DISPERSAL OF CORAL LARVAE:
A modelling perspective on its determinants and implications

Thesis submitted by
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Nature has been defined as a principle of motion and change, and it is the subject of our inquiry. We must therefore see that we understand the meaning of motion for if it were unknown, the meaning of nature too would be unknown

(Aristotle, Physics, III, 1)

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ABSTRACT

In this thesis, I investigate the mechanisms and implications of coral larvae dispersal using spatially explicit and spatially realistic models. *Chapter 1* presents an introduction to the relevant theoretical background and a thesis outline.

Chapter 2 investigates the effects of different combinations of larval type (brooders vs. spawners) and current pattern (non-directional flow vs. strongly directional flow) on settlement, connectivity among reefs by larvae, and evenness and diversity of sources of the larval input to reefs. Despite their simplicity, the models revealed complex dynamics, and significant differences in results were found for different larval types, hydrodynamics conditions, and individual reefs. Settlement was higher for brooders than spawners, because their larvae suffered lower mortality during shorter pre-competent and competent periods. Increasing advection in the currents increased non-local settlement, however connectivity (the number of reefs connected) was not necessarily increased. The traditional view of connectivity being higher in spawners than brooders was often not supported when the currents were strong. Reefs or reefal systems with high evolutionary-scale connectivity did not necessarily have high ecological-scale connectivity. Moreover, different current patterns produced different effects on each larval type. These differences were quantitative for settlement and connectivity, but qualitative for the diversity of the settling larvae (an increase in advection increased diversity for brooders and decreased it for spawners).

Chapter 3 examines the effect of water retention at reefs on the settlement, connectivity, and evenness and diversity of sources of the larval input of different larval types under varying current patterns. Of the common predictions about the effects of an increase in the level of water retention at reefs only the increases in total and local settlement were fully supported. The other predictions (reduction in non-local settlement, connectivity, evenness, and diversity) were supported, but only at medium and high levels of water retention. At low retention levels and when the currents had a steady and strongly directional flow (the most common current conditions) the predictions were not met in many cases. In the absence of retention, settlement, connectivity, and diversity could be very low, especially for larvae with long pre-competent and competent periods (i.e. spawners). It was concluded that some level of larval retention at the reefs must exist, at least for spawners, in order to obtain settlement and connectivity values comparable to those found by ecological and genetic studies. Moreover, only very small levels of retention were required to produce dramatic increases in settlement rate, and these levels did not substantially reduce connectivity or diversity. In fact, these levels of retention could increase the connectivity of spawners when the currents had a strongly directional flow, as their larvae could become trapped in the circulation of reefs other than their natal. Notably, the estimated level of retention for a typical reef in the central Great Barrier Reef (GBR) provided the most favourable conditions for spawning corals in the models (which included reef densities and current speeds similar to those found in this region); this retention level maximised evolutionary-scale connectivity, yielded a high ecological-scale connectivity, and vastly increased settlement in spawning corals.

Chapter 4 investigates settlement and the mechanisms determining it on the GBR. The models reproduced many patterns of settlement and connectivity previously described by empirical studies, including the latitudinal settlement patterns of spawners and their proportion in the total settlement. It was concluded that a significant part of the large spatial and temporal variation in recruitment observed in the field might be related to variation in the factors included in the models, rather than to purely stochastic variation as often assumed. Therefore, settlement may be predictable to a certain extent if enough physical and biological information is available at the relevant spatial and temporal scales. Discrepancies between the models and field observations most likely reflect the importance of factors not included in the models, such as the decrease in temperature with latitude. Although all the models for brooders predicted a decline in settlement from the central to the southernmost GBR, none of them accurately reproduced the recruitment patterns of the northern GBR (all underestimating recruitment in this area). The models that best reproduced the latitudinal patterns of recruitment of spawners included fecundity, indicating the importance of this process in determining regional-scale recruitment. The proportion of spawners in the total settlement was best predicted when the models included retention and adult abundance (fecundity data was not available for brooders). Large differences in settlement and connectivity patterns occurred in space (even among nearby reefs) and among taxa in the models, suggesting the danger of generalising results obtained by empirical studies sampling a small number of reefs and/or species.

