

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.

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Chapter 1: **GENERAL INTRODUCTION**

The life histories of coral reef animals and plants usually comprise a long adult benthic phase and a relatively short ‘juvenile’ pelagic phase (e.g. Thorson 1950, Mileikovsky 1971, Reed et al. 1988, Strathmann 1993). The benthic phase is predominantly sedentary, although to different extents depending on the organism. In fishes the adult phase is not strictly benthic or sedentary, but tropical reef fishes generally do not move significant distances away from the location where they recruit despite their capabilities for mobility. In most invertebrates and plants the benthic phase is mainly stationary. In fact, in many species the adult is attached to the substratum and completely immobile, except for some dispersive processes that occur at very small spatial scales, such as directional growth. In corals, only a few species, mainly belonging to the family Fungiidae, are free-living or unattached, displaying some passive mobility dependent on the local hydrodynamic conditions and limited active mobility by using their tentacles and inflating soft tissues (Veron 1986a). In other coral species, fragmentation of live colonies can also provide passive short-distance dispersal (e.g. Tunnicliffe 1981, Wallace 1985, Hughes 1999). Long-distance dispersal can occur in some species via rafting of colonies after their attachment to floating objects (Jokiel 1984). However, although rafting may connect populations genetically to a certain extent, it is probably not very significant ecologically. The ‘juvenile’ pelagic phase usually occurs in the form of a dispersive larva, with different dispersing capabilities depending on the species. In most cases, the larva is planktonic and has the potential to connect populations on separate reefs, both genetically and ecologically (e.g. Harrison and Wallace 1990, Mc Edward 1995).

Populations can change in size by only four processes: birth, death, immigration, and emigration. The first two sources of change are local processes; the latter two are regional processes that couple the dynamics of many local populations, adding enormous complexity to the dynamics of the ecosystem (e.g. Gaines and Lafferty 1995). When immigration and emigration processes are important, the dynamics of a single local population cannot be understood without considering the demography of other populations. Together they form a population of connected local populations (or sub-populations), for which the term ‘metapopulation’ has been derived (Levins 1971). Marine species with this kind of life history can be considered to be ‘open’ (e.g. Caley

et al. 1996), and the most appropriate way to study these species is at the metapopulation level (e.g. Mumby 1999). For many of the organisms inhabiting coral reefs, immigration and emigration processes occur almost exclusively during the pelagic larval phase. Traditionally, most ecological studies on coral reefs have investigated the abundance or diversity of individuals in the adult phase. In the last 20 years more attention has been devoted to the larval phase, especially for commercially important species. The term ‘supply-side ecology’ was coined in recognition of the important role of larval input in determining the size of local adult populations (e.g. Underwood and Fairweather 1989). Only recently, the converse relationship between adult stocks and larval output has begun to receive attention (e.g. Hughes et al. 2000). However, integrating adult and larval phases (Gaines and Bertness 1993, Gaines and Lafferty 1995) and local and regional processes (Hughes et al. 1999) in the same study is rare due to logistic constraints. Consequently, we are still far from having a clear picture of the complete population dynamics of most coral reef species.

Connectivity among local populations on distinct reefs provided by larval dispersal has important implications not only for their demography (e.g. Gaines and Roughgarden 1985, Crossland 1988, Doherty 1988, Hughes 1990, Karlson and Levitan 1990), but also for many aspects of the biology of marine organisms such as their biogeography (e.g. Stehli and Wells 1971, Veron 1995, Scheltema 1986), genetics and evolution (e.g. Jablonski 1986, Palumbi 1995, Palumbi et al. 1997). As a result, understanding patterns of larval dispersal and settlement is essential for the appropriate management of coral reef ecosystems (e.g. Man et al. 1995, Roberts 1997, Hughes et al. 1999). Moreover, because larval dispersal from local reefs implies that variation in recruitment will not necessarily match variation in adult abundance, as suggested by Hughes and colleagues (1999) “...management of natural resources based on sound knowledge of processes and mechanisms will be far more robust than the traditional approach that has centred on monitoring patterns of abundance”.

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

Field observations, experiments, and modelling have provided valuable insights into the potential for dispersal and patterns of settlement of larvae. However, research on the realised dispersal ability of marine larvae has been limited (Palumbi 1995). Plankton tows have documented the presence of larvae of a wide range of species throughout the world's oceans, and the discovery of the larvae of coastal species far out to sea shows that long range movement is possible (e.g. Scheltema 1986). Nevertheless, in the field it is very difficult to track movements of larvae, establish their source and destination, and assess their ability to successfully settle and metamorphose into adults (Palumbi 1995). Tracing the invasion of introduced species has also provided some insight into the dispersal abilities of these species (Carlton and Geller 1993), but it is not clear if dispersal dynamics into a new habitat and between habitats already occupied by the species are similar (Palumbi 1995). In corals, fieldwork presents important logistic and financial constraints (e.g. Willis and Oliver 1990). This is mainly owing to the properties of the coral larvae and gametes (small size and taxonomic uncertainty) and their release (in variable and generally huge numbers, simultaneous in numerous reefs, with exact timing difficult to predict and extreme dilution after long periods in the water, and often -frequently in brooders and occasionally in spawners- in multiple episodes). Investigation of the dispersal of coral larvae in the field has mainly consisted of visually tracking the 'slicks' of gametes after a mass-spawning event (e.g. Willis and Oliver 1990, see *Section 1.2.B.2*). This is costly and can only be done for a limited time as hydrodynamic processes diffuse the slicks after 2 or 3 days (e.g. Olivier and Willis 1987). The settlement of coral larvae has been frequently investigated using recruitment plates (e.g. see Hughes et al. 2002a for a meta-analysis of the settlement studies in the Great Barrier Reef (GBR)); but this per se does not reveal dispersal patterns, only their consequences for the subset of species that readily recruit on plates. The combination of field recruitment data with information on adult abundance and fecundity has, nevertheless, provided some insights into the spatial scales of dispersal in the GBR (Hughes et al. 2000).

Different experimental approaches have been used in the laboratory, these include: the analysis of energy reserves and respiration requirements of larvae (e.g. Richmond

1981), and the study of settlement patterns in aquaria (e.g. Baird 1998, Wilson and Harrison 1998). Both of these techniques provide only an indication of the dispersal potential of the larvae. In addition, there may be difficulties in the extrapolation of such laboratory studies to natural conditions (Pechenik 1990).

Because of the limitations inherent in field and experimental studies, the only way to fully explore the actual realisation of the potential for dispersal of larvae has been the use of indirect methods. The most common approach is to examine the genetic structure of local populations using molecular methods, mainly enzyme electrophoresis and more recently DNA-based techniques, from which gene flow and dispersal can be inferred. However, these methods also have associated problems. They are expensive and concentrate on a few reefs (but see Ayre and Hughes 2000 for a large-scale hierarchical study), usually not revealing the source of the genes. Genetic studies can also be limited by the presence of low amounts of overall genetic variation in the species or areas investigated, precluding the detection of differences among populations (Thorrold et al. 1998, but see Avise 1994). Furthermore, molecular methods reveal connectivity at a genetic scale, and because only a few migrants per generation are required to maintain genetic homogeneity among populations this connectivity may not be important ecologically (e.g. Thorrold et al. 1998). In addition, they present some conceptual problems when applied to infer the dispersal levels of larvae, as most of the models used in genetic analysis are simplistic and incorporate unrealistic assumptions. For example, they generally assume that all populations are equal sources of migrants (e.g. Sork et al. 1999) and that genetic differences among populations are originated exclusively by drift, disregarding differences in selective pressures (e.g. Schulman 1998, Planes 2002, Mora and Sale 2002). Recently, chemical analysis of otoliths in fish recruits (on its own or in combination with genetic methods) has also been used to estimate the proportion of local recruitment in reef fishes (Jones et al. 1999, Swearer et al. 1999, Jones et al. 2005). This technique also presents important logistic (e.g. capturing all new recruits to a population) and financial limitations, and similarly to the genetic methods it can only focus on a few reefs, usually not revealing the source of the recruits (except for those of local origin). Moreover, it cannot be used for marine invertebrates such as corals, the taxa of interest in this thesis, which have very different dispersal qualities to fishes.

Simulation models are not hindered by many of the limitations of the empirical approaches to the study of larval dispersal. For example, modelling allows relatively

easy and inexpensive use of a wide range of different spatial and temporal scales as well as the integration of different life-history phases (e.g. adult benthic phase and larval pelagic phase) in a single study. As a consequence, simulation models can provide alternative insights. Models also present drawbacks; their main limitation being that they are simplifications of reality. However, this can also be one of their greatest virtues, as this simplification may let us see the ‘wood from the trees’, allowing the discovery of patterns and insights into processes which could not be identified otherwise. In fact, given the complexity of larval dispersal, the combination of empirical (field and laboratory) and theoretical methods constitutes the best chance of assessing and understanding this process, its causes and consequences.

Throughout this thesis I shall take advantage of the models qualities by using spatially explicit and spatially realistic models (see *Appendix IV* and *Chapter 2*) to investigate the dispersal of coral larvae, the factors determining it, and its implications for the ecology, genetics, and biogeography of corals (for a more detailed description of the material included in this thesis see the last section of this chapter, *Thesis Outline*). To do so I will extensively make use of empirically obtained data both in the design of the models and the evaluation of their results. The reproductive biology of corals, together with the swimming capabilities, behaviour, and mortality of their larvae are crucial and recurrent themes in the remaining chapters of this thesis; therefore I will introduce them here first.

1.2. CORAL REPRODUCTIVE BIOLOGY AND LARVAL COMPETENCE PATTERNS

Corals can reproduce asexually and sexually; however, the precise mechanisms by which both reproduction types occur can vary greatly among taxonomic groups. Both reproduction types are described below.

1.2.A. Asexual reproduction

In corals separation of polyps, or clumps of polyps, from a colony can occur as a consequence of external disturbances such as storms, bioerosion, disease, or predation. This process is called fragmentation or fission, and it is the most widespread mechanism

of asexual reproduction in corals (e.g. Tunnicliffe 1981, Wallace 1985). Moreover, fragmentation can be the prime mode of proliferation for some species in some locations, such as the branching *Acroporas* in the Caribbean (Hughes et al. 1992). Fragmentation can also occur without any apparent exogenous mechanism, as some colonies seem to be able to undergo natural autotomy. A number of coral species have evolved specific morphological structures, such as buds, polyp-balls, and stolons, that promote asexual reproduction (Harrison and Wallace 1990). Some brooding species can also produce planktonic larvae asexually via parthenogenesis (Harrison and Wallace 1990). Different individuals of the same species of coral can show different mechanisms of asexual reproduction depending on the location and environmental conditions, and sometimes several mechanisms can be found in a single colony (see Fautin 2002 for a review on asexual reproduction in cnidaria).

1.2.B. Sexual reproduction

Corals exhibit overlapping iteroparity (overlapping generations breeding repeatedly). The end product of the annual reproductive cycle is a ciliated planula larva. The larval life of corals, as in other marine invertebrates, consists of up to three consecutive stages: pre-competent period, competent period, and a post-competent period. The pre-competent period is the time of continuous rapid morphological and physiological development that occurs after larval release (in brooders) or fertilisation (in spawners, see *below*) (e.g. Scheltema 1986, Pechenik 1990). This period ceases once the larva has reached a certain developmental stage, competence, in which it is able to settle and metamorphose into the adult phase (a dividing polyp in corals) if suitable habitat is found. The larvae of some brooding species can settle within minutes after release (e.g. Harrison and Wallace 1990), thus they may be competent on release (i.e. they may lack a pre-competent period). The period between the attainment of the ability to settle and metamorphose and the actual occurrence of these events, or the loss of these capabilities, is the competent period. The arrival of new juveniles to a population is known as recruitment. Settlement and metamorphosis are processes that require energy (Scheltema 1986). If the energy level of the larva is reduced below a certain threshold, successful settlement and metamorphosis may not be possible (Lucas et al. 1979, Kempf 1981). Therefore, there is a limit to the time that the larva can delay settlement (Scheltema 1986), although larval life may be extended in a post-competent period (Richmond 1987, Pechenik 1990). Post-competent larvae have been observed to

experience spontaneous settlement (i.e. in the absence of cues), abnormal metamorphosis, or the loss of their ability to settle and metamorphose ultimately resulting in degradation and death (Pechenik 1990).

The duration of the competent period in the field is variable as the larva generally can delay settlement (e.g. Scheltema 1986, Pechenik 1990). The delay can be quite long, especially if the appropriate conditions for settlement are not present (Baird 1998, 2001). Larvae typically detect suitable habitat for settlement via stimulation cues (e.g. Scheltema 1986, Pechenik 1990), which generally take the form of soluble pheromone-like compounds or surface recognition substances (Scheltema 1986). Observed stimuli for settlement in different species of corals include: the presence of previously settled juveniles and colonies of conspecifics (Lewis 1974), the existence of crustose coralline red algae (Morse et al. 1988), and particular light intensities (Lewis 1974, Maida et al. 1994, Babcock and Mundy 1996, Mundy and Babcock 1998). Furthermore, not all the larvae in a cohort display the same duration of pre-competent and competent periods, even if they are under the same environmental conditions (e.g. Atoda 1947a, Wilson and Harrison 1998). Most of the larvae settle soon after they reach competency (in hours or a few days depending on the species) if suitable substratum is found, but a few others may remain planktonic much longer (for weeks or even months in some species) (e.g. Harrison et al. 1984, Richmond 1987, Morse et al. 1996, Wilson and Harrison 1998). Therefore, the larvae of marine invertebrate species differ not only in the mean duration of their pre-competent and competent periods, but also in the variance of the duration of these periods within cohorts (Scheltema 1986, Pechenik 1990, Baird 2001).

The lengths of the pre-competent and competent periods limit the connectivity among reefs by larvae, influencing the flow of individuals and genes among them, and thereby the ecology, evolution, and distribution of the species (e.g. Connell 1973, Jablonski 1986, Scheltema 1986, Palumbi 1997). Environmental factors, such as temperature and salinity, affect the rate of larval growth and consequently the length of the pre-competent period and overall larval life span (Pechenik 1987, 1990). However, their effect on the competent period is less clear (Scheltema 1986, Pechenik 1990, Zaslav and Benayahu 1996). The extent of the competent period is intrinsically related to the provision and expenditure of energy by the larva (e.g. Richmond 1982). The sources of energy available to coral larvae include: stored energy reserves available upon release (e.g. Richmond 1989), translocated metabolites from zooxanthellae (when these are present in the larva) (e.g. Richmond 1981, Glynn et al. 1991), and larval

nourishment. Coral larvae are typically non-feeding. However, the larvae of some corals have been observed to feed on food particles, and phytoplankton using a number of mechanisms, including: mucus nets and/or ciliary currents (in *Caryophyllia smithi*, Tranter et al. 1982), mesenterial filaments and/or tentacles following temporal metamorphosis into a planktonic polyp-like state or a sessile benthic form (in *Pocillopora damicornis*, Richmond 1985, 1988), or simply using their oral pore to capture food (in *Cyphastrea ocellina*, Wright 1986). Uptake of dissolved organic matter (DOM) has also been proposed as a potential source of energy for the larvae of corals (Fadlallah 1983, Zaslow and Benayahu 1996). However, although DOM uptake has been empirically demonstrated for the larvae of some other marine invertebrates (Jaekle 1994, Hoegh-Guldberg 1994, Hoegh-Guldberg and Pearse 1995, Schilling et al. 1996), it is probably not significant in larval nutrition because of the low concentrations of DOM in sea waters (Johannes 1974, Hoegh-Guldberg et al. 1997). Expenditure of energy by the larva depends not only on the duration of its pre-competent and competent period, but also on its metabolic rate. For example, the larvae of two different morphotypes of the same species of coral were found to have very different metabolic qualities (i.e. energy reserves and metabolic rates), with the smaller (less provisioned) larval form being predicted to have a competent period three times longer than the larger one (Richmond 1987).

The sexual reproduction strategies in corals can be grouped into two broad types: brooders and broadcast spawners. This classification is important because the two reproductive types are ecologically distinct, as outlined below.

1.2.B.1. Brooders

Brooding corals include the family Pocilloporidae (although some species also spawn); most species in the families Dendrophylliidae and Agariciidae; many in the Poritidae; some in the Caryophylliidae, Faviidae, Fungiidae, Meandrinidae, Mussidae, Oculinidae, and Siderastreidae; and the sub-genus *Isopora* of the Acroporidae (Fadlallah 1983, Harrison and Wallace 1990). Corals of this type are viviparous and typically hermaphrodites; they release sperm but not eggs, which are internally fertilised. Zygotes develop within the polyp -at least partially- to form planulae, so that by the time they are released they are relatively large (e.g. Harrison and Wallace 1990 and references within). The release of planulae occurs for up to 12 months per year, following a lunar cycle (reviewed by Tanner 1996a). The number of planulae releases per year, and the

length and synchrony with the moon-phase of the monthly cycle varies among species and locations. Being released in a rather advanced ontogenetic stage implies that the larvae have a short pre-competent period, ranging from virtually nil (i.e. minutes or competent on release) to two days depending on the species (Harrison and Wallace 1990). However, if planulae are not presented with suitable settlement substratum they can remain competent to settle for a few days, and in some species for weeks. Richmond (1987) estimated from analysis of their energy reserves and respiration demands, that the brooded larvae of *Pocillopora damicornis* can survive approximately 100 days and still settle successfully. He also demonstrated through direct observation that larvae of this species could settle and metamorphose in aquaria after 103 days. Numerous factors contribute to the potentially long competent period of *P. damicornis* larvae. They contain large energy reserves (Richmond 1987), and they can also acquire energy by several mechanisms including autotrophy through their photosynthetic zooxanthellae, planktotrophy via mesenterial filaments and temporal metamorphosis into a planktonic polyp (Richmond 1985). The presence of zooxanthellae is characteristic of the larvae of most brooding coral species, except from those in the Dendrophylliidae and Isoporan species (Kojis and Quinn 1981a, Fadlallah 1983, Richmond 1988, Harrison and Wallace 1990).

