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

Thesis submitted by
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James Cook University
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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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

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>STATEMENT OF ACCESS</td>
<td>ii</td>
</tr>
<tr>
<td>ELECTRONIC COPY</td>
<td>iii</td>
</tr>
<tr>
<td>STATEMENT OF SOURCES</td>
<td>iv</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>v</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>vi</td>
</tr>
<tr>
<td>TABLE OF CONTENTS</td>
<td>ix</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>xvi</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>xviii</td>
</tr>
</tbody>
</table>

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

1.1. TECHNIQUES USED IN THE STUDY OF DISPERAL 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
TABLE OF CONTENTS

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
# Table of Contents

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.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
# TABLE OF CONTENTS

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 km² 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