Chapter 5 explores the putative relationship between the potential for dispersal provided by the larvae of scleractinian corals and the extent of their geographic ranges in the Indo-Pacific (IP). Both the extent of the geographic range and the dispersal variables computed by the models varied substantially among the species in the study. Nevertheless, the potential for dispersal provided by the larvae of coral species was a poor predictor of the size of their geographic ranges. Notably, there was a tentative relationship between estimates of gene flow and some of the variables calculated by the dispersal models (particularly evolutionary-scale connectivity). The dispersal potential of the larvae is an important factor determining the geographic ranges of coral species, but the dispersal hypothesis per se cannot explain the geographic distributions of corals in the IP. The distribution of corals is also influenced by many other factors that mask the effect of the dispersal potential of the larvae in determining the geographic ranges of coral species in the IP.

Chapter 6 investigates the mechanisms by which the patterns of species richness in the IP may have arisen, using a 'Topological Model' of coral reef biogeography of this region that included speciation, dispersal, and local extinction processes. In the model dispersal occurred randomly (i.e. exclusively by diffusion) over a spatially realistic representation of the IP. This model produced a good approximation (better than previous models) to the present patterns of coral species richness in the IP. It was concluded that currents might not be the dominant factor shaping the geographic distribution of tropical inshore species as previously suggested, the topology of the habitats of the species being at least as important. In the 'Topological Model' the spatial attributes and relationships among habitats were sufficient for the central IP to act simultaneously as a centre of 'origin', 'accumulation', and 'refuge' (without the need of assuming particular properties for this area and/or the currents it receives), consequently generating a centre of species richness. The 'Topological Model', alone or in combination with a hydrodynamic model, can be used as a null-model against which the patterns of species richness in the IP can be contrasted.

The spatially explicit and spatially realistic models used in this thesis provided significant insights into the factors determining the dispersal and settlement of larvae and their consequences. These models can be used for guiding the conservation and management of marine populations; they should, however, be adapted to each specific problem, and contain adequate information about the physical conditions and organisms in question.