1.2.B.2. Broadcast spawners

Hermatypic corals differ from other clonal marine invertebrates in that at least two thirds of their species spawn gametes rather than brood larvae (Jackson 1986). Broadcast spawners include the families Acroporidae (except for the sub-genus *Isopora*), Fungiidae (although some species also brood), Merulinidae, and Pectiniidae; most species in the families Caryophyllidae, Faviidae, and Mussidae; many species in the Poritidae; and some species in the Agariciidae, Meandrinidae, Oculinidae, and Siderastreidae (Fadlallah 1983, Harrison and Wallace 1990). Corals of this type are generally oviparus hermaphrodites; they release both spermatozooids and eggs simultaneously into the water, where fertilisation and larval development occur (Harrison et al. 1984, Harrison and Wallace 1990). Broadcast spawning species frequently have an annual gametogenic cycle; gamete release occurring once a year in a multi-species spawning event that lasts a few nights (Harrison et al. 1984). The synchronicity of the spawning is thought to increase fertilisation success and enhance genetic exchange via cross-fertilisation (e.g. Stobart 1992, Willis 1992), as well as

reduce the mortality of gametes and larvae through predator satiation (Harrison et al. 1984). Annual mass spawning generally occurs in periods of warm sea water temperature, low heavy rainfall, and small tidal amplitude (e.g. Harrison and Wallace 1990, Mendes and Woodley 2002); its timing determined by the cycles of annual temperature, the Moon, and diurnal light (e.g. Babcock et al. 1986, Harrison and Wallace 1990). In regions where environmental cycles are not evident (i.e. where environmental variables do not fluctuate significantly) the multi-species spawning season can extend for many months (e.g. Red Sea: Shlesinger and Loya 1985, Japan: Heyward et al. 1987, Hayashibara et al. 1993, Micronesia: Richmond and Hunter 1990, Caribbean: Szmant 1986), with different colonies spawning in different lunar cycles (Baird et al. 2002). Even in regions with well-defined environmental cycles some species may spawn more than once (i.e. 'split spawning' sensu Willis et al. 1985) in special years, and in all regions colonies of species that typically participate in mass spawning episodes may miss one or more reproductive seasons (Baird et al. 2002). Nevertheless, larval production and consequently recruitment are generally much more seasonal for spawning than brooding corals (e.g. Hughes et al. 2001). After the mass spawning event the gametes and newly formed larvae often aggregate on the surface forming 'slicks' (e.g. Olivier and Willis 1987, Willis and Oliver 1990). The slicks are initially transported away from the reef by the currents, winds, and tides; but they gradually dispel within one or two days.

Larvae of broadcast spawners are typically smaller and therefore believed to contain fewer energy reserves than those of brooders (e.g. Fadlallah 1983, Harrison and Wallace 1990). Externally fertilised larvae generally lack zooxanthellae, except for the Acroporidae genus *Montipora* and the Poritidae species that develop from eggs containing zooxanthellae (Kojis and Quinn 1981a, Babcock and Heyward 1986). Nevertheless, the larvae of some species of fungiids have been observed to uptake zooxanthellae after fertilisation (Krupp 1983), and this may be possible in all species (Baird personal communication). Because the origin and entire development of the larvae occurs in the water column, they need longer time to reach competence than their brooded counterparts. The pre-competent period of the larvae of broadcast spawning corals generally lasts between 2 and 7 days (e.g. Babcock and Heyward 1986, Harrison and Wallace 1990, Baird 2001). However, the larvae may remain viable for much longer, weeks and even months (e.g. Harrison et al. 1984, Wilson and Harrison 1998, Baird 2001).

1.3. LARVAL MORTALITY

Unfortunately we know little about the mortality of marine larvae and its variation in space, time, and among taxa. Reliable estimates of larval mortality are rare owing to the inherent difficulty of repeatedly sampling the same cohort in the plankton. Although the accuracy of estimated larval mortality rates vary, mortality appears to be high for most invertebrate larvae, with instantaneous mortality ($M = \ln(N_t/N_0)/-t$, where N_0 =initial larvae abundance, N_t =larvae abundance at time t) ranging from 0.0161 to 1.01 (~ daily mortality: 0.0111 to 0.636) (Morgan 1995). However, most of the available data come from commercially important species of molluscs and crustaceans, and there are no studies of larval mortality in the field for coral species.

Ideally, the mortality rate of planktonic larvae should be estimated for young and old larvae in a variety of larval habitats. Mortality in marine invertebrates is generally greater in the earlier stages of development (e.g. Rumrill 1984, Pennington et al. 1986, Scheltema 1986), being best described by a type III survivorship curve (Pearl 1928, Deevey 1947). However, some authors have suggested that corals fit a survivorship curve type II, and others believe that the curve type may vary depending on the environmental conditions and species (Baird personal communication). Improved estimates of larval mortality can be obtained by partitioning mortality into its various sources, but our knowledge of the factors causing mortality is limited. In long-term cultures, mortality of larvae of marine invertebrates appears to be due to environmental factors rather than senescence (Kempf 1981). However, coral larvae in culture are remarkably resistant to contamination (Babcock et al. 2003). In the field, it seems that larvae are well adapted to their planktonic existence, with relatively few larvae dying of starvation, disease, or natural senescence (Morgan 1995). Predation appears to be the most important source of larval mortality for marine invertebrates in their natural environments (e.g. Thorson 1950, Day and McEdward 1984, Young and Chia 1987, Rumrill 1990). Because of the concentration of predators at the reefs intense predation on coral larvae can occur in them (Westneat and Resing 1988), generally much greater than in the open water (Johannes 1978, Hamner et al. 1988). The greater levels of predation at the reefs together with the greater mortality in the earlier stages of larval development strongly suggest that total larval mortality is higher within than between reefs.

In many marine invertebrate species brooded larvae have lower mortality than spawned larvae; their daily mortality rates often differing by up to one order of magnitude (e.g. Morgan 1995 and references within). This disparity is most likely attributable to differences in habitat preferences between both types of larvae and the fact that brooded larvae are released at a more advanced ontogenetic stage avoiding much of the early larval mortality of spawners. However, corals may not fit the conventional pattern. The larvae of many brooding molluscs and crustaceans are benthic or demersal, while the larvae of brooded corals are frequently pelagic and presumably exposed to the same planktonic dangers as spawned larvae. In addition, spawning corals release their gametes in a multi-species mass-spawning event (Harrison et al. 1984), which may reduce the initial loss of gametes and newly formed zygotes due to predator satiation (Harrison et al. 1984). Moreover, spawning occurs nocturnally when predation is less intense (e.g. Babcock et al. 1986). Paradoxically, mass spawning can also expose corals to catastrophic losses. For example, a heavy rain squall coincided with the spawning event of 1981 in the fringing reefs of Magnetic Island lowering the salinity of the sea water, thus destroying the propagules on the sea surface and severely reducing the larval production of that year (Harrison et al. 1984). Brooders, on the other hand, generally distribute their larval production over the year, spreading the risk of mortality of their offspring due to unpredictable disturbances. Additionally, differences in larval mortality are likely to be common among coral species. Important differences in larval mortality have been found among some species, consequence of the differential palatability to predators (Pratchett et al. 2002) and antimicrobial properties (Marquis et al. 2005) of their larvae. Nevertheless, despite the variation of instantaneous mortality rate in space, time, and among species, larvae of spawning corals generally have higher absolute mortality, solely because of their longer pre-competent and often competent periods.

1.4. LARVAL SWIMMING CAPABILITIES AND BEHAVIOUR

The swimming capabilities of the larvae of marine organisms vary among taxa (e.g. Leis and Carson-Ewart 1997a, Trnski 2002, Fisher and Wilson 2004, McHenry 2005), developmental stages and/or sizes (e.g. Bellwood and Fisher 2001), and environmental

conditions such as temperature and salinity (e.g. Young 1995, Green and Fisher 2004, Brooke and Young 2005). The larvae of many fishes (e.g. Leis and Carson-Ewart 1997a, Clark et al. 2005, Fisher 2005), ascidians, crustaceans, and cephalopods (e.g. Mileikovsky 1973, Chia et al. 1984 and references within) can, once they reach a certain developmental stage and/or size, swim for extended periods at speeds greater than the average currents speeds in their environments (i.e. typical horizontal current speeds range between 10-30 cm.s^{-1} , and many of these larvae can swim at least at 10-25 cm.s^{-1} , and some species at more than 50 or 65 cm.s^{-1}). The larvae of other marine invertebrates, however, can only swim at modest speeds, generally between 0.1 and 1 cm.s^{-1} (e.g. Mileikovsky 1973, Chia et al. 1984 and references within). The few swimming speeds reported for the larvae of corals fall in this range (e.g. 0.33 cm.s^{-1} for *Seriatopora histrix* - Atoda 1951, and 1-3 cm.s^{-1} for *Caryophylliidae smithi* - Tranter et al. 1982), and consequently are not fast enough to override the currents in most reef locations.

Another major aspect of the locomotion of marine larvae is their vertical migration in the water column. By altering their vertical position in the water column larvae can potentially avoid predation, improve feeding, modify dispersal patterns, affect their spread with respect to other larvae and adults, and facilitate settlement (e.g. Young 1995, Kingsford et al. 2002). Often migration is a behavioural response to environmental cues. Numerous environmental cues have been identified for marine larvae, including: light intensity and polarity, gravity, pressure, current direction, temperature, chemicals (of biotic origin such as amino acids, and abiotic origin such as salinity), magnetism, images, sound, vibrations, and texture (i.e. solid objects) (e.g. Kawaguti 1941, Young 1995, Kingsford et al. 2002, Simpson et al. 2005). For the larvae of marine invertebrates light and gravity are the two major environmental cues for orientation during dispersal, while chemical and texture cues influence the location and timing of larval settlement (e.g. Young 1995, McHenry 2005). The larvae of most species of corals (and other marine invertebrates) initially migrate to the water surface, and later descend in the water column (e.g. Szmant-Froelich et al. 1980, Babcock and Heyward 1986) or (generally shortly before settlement) become demersal (e.g. Atoda 1951, Svane and Young 1989, Young 1995, McHenry and Strother 2003). These vertical migration patterns are usually attributed to an ontogenetic reversal in phototactic and/or geotactic responses (i.e. from positive phototaxis and/or negative geotaxis to negative phototaxis and/or positive geotaxis) (e.g. Edmonson 1946,

Fadlallah 1983, McHenry and Strother 2003, Brooke and Young 2005). It has also been suggested that the changes in vertical distribution of the larvae in the water column can be due, at least partially, to changes in buoyancy during their development (Harrison and Wallace 1990), possibly associated to the use of lipid reserves (Richmond 1987). Nevertheless, little is known about the vertical distribution of coral larvae throughout most of their life. Their limited swimming capabilities in combination with the currents patterns commonly present in coral reef environments (i.e. strong currents in relatively deep water over varying bathymetry, usually leading to turbulent vertical speeds of 0.1-1.5 cm.s⁻¹) suggest that vertical migration of coral larvae in the water column is often prevented or at least limited (Mileikovsky 1973, Black 1993). However, a number of studies indicate that the larvae of some species may undergo a diurnal vertical migration cycle (Kawaguti 1940, Hodgson 1985a, 1985b).

The majority of studies on the swimming capabilities, responses to environmental cues, and mortality of marine larvae have been conducted in small aquaria in the laboratory (e.g. Morgan 1995, Young 1995, and references within). However, it is not clear whether larvae behave similarly under natural conditions (e.g. Fadlallah 1983, Young 1995). There is still a lot to be learned about the behaviour and mortality of coral larvae (particularly in the field), as in many other areas of larval biology such as development, nutrition, and physiology.

1.5. THESIS OUTLINE

This thesis is conceptually composed of three parts. *Part 1* is mainly theoretical, while *Parts 2* and *3* are more empirically based. *Part 1*, the most extensive, deals with the dispersal process of coral planulae. It investigates the factors determining dispersal and their consequences for the spatial patterns of larval settlement and connectivity among reefs. *Part 1* is subdivided into two chapters (*Chapter 2* and *Chapter 3*). *Chapter 2* explores the patterns of settlement and connectivity produced by the two ecologically distinct larval types of corals (brooders and broadcast spawners) under different current types. It also serves as a general introduction to the design and functioning of the most common model type in this thesis. *Chapter 3* examines the effects of water retention at the reefs on larval settlement and connectivity among reefs.

In *Part 2 (Chapter 4)*, the dispersal of larvae released by brooding and spawning corals is modelled within six zones of the GBR. The main aim of this chapter is to explore the mechanisms generating the patterns of coral larvae settlement in the GBR. In order to do this, varying levels of physical and biological information (e.g. spatial description of the reefs, hydrodynamics of the area, coral cover and fecundity) are included in the implementations of the models, and the results of the different models are contrasted with the information available in the literature. The results are also compared among and within areas, and a qualitative assessment is made of how representative localised field studies are of the zones in which they are conducted and of the GBR as a whole.

Part 3, subdivided in two chapters (*Chapter 5* and *Chapter 6*), investigates the relationships between larval dispersal and biogeography in corals. *Chapter 5* first explores the influence of the pre-competent and competent periods (i.e. their length, and the proportion of larvae in the cohort available for settlement throughout the competent period) on the potential for dispersal of larvae, and then the relationship between this potential and geographic range size. For this, competence patterns estimated in the laboratory for a range of coral species are used in the models. Then, different measures of the extent of the geographic ranges of these species are calculated. Finally, the putative relationship between the potential for dispersal of the larvae and the extent of the geographic range of the species is assessed. In *Chapter 6*, the role of habitat topology (i.e. spatial relationships among settlement substrata) as a potential mechanism underlying the patterns of species richness in the Indo-Pacific is investigated. In order to do this a ‘Topological Model of Coral Reef Biogeography’ was developed. This model consists of two sub-models: a ‘Dispersal Sub-model’ including a spatially realistic representation of the Indo-Pacific, and a ‘Biogeography Sub-model’ that integrates stochastic representations of speciation, extinction, and dispersal processes.

To conclude, a general discussion of the findings of this research is provided in *Chapter 7*. Additionally in this chapter, the implications of the results and applications of the models for management and conservation are examined, the main problems in the implementation of the models are revised, and directions for future research are suggested. *Appendices* offer additional information on the functioning (*Appendix I*) and theoretical background (*Appendices II* and *III*) of the models, and a glossary including

definitions of the most commonly used concepts in the thesis and the variables computed by the models (*Appendix IV*).

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

2.1. INTRODUCTION

The dispersal of planktonic larvae by most marine invertebrates enables communication among geographically separated reefs. Because the adult phase in marine invertebrates is benthic and mostly sedentary, this connectivity provides a mechanism for exchange of individuals and genes between populations that would otherwise be isolated. High spatial and temporal variability in the abundance of larvae at settlement (e.g. Barnes 1956, Milicich 1994, Hughes et al. 2000) indicates the complexity of larval dispersal. However, dispersal is not a random process (e.g. Willis and Oliver 1990, Palumbi et al. 1997), and different factors have been identified as determining its outcome. These include: the topology of the reefs (size, morphology, and distribution) (e.g. Johnson and Preece 1992, Archambault and Bourget 1999), the hydrodynamic processes occurring during dispersal (direction and speed of advection by currents, degree of diffusion, and level of water retention at reefs) (e.g. Sammarco and Andrews 1988, Black et al. 1991, Milicich 1994, James et al. 1996), and the biology of the larvae (competence patterns, condition, behaviour, and mortality) (e.g. Grosberg 1982, Richmond 1987, Underwood and Fairweather 1989, Morgan 1995, Wilson and Harrison 1998). The topology of the reefs provides the dispersal setting; the hydrodynamic processes supply the main transport mechanisms, at least for the larvae of marine invertebrates with limited motile abilities such as corals (see *Chapter 1, Section 1.4.*); while larval competence patterns, condition and mortality dictate the effective dispersal time. The behaviour of the larvae, specially that influencing their vertical positioning within the water column, can also have drastic effects on the outcome of the dispersal process (e.g. Boicourt 1982, Grosberg 1982, and see *Chapters 1 and 3.*) Unfortunately, our knowledge of *in situ* larval behaviour is limited, particularly in corals.

The hydrodynamic transport processes operating in coral reef systems can be classified into three groups or bands according to their frequency: (1) tides (semi-diurnal and diurnal frequencies), (2) weather-band currents (daily to monthly

frequencies), and (3) background currents (seasonal frequencies or almost constant). Each band has different effects on the transport of water particles and the dispersal of larvae (Williams et al. 1984). Tides are important for flushing individual reefs, weather-band currents for flushing the reefs and for meso-scale communication among reefs, and background currents for communication at the scale of the continental shelf. Background currents are also known as drift, residual, or seasonal currents. Typically they are broad and slow currents with very low frequency and long duration, induced by steady or very low frequency wind stress and/or longshore pressure gradients. These currents are essential in ecological terms, as they are the component of ocean circulation that transports nutrients and biota over very long distances, and their flow patterns determine the upstream and downstream directions in coral reef systems such as the Great Barrier Reef (GBR) (Andrews and Pickard 1990).

