ……………………………… 13
2.3.3. Temporal patterns of injury ………………………………… 13
2.3.3.1. The fate of injuries ………………………………... 14
2.3.3.2. The addition of new injuries ……………………… 15
2.4. Results ……………………………………………………..…….. 16
2.4.1. General summary of results …………………………….…... 16
2.4.2. Spatial patterns of injury …………………………………….. 16
2.4.2.1. Patterns of tissue loss between sites ……...……… 16
2.4.2.2. The effect of morphology and colony size
on injury patterns at the four sites ………………… 18
2.4.2.3. Coral community composition and size-
structure among sites ……………………………… 20
2.4.3. Temporal patterns of injury ……………………….………... 24
2.4.3.1. Initial status of injuries …………………….……... 24
2.4.3.2. Fate of injuries ……………………………………..… 27
2.4.3.3. New injuries …………………………………….…… 29
2.4.3.4. Frequency of injury ……………………….……… 33
2.5. Discussion ……………………………………………………….. 34
2.5.1. Spatial patterns of injury ……………………….…………… 34
2.5.2. Temporal patterns of injury ……………………………….… 36

**Chapter 3 Interspecific differences in the regeneration of artificial
injuries on scleractinian corals.** ……………………………………… 41

3.1. Abstract ……………………………………………….…………..… 41
3.2. Introduction ………………………………………………………… 42
3.3. Materials and Methods ……………………….……………………….. 46
3.3.1. Experiment 1 (Interspecific differences in recovery and
injury position within colonies) ………………..…………… 47
3.3.2. Experiment 2 (Interspecific differences in recovery and
injury types) ………………………………………………..… 48
3.3.2.1. Tissue removal versus scraping injuries …..……….. 48

3.3.2.2. Tissue loss versus branch removal ………………… 50
3.3.3. Statistical analysis ……………………………………………. 50
3.4. Results ………………………………………………………………... 51
3.4.1. Experiment 1 (Interspecific differences in recovery and injury position within colonies) ……………………………. 51
3.4.2. Experiment 2 (Interspecific differences in recovery and injury types) ………………………………………… 53
3.5. Discussion ……………………………………………………………. 56
3.5.1. Interspecific differences in regeneration ……………………. 56
3.5.2. Injury characteristics ……………………………………….. 58

Chapter 4 The response of *Acropora hyacinthus* and *Montipora tuberculosa* to scraping injuries, tissue mortality and breakage ……… 61

4.1. Abstract …………………………………………………………..… 61
4.2. Introduction ………………………………………………………… 62
4.3. Materials and Methods ……………………………………………... 65
4.3.1. Amount of regeneration ……………………………………. 66
4.3.2. Amount of algal settlement ……………………………….… 66
4.3.3. Zone of tissue available for regeneration …………………… 68
4.3.4. Analysis of data …………………………………………..… 68
4.4. Results ………………………………………………………………... 69
4.4.1. Amount of regeneration ……………………………………. 69
4.4.2. Amount of algal settlement ………………………………….. 70
4.4.3. Zone of tissue available for regeneration …………………… 73
4.5. Discussion ……………………………………………………………... 75

Chapter 5 To survive or reproduce: The response of scleractinian corals to damage ……………………………………………… 79

5.1. Abstract 79
5.2. Introduction 81
5.3. Materials and Methods 83
5.3.1. Response to injury: experimental design 83
5.3.2. Effects of injury on colony growth, regeneration and survival 85
5.3.3. Effects of injury on reproduction 86
5.3.4. The loss of reproductive output as a result of injury 87
5.4. Results 88
5.4.1. Response to injury by scleractinian corals 88
5.4.2. The effect of injury on colony growth, regeneration and survival 88
5.4.3. The effect of injury on reproduction 89
5.4.3.1. Colony-wide effect of injury on reproduction 89
5.4.3.2. Localised effects of injury on reproduction 91
5.4.4. Loss of reproductive output associated with injury 95
5.5. Discussion 98
5.5.1. Response to injury 98
5.5.2. Strategies of resistance 99
5.5.3. Trade-offs between growth, reproduction and survival 100

Chapter 6 General Discussion 104

References 110

LIST OF TABLES **Page**

Table 2.1. The number of small and large injuries present at South Island, Lizard Head, Washing Machine and North Reef, Lizard Island ………….. 17

Table 2.2. The distribution of colonies within injury categories amongst sites for morphological groups and colony size ……………………………………. 19

Table 2.3. The results of the logistic regression analyses assessing the effects of site, morphology, and colony size on (1) uninjured and injured colonies and (2) injured colonies with ≤ 5% and > 5% partial mortality …. 20

Table 2.4. The percentage of uninjured colonies among morphological groups and colony sizes and the percentage of colonies with low and high amounts of partial mortality for morphological groups ………………. 21

Table 2.5. A summary of the analysis of variance (ANOVA) results testing for differences in mean number of colonies per transect and (b) mean percent cover between sites and morphological groups ……………………….…... 22

Table 2.6. The results of logistic regression analysis assessing the effects of morphological group and sites on the distribution of small and large colonies ……………………………………………………….... 24

Table 2.7. The number of injuries that regenerated, shrank, stayed the same, or grew over 12 months, cross-classified by initial state, species and census interval ……………………………………………………..…… 30

Table 2.8. A repeated measures ANOVA testing the effect of species and colony size on the number of new injuries per colony over time for the two consecutive censuses ………………………………………………………. 31