TABLE OF CONTENTS

STATEMENT OF ACCESS .... **ii**

ELECTRONIC COPY .... **iii**

STATEMENT OF SOURCES .... **iv**

ACKNOWLEDGEMENTS.................................... **v**

ABSTRACT .... **vi**

TABLE OF CONTENTS.................................... **ix**

LIST OF TABLES.................................... **xvi**

LIST OF FIGURES.................................... **xviii**

Chapter 1: **GENERAL INTRODUCTION** **1**

1.1. TECHNIQUES USED IN THE STUDY OF DISPERSAL AND SETTLEMENT OF MARINE LARVAE 3

1.2. CORAL REPRODUCTIVE BIOLOGY AND LARVAL COMPETENCE PATTERNS 5

1.2.A. Asexual reproduction 5

1.2.B. Sexual reproduction 6

1.2.B.1. Brooders 8

1.2.B.2. Broadcast spawners 9

1.3. LARVAL MORTALITY 11

1.4. LARVAL SWIMMING CAPABILITIES AND BEHAVIOUR 12

1.5. THESIS OUTLINE 14

Chapter 2: **LARVAL TYPES, CURRENTS, and their INTERACTION** **17**

2.1. INTRODUCTION 17

2.1.A. Aims of the study 20

2.2. MATERIALS and METHODS 21

2.2.A. General design 21

2.2.B. Model inputs 22

2.2.B.1. Spatial representations: Charts 22

2.2.B.2. Currents 26

2.2.B.3. Larval life 27

2.2.B.4. Fixed parameters 28

2.2.C. Model functioning and rules 29

2.2.D. Model outputs ... 30
2.2.E. Results analysis ... 31
2.2.F. Results presentation ... 36
2.3. RESULTS ... 37
2.3.A. Settlement rate ... 37
2.3.B. Settlement distribution: local vs. non-local settlement ... 39
2.3.C. Connectivity among reefs by larvae ... 39
2.3.D. Evenness and Diversity of reef receptors of the settling larvae ... 41
2.4. DISCUSSION ... 43
2.4.A. Settlement of larvae ... 43
2.4.B. Settlement distribution: local vs. non-local settlement ... 44
2.4.C. Connectivity among reefs by larvae ... 45
2.4.D. Evenness and diversity of reef receptors of the settling larvae ... 46
2.4.E. Variation among reefs in the studied dispersal variables ... 47
2.4.F. Model Limitations ... 47
2.4.F.1. General design ... 47
2.4.F.2. Hydrodynamic conditions ... 48
2.4.F.3. Larval competent periods ... 49
2.4.F.4. Larval mortality ... 49
2.4.F.5. Accuracy of the models and concluding remarks ... 50
2.4.G. Summary and Conclusions ... 50
Chapter 3: **EFFECTS OF LARVAL RETENTION ON REEFS ... 52**
3.1. INTRODUCTION ... 52
3.1.A. Evidence for dispersal and retention of larvae ... 52
3.1.A.1. Oceanographic evidence ... 52
3.1.A.2. Behavioural evidence ... 54
3.1.A.3. Ecological evidence ... 55
3.1.A.4. Genetic evidence ... 57
3.1.B. Aims of the study ... 58
3.2. MATERIALS and METHODS ... 59
3.2.A. Spatial representation of the reefs: Charts ... 59
3.2.B. Hydrodynamic patterns ... 60
3.2.C. Competence patterns of the larvae ... 60
3.2.D. Other parameters ... 64

3.2.E. Data analysis and presentation 65
3.3. RESULTS 66
3.3.A. Retention level, settlement rate, and fate of larvae 66
3.3.B. Retention level and local vs. non-local settlement 68
3.3.C. Retention level and connectivity among reefs 70
3.3.C.1. Evolutionary-scale connectivity 70
3.3.C.2. Ecological-scale connectivity 72
3.3.D. Retention level and evenness of the larval input 74
3.3.E. Retention level and diversity of the larval input 74
3.4. DISCUSSION 76
3.4.A. Consequences of the level of water retention in the models 77
3.4.A.1. Settlement rate and larval fate 77
3.4.A.2. Non-local vs. local settlement 78
3.4.A.3. Connectivity among reefs by larvae 79
3.4.A.4. Evenness and diversity of reef sources of the larval input to the reefs 80
3.4.B. Larval retention: implications and applications 81
3.4.B.1. Implications of larval retention 81
3.4.B.2. Applications to management and conservation 82
3.4.C. Model Limitations 83
3.4.D. Summary and Conclusions 85
***Chapter 4:* DISPERSAL OF LARVAE ON THE GREAT BARRIER REEF 87**
4.1. INTRODUCTION 87
4.1.A. Climatic and biological latitudinal patterns on the GBR 88
4.1.B. Aims of the study 91
4.2. MATERIALS and METHODS 92
4.2.A. Model Inputs 92
4.2.A.1. Spatial representations: Charts 92
4.2.A.2. Physical Oceanography 96
4.2.B. Model Types 98
4.2.C. Data Analysis 99
4.2.C.1. Aim 1: Patterns of larval dispersal and their effects in six zones of the GBR 99
4.2.C.2. Aim 2: Mechanisms underlying the latitudinal recruitment patterns on the GBR 100