Research on the effects of the factors determining dispersal on settlement and connectivity is essential given the significance of these processes for the ecology, evolution, and management of corals (see *General Introduction* and references within). Variability in hydrodynamics (e.g. speed and direction of the currents) and biological processes (e.g. production, mortality, and behaviour of the larvae) makes the dispersal of larvae complex and difficult to study (e.g. Palumbi 1995). Empirical observation of dispersal in the field is restricted by logistic and financial constraints. Generally, larvae can only be tracked for a very limited time, 2 or 3 days at most (e.g. Olivier and Willis 1987, Willis and Oliver 1990). Settlement on recruitment plates does not provide information on the dispersal process itself, solely on its consequences. Furthermore, this information is only supplied for the subset of species that readily recruit on plates. Laboratory observations (e.g. Richmond 1988, Baird 2001) provide only an indication of the potential for dispersal of larvae. Genetic studies of a population supply estimates on gene flow and levels of local recruitment, but generally do not reveal the source of the genes or mechanisms involved in the genetic exchange among populations. Hierarchical large-scale studies (e.g. Sale 1984, Hughes et al. 1999, Ayre and Hughes 2000) and meta-analysis of several independent, spatially scattered, small-scale studies (Hughes et al. 2001) constitute a better approach to the investigation of the regional dynamics of dispersal, although they are not exempt from difficulties. In any case, the study of all the local populations comprised in a functional metapopulation and their inter-relationships is usually impossible. Simulation models are not limited by many of the constraints found in the fieldwork. Moreover, they can integrate physical

descriptions of the environment and biological data obtained in the laboratory, and their predictions can be compared to information acquired from ecological and genetic studies, providing an alternative approach with which to gain insights into larval dispersal and its consequences. In this chapter I present an investigation of the effects of factors determining larval dispersal on settlement and connectivity among reefs using a modelling approach.

Given the importance of the topology of the reefs and hydrodynamic processes for the dispersal of larvae, incorporating a spatial component in the models is crucial. Spatially structured models consider that the environment consists of a number of sites or populations (reefs in the models presented in this thesis) linked by dispersal (Figure 2.1.). Some spatially-structured models also incorporate the geometry of the set of sites included in the models, accounting for spatial relationships such as their relative positions and the distances separating them (e.g. Comins et al. 1992). The models in this subset are known as spatially explicit. In reality, not all populations in a metapopulation are homogeneous units (e.g. Nunney 2001); they vary both in space and time. Reefs, for example, differ in size, shape, coral cover and fecundity across spatial and temporal scales. Another subset of spatially-structured models accounts for this spatial and/or temporal heterogeneity (e.g. McPeck and Holt 1992). The most accurate representations of spatial processes are provided by the models in the intersection of both subsets, that is, the models including both the geometry and the spatial and/or temporal heterogeneity of the sites (Travis and Dytham 1998). These are called spatially realistic models.

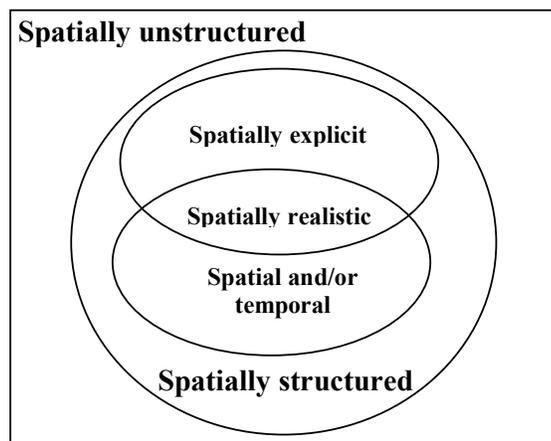


Figure 2.1. Types of population models according to their representation of space. Population models can be classified into two distinct sets: spatially-unstructured and spatially-structured. A subset of the spatially-structured models, the spatially-explicit models, includes the geometry of sites. Another subset introduces the spatial and/or temporal heterogeneity of sites. The intersect between these two subsets provides the most spatially realistic modelling alternative (from Travis and Dytham 1998).

Most of the modelling efforts dealing with the dispersal of marine larvae have taken a hydrodynamic approach. The aim of some of these models is simply to gain insights into the transport mechanisms of larvae (e.g. Black 1993). Other models are spatially realistic, incorporating detailed spatial information of an area, and their objective is to predict the destinations and amount of larvae reaching individual sites (such as reefs) in the area (e.g. James et al. 1996). These models generally lack biological information (e.g. duration of the larval competent period or mortality rates of the larvae), and what they in fact predict is the destination of particles of water or passive objects embedded in the water mass. A number of models incorporate information on the biology of larvae. This type of model has been used, for example, to study the influence of marine reserves in populations of fishes (Man et al. 1995), recovery from disturbance in corals (Johnson and Preece 1992, Preece and Johnson 1993), and the effect of habitat destruction in corals (Stone et al. 1996). Although these models study the relationship between larval dispersal and some ecological process, they often pay little attention to the physical aspects of dispersal. They generally use basic representations of the dispersal environment and include simple descriptions of the hydrodynamic conditions. The areas where dispersal occurs are theoretical, their designs chosen for their spatial characteristics (e.g. reef size and distance among reefs). It is only recently that a model has combined both high-resolution physical sub-models (i.e. including spatially realistic hydrodynamics and topology) and moderately realistic representations of larval biology to explore the dispersal of fish larvae in the Caribbean (Cowen et al. 2006).

2.1.A. Aims of the study

The main aim of this chapter is to use spatially explicit and spatially realistic models to explore the effects of factors determining dispersal (and their interaction) on settlement and connectivity among reefs. The models include descriptions of the topology of the reefal systems, the hydrodynamic patterns in the systems caused by background currents, and the biology of the larvae. I concentrate on the effect of 2 factors. (1) Larval type: brooders vs. broadcast spawners, and (2) current pattern: random or non-directional current flow (diffusion) vs. strongly directional current flow (diffusion + advection). The aim of this study is not to predict the exact destinations or amounts of larvae that settle, but to gain insights into the effects of these factors (and their interaction) on larval settlement and connectivity among reefs.

This chapter also serves as an introduction to the design and functioning of most of the models in this thesis. Variations in the relatively simple model type described and used in this chapter are used in the remainder of this thesis, either on their own (*Chapters 3 to 5*) or coupled with other types of models (*Chapter 6* and see *Chapter 7*).

2.2. MATERIALS and METHODS

The design, functioning, formats of the input and output files of the models in this chapter, together with the methods used in the analysis and representation of the results are presented below. These themes are common to the majority of the models in this thesis. Therefore, I will describe the general model in detail here, along with the specific design features relevant to this chapter, and only a brief overview of alternative possibilities. In the materials and method sections of subsequent chapters I will describe only the specific modifications and additions to the design and functioning of the general model relevant to those chapters.

2.2.A. General design

All the models were implemented using C programming language, under the formalism of a coupled lattice (CL) (see *Appendix IV*). CL models are a generalisation of the more commonly used in ecology cellular automata (CA) models. Traditional CA models consist of a regular lattice of cells, the state of each cell being represented by a discrete variable or set of variables. Time advances in discrete steps. In each step, every cell in the CA updates its state according to rules that depend on its current state and the states of its neighbours. CLs differ from traditional CAs in that cells can contain continuous values (i.e. their state is represented by continuous variables) and their state can be updated using more information than solely the state of the cells in the neighbourhood. CA and CL models are particularly appropriate for the study of processes with an important spatial component (e.g. Wolfram 1984). They can be constructed using simple rules and are capable of very complex behaviour. As a consequence, they have proved useful in gaining insights into the interplay between ecological processes that can occur at different spatial and/or temporal scales (e.g. Fahrig 1992, Levin 1992).

2.2.B. Model inputs

The main inputs to the general CL model were: a spatial representation of the physical environment, flow directions and speed of the background current, retention level of larvae at the reefs, lengths of the pre-competent and competent periods, mortality rate of the larvae, coral cover, and coral fecundity for each reef (Table 2.1.). The results presented in this chapter were obtained running simulations on 224 models, each of them representing a unique combination of the following inputs: environment representation, current patterns, and lengths of the pre-competent and competent periods of the larvae (Table 2.2.). The values for the rest of the inputs were kept constant across all the models.

2.2.B.1. *Spatial representations: Charts*

‘Charts’ were used as spatial representations of the physical environment. Each chart consisted of a matrix of cells, in which each cell depicted a square area (1 km x 1 km in this chapter) and contained a code symbolising its land-type. Four broad land-type categories were used: reef (marine substratum suitable for coral settlement and development), water (marine floor not suitable for coral settlement and development, effectively open water for the larvae), land (any emerged land, including: mainland, foreshore, islands, cays, and rocks), and mangrove (areas occupied by mangroves). To distinguish each reef in the chart, a unique code was assigned to each of them. Therefore each cell in the chart contained one of $n+3$ possible values; n values for the codes representing each of the n reefs, and the remaining 3 values representing water, land, and mangrove land-types (Figure 2.2.). In this way the size, shape and location of the main spatial features in the area of interest could be accurately represented. Each chart was used as a mould underlying the corresponding CL models (4 models per chart: 2 larval types x 2 current patterns, Table 2.2.).

In order to provide a wide range of dispersal environments, 55 different charts were used in the simulations (Table 2.2). Forty-nine were representations of theoretical areas, differing in various aspects of the topology of their reefs. Nine charts differed exclusively in their number of reefs, nine (1 in the previous subset and another 8) in the size of their reefs, ten in their reef density by varying their number of reefs, ten in their reef density by varying the size of their reefs (1 in the previous subset and another 9), and sixteen in their reef layout (1 in the first subset and another 15) (Table 2.3.). The

Table 2.1. General description of the spatially explicit and spatially realistic models of reefal systems used in *Chapter 2*. The current patterns values shown in brackets represent the probability of a water particle remaining in its cell or moving into each of the neighbouring cells in 8 cardinal directions (C = Central cell, N = North, NE = North-East, E = East, SE = South-East, S = South, SW = South-West, W = West, NW = North-West).

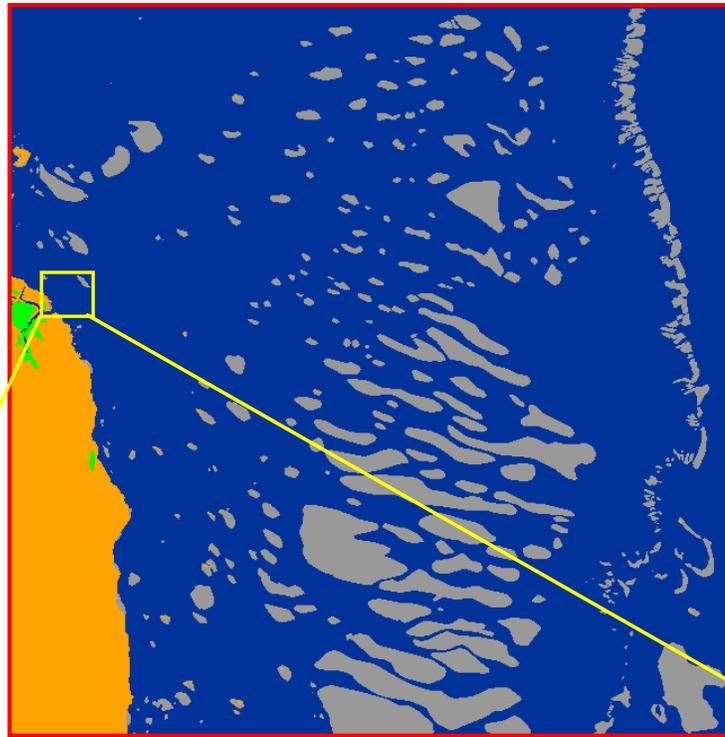
General design	Type	Coupled lattice
	Number of cells	400 to 32,400
	Cell size	1 km ²
Reefs	Reefs number	1 to 100
	Reefs size	1 to 100 km ²
	Reefs density	0.25% to 25%
	Reefs distribution	Uniform, Aggregated, Random
Fixed parameters	Currents speed	605 m.h ⁻¹ \approx 0.17 m.s ⁻¹
	Larval mortality	50% day ⁻¹ (M = 0.69)
	Larval retention	0%
	Coral cover and fecundity	10 ⁶ larvae per km ² of reef
Variables investigated	Larval competent period	Brooders: 0.5 to 7 days
		Spawners: 3 to 30 days
	Current patterns (C:N:NE:E:SE:S:SW:W:NW)	Diffusion: (0.000:0.125:0.125:0.125:0.125:0.125:0.125:0.125:0.125) Diffusion + Advection: (0.000:0.040:0.040:0.040:0.200:0.400:0.200:0.040:0.040)

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.

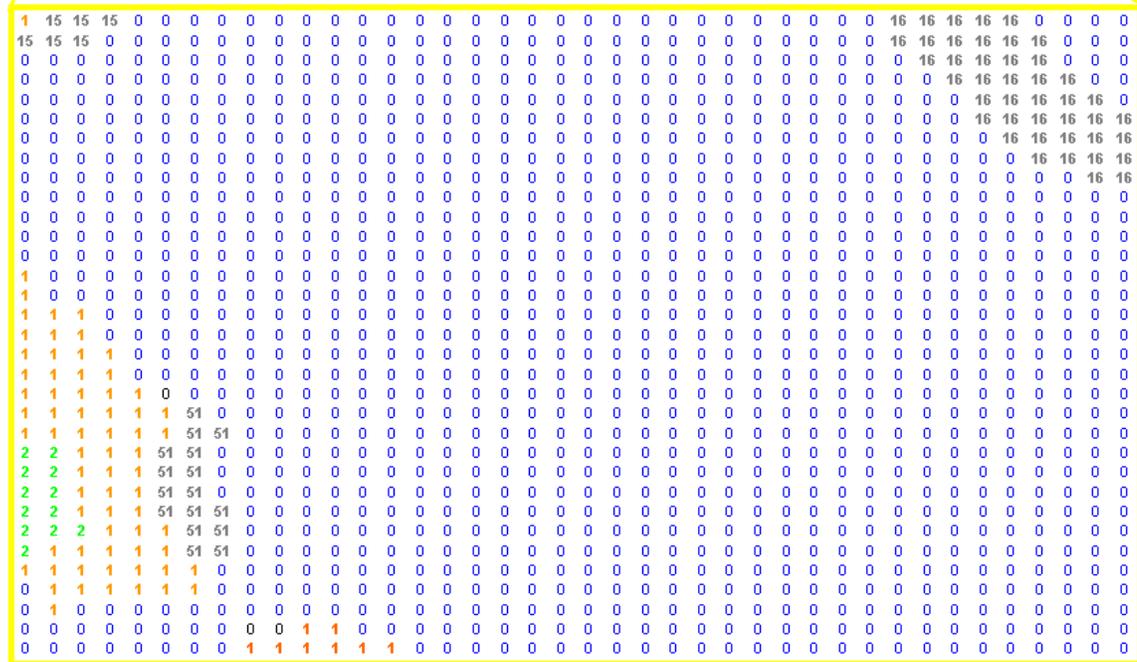
Charts	Larval types	Current patterns	Number of models
Theoretical (49)	Brooders	Random, non-directional (diffusion)	49 x 2 x 2 = 196
		Strongly directional (diffusion + advection)	
	Broadcast spawners	Random, non-directional (diffusion)	
		Strongly directional (diffusion + advection)	
GBR zones (6)	Brooders	Random, non-directional (diffusion)	6 x 2 x 2 = 24
		Strongly directional (diffusion + advection)	
	Broadcast spawners	Random, non-directional (diffusion)	
		Strongly directional (diffusion + advection)	
Total number of models			200 + 24 = 220

Table 2.3. Spatial features of the theoretical charts used in *Chapter 2*. *Topological attribute*: Aspect of the topology of the reefs in which the subset of charts differ. *Reef distribution*: Layout of the reefs in the chart (*Uniform*: regularly distributed, *Aggregated – 2*: aggregated in 2 groups of reefs and randomly distributed within each group, *Aggregated – 4*: aggregated in 4 groups of reefs and randomly distributed within each group, *Random*: randomly distributed all over the chart). *Reef size*: Number of cells in each reef, in brackets the number of cells on the sides of the reef. *Grid size*: Number of cells in the chart, in brackets the number of cells on the sides of the chart.

Topological attribute	Chart number	Reef distribution	Reef number	Reef size (no. cells)	Reef density	Grid size
Reef size	1	Uniform	16	1 (1x1)	4 %	400 (20x20)
	2	Uniform	16	4 (2x2)	4 %	1,600 (40x40)
	3	Uniform	16	9 (3x3)	4 %	3,600 (60x60)
	4	Uniform	16	16 (4x4)	4 %	6,400 (80x80)
	5	Uniform	16	25 (5x5)	4 %	10,000 (100x100)
	6	Uniform	16	36 (6x6)	4 %	14,400 (120x120)
	7	Uniform	16	49 (7x7)	4 %	19,600 (140x140)
	8	Uniform	16	64 (8x8)	4 %	25,600 (160x160)
	9	Uniform	16	81 (9x9)	4 %	32,400 (180x180)
Reef number	10	Uniform	1	16 (4x4)	4 %	400 (20x20)
	11	Uniform	4	16 (4x4)	4 %	1,600 (40x40)
	12	Uniform	9	16 (4x4)	4 %	3,600 (60x60)
	4	Uniform	16	16 (4x4)	4 %	6,400 (80x80)
	13	Uniform	25	16 (4x4)	4 %	10,000 (100x100)
	14	Uniform	36	16 (4x4)	4 %	14,400 (120x120)
	15	Uniform	49	16 (4x4)	4 %	19,600 (140x140)
	16	Uniform	64	16 (4x4)	4 %	25,600 (160x160)
Reef density by increase in size (number fixed)	18	Uniform	36	1 (1x1)	0.25%	14,400 (120x120)
	19	Uniform	36	4 (2x2)	1.00%	14,400 (120x120)
	20	Uniform	36	9 (3x3)	2.25%	14,400 (120x120)
	14	Uniform	36	16 (4x4)	4.00%	14,400 (120x120)
	21	Uniform	36	25 (5x5)	6.25%	14,400 (120x120)
	22	Uniform	36	36 (6x6)	9.00%	14,400 (120x120)
	23	Uniform	36	49 (7x7)	12.25%	14,400 (120x120)
	24	Uniform	36	64 (8x8)	16.00%	14,400 (120x120)
	25	Uniform	36	81 (9x9)	20.25%	14,400 (120x120)
Reef density by increase in number (size fixed)	26	Uniform	36	100 (10x10)	25.00%	14,400 (120x120)
	27	Uniform	1	36 (6x6)	0.25%	14,400 (120x120)
	28	Uniform	4	36 (6x6)	1.00%	14,400 (120x120)
	29	Uniform	9	36 (6x6)	2.25%	14,400 (120x120)
	6	Uniform	16	36 (6x6)	4.00%	14,400 (120x120)
	30	Uniform	25	36 (6x6)	6.25%	14,400 (120x120)
	22	Uniform	36	36 (6x6)	9.00%	14,400 (120x120)
	31	Uniform	49	36 (6x6)	12.25%	14,400 (120x120)
	32	Uniform	64	36 (6x6)	16.00%	14,400 (120x120)
	33	Uniform	81	36 (6x6)	20.25%	14,400 (120x120)
Reef distribution	34	Uniform	100	36 (6x6)	25.00%	14,400 (120x120)
	14	Uniform	36	16 (4x4)	4.00%	14,400 (120x120)
	35-39	Aggregated – 2	36	16 (4x4)	4.00%	14,400 (120x120)
	40-44	Aggregated – 4	36	16 (4x4)	4.00%	14,400 (120x120)
	45-49	Random	36	16 (4x4)	4.00%	14,400 (120x120)



2.2.a.