Table 2.9. The number of censuses in which colonies sustained injuries recorded over 3 - 4 monthly intervals from 1994 - 1995 and 1995 - 1996 for small and large colonies of *G. retiformis*, *A. hyacinthus* and *A. gemmifera* …………………………………………… 33

Table 3.1. A list of studies showing the places and scleractinian corals for which experimental studies on injury and regeneration have been conducted …… 45

Table 3.2. The mean colony diameter ± SE (cm) for the study species ………….. 47

Table 3.3. An ANOVA table for the comparison of the amount of regeneration between species and injury position for experiment 1 at North Reef, Lizard Island …………………………………………….………… 52
Table 3.4. (a) Linear extension of new growth for the two injury types (tissue removal and branch removal) inflicted on *A. millepora* and *A. gemmifera* in experiment 2b. (b) Injury size and regeneration for the two injury types inflicted on *A. millepora* and *A. gemmifera* in experiment 2b ………………………………………………..………….. 55
Table 4.1. A summary of the repeated measures ANOVA testing for differences in regeneration between species and injury types, and how these patterns change between censuses …………………………………………………... 71
Table 4.2. A summary of the repeated measures ANOVA testing for differences in the amount of algal colonisation between species and injury types, and how these patterns change over time …………..……………..…….. 73
Table 4.3. The zone of tissue available for regeneration to original injury area for each injury type and species, and the results of the t-test analysing differences between species in the amount of tissue available for regeneration for each injury type …………………………………...…… 74
Table 4.4. A summary of the repeated measures analysis of covariance (ANCOVA) testing for differences in regeneration between species for breakage injuries and how these patterns change between census after the effect of tissue area available for regeneration has been adjusted for. ……………………….………………….…..… 75
Table 5.1. A summary of ANCOVA results testing the effects of injury size and frequency of damage on colony growth (cm^2) and regeneration (cm^2) for each species ……………………………………………………………….. 92
Table 5.2. A summary of ANOVA results testing colony-wide effects of injury size and frequency of damage on egg volume per polyp (mm^3) and polyp fecundity for the three species …………………………………...….. 93
Table 5.3. A summary of ANOVA results testing the effects of injury (size and frequency of damage) and position (samples taken close to and away from the injury site) on egg volume per polyp (mm^3) and

polyp fecundity for the three species ……………………………………..... 94
Table 5.4. The mean egg number per polyp and mean egg size for samples collected close to and away from the injury site for colonies of *A. hyacinthus*, *A. gemmifera* and *G. retiformis* …………………………..….. 98

LIST OF FIGURES **Page**

Figure 2.1. A map of Lizard Island showing the location of study sites ………..… 11

Figure 2.2. The mean partial mortality per transect for the four study sites around Lizard Island ………………………………….………………..… 17

Figure 2.3. The number of colonies per transect among morphological groups at each site around Lizard Island ……………………………….. 23

Figure 2.4. The coral cover per transect of morphological groups at each site around Lizard Island ………………………..…………………… 23

Figure 2.5. The distribution of small and large colonies among morphological groups and sites at Lizard Island ………………………….. 24

Figure 2.6. The number of small and large injuries on colonies of *G. retiformis*, *A. gemmifera* and *A. hyacinthus* in February 1994 and February 1995 ………………………………………………..….. 25

Figure 2.7. The range and average numbers of injuries per colony present on large and small colonies of *G. retiformis*, *A. gemmifera* and *A. hyacinthus* at the start of each census ……………………………..….. 26

Figure 2.8. The distribution of injuries between small and large colonies in February 1994 and February 1995 ……………………….…………… 27

Figure 2.9. A classification tree showing the relationship between fate and initial state, species and census ………………………………..…….. 28

Figure 2.10. The mean number of new injuries per colony over time for large and small colonies of *G. retiformis*, *A. gemmifera* and *A. hyacinthus* . 32

Figure 3.1. A photographic series showing the recovery of the tissue and scraping injuries inflicted on *Porites* over time ……………………………. 49

Figure 3.2. The amount of regeneration of a central and edge injury for several common reef-crest species over 71 days ……………..………… 52

Figure 3.3. The percentage of injury regeneration over time for *P. australiensis* and *A. cytherea* ……………………………………..………………..…. 54

Figure 4.1. Photographs of the different injury types for *A. hyacinthus*

and *M. tuberculosa* showing the size of the injury and the zone of tissue available for regeneration …………………..…………………… 67
Figure 4.2. The mean regeneration of injuries for injury type and species after 12 and 24 days ………………………………………………..… 70
Figure 4.3. The mean algal settlement for injury type and species after 12 and 24 days ……………………………………………………...…. 72
Figure 4.4. A scatter plot of the relationship between the amount of regeneration (cm^2) and the amount of algal settlement (cm^2) over 12 and 24 days ………………………………………………..… 72
Figure 5.1. An outline of the injury regimes inflicted on the three species ………. 84
Figure 5.2. (a) Final colony size (cm^2) adjusted for initial colony size by ANCOVA showing the effects of injury size and frequency of damage on absolute colony growth for each species. The amount of regeneration (cm2) over nine months, adjusted for initial injury size by ANCOVA, for each injury treatment by species ……………………….. 90
Figure 5.3. The proportion of polyps with mature gonads averaged over colonies for injury treatments and position effects within colonies for the three species …………………………………………..…… 96
Figure 5.4. The average egg volume per polyp (mm^3) for injury treatments and position effects within colonies for the three species …………………. 97