4.2.C.3. Aim 3: Patterns of larval dispersal among reefs within zones 101
4.3. RESULTS 101
4.3.A. *Aim 1*: Patterns of larval dispersal in zones of the GBR................................ 101
4.3.A.1. Settlement rates 101
4.3.A.2. Origin of settled larvae: local vs. non-local settlement 103
4.3.A.3. Relationships among reefs 103
4.3.A.3.a. Connectivity at an evolutionary-scale 103
4.3.A.3.b. Connectivity at an ecological-scale... 105
4.3.A.3.c. Evenness of larval input 105
4.3.A.3.d. Diversity of larval input 105
4.3.B. *Aim 2*: Mechanisms contributing to the latitudinal recruitment patterns on the GBR.. 107
4.3.C. *Aim 3*: Patterns of larval dispersal among reefs within zones......................... 112
4.4. DISCUSSION 114
4.4.A. Patterns of dispersal among and within sectors in the GBR............................ 114
4.4.A.1. Settlement rate 114
4.4.A.2. Relationships among reefs 115
4.4.B. Mechanisms contributing to the latitudinal recruitment gradients in the GBR 116
4.4.B.1. Latitudinal recruitment gradients in brooders and spawners..................... 116
4.4.B.2. Latitudinal gradient in the proportion of spawners in the total settlement.. 117
4.4.C. Model Limitations 119
4.4.D. Summary and Conclusions 123
Chapter 5: **LARVAL COMPETENT PERIOD and SIZE OF GEOGRAPHIC RANGE IN CORALS 125**
5.1. INTRODUCTION 125
5.1.A. Relationship between dispersal potential and geographic range size............... 126
5.1.B. Aims of the study.. 129
5.2. MATERIALS and METHODS 130
5.2.A. Species of coral used in the study 130
5.2.B. Geographic range sizes 130
5.2.C. Potential for dispersal of larvae.. 130
5.2.C.1. Dispersal environment 132

5.2.C.2. Competence patterns of the larvae 134
5.2.C.2.a. Linear representation of the larval competence patterns 134
5.2.C.2.b. Non-linear representation of the larval competence patterns 135
5.2.C.3. Data analysis 138
5.2.D. Relationship between potential for dispersal and geographic range size 139
5.3. RESULTS 139
5.3.A. Geographic ranges 139
5.3.B. Potential for dispersal provided by the larvae 141
5.3.B.1. Broadcast spawners, linear representation 141
5.3.B.2. Broadcast spawners, non-linear representation 141
5.3.B.3. Brooders, non-linear representation 146
5.3.C. Relationship between larval dispersal potential and geographic range size 148
5.4. DISCUSSION 148
5.4.A. Variation in range sizes of corals in the Indo-Pacific 148
5.4.B. Variation in larval dispersal potential of corals in the Indo-Pacific 150
5.4.C. Relationship between larval dispersal potential and geographic range size 152
5.4.D. Study limitations 157
5.4.D.1. Experimental limitations 157
5.4.D.2. Model limitations 158
5.4.D.3. Statistical analysis limitations 158
5.4.E. Summary and Conclusions 159
Chapter 6: **LARVAL DISPERSAL, HABITAT TOPOLOGY, and SPECIES RICHNESS IN INDO-PACIFIC CORALS 161**
6.1. INTRODUCTION 161
6.1.A. Patterns of species richness in the tropical Indo-Pacific 161
6.1.B. Theories proposed to explain the patterns of species richness in the tropical Indo-Pacific 162
6.1.C. Processes determining species richness patterns and the ‘Vortex Model’ 166
6.1.D. Limitations of the ‘Vortex Model’ 167
6.1.E. Aims of the study 168
6.2. MATERIALS and METHODS 169
6.2.A. ‘Dispersal Sub-model’ 169
6.2.A.1. Charts: spatial representations of the environment 171
6.2.A.2. Currents 172