2.2.b.

Figure 2.2. Example of the representation of reefal systems using ‘charts’. (2.2.a.) Chart representation of an area of the northern GBR. (2.2.b.) Internal computer representation of a portion of the chart. The land-types are colour-coded in the graphics and number-coded in the computer memory: blue (0) = water; orange (1) = land; green (2) = mangrove; grey (>2) = reefs.

remaining six charts represented mapped areas of the GBR (see *Chapter 4* for a detailed description of these charts). The theoretical areas included only cells occupied by reef and water, while the GBR charts also included land and (in 5 cases) mangrove land-types. The sizes of the charts ranged from 20 x 20 (400) cells to 180 x 180 (32,400) cells; reefs numbers from 1 to 100; reefs sizes from 1 to 100 cells; and reef density (percentage of reef cells in the chart) from 0.25% to 25%.

2.2.B.2. Currents

The flow patterns of the background currents in the modelled coral reef systems were represented by a set of nine values, indicating the probabilities of a particle of water remaining in the same cell or of moving into each of the eight neighbouring cells in the next iteration (i.e. remaining in the same area or moving North, North-East, East, South-East, South, South-West, West, or North-West) (Table 2.1.). These probabilities are mutually exclusive and add up to 1. The same current conditions were applied to the whole chart during the whole simulation. That is, the current set was kept constant in space and time, applying it to each cell in each of the iterations of the simulation.

For the purpose of this chapter two sets of currents were used, the ‘random set’ and the ‘southward set’. In both, larvae can disperse in any direction, but with different probabilities in each case. In the first set the flow of the currents occur with equal probability in any direction (0.000:0.125:0.125:0.125:0.125:0.125:0.125:0.125:0.125), while in the second set the flow is mainly to the South (0.000:0.040:0.040:0.040:0.200:0.400:0.200:0.040:0.040) (values indicate the probabilities of a water particle being found in the Central:North:North-East:East:South-East:South:South-West:West:North-West cells -relative to its present position- in the next iteration). The random set represents transport exclusively by diffusion, while the southward set represents both diffusion and advection towards the South. Diffusion differs between current sets. It is implemented with equal probability in all directions in the random set, but is greater towards the South-East and South-West (i.e. in the directions adjacent to the direction of advection) in the southward set to more accurately simulate what occurs in nature. The random set especially is an idealistic case, but its comparison with a strongly directional current set (i.e. null advection vs. strong advection) can provide insights into the effect of background currents on the dispersal, settlement, and connectivity among reefs by larvae. Furthermore, this approach can also be used to represent dispersal conditions over longer periods of time, integrating several dispersal episodes. In this case, the first

current set would represent an area with a highly variable current direction (e.g. Torres Strait and northern part of Cape York in the GBR) and the second one would depict an area with a more consistent current direction (e.g. the Central and Southern GBR) (see *Appendix III*).

In other chapters the currents sets for water and reef cells may differ (*Chapters 3 to 6*). This difference represents the distinctive flow conditions that may exist at the reefs, where retention of water can occur for some period of time. In this chapter, the level of larvae retention at the reefs was set to 0 (by setting the probability of the central cell in the current sets to 0), i.e. no retention was included in the models in order not to confound its effects with those of the factors being examined. *Chapter 3* specifically deals with the effect of water retention on settlement and connectivity among reefs.

2.2.B.3. Larval life

In this chapter, larval life was represented by two values; the time elapsed since larval release for brooders and fertilisation for broadcast spawners until the start and end of the competent period. In between these two times the competent period was represented linearly, assuming that at any given time the same proportion of larvae is ready to settle and metamorphose in the cohort (the entire cohort in this case). This representation corresponds to the hypothetical situation where the competent periods of all larvae in a cohort are synchronised.

The models in this chapter used representations of the archetypical larvae of both reproductive and ecologically distinct types of corals: brooders, and broadcast spawners. The limits of their competent periods were (in days) set to: 0.5 to 7 for the ‘classic brooder’ and 3 to 30 for the ‘classic spawner’. The limits chosen for the classic brooder are comparable to the duration of the competent period observed in the laboratory for *Pocillopora damicornis* (Stephens 1931) and *Stylophora pistillata* (Atoda 1947b). Likewise, the limits chosen for the classic spawner are close to the duration observed for *Cyphastrea serailia* (Wilson and Harrison 1998) and *Cyphastrea ocellina* (Edmonson 1929), and similar to the value estimated by analysis of the energy reserves and respiration requirements for the larvae of *Acropora tenuis* (Richmond 1988).

2.2.B.4. Fixed parameters

Current speed and larval mortality rate can be set for each model, but remain the same throughout the chart during the whole simulation. In this chapter the same current speed and mortality rate were applied in all models. A current speed of 605 m.h^{-1} ($\sim 17 \text{ cm.s}^{-1}$) was used. Similar background current speeds are common, for example, in the central GBR (17.5 cm.s^{-1} , Kelly and Andrews 1985) and in the Western and Central Pacific (18 cm.s^{-1} , Jokiel 1984). However, only a proportion of the larvae transported between two cells cover the distance between the cells in the time suggested by the speed of the currents (i.e. they travel, for example, between two cells which centres are $\sim 6 \text{ km}$ away in 10 h). The remaining larvae, although they move at the same speed, take longer because they are not transported in a straight line due to diffusion (i.e. they are ‘under-dispersed’ relative to those transported in a straight line). In fact, the number of possible routes between any two cells in a chart is virtually infinite, although few or no larvae would follow many of these routes (see also *Section 2.2.B.2.*).

The average distance between the centre of a cell and the centres of the 8 adjoining cells was 1.21 km (the 4 cells on the sides distanced 1 km, while the 4 cells on the corners distanced 1.414 km), so a speed of 605 m.h^{-1} was equivalent to 0.5 cells.h^{-1} . In other words, each iteration in the models (i.e. the period during which the larvae could move to adjacent cells) corresponded to two hours in the real world. Pre-settled larvae suffered a daily mortality of 0.5 in the models (instantaneous mortality rate, $M \sim 0.69$). This was implemented by applying a survival rate of 0.943874 to the larvae in each of the iterations. This mortality rate represents both endogenous mortality (i.e. due to larval senescence) and exogenous mortality (e.g. due to predation and disease). In the remaining chapters, where non-linear representations of the competence patterns of the cohorts are used, mortality rates are lower as endogenous mortality is included in this type of representation.

The percentage cover and fecundity rate of the corals can be set for each reef, but in this chapter they were kept the same for all reefs within a model and across all models. Because coral cover and fecundity were equal in all reefs, the production of larvae by a reef was simply made proportional to its area. Each reef cell (1 km^2) was assumed to produce a million larvae. The value used is not really important, as the purpose of the study is not predictive, but comparative.

2.2.C. Model functioning and rules

Larvae are produced and dispersed from each reef-cell successively, following the rules described in the next three paragraphs. That is, dispersal is simulated from one reef-cell at a time. Only when dispersal from a reef-cell is completed (see below) and the results for that cell have been added to the entry for the reef that the cell belongs to in the database containing the raw results (see *Section 2.2.D.*), dispersal from the next reef-cell (under the same conditions) begins. In this way, the individual results for each reef are tracked independently. For each reef-cell, all larvae are released simultaneously, and their dispersal is deterministic and followed collectively (i.e. the models are not stochastic or individually-based). This makes the simulations much more efficient in terms of running time, and it should not greatly affect the results obtained given the large number of larvae released in each reef-cell.

To track dispersal, each cell in the CL contains a value that indicates the likelihood of the cell to contain at a particular time (i.e. iteration) a larva released in the reef cell for which dispersal is being simulated. Because dispersal is simulated collectively and deterministically for all the larvae released from a particular reef-cell, the values contained in the cells also represent the proportion of the total larvae released in the source reef-cell (i.e. the cell for which dispersal is being simulated) contained in the cell at a given time. At the start of the simulation of dispersal from a reef-cell, the cell is initialised with a value of 1. In other words, at time 0 (representing larval release for brooders and fertilisation for broadcast spawners) all larvae are concentrated in the reef cell of origin (probability = 1). During dispersal larvae can settle on the natal reef or another reef, die, become post-competent, fall into a mangrove area, or disperse out of the simulation area. These outcomes are mutually exclusive and their probabilities add to 1. The probabilities of each of the outcomes are calculated during the simulation for the larvae produced at each reef (one reef-cell at a time).

The larvae in water-cells are subjected to mortality and dispersal according to the current patterns described by the model inputs. That is, in each of the iterations the surviving larvae in each cell are dispersed to the cells in its neighbourhood according to the probabilities contained in the relevant current set (see *Section 2.2.B.2.*). Because retention is not included in the models used in this chapter, the reef-cells effectively behave like water-cells before the larvae are competent to settle. If the larvae in a reef-cell are competent to settle they will, by being removed from the dispersal matrix and

stored in a database according to their reef source and reef destination (see *Section 2.2.D.*). Land-cells act as mirrors; in other words, larvae that fall into them immediately bounce back to their cell of origin (in reality they simply remain in their cell) only suffering mortality, and if they survive they will be available for dispersal or settlement in the next iteration. Larvae that fall into a mangrove-cell are exposed to mortality but not dispersal; that is, they get trapped in the mangrove areas. These processes are repeated each iteration. The model iterates until all larvae become non-competent or until no cell in the CL contains a probability of having competent larvae higher than an established threshold (a probability of 10^{-12} in the models presented in this chapter). That is, the simulations were run until all or the vast majority of larvae had settled, died, or ceased being competent, and therefore dispersal was virtually finished.

A problem presented using CL models is that posed by the outer cells of the lattice, as their neighbourhoods are different to the ‘standard 9-cell neighbourhood’ described above for cells elsewhere. This is known as the ‘edge effect’. The common approaches to this problem are: joining the top and bottom ends and the left and right ends in an structure known as ‘torus’; making the edges reflective (i.e. larvae bounce back into the lattice in a position symmetrical to what they would have had outside the grid using the outermost cell as a mirror); or making the edges absorbent (i.e. larvae dispersed away from the lattice disappear and never come back into the system). Because some of the charts used in this chapter represented actual reefal areas, the torus and reflecting edges designs were not appropriate and instead a modification of the absorbing edges strategy was employed. A rim with a thickness of 10 water cells was added to the charts; this acted as buffer zone, giving the larvae that reached the cells in the rim the chance to return to the original chart area. If the larvae reached the outer edge of the buffer zone they were absorbed, but this was rare because few larvae reached the original chart edge and those that did could return inside it or suffered mortality for at least ten more iterations before they could reach the outer edge of the buffer zone.

2.2.D. Model outputs

The models sequentially produce three outputs, each of them consisting of a database (Figure 2.3.). The first database is created during the simulation of dispersal and retention (when present) of larvae from each reef-cell, and it describes the fate of the larvae expressed in terms of probability. This includes for each source reef the

proportion of the larvae released that: settled in each reef and in total, died, became post-competent, fell into a mangrove area, and dispersed out of the modelled area during the simulation (Figure 2.3.).

The second database is obtained by combining the results contained in the first database with the information about each reef. First, the total production of larvae by each source reef is estimated using information on their area, coral cover and fecundity. Then, the probability values representing the fate of the larvae released by each reef in the first database are converted into absolute numbers of larvae by multiplying each probability by the estimated total larval production of the reef (Figure 2.3.). This database is therefore similar in structure to the previous one, containing the same concepts mentioned above but expressed in absolute numbers of larvae. It also includes information on the larvae settled on each reef and their origins. That is, in the second database the reefs are considered not only as sources of larvae but also as receptors, so that both the larval outputs and inputs of each reef are described in detail (Figure 2.3.).

The final output of the models, the third database, is a product of the analysis of the results in the second database and it contains summary statistics of the computed variables. This is described in detail in the next section.

2.2.E. Results analysis

The analysis and summary of the results obtained for each simulation is built into the program implementation of the model. For the effects of this chapter, a total of 14 variables for each reef were computed and stored in a database (3rd database) during the data analysis (Table 2.3) (in reality a total of 53 variables are computed by the program, see *Appendix I*). The total, average and standard deviation values of these variables for the reefs in the reefal system (chart) were also computed and stored in the database. These variables can be classified into three broad groups: larval fate variables, variables describing the degree of connectivity among reefs, and variables related to the diversity of the larvae settling on the reefs.

The larval fate variables can be further classified into three sub-types: output, input, and success variables (Table 2.4., *Appendix I*). Output variables consider the reefs as sources of larvae, while input variables consider them as receptors (Figure 2.4.). The term ‘receptor’ is preferred over ‘sink’, as many reefs receive larvae without acting as sinks (traditionally the term ‘sink’ is used for reefs that receive more larvae than they

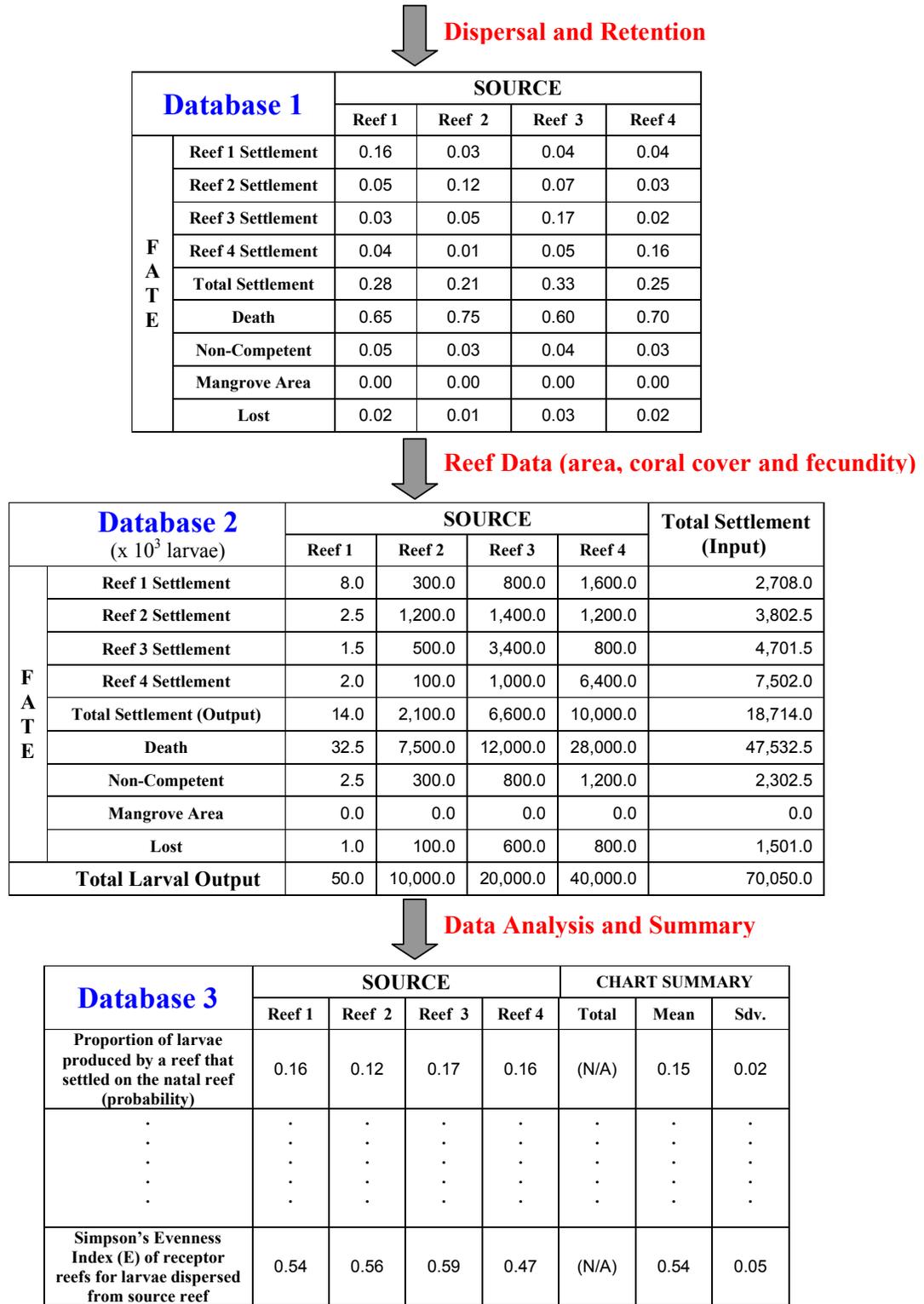


Figure 2.3. Information flow and outputs (3 databases) in the general model. The 1st database, produced after the simulation of dispersal and retention, contains probabilities representing the fate of the larvae released on each reef. The 2nd database, obtained by combining the 1st database with information on the reefs (area, coral cover and fecundity), express the larval fate in absolute numbers of larvae, considering the reefs both as sources and receptors. The 3rd database is obtained by the analysis and summary of the data in the 2nd database (N/A = Non-Applicable).

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).

Fate of Larvae	Output	Proportion of the total larvae produced by a reef that settled on the natal reef
		Proportion of the total larvae produced by a reef that settled on non-natal reefs
		Proportion of the total larvae produced by a reef that died
		Proportion of the total larvae produced by a reef that became non-competent
		Proportion of the total larvae produced by a reef that fell in mangrove areas
		Proportion of the total larvae produced by a reef that was lost outside the chart
	Input	Proportion of the total larvae settled in a reef that came from that reef
		Proportion of the total larvae settled in a reef that came from other reefs
	Success	Larvae settled in a reef per million larvae produced by the reef
Connectivity among Reefs	Output	Richness (number) of receptor reefs of larvae dispersed from a source reef at a threshold > 0 larva
		Richness (number) of receptor reefs of larvae dispersed from a source reef at a threshold ≥ 1 larva
		Richness (number) of receptor reefs of larvae dispersed from a source reef at a threshold ≥ 1000 larvae
Diversity Indices	Output	Simpson's Diversity Index (D) of receptor reefs of the larvae dispersed from a source reef
		Simpson's Evenness Index (E) of receptor reefs of the larvae dispersed from a source reef

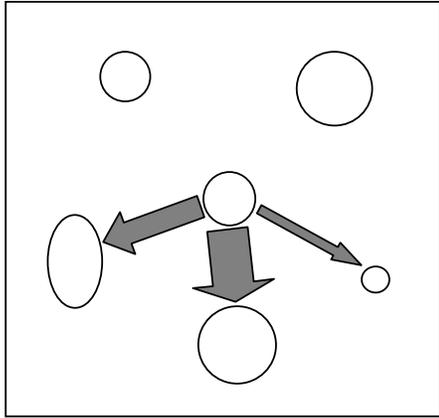


Figure 2.4.a.

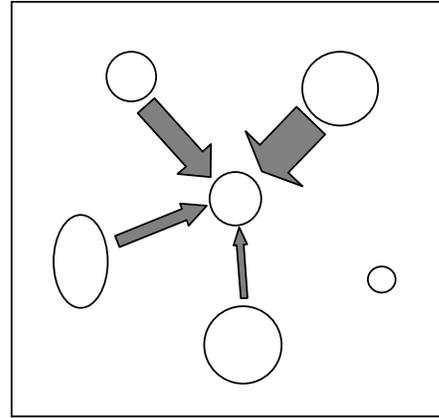


Figure 2.4.b.

Figure 2.4. Larval output and input of a reef. (2.4.a.) Output variables refer to the larvae produced by a reef. For example, output connectivity is the number of receptor reefs of the larvae produced by a reef (3 in the example diagram). (2.4.b.) Input variables refer to the larvae settling on a reef. For example, input connectivity is the number of source reefs of the larvae settled in a reef (4 in the example diagram). The amount of larvae connecting reefs can also vary among reef pairs as expressed by the thickness of the arrows.

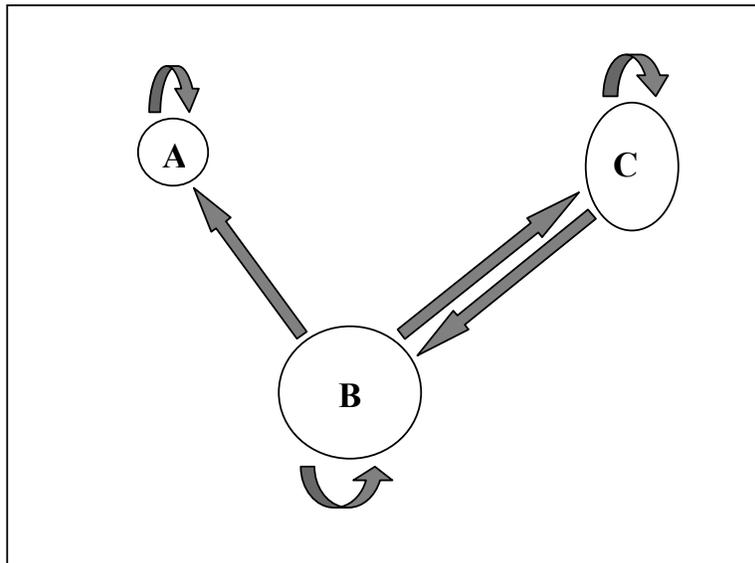


Figure 2.5. Larval output and input connectivity. The values of the output and input versions of the connectivity and diversity variables may differ at the level of individual reefs, but are equal at the reefal system (i.e. chart) level. For example, the larval output of all the reefs considered together reaches as many reefs as the number of reefs where the larval input comes from. In the 3 reefs (A,B,C) system in the picture the total output connectivity is 6 (A = 1; B = 3; C = 2) and the total input connectivity is also 6 (A = 2; B = 2; C = 2).

produce; see below and *Appendix IV*). The larval fate variables that consider the reefs as sources of larvae (output sub-type) include the proportion of larvae produced by each reef that: settles on the natal reef, settles elsewhere, dies, becomes post-competent, falls into a mangrove area, and is lost out of the chart during the simulation. The larval fate variables that consider the reefs as receptors of larvae (input sub-type) include the proportion of larvae settled on each reef from local and non-local sources. The last sub-type of the larval fate variables measures settlement success. This is estimated by computing the number of larvae settled per million of larvae released.

The connectivity variables represent the number of reefs connected to each other by larvae at different levels or thresholds (Figure 2.4.). A connectivity threshold is the minimum number of larvae that have to disperse between two reefs for them to be considered as connected. Three thresholds were used in this chapter: > 0 larva (there is a possibility of connection, although on average there may be less than one larva connecting the reefs per dispersal episode; that is, the reefs may only be connected occasionally rather than in all dispersal events), ≥ 1 larva, and ≥ 1000 larvae. The last threshold is important at ecological time scales, while the first two are important mainly at evolutionary time scales. Connectivity can be computed considering the reef as a source of larvae (output connectivity) or as a receptor of larvae (input connectivity). Output connectivity indicates the number of reefs on which at least a certain amount (threshold) of larvae produced by a given reef settle, and input connectivity indicates the number of reefs that produce at least a certain amount (threshold) of the settlers on a given reef.

Describing the relationships among reefs exclusively in terms of the number of reefs connected by larvae can be misleading, as it lacks information on the amount of larvae exchanged among reefs (Figure 2.4.). To complete the picture provided by the connectivity variables, the models also compute evenness and diversity variables for both the larval output and input of each reef. The evenness (or equitability) variables estimate the symmetry with which the larvae produced by one reef settle on the receptor reefs (larval output evenness) and with which the larvae received by one reef were originated (larval input evenness). The diversity variables take into account both connectivity and evenness, combining them into a single variable. They refer to the extent to which different receptor reefs are represented as settling locations for the larvae produced by a reef (output diversity) and different source reefs are represented as origins of the larvae settled in a reef (input diversity). The evenness and diversity

variables in the models are based on the species' evenness and diversity indices (E and D indices respectively) developed by Simpson (e.g. Begon et al. 1990) (but see *Appendix I* for additional implementations). In a similar fashion, connectivity can be considered equivalent to species richness, representing in this case the abundance of receptor or source reefs rather than species abundance.

At the individual reef level the values of the output and input versions of the connectivity and diversity variables can differ among reefs (e.g. a reef can send its larvae to more reefs than it receives larvae from). However, at the reefal system (i.e. chart) level both versions have equal values since the total number of reef connections is the same for the larval output and input (Figure 2.5.). Because in this chapter the interest is primarily on the behaviour of the variables at the system level only one value was reported for each of the connectivity and diversity variables (however, for clarity I arbitrarily refer to these variables as output variables). In chapters where the charts represent real reefs (Great Barrier Reef in *Chapter 4*) or reefal systems (Indo-Pacific in *Chapter 6*) rather than theoretical systems, both the output and input variable subtypes (and their differences) are presented as the interest is on the behaviour of the variables at both the system and the individual reef level.

Given the heuristic (rather than predictive) nature of the models in this chapter (see *Section 2.1.A.*) their results must be interpreted on a relative scale (i.e. the subject of interest are the relative, rather than the absolute, values obtained for the different reproductive type-current pattern combinations). This is particularly true for connectivity among reefs (at all thresholds), as the models used an arbitrary fecundity rate (see *Section 2.2.B.4.*). This is also the reason why settlement is reported as two rates (i.e. proportion of larvae settled per total and per million larvae produced), rather than in absolute terms. Although in this thesis evenness and diversity are also used in relative terms, they are suitable for direct comparison even between different reefal systems (as they do not depend on the total number of larvae settled, but on their proportions).

2.2.F. Results presentation

The results of the 220 models (Table 2.2.) were grouped by life history–current pattern combination (i.e. brooders with diffusion, brooders with diffusion + advection, spawners with diffusion, spawners with diffusion + advection). For each of these four combinations the average of the variables describing the whole reefal system (i.e. total,

mean, and variance of all reefs) in the data analysis databases were computed and presented graphically.

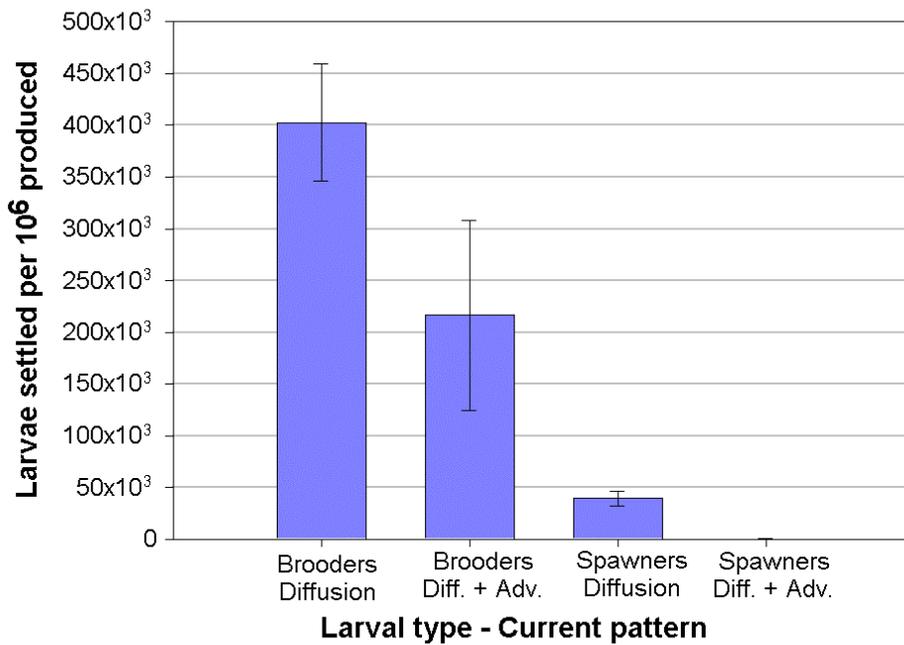
Although 55 different charts were used in the models to provide a broad range of dispersal environments for the larvae, only the effects of the grouping criteria (life history, current pattern, and their combination) on larval settlement and reef connectivity are considered in this chapter. The effects of the spatial features of the reefs (e.g. number, size, density, and layout) on the settlement of larvae and connectivity among reefs in the 49 theoretical charts will be published elsewhere. The particular outcomes of the spatially explicit and spatially realistic models for the 6 zones of the GBR are presented in *Chapter 4*.

2.3. RESULTS

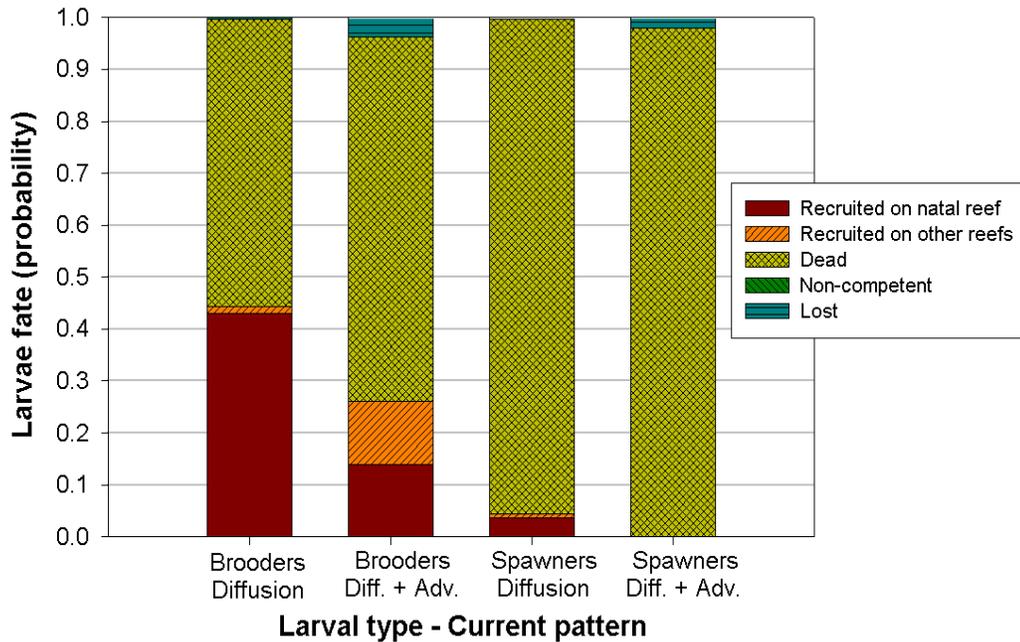
2.3.A. Settlement rate

The proportion of larvae settled on reefs relative to the total production of larvae was greater in brooders than spawners, and within each group settlement was greater when current flow was not strongly directional (Figure 2.6.a.). The effect of the larval type was greater than the effect of the currents (at least with the range of currents examined in this chapter). In fact, even the settlement of brooders under the most unfavourable hydrodynamic conditions for settlement (strongly directional flow) was almost 6 times larger (26.14% vs. 4.5%) than that of spawners under the most favourable conditions (transport only by diffusion) (Figure 2.6.a.). Current pattern affected settlement differently in each larval type; settlement was nearly 10 times higher in brooders than spawners in the absence of advection (44.33% vs. 4.5% of the total production of larvae), but almost 900 times higher when the current flow was strongly directional (26.14% vs. 0.03%) (Figure 2.6.a.). When the currents have a major directional component, there was greater variation from reef to reef in the amount of larvae settled (error bars in Figure 2.6.a.) since the reefs downstream received a much higher proportion of larvae than the reefs upstream and those outside the dispersal path.

The reason for the substantial differences in settlement rates between brooders and spawners lies in the much longer pre-competent period of the larvae produced by the latter, during which the larvae were decimated by mortality (95.26% and 97.97% of the



2.6.a.



2.6.b.

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. Error bars represent average standard deviation of all reefs and simulations for each larval type - current pattern combination.

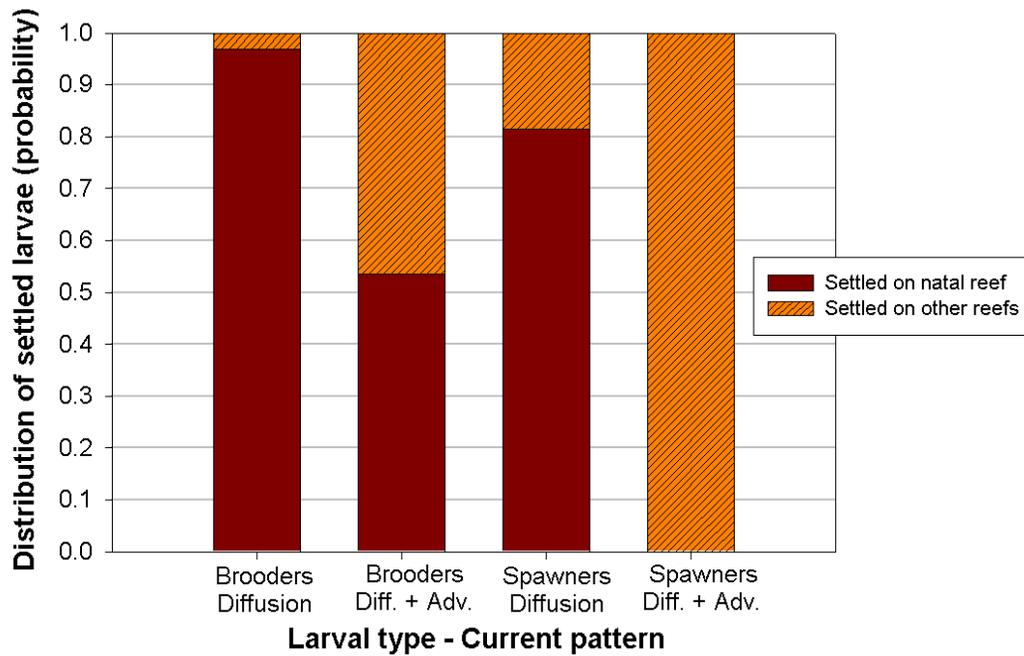
larvae of spawners died in non-directional and directional currents respectively, while only 55.44% and 70.10% of the brooded larvae died in the same conditions) (Figure 2.6.b.). In fact, the combined proportion of larvae settling and dying was very similar in all reproductive type-current pattern combinations (~96%-99%), indicating that mortality was the main reason for their differences in settling success. The remaining ~1%-4% in all combinations corresponded mainly to larvae dispersing out of the charts, and to a lesser extent to larvae becoming post-competent during the simulations. Within each of the life history strategies, the proportions of larvae that died and were lost out of the chart during the simulation were greater when the currents included a strongly directional flow.