6.2.A.3. Pre-competent and competent periods of the larvae 173
6.2.A.4. Fixed parameters 174
6.2.B. 'Biogeography Sub-model' 174
6.2.C. Data Analysis and Results Presentation 176
6.3. RESULTS 178
6.4. DISCUSSION 184
6.4.A. Evidence in support of the 'Topological Model of Coral Reef Biogeography' 184
6.4.B. Potential evidence against the 'Topological Model of Coral Reef Biogeography' 185
6.4.C. Comparison of the 'Topological Model' with other theories including habitat topology 187
6.4.D. The 'Topological Model of Coral Reef Biogeography' as a null model 188
6.4.D.1. Central Indo-Pacific 188
6.4.D.2. Central and Eastern Pacific 188
6.4.D.3. Arafura Sea 189
6.4.D.4. Great Barrier Reef 189
6.4.E. Model limitations 190
6.4.F. Summary and Conclusions 191
***Chapter 7:* GENERAL DISCUSSION** **193**
7.1. OVERVIEW AND DISCUSSION OF THE MAIN FINDINGS IN THE THESIS 193
7.1.A. *Chapter 2:* Larval types, currents patterns, and their interaction 193
7.1.B. *Chapter 3:* Effect of larval retention on reefs 196
7.1.C. *Chapter 4:* Dispersal of larvae on the Great Barrier Reef 197
7.1.D. *Chapter 5:* Larval competent period and size of geographic range in corals 199
7.1.E. *Chapter 6:* Larval dispersal, habitat topology, and species richness in Indo-Pacific corals 200
7.2. APPLICATIONS: CONSERVATION and MANAGEMENT 202
7.3. SUGGESTIONS FOR FURTHER WORK 205
7.3.A. Empirical work 206
7.3.B. Modelling work 207
7.4. CONCLUSIONS 210

REFERENCES **212**

Appendix I: **LIST OF VARIABLES CALCULATED BY THE LARVAE DISPERSAL PROGRAM** **239**

Appendix II: **GEOGRAPHIC SETTING OF THE GREAT BARRIER REEF** **242**

Appendix III: **PHYSICAL OCEANOGRAPH OF THE GREAT BARRIER REEF** **246**

Appendix IV: **GLOSSARY** **253**

LIST OF TABLES

Chapter 2: **LARVAL TYPES, CURRENTS, and their INTERACTION**

Table 2.1. General description of the spatially explicit and spatially realistic models of reefal systems used in *Chapter 2* 23

Table 2.2. Types of spatially explicit and spatially realistic models of reefal systems used in *Chapter 2* grouped by type of input being investigated 23

Table 2.3. Spatial features of the theoretical charts used in *Chapter 2* 24

Table 2.4. List of variables computed by the data analysis module in the models of reefal systems used in *Chapter 2* (contained in the 3rd database output) 33

Chapter 3: **EFFECTS OF LARVAL RETENTION ON REEFS**

Table 3.1. Current sets used in the models of reefal systems in *Chapter 3* 61

Table 3.2. Types of spatially explicit models of reefal systems used in *Chapter 3* grouped by type of data input being investigated 64

Chapter 4: **DISPERSAL OF LARVAE ON THE GREAT BARRIER REEF**

Table 4.1. Location of the Great Barrier Reef zones represented by the charts used as data input to the models in *Chapter 4* 95

Table 4.2. Sectors of the Great Barrier Reef used in *Chapter 4,* their latitudinal boundaries, and references used in the representation of their hydrodynamic patterns 95

Table 4.3. Current sets used in *Chapter 4* 97

Table 4.4. Coral cover and adult fecundity in the 6 zones of the GBR used in *Chapter 4* 98

Table 4.5. Comparison of the number of reefs and reefal area (total area of the reefs) between the polygon coverages (closest to the real world) and the charts (used in the models) representing each zone 120

Table 4.6. Contribution of larvae to the 6 study reefs in each zone by 8 reefs located adjacent (in the 8 cardinal directions) to the charts used in *Chapter 4* 121