2.3.B. Settlement distribution: local vs. non-local settlement

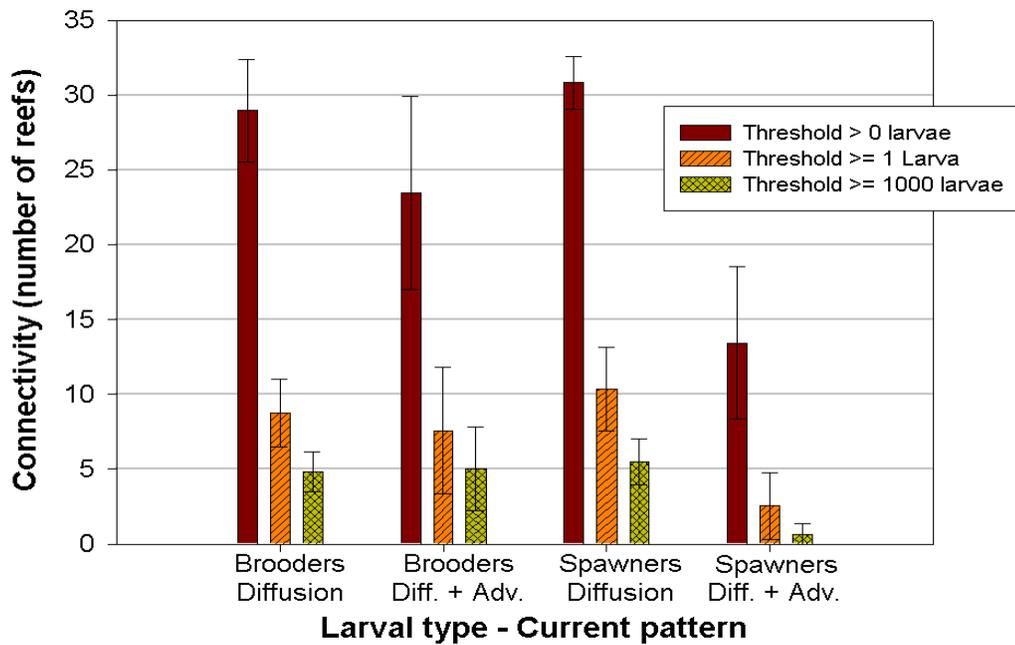
When the currents flowed mainly in one direction non-local settlement was much higher than under non-directional currents (46.40% and ~100% for brooders and spawners respectively under strongly directional currents vs. 3.09% and 18.67% under non-directional currents) (Figure 2.7.a.). In fact, when the currents had a strongly directional component the majority of the larvae were washed relatively far away from the natal reef before they completed their pre-competent period. However, in the absence of advection, larvae were transported in random directions so that most of the larvae were not carried far, and a greater proportion of them returned to their reefs of origin while they were still competent to settle. Under each current scenario spawners showed a much higher proportion of non-local settlement than brooders (Figure 2.7.a.). This was particularly true when the flow was strongly directional; in this case settlement by spawners on natal reefs was practically negligible.

2.3.C. Connectivity among reefs by larvae

Connectivity at an evolutionary scale was high for both brooders and spawners. However, connectivity at an ecological scale was much lower in both reproductive types. At all scales connectivity was lower when the currents had a strongly directional component than when only diffusion was present (Figure 2.7.b.). Therefore, even though many more larvae settled away from the natal reef when advection occurred (Figure 2.7.a.), they did so on fewer reefs. As a consequence, there was greater variation among reefs in terms of connectivity when the currents had a directional flow (error



2.7.a.



2.7.b.

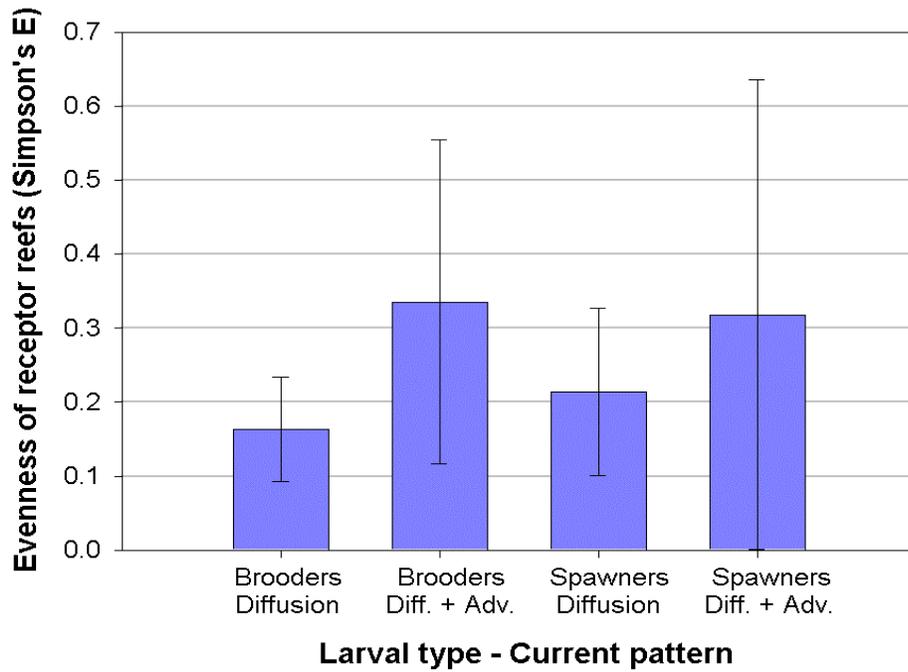
Figure 2.7. Effect of larval type - current pattern combination (brooders with diffusion; brooders with diffusion + advection; spawners with diffusion; spawners with diffusion + advection) on: (2.7.a.) proportion of larvae settling locally and away from their natal reef; (2.7.b.) connectivity among reefs at different larval thresholds. Error bars represent the average standard deviation of all reefs and simulations for each larval type - current pattern combination.

bars in Figure 2.7.b). The effect of current pattern on connectivity among reefs was stronger in spawners than in brooders at all thresholds (evolutionary and ecological scales). This effect was so large in spawners that in the absence of advection they showed the highest connectivity of all the larval type-current pattern combinations, but the lowest in its presence (Figure 2.7.b.).

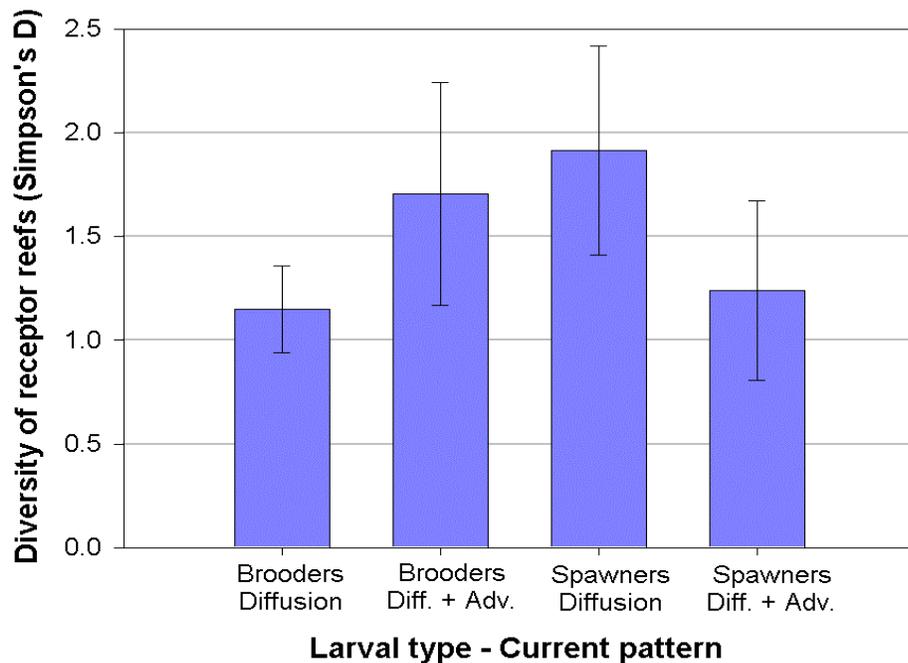
2.3.D. Evenness and Diversity of reef receptors of the settling larvae

The amount of larvae settled on each receptor reef was always more even in the presence of advection (Figure 2.8.a.). When only diffusion occurred, the natal reef received most of the larvae, followed by the reefs close to it, and progressively fewer larvae settled farther away. On the other hand, when advection was also present, the reefs where settlement occurred tended to receive more similar amounts of larvae. The increase in evenness due to advection was smaller in spawners (0.21 to 0.32 = 52% increase) than in brooders (0.16 to 0.34 = 112.5% increase). In fact, when advection was not included as a transport mechanism brooders showed the lowest evenness (0.16) of all the larval type-current pattern combinations, whereas in its presence they showed the highest evenness (0.34) (Figure 2.8.a).

There was, therefore, a very different quantitative effect of current pattern on the connectivity and evenness of both larval types. As a consequence, increasing advection produced an opposite effect on the diversity (which combines in a single variable connectivity and evenness, see *Section 2.2.E.* and *Appendix IV*) of receptor reefs of the settling larvae of spawners and brooders (Figure 2.8.b). In brooders, advection produced only a small decrease in connectivity and a very large increase in evenness, leading to an increase in diversity (Figures 2.7.b., 2.8.a., and 2.8.b.). In spawners, on the other hand, advection produced a large decrease in connectivity and a moderate increase in evenness, leading to a reduction in diversity (Figures 2.7.b., 2.8.a., and 2.8.b.). Variability in diversity and especially evenness of receptor reefs among individual source reefs was very large (error bars in Figures 2.8.a. and 2.8.b.). This variation was greater for currents with a strongly directional flow than for those including only diffusion.



2.8.a.



2.8.b.

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). Error bars represent the average standard deviation of all reefs and simulations for each larval type - current pattern combination.

2.4. DISCUSSION

2.4.A. Settlement of larvae

The models indicated a higher settlement rate for larvae released by brooding corals than for larvae produced by spawners. This was a result of the shorter pre-competent period of the larvae of brooders, which reduced the time they spent exposed to potential sources of mortality while in the plankton. In addition, settlement rate was lower when the currents had a strongly directional flow. On average (for all reefs and charts) larval type was more important in determining settlement rate in the simulations than current pattern, although the latter could produce larger variation in settlement among reefs (e.g. between reefs up- and down-stream). Nevertheless, the difference in total settlement between both larval types depended on the current pattern, and was much higher (90 times) in currents with a strong directional flow than in the absence of advection. The complexity of these results, obtained using relatively simple models where only two variables were modified among simulations, denotes the inherent difficulties in the study and management of marine metapopulations.

The settlement results obtained in the simulations were expressed as proportions of the total production of larvae by the corals. In the models the production of larvae by brooders and spawners was set to be equal. However, broadcast spawners produce many more larvae in mass spawning events than brooders release when they breed. On the other hand, brooders typically release larvae throughout the year (reviewed by Tanner 1996a). Richmond (1988) estimated that the annual fecundity per colony for the spawner *Acropora tenuis* and the brooder *Pocillopora damicornis* are similar (for colonies of similar size). If this was the norm among brooding and spawning coral species and their annual productions of larvae were in fact comparable, there would also be an advantage in the absolute number of larvae settled annually for brooders. Nevertheless, brooding corals require a greater investment of time and energy to produce larvae and nurture them within the polyp. These energetic costs may be detrimental to other processes of the adult brooding corals. Richmond (1988) found that the average caloric content of *P. damicornis* larvae is 0.74 calories and that of *A. tenuis* is 0.29 calories. Assuming that the cost to produce a calorie of larva is similar in the two compared species (which may not necessarily be true if the proportion of lipids, carbohydrates and proteins differ significantly between both larval types), expressing

the number of larvae settled per calorie of larvae produced can be used to compare settlement rates in terms of their energetic cost to the coral. Using the caloric values found by Richmond as representative of the energy content of the larvae of brooders and spawners, the settlement rate per calorie of larvae produced would be 3.81 times higher in brooders than spawners (59.11 vs. 15.52) if diffusion was the only transport mechanism and 227 times (34.85 vs. 0.104) when there was a strongly directional flow in the currents. Although values would vary among particular pairs of species, energetic differences of this type are likely to be common between the larvae of brooders and spawners as the former are larger and have greater energy reserves. Hence, although the difference in settlement rate between both reproductive groups would be smaller when expressed in relation to the energetic cost of producing the larvae, settlement rate would likely be greater for brooders, and this difference would remain very large when the currents have a strongly directional flow (the most common current condition).

2.4.B. Settlement distribution: local vs. non-local settlement

Local settlement on natal reefs was considerably higher in brooders than spawners under all current patterns. The longer pre-competent and usually competent periods of spawned larvae allowed them to reach and settle on non-natal reefs in higher proportions. Nevertheless, in the models current pattern had an even greater effect on determining the proportion of larvae settling locally and away from the natal reefs, with advection dramatically increasing the proportion of non-local settlement.

Genetic (Ayre and Hughes 2000) and ecological (Sammarco and Andrews 1988, 1989) studies of corals in the GBR have found that recruitment in most coral species relies primarily upon self-seeding. Much of the GBR is subjected to relatively constant advection conditions due to background currents, comparable to those used in the models representing transport by currents with directional flow (e.g. Kelly and Andrews 1985, Wolanski 1994, and see *Chapter 4* and *Appendix IV*). However, in the models with this type of current local settlement decreased relative not only to total larval production, but also to non-local settlement. In fact, under these current conditions, non-local settlement amounted to almost half of the total settlement in brooders and practically accounted for all the settlement in spawners. Although a controversial issue (see *Chapter 3*), retention of water particles at reefs has been predicted by meso-scale hydrodynamic models of coral reefs (e.g. Black et al. 1991, Black 1993) and confirmed

by field observations and measurements (e.g. Hamner and Hauri 1981, Wolanski 1994). In the models presented in this chapter all transport of larvae occurred by advection and/or diffusion; retention at reefs was deliberately not included. Nevertheless, at least for spawners the models would require some level of larval retention at the reefs for the simulated coral populations to display the levels of gene flow estimated by the genetic studies, suggesting the importance of retention.

Current patterns are also variable in space and time, with the direction and speed of the current flow varying in different areas of a reefal system and within and among dispersal episodes. If variable (in direction and/or speed) rather than constant advection had been implemented in the models, the results obtained would have been intermediate between the models with and without constant advection, and consequently closer to the findings by the genetic studies. Nevertheless, some level of larval retention still would be necessary to replicate the levels of local settlement observed in the field.

2.4.C. Connectivity among reefs by larvae

Connectivity among reefs varied greatly depending on the threshold of larvae used to describe two reefs as connected. In agreement with ecological (e.g. Sammarco and Andrews 1988, 1989, Hughes et al. 2000) and genetic (e.g. Ayre and Hughes 2000, Nishikawa and Sakai 2005) studies, at an ecological scale reefs were usually only connected to a few close reefs, but at an evolutionary scale corals formed vast metapopulations.

Current pattern and larval type interacted in complex ways in terms of connectivity. Spawners showed greater connectivity than brooders when only diffusion was used in the models, but lower when advection was included. The traditional view that the larvae of spawners display higher connectivity (e.g. Harrison et al. 1984) may not be true in all hydrodynamic and/or topological conditions. In dense reef systems when advection is a significant element in the transport of larvae, brooders can be connected to more reefs (for an equal larval production), particularly at ecological scales, due to their lower mortality.

From the results obtained here, it seems essential that when connectivity is mentioned for a reef (with defined hydrodynamic and topological conditions) the relevant taxa and scale (i.e. threshold) are also specified. That is, a reef that displays high connectivity for one species may not do so for another with different pre-competence and competence patterns. Similarly, high connectivity of a species (relative

to other species) at evolutionary scale does not imply high connectivity at ecological scale and vice versa. Furthermore, low connectivity (i.e. few reefs being connected by larvae) does not necessarily mean high proportions of local recruitment. For example, in the models for spawners under a strongly directional current flow, a high proportion of the larvae did not settle locally and connectivity among the reefs was low. The reason for this was that although most larvae settled non-locally, they settled only on the few reefs encountered by the current path during their competent period.

2.4.D. Evenness and diversity of reef receptors of the settling larvae

One of the most important results of this study was the differential effect of the distinct current patterns on the two reproductive groups in terms of diversity of reef receptors of larvae. Diversity combines connectivity among reefs and evenness of settlement in a single descriptive variable, which can be used to effectively summarise the dispersal of larvae in a reef system (see *Section 2.2.E.*). Therefore, diversity describes an essential component of the ecology and evolution of marine organisms. Although the inclusion of advection in the models led to a decrease in the number of reefs connected (see *Section 2.3.C.*) and an increase in evenness (see *Section 2.3.D.*) in brooders and spawners, the sizes of these effects were different for both reproductive types of coral. The decrease in connectivity was small for brooders and large for spawners, while the increase in evenness was very large for brooders and moderate for spawners. In brooders the small decrease in connectivity and very large increase in evenness produced an increase in the diversity of reef receptors of their larvae. In contrast, in spawners the large decrease in connectivity and a moderate increase in evenness resulted in a reduction in the diversity of their receptor reefs. This indicates once more the complexity of larval dispersal and the difficulties in the management of marine communities. Moreover, different current patterns are likely to also produce distinct effects on the diversity of receptor reefs of particular larval types (i.e. at species level). *Chapter 5* examines the differences in settlement, connectivity, evenness and diversity among larvae of coral species with known pre-competent and competent periods under different current patterns.

2.4.E. Variation among reefs in the studied dispersal variables

There was substantial variation among individual reefs for all the variables studied. Similarly, field studies show that settlement by larvae of brooding and spawning corals is highly variable among reefs (e.g. Hughes et al. 1999). The differences among reefs were larger under a strongly directional flow (the most common current pattern). This is in agreement with empirical findings (e.g. Benzie and Stoddart 1992) and hydrodynamic research (e.g. Wolanski 1994), in which some reefs are more likely to receive larvae than others as a result of the patterns of current flow. There were also differences in the amount and patterns of variability among reefs in the variables studied between both larval types. Variability among reefs was generally larger for spawning than brooding corals in the models, particularly when the currents and the spatial layout of the reefs were not homogenous in space (i.e. strongly directional flow and random distribution of the reefs), as a consequence of their longer pre-competent and competent periods. The extensive variability among reefs together with the complex interactions between larval type and current pattern, further emphasise the difficulty in the study of larval dispersal, the assessment of its ecological and evolutionary consequences, and the management of marine communities.

2.4.F. Model Limitations

The models presented in this chapter, as all models, are an idealisation. Some of the simplifying assumptions and limitations of the models are discussed below.

2.4.F.1. General design

The edges of the CL models were absorbent (see *Section 2.2.C*). Absorbent edges present the problem of losing individuals (i.e. larvae) relevant to the simulated processes out of the modelled space. To minimise this problem an extra rim of 10 water cells was placed around the chart. A greater number of larvae were lost when the currents had a strongly directional flow. The maximum loss, 3.7% of the total larvae produced, occurred when the larvae released by brooding corals dispersed under these hydrodynamic conditions. On average less than 1.4% of the larvae were lost out of the chart per simulation. Therefore the CL edge effect did not affect greatly the results obtained in the simulations and the model design seems appropriate.

2.4.F.2. Hydrodynamic conditions

Despite the importance of oscillating currents (tides and weather-band currents) for flushing, mixing and transporting water particles at small and medium scales (Williams et al. 1984), only background currents were represented in the models. Background currents are a stable component (low frequency or almost constant) of the ocean circulation that usually operates over medium to long distances, and are essential for the transport of larvae (Andrews and Pickard 1990). Furthermore, coral mass spawning events on some reefal systems, such as the GBR, coincide with periods of neap tides, so at least during the early phases of larval dispersal the transport provided by the tides is likely to be relatively small.

Current patterns were constant in space and time in the models. In reality, even steady background currents flow with different directions and speeds in different areas of a reefal system due to topographical and meteorological constraints. Similarly, diffusion is generally greater near topographical features and on the edge than the centre of background currents. As a consequence, in nature larvae follow more similar routes (since less larvae are transported in non-straight routes and the non-straight routes are less convoluted) and therefore have more similar ‘overall’ dispersion speeds (i.e. a lower proportion of larvae are under-dispersed, see *Section 2.2.B.4.*) in the centre of the currents. The uniform flow implemented in the models (see *Section 2.2.B.2.*) could be thought of as a background current wide enough to encompass the whole area represented by the chart. However, current patterns also experience temporal variability, mainly associated with weather changes (e.g. changes in the prevailing winds and seasonal cycles). Including this sort of detail in the models would have made them more realistic, but also more complex. The extra detail would make the analysis and interpretation of the model results more difficult as there would be further parameter combinations to explore. Moreover, given the heuristic nature of the models (see *Section 2.4.1.*) using high-resolution hydrodynamics is not essential. The current speed in the models (17 cm.s^{-1}), chosen in part for simplicity of design, is common, for example, in the central GBR (17.5 cm.s^{-1} , Kelly and Andrews 1985) and the Western and Central Pacific (18 cm.s^{-1} , Jokiel 1984). However, background currents usually range between 5 and 60 cm.s^{-1} , so the current speed used in the models may not be representative of other reefal systems.

In addition, incorporating larval retention at reefs could add realism, although it would also increase the complexity of the models and the interpretation of the results. The effects of larval retention on settlement and connectivity in brooding and spawning corals are examined in detail in *Chapter 3*.

2.4.F.3. Larval competent periods

The competent periods of the larvae in a cohort were represented linearly. This is quite a simplistic representation as it assumes that all the larvae in the cohort begin and cease competence simultaneously. Laboratory studies have shown that the proportion of larvae competent to settle increases very rapidly after the first few competent larvae appear until it reaches a peak, then declines, at first rapidly and then progressively more slowly, with a small proportion of the larvae remaining capable of settlement for long periods (e.g. Wilson and Harrison 1998, Baird 2001). Non-linear representations of the competent periods of the larvae in a cohort are used in other chapters in this thesis. *Chapter 5*, in particular, explores the dispersal capabilities of specific species of corals (derived from their competence patterns) in relation to their geographic ranges.

2.4.F.4. Larval mortality

Larval mortality in marine invertebrates is quite high, daily larval mortality ranging from 0.0111 to 0.636 (instantaneous mortality, $M \approx 0.0161$ to 1.01) (e.g. Morgan 1995 and references within). A larval mortality included in this range was used in the models (daily larval mortality = 0.5, $M \approx 0.69$). Unfortunately the accuracy of the estimated larval mortalities vary, and most of the available data come from commercially important species of molluscs and crustaceans, with no studies on mortality in the field for the larvae of coral species. Additionally, in the models, larval mortality was constant in space and time within each simulation. However, the mortality of larvae in marine invertebrates appears to be greater in the early stages of development of the larvae (e.g. Scheltema 1986), and the mortality of coral larvae is likely to be greater within than between reefs (see *Chapter 1, Section 1.3*). Similarly, equal mortality rates were used for both reproductive groups in the models, but the larvae of spawning corals may suffer higher mortality than brooded larvae, at least in the early larval stages, since their development is completely external. In any case, our knowledge of larval mortality in

corals is still very limited and needs to be further developed before accurate and complete descriptions can be included in the models.

2.4.F.5. Accuracy of the models and concluding remarks

The design and implementation of the models involved a number of simplifying assumptions. These assumptions were justified, as the aim of this study was not to provide an accurate prediction of the destination and abundance of the larvae in a particular reefal system, but to investigate the effect of larval type and current pattern on settlement and connectivity among reefs. Further assumptions in the models resulted from the constraints presented by our limited knowledge, especially on the biology of coral larvae.

Implementing more combinations of the factors affecting the dispersal of coral larvae (e.g. using other charts and/or other hydro-dynamic patterns) and investigating the impact of parameters that were kept constant in the models (e.g. mortality, retention level at the reefs, and current speed) would have helped to provide further insights into the effects of these factors on the settlement and connectivity among reefs. However, this would have made the analysis and interpretation of the results more complex. Some of these questions are investigated in *Chapters 3 and 4*.

2.4.G. Summary and Conclusions

Despite their simplicity, the models revealed complex dynamics and interesting insights into coral larvae dispersal, settlement, and connectivity. Significant differences were found for different larval types, hydrodynamic conditions, and individual reefs. Moreover, the interactions among these factors were also complex, with different current flow patterns producing different effects on distinct larval types and reefs. Larval type was the main determinant of the larval settlement rate. Settlement rates were higher for brooders than spawners because the larvae of the latter suffered higher mortality during their longer pre-competent and competent periods. Current pattern constituted the main influence on the spatial distribution of settlers (i.e. local vs. non-local settlement) and connectivity. Advection increased non-local settlement, but it decreased connectivity (i.e. instead of settling on the natal and nearby reefs larvae settled mostly in a few reefs farther away). In the presence of advection local settlement was practically negligible for species with long pre-competent and competent periods,

suggesting that at least for these species some mechanism of retention must exist at the reefs (see *Chapter 3*). Reefal systems and reefs with high evolutionary-scale connectivity did not necessarily have high ecological-scale connectivity and vice-versa. Notably, the two current patterns studied had opposite effects on the diversity of receptor reefs of both larval types (advection increased diversity in brooders and decreased it in spawners). The dynamics of dispersal and settlement of coral larvae have important implications for the management of coral reefs (e.g. Roberts 1997, Mumby 1999). The complexity of these dynamics makes management of marine reserves a difficult task (Sale 1999, Hughes et al. 1999) that should be specific to each case, and periodically reassessed as the understanding of the functioning and information on the evolution of the particular system increase.

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

3.1. INTRODUCTION

One of the biggest controversies in marine biology in the last 30 years has been to what extent larvae produced by marine species are widely dispersed or retained locally (e.g. Harrison and Wallace 1990, Sponaugle et al. 2002). How far the propagules travel, their settlement distribution, and the proportion recruiting within natal populations remain largely unknown (Palumbi 1994, Schulman 1998). Results from different studies often appear contradictory. Below, I review the evidence for wide dispersal and local retention. These issues are of considerable importance as the life history of at least 70% of marine organisms includes a larval phase (Thorson 1950) that is often pelagic. The level of dispersal and retention of larvae determines whether populations of marine species are mainly open (i.e. reliant on externally produced larvae) or closed (i.e. self-replenishing) (e.g. Caley et al. 1996, Mora and Sale 2002), which is essential for many aspects of the biology of the species, including their demography, genetic structure, and evolution (see *Chapters 1 and 7*).

3.1.A. Evidence for dispersal and retention of larvae

3.1.A.1. Oceanographic evidence

Ocean currents provide great potential for the dispersal of larvae. In particular, background or drift currents, originating from steady or low frequency pressure gradients like the rotation of the Earth and seasonal winds, offer a mechanism for large-scale transport and connectivity among distant populations (Williams et al. 1984, Andrews and Pickard 1990, see *Chapter 2*).

In contrast, many other hydrodynamic mechanisms that are capable of extending the residence times of water particles in an area for periods longer than the pre-competent period of the larvae have also been described. Some of the most ubiquitous mechanisms are gyres, eddies, and their associated secondary circulations. Both, gyres and eddies, consist of horizontal circular-moving loops of water. Gyres are large-scale currents generally flowing around the periphery of the ocean basins centred in subtropical high-pressure regions (e.g. Garrison 2002, Thurman and Trujillo 2002). Eddies are formed on

the side of main currents, produced when the main current encounters an obstacle (such as a shoreline or seabed topography) (e.g. Pingree et al. 1978, Loder 1980, Pingree and Maddock 1985) or another current (e.g. Garrison 2002, Thurman and Trujillo 2002). Eddies are now considered as part of the normal circulation patterns, and are frequently associated with islands and isolated platform reefs (Hamner and Hauri 1981, Wolanski et al. 1984, Black et al. 1991, Wolanski 1994). They can contain dense aggregates of plankton (Hamner and Hauri 1981), and have long been proposed as important physical mechanisms that minimise the loss of eggs and larvae of coral reef fishes due to transport away from suitable settlement sites (Boden 1952, Sette 1955, Randall 1961, Sale 1970). There are now numerous cases where larval retention has been proven or inferred to be caused by gyres (e.g. Hill et al. 1994, Pedrotti and Fenaux 1996, Withler et al. 2001) or eddies (e.g. Sammarco and Andrews 1988, Bailey et al. 1997, Vargas et al. 1997, Chiswell and Roemmich 1998).

Other widespread mechanisms involved in larval retention are associated with tides. Typically, retention is produced by a net onshore flow of the residual currents produced by external tides (e.g. Rowe and Epifanio 1994, Chen et al. 1997, Thiebaut et al. 1998, Ishii et al. 2001, Jager 2001). Dense aggregations of plankton (Alldredge and Hamner 1980) and invertebrate larvae (Gay and Andrews 1994) have also been discovered in these currents. In addition, tidal bores and internal waves have been proposed as a mechanism for larval retention too (e.g. Shanks 1986, Kingsford and Choat 1986, Pineda 1999).

'Long-shore' circulation around topographic features, due to the interaction of these features and near-shore onshore flow, is also a potential mechanism for larval retention around islands (Cowen and Castro 1994) and reefs (Black 1993). Other mechanisms that have been associated with larval retention include: vertically stratified flows in which the direction and speed of the current vary with depth (e.g. Scheltema 1986), onshore countercurrents (Mullineaux and Mills 1997, Chiswell and Roemmich 1998), onshore movement of relaxing upwelling fronts (Shanks et al. 2000), river plume flows in estuaries (Thiebaut et al. 1998), very localised (mini-scale phenomena) circulation features produced by the reef structure (Shanks 1983, Kingsford and Choat 1986, Shanks 1986, Wolanski and Hamner 1988, Kingsford 1990), or simply the location of natal populations in low flow and/or slow current zones (Frith and Mason 1986, Boehlert et al. 1992, Cowen and Castro 1994).

However, field and modelling work have shown that mechanisms that normally promote larval retention in natal populations can be easily disrupted by weather conditions. Wind direction and strength are crucial, being capable of interrupting retention by altering the prevalent current conditions (e.g. Young et al. 1998, Thiebaut et al. 1998, Ellien et al. 2000, Nakata et al. 2000, Jager 2001). Seasonal weather variation (Swearer et al. 1999), storms (Bailey et al. 1997) and other short-term climatic variations (Cowen 1985, Corten 1986) can also decrease retention, increasing the potential for dispersal.

3.1.A.2. Behavioural evidence

Specific adult and larval behaviour can help to exploit the potential for larval aggregation, dispersal or retention provided by hydrodynamic mechanisms (e.g. Scheltema 1986, Rothlisberg et al. 1995).

The timing and location of spawning by adults are critical. In corals on the Great Barrier Reef (GBR), mass spawning occurs each year during a brief period of neap tides when dispersion of gametes and larvae is minimised (Harrison et al. 1984, Babcock et al. 1986). Although this reproductive behaviour is likely to have evolved to increase fertilisation (e.g. Stobart 1992), it can also lead to reduced dispersal. Many fishes also spawn during periods in which the hydrodynamic mechanisms are most likely to retain larvae in the vicinity of the natal population (Lobel 1978, 1989, Lima and Castello 1995, Paula 1998). Other fishes release their eggs or larvae in near-shore eddies that transport larvae back to the parent population (Johannes 1978). However, numerous species reproduce year-round, and the vast majority of these reproduce in locations that vary greatly in hydrodynamic conditions (sometimes favouring dispersal, sometimes favouring retention).

In many instances larvae do not behave simply like passive particles, and the predicted outcomes from the transport mechanisms of water may be modified. For example, the larvae of many ascidians (e.g. Young 1986, Bingham and Young 1991, Stoner 1992), amphipods (e.g. Hogh and Naylor 1992), decapods (e.g. Cronin and Forward 1986, Young 1995), and fishes (e.g. Cowen and Castro 1994, Leis and Stobutzki 1999, Paris and Cowen 2004) can migrate vertically in the water column interacting with vertically stratified flows, potentially enhancing their chances of retention. In coral larvae, vertical migration often follows an ontogenetic cycle; initially migrating upwards to the water surface, and towards the end of their planktonic life

migrating downwards in search for suitable substratum (e.g. Atoda 1951, Harrison and Wallace 1990). Some studies suggest that the larvae of some coral species may also undergo a diurnal vertical migration cycle (Kawaguti 1940, Hodgson 1985a, 1985b). However, the modest swimming capabilities of coral larvae (see *Chapter 1, Section 1.4.*) in combination with the currents patterns in coral reef environments (frequently involving significant turbulent vertical speeds) are likely to often limit or prevent their vertical migration (Mileikovsky 1973, Black 1993). In reality, little is known about the vertical distribution and behaviour of coral larvae during most of their planktonic life, particularly in the field (see *Chapter 1, Section 1.4.*). In any case, vertical migration and other behavioural characteristics of the larvae of marine invertebrates and fishes, such as their abilities to respond to visual and chemical cues (e.g. Kobayashi 1989, Leis et al. 1996, Doherty and Carleton 1997, Stobutzki and Bellwood 1998, Simpson et al. 2005) and their swimming capabilities (e.g. Leis and Carson-Ewart 1997b, Stobutzki and Bellwood 1997, Chiswell and Booth 1999, Leis and Stobutzki 1999, Fisher 2005) can not only be used to enhance retention, but also to promote dispersal. Furthermore, larval behaviour can vary not only among species, but also within the reproductive output of a single individual. *Goniastrea aspera* both broods and spawns in Okinawa; its brooded larvae settle soon after release, while its spawned larvae are planktonic (Sakai 1997). Larval behaviour has been found to vary even among the larvae within a cohort. A proportion of the larvae released by *Goniastrea australensis* have a period of benthic development (~ 5 days) before pelagic dispersal, while the remaining larvae have complete planktonic development (Kojis and Quinn 1981b). The brooded larvae in *G. aspera* and the larvae with partial benthic development in *G. australensis* are likely to increase local settlement, while the larvae with fully planktonic development in both species may promote dispersal.

3.1.A.3. Ecological evidence

Until recently, the commonly held view was that eggs and larvae form part of the plankton where they are transported by currents, sometimes for long distances, interconnecting populations despite being subjected to high mortality (e.g. Williams et al. 1984, Sale 1990, Boehlert 1996, Roberts 1997). Many field and experimental observations indirectly support this broad dispersal hypothesis. The larvae of many marine organisms are long-lived, providing the potential for long-range dispersal (e.g.

Thorson 1950, Bikerland et al. 1971, Pechenik et al. 1984, Richmond 1987, Wilson and Harrison 1998). Larvae of numerous marine species have been collected in open water, some at great distance from shore (e.g. Ahlstrom 1972, Richards 1984, Young et al. 1986, Clarke 1991). After mass spawning events, coral larvae frequently aggregate into slicks on the water surface that are transported away from the reefs within one or two days, after which they usually dissipate (e.g. Willis and Oliver 1990, Olivier et al. 1992, Nadaoka et al. 2002). Spawning and recruitment in damselfishes are correlated in time but not in terms of magnitude, which may imply that recruitment is largely determined by planktonic dispersal (Meekan et al. 1993). Nevertheless, decoupling of this type could also be due to spatial patterns of larvae mortality (Danilowicz and Sale 1999).