Chapter 5: **LARVAL COMPETENT PERIOD and SIZE OF GEOGRAPHIC RANGE IN CORALS**

Table 5.1. Description of the spatially explicit models of reefal systems used in *Chapter 5* grouped by data inputs types 132

Table 5.2. Current sets used in the models 133

Table 5.3. Reproductive type and competence patterns for the species used in the models in *Chapter 5* 135

Table 5.4. Relationship among biogeographic variables and the dispersal variables obtained with the models for broadcast spawning corals............................. 149

Table 5.5. Dispersal potential of larvae computed by the models in *Chapter 5* and gene flows estimated in the GBR (Ayre and Hughes 2000) for 3 brooding and 3 spawning coral species 154

Table 5.6. Relationships among the variables describing the dispersal potential of the larvae computed by the models in *Chapter 5* (using non-linear representations of the larval competent period) and the gene flows observed in the GBR (Ayre and Hughes 2000) for 5 species of coral (*P. damicornis*, *S. pistillata*, *S. histrix, A. millepora* and *A. valida*) 156

Chapter 6: **LARVAL DISPERSAL, HABITAT TOPOLOGY, and SPECIES RICHNESS IN INDO-PACIFIC CORALS**

Table 6.1. Description of the current conditions used in the 'Dispersal Sub-model' of the 'Topological Model' of coral reef biogeography of the Indo-Pacific.. 173

Appendix I: **LIST OF VARIABLES CALCULATED BY THE LARVAE DISPERSAL PROGRAM**

Table ApI.1. Larval fate variables………………………………………..………..240

Table ApI.2. Connectivity and diversity variables……………………………...241

LIST OF FIGURES

Chapter 2: **LARVAL TYPES, CURRENTS, and their INTERACTION**

Figure 2.1. Types of population models according to their representation of space........ 19

Figure 2.2. Example of the representation of reefal systems using 'charts' 25

Figure 2.3. Information flow and outputs (3 databases) in the general model 32

Figure 2.4. Larval output and input of a reef 34

Figure 2.5. Larval output and input connectivity 34

Figure 2.6. Effect of larval type - current pattern combination (brooders with diffusion; brooders with diffusion + advection; spawners with diffusion; spawners with diffusion + advection) on: (2.6.a.) settlement success of larvae; (2.6.b.) fate of the larvae produced.. 38

Figure 2.7. Effect of larval type - current pattern combination (brooders with diffusion; brooders with diffusion + advection; spawners with diffusion; spawners with diffusion + advection) on: (2.7.a.) proportion of larvae settling locally and away from their natal reef; (2.7.b.) connectivity among reefs at different larval thresholds 40

Figure 2.8. Effect of larval type - current pattern combination (brooders with diffusion; brooders with diffusion + advection; spawners with diffusion; spawners with diffusion + advection) on: (2.8.a.) evenness of reef receptors of larvae (Simpson's E index); (2.8.b.) diversity of reef receptors of larvae (Simpson's D index) 42

Chapter 3: **EFFECTS OF LARVAL RETENTION ON REEFS**

Figure 3.1. Non-linear representation of the cohort competence patterns...................... 63

Figure 3.2. Effect of the level of water retention at the reefs on the larval settlement of a cohort.. 67

Figure 3. 3. Effect of the level of water retention at the reefs on the fate of the larvae of a cohort.. 69

Figure 3.4. Effect of the level of water retention at the reefs on the spatial distribution of the settled larvae of a cohort.. 71

Figure 3.5. Effect of the level of water retention at the reefs on the connectivity among reefs by the larvae of a cohort.. 73

Figure 3.6. Effect of the level of water retention at the reefs on the evenness of reef sources of the larval input to the reefs 75

Figure 3.7. Effect of the level of water retention at the reefs on the diversity of reef sources of the larval input to the reefs 75

Chapter 4: **DISPERSAL OF LARVAE ON THE GREAT BARRIER REEF**

Figure 4.1. Map of the GBR and its sectors..................... 88

Figure 4.2. Variation in the proportion of spawner recruits in the total recruitment in the Great Barrier Reef..................... 90