Conversely, considerable circumstantial and direct evidence also indicates that the larvae of some species can be retained and recruited to their original population. Communities of marine organisms survive and persist in the absence of an up-current source (Schultz and Cowen 1994). Endemic species with pelagic larvae exist round isolated oceanic islands (Hourighan and Reese 1987, Robertson and Allen 1996). Marine populations established by man after new introduction (Baltz 1991) or reintroduced following disturbance (Southworth and Mann 1998) persist by self-seeding. Invertebrate assemblages of muddy-fine sand communities are often stable in space and time, despite the potential for dispersal of the larvae of many of the organisms involved, including annelids, molluscs, and echinoderms (Thiebaut et al. 1997). Likewise, short-range dispersal has been found in numerous marine invertebrates despite their high dispersal potential (e.g. Olson 1985, Frith and Mason 1986, Knowlton 1986, Young et al. 1986). In corals, a large-scale survey of the recruitment patterns by larvae of broadcast spawners on the GBR concluded that they exhibit a stock-recruitment relationship, where variation in fecundity among reefs explained over 70% of their variation in recruitment (Hughes et al. 2000). The high spatial correlation between fecundity and recruitment suggests that the majority of their larvae do not undergo large-scale movements. Another study of recruitment by corals near a reef in the central GBR showed that plates located close to the reef had higher recruitment, while settlement declined dramatically with distance from the reef (Sammarco and Andrews 1988, 1989). Similarly, larvae of fishes from temperate rocky shores (Marliave 1986, Kingsford et al. 1989) and tropical reefs (Powles 1977) were concentrated within a few metres of their population of origin, but rare or absent farther away. However, in these cases higher concentrations of larvae in their natal populations

could be, at least partially, an artefact due to the diffusion experienced by the larvae during dispersal. Analysis of the chemical composition of otoliths has revealed coastal development for approximately 70% of the recruits of the wrasse *Thalassoma bifasciatum* in St. Croix (Virgin Islands, Caribbean), which suggests the existence of larval retention (Swearer et al. 1999). Direct evidence of larval retention has been obtained using ‘mark and recapture’ experiments, where larval otoliths were marked with tetracycline (in some cases combined with parental analysis), for the damselfish *Pomacentrus amboinensis* on Lizard Island (GBR) (15-60% of larvae settled into their natal population, Jones et al. 1999), and the clownfish *Amphiprion polymnus* on Schumann Island (Papua New Guinea) (~32% of larvae settled within tens of metres of their hatching location, Jones et al. 2005).

3.1.A.4. Genetic evidence

Population genetics can help us determine how much of the potential for dispersal of the larvae is actually realised and how frequently retention occurs in the natal population (Palumbi 1995, Schulman 1998). Many populations of marine species are genetically homogeneous over a large spatial scale (e.g. Rosenblatt and Waples 1986, Palumbi 1992, Grijalva-Chon et al. 1994, Doherty et al. 1995, Schulman and Bermingham 1995, Gold and Richardson 1998), but numerous cases of significant genetic subdivision (implying low gene flow) have also been found (e.g. Bell et al. 1982, Planes 1993, Weber and Levy 2000). The high levels of genetic subdivision among populations of some species can be explained by isolation due to geographic distance (e.g. Stepien et al. 2000) or to the life history of the species (e.g. non-pelagic eggs or larvae with a short planktonic life, Schulman and Bermingham 1995). However, important genetic subdivision among nearby and environmentally homogeneous populations can also occur even in species with extended pelagic larval periods (e.g. Burton and Feldman 1982, Stepien 1999, Withler et al. 2001, Taylor and Hellberg 2003). In these cases, genetic sub-division may be caused by some mechanism of larval retention (e.g. a gyre in Withler et al. 2001, and behaviour in Taylor and Hellberg 2003).

A problem presented by genetic studies is that they show connectivity among populations at a genetic scale, which may be trivial ecologically as only a few migrants per generation are required to maintain genetic homogeneity among populations (e.g. Thorrold et al. 1998). Furthermore, genetic-scale connectivity between two populations

can be the result of a multi-generational sequence of ‘steps’ involving intermediate ‘stepping-stone’ populations, rather than of a direct exchange of individuals between the populations (e.g. Ayre and Hughes 2004). Despite this, a common finding in the genetic analysis of marine species is that although dispersal among populations provides enough gene flow to maintain panmixis, genetic subdivision is at least noticeable implying that the populations have an important self-seeding component (e.g. Graves et al. 1992, Gold et al. 1997, Ayre and Hughes 2000, Nishikawa and Sakai 2005). Further limitations of genetic studies, relevant to the investigation of the levels of larval dispersal and retention in marine metapopulations, include the presence of low amounts of overall genetic variation in the species and/or area investigated (preventing the detection of genetic differences among local populations), and the incorporation of simplistic and unrealistic assumptions in the models used in genetic analysis (see *Chapter 1 Section 1.1.* and references within).

In summary, there is considerable evidence from oceanographic, behavioural, ecological and genetic studies for both long distance dispersal and retention of larvae. In addition, although retention may be a widespread phenomenon, it is highly variable in space (e.g. Willis and Oliver 1988a, Swearer et al. 1999), time (e.g. Voss et al. 1999, Ellien et al. 2000), and among taxa (e.g. Brogan 1994). In a recent review of dispersal and retention processes in coral reefs fishes, Mora and Sale (2002) concluded that “at present, the extent to which reef fish populations are open or closed must be regarded as unknown”. Our knowledge of these processes in corals is even more limited.

3.1.B. Aims of the study

Although a considerable number of studies have attempted to establish the level of larval retention in numerous species and locations, little attention has been paid to the implications of these processes for the biology of the species. It is often simply assumed that an increase in the level of larval retention must increase settlement and decrease connectivity among reefs.

In this chapter I use spatially explicit models to investigate the effect of water retention at reefs on aspects of larval settlement and reef connectivity. In the models I simulate the dispersal and retention of larvae produced by brooders and broadcast spawners corals under two different hydrodynamic conditions: non-directional flow (diffusion alone) and strongly directional flow (diffusion + advection). I specifically

assess the effects of increasing levels of retention for each of these 4 cases (2 coral reproductive types x 2 current patterns) and compare their outcomes with the expectations based on the literature. The predictions tested by the models are that an increase in the level of retention results in:

- (1) An increase in the total settlement of larvae.
- (2) (a) An increase in the amount of larvae settled locally, and
(b) A decrease in the amount of larvae settled on reefs other than natal.
- (3) A decrease in the connectivity among reefs by larvae at all scales (evolutionary and ecological scales, see *Chapter 2* and *Appendix IV*).
- (4) A decrease in the evenness of reef sources of the larvae settling on the reefs, as an increasingly greater proportion of the settling larvae originate locally.
- (5) A decrease in the diversity of larvae settling on the reefs in terms of their source reefs.

After testing these predictions, the dispersal vs. retention controversy is reassessed in light of the results. Finally, the implications of larval retention for the biology of marine organisms, and its significance for the management and conservation of marine populations are briefly discussed.

3.2. MATERIALS and METHODS

The general design of the models, input types, coupled lattice (CL) functioning and rules, output files, and data analysis were similar to those described in *Chapter 2*. The main differences were in the data input. In particular, given the aims of this chapter, the hydrodynamic patterns in the different models included varying levels of water retention at the reefs. The particular data inputs used in this chapter are described in detail below.

3.2.A. Spatial representation of the reefs: Charts

A chart (representation of a unique reefal system, see *Chapter 2* and *Appendix IV*) with 36 reefs of 4 x 4 cells distributed uniformly in a grid of 120 x 120 cells was used in all the simulations in this chapter. Each cell was square and represented an area of 1 km². The reef density of this chart was 4.00% (36 reefs of 16 cells in a 14,400 cells grid). Similar reef densities are found in many areas of the Great Barrier Reef (GBR),

especially in the Northern and Central Sectors (see *Appendix II*). The grid was surrounded by a buffering rim of 10 cells to minimise the edge-effect problem in CL models (see *Chapter 2*), and therefore the effective grid size was 140 x 140 cells.

3.2.B. Hydrodynamic patterns

Current sets were used to define the transport of water particles (see *Chapter 2*). Each current set consisted of a set of values representing the probabilities of a water particle remaining in its previous location and moving into each of the 8 neighbouring cells (i.e. moving: N, NE, E, SE, S, SW, W, NW). As in *Chapter 2*, two mechanisms of transport of water particles were used: diffusion alone, and diffusion combined with advection. In the former, transport occurred in any direction with equal probability (non-directional flow). In the latter, transport could also occur in any direction, but its probability differed among directions. In the models used in this chapter (as in *Chapter 2*) advection was represented by a strongly directional flow to the South (Table 3.1.b.).

Varying levels of water retention at the reefs were modelled for each transport type (Tables 3.1.a. and 3.1.b.). Retention was implemented by increasing the probability of retainment of water particles in the central cell of the neighbourhood and proportionally reducing the probabilities of dispersal to the surrounding cells when transport occurred over a reef area (i.e. when the cell land-type in the underlying chart was reef, see *Chapter 2*). In this representation of retention, the water was not indefinitely retained in the reefs, but gradually flowed out while being replaced, resembling what occurs in nature. Twenty-seven levels of retention were implemented, ranging from 0% to 100% (Tables 3.1.a. and 3.1.b.). Each level of retention represented the proportion of water particles retained in a reef after 10 days (i.e. 120 iterations). This length of time was chosen because it is biologically significant and has previously been used to describe the levels of water retention at coral reefs (e.g. Black et al. 1990, Black et al. 1991, Black 1993).

3.2.C. Competence patterns of the larvae

A non-linear representation of the competence patterns of the larvae was used (Figure 3.1.). This type of representation includes not only the beginning and end of competence in the cohort (as in the linear representation, see *Chapter 2*), but also the proportion of larvae in the cohort competent to settle at different times. This approach emulates more closely the findings in the laboratory (e.g. Wilson and Harrison 1998),

where the larvae in a cohort are not synchronised at the start or end of their competence. In general, most larvae become competent soon after the first one does (peak in Figure 3.1.) and cease being competent at very different times (long tail in Figure 3.1.).

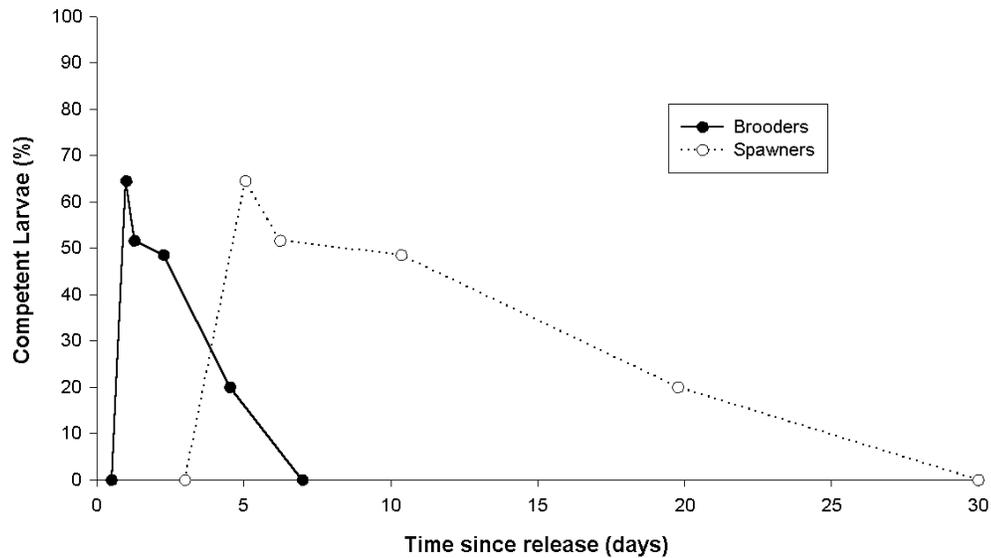


Figure 3.1. Non-linear representation of the cohort competence patterns. The proportion of larvae in the cohort competent for settlement and metamorphosis varies with time (Atoda 1947a, 1947b, 1951, Baird 1998, 2001).

Two different competent patterns were used in the simulations (Figure 3.1.). The first one representing a ‘classic brooding coral’ with short pre-competent and competent periods, and the second one representing a ‘classic spawning coral’ with a relatively long pre-competent period and an extended competent period (see *Chapter 2*). The proportion of larvae in the cohort settling at each inflexion point (i.e. heights of the peak and peak-tail transition points) were kept the same for both reproductive types of coral and only the times at which these points occurred varied among them (Figure 3.1.). The same competence curves (i.e. patterns) were used for all the larvae within the same coral reproductive type (i.e. brooders and spawners) regardless of their reef of origin. The chart used in this chapter represents a relatively small area (120 x 120 km), so no geographic variation in competence patterns needed to be assumed in the models.

Moreover, presently there is not sufficient information on the spatial variation in the competence patterns of corals to allow the inclusion of this kind of detail in the models. It seems clear that the length of the competent period increases with latitude due to the associated decrease in temperature, but it is not obvious how these gradients affect the shape of the competence curves, or if brooders and spawners are influenced to different extents and/or ways.

3.2.D. Other parameters

The mortality rate of the larvae was set to 0.25 day^{-1} (instantaneous mortality rate, $M \approx 0.29$). This was based on the values found for the larvae of marine invertebrates (their M ranging from 0.005 to 1.03, with a mean value of 0.22, Morgan 1995). The values of the rest of the parameters in the simulations were as described in *Chapter 2*.

In total, 108 simulations were run (one per model, Table 3.2.). These were the result of the combination of: 27 levels of water retention at the reefs x 2 current patterns (non-directional vs. strongly directional flow) x 2 competence patterns (classic brooder vs. classic spawner).

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

Input Type	Variants	Number
Chart	36 reefs of 16 km^2 uniformly distributed in a 140×140 cells grid (reef density $\approx 4.00\%$)	1
Retention Level	Percentage of water retained in the reef after 8 days: 0%, 0.001%, 0.01%, 0.1%, 1%, 2%, 4%, 6%, 8%, 10%, 15%, 20%, 25%, 30%, 35%, 40%, 45%, 50%, 60%, 70%, 80%, 90%, 100%.	27
Current Pattern	Diffusion	2
	Diffusion + Advection	
Life History	Typical brooders	2
	Typical broadcast spawners	
Total Number of Models		$1 \times 27 \times 2 \times 2 =$ 108

3.2.E. Data analysis and presentation

The analysis and summary of the results were similar to those described in *Chapter 2*. In this chapter two larval thresholds were used to define connectivity. In the first, representing connectivity at an evolutionary-scale, any amount of larvae (> 0 larva) was enough to consider two reefs as connected. In the second threshold, representing connectivity at an ecological-scale, at least 1000 larvae (≥ 1000 larvae) were required to define the reefs as connected (see *Chapter 2* and *Appendix IV*).

Two types of graphs were used to illustrate the changes in settlement rate, connectivity, evenness and diversity with increasing levels of retention. The first type expressed the level of water retention after 10 days on a decimal scale, while the second type used a logarithmic scale. The former gave an overall view of the effect of varying the level of retention on the studied variables. The latter displayed its effect more clearly when the level of water retention was very low (0%-1%). These early small increases in the level of retention are expected to produce the largest and most complex variation on the studied variables. However, the level of retention at the reefs is likely to range from 0% (no retention) to at least 10% (low to medium retention), so both representations are required to produce a complete picture. In addition, settlement at the different retention levels was expressed in two different ways: as the amount of larvae settled per million larvae produced, and as a proportion of the maximum settlement (occurring with 100% retention) for that particular larval type - current pattern combination. In the remainder of this chapter I will refer to the former as settlement rate and the latter as settlement proportion. Settlement rate graphics indicate the variation in settlement success with retention level of the larval type - current pattern combinations. However, different larval types may have very different settlement rates even when retention is total (100%), making it difficult to compare among larval types. For example, a small increase in settlement rate with the increase in retention level for a species with low settlement success may constitute a very large increase in settlement proportion. Therefore, four graphics were used to represent settlement, two for settlement rate and two for settlement proportion, each of them expressed in decimal and logarithmic scale.

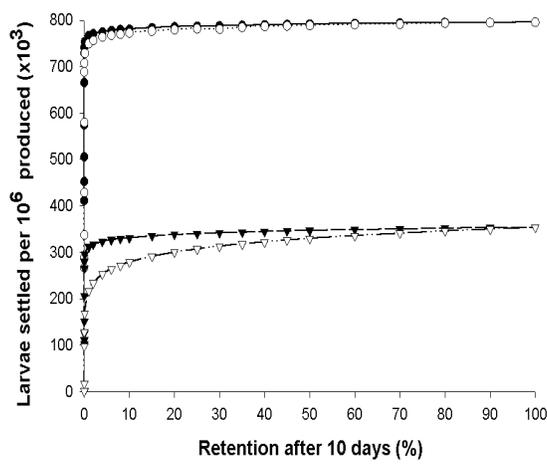
3.3. RESULTS

3.3.A. Retention level, settlement rate, and fate of larvae

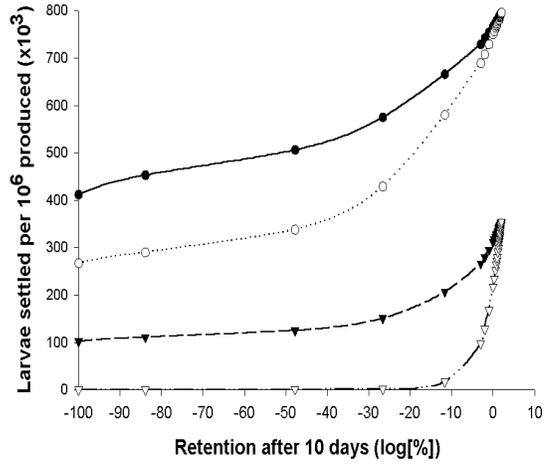
As predicted, an increase in the level of water retention at the modelled reefs increased settlement rate in all larval types and current conditions (Figures 3.2.a. and 3.2.b.). In all cases the increase in settlement rate was asymptotic, with a dramatic increase between retention levels of 0% - 10%, and only slight gains with further increases in retention (Figure 3.2.a.). With 10% retention after 10 days settlement ranged between 78.6% and 98.1% of the maximum settlement (obtained with 100% retention) depending on the larval type and current conditions, and with 20% retention between 84.5% and 98.7% (Figure 3.2.c.). In fact, an increase in retention level from 0% to just 0.001% produced an increase in settlement proportion between 27.5% (from ~0% to 27.5% in spawners under diffusion and advection) and 53% (from 33.5% to 86.5% in spawners under only diffusion) (Figure 