Figure 4.3. Maps of the GBR and the 6 zones used in the models 93

Figure 4.4. Average settlement rates (larvae settled per km^2 of receptor reef) for the 6 study reefs in each of the 6 zones of the GBR provided by model type 1 102

Figure 4.5. Average origin (local vs. non-local) of the settled larvae for the 6 study reefs in each of the 6 zones of the GBR provided by model type 1 102

Figure 4.6. Average connectivity among reefs by larvae for the 6 study reefs in each of the 6 zones of the GBR provided by model type 1 104

Figure 4.7. Average evenness and diversity of reef sources of the larvae settled on the 6 study reefs in each of the 6 zones of the GBR provided by model type 1 106

Figure 4.8. Rank - Contribution graphics for the 6 modelled zones of the GBR provided by model type 1..................... 108

Figure 4.9. Comparison between settlement results in the models without retention and field recruitment data 109

Figure 4.10. Comparison between settlement results in the models with retention and field recruitment data 110

Figure 4.11. Level of variation in the modelled dispersal variables among the 6 study reefs within zones 113

Chapter 5: **LARVAL COMPETENT PERIOD and SIZE OF GEOGRAPHIC RANGE IN CORALS**

Figure 5.1. Geographic ranges of the 15 species of corals whose competent periods were used in the models..................... 131

Figure 5.2. Competence patterns of the larvae of the five broadcast spawning coral species used in the non-linear models..................... 137

Figure 5.3. Competence patterns of the larvae of the three brooding coral species (substratum offered) used in the non-linear models 138

Figure 5.4. Variation in the geographic range sizes of the coral species used in the models 140

Figure 5.5. Simulation results for the larval dispersal of broadcast spawners in the absence of retention using a linear representation of the competent periods.......... 142

Figure 5.6. Simulation results for the larval dispersal of broadcast spawners in the presence of retention using a linear representation of the competent periods......... 143

Figure 5.7. Simulation results for the larval dispersal of broadcast spawners in the absence and presence of retention using a non-linear representation of the competent periods 145

Figure 5.8. Simulation results for the larval dispersal of brooders in the absence and presence of retention using a non-linear representation of the competent periods.. 147

Figure 5.9. Relationship between the evolutionary-scale connectivity values computed by the models (using non-linear representations of the larval competent period) and the gene flows estimated in the GBR (Ayre and Hughes 2000) for 5 species of coral . 156

Chapter 6: **LARVAL DISPERSAL, HABITAT TOPOLOGY, and SPECIES RICHNESS IN INDO-PACIFIC CORALS**

Figure 6.1. Digitised map of the Indo-Pacific used in the simulations in *Chapter 6* 172

Figure 6.2. Competence patterns of the larvae of broadcast spawning coral *Acropora valida,* used in the models in *Chapter 6* 173

Figure 6.3. Information flow and use in the 'Topological Model of Indo-Pacific Coral Reef Biogeography' 177

Figure 6.4. Example of species dynamics over 200 iterations produced by the 'Topological Model of Indo-Pacific Coral Reef Biogeography', illustrating the emergence of a CIP hotspot.. 181

Figure 6.5. Comparison between the species richness patterns found in the IP and the results produced by the 'Vortex' and 'Topological' Models of Indo-Pacific Coral Reef Biogeography 183

Chapter 7: **GENERAL DISCUSSION**

Figure 7.1. Mechanisms and implications of the dispersal of coral larvae and their investigation in this thesis 194

Appendix III: **PHYSICAL OCEANOGRAPHY OF THE GREAT BARRIER REEF**

Figure ApIII.1. Background currents influencing the water circulation in the GBR….247

Figure ApIII.2. Topography and hydrodynamics of the Capricorn – Bunker Groups sector…………………………………………………………………………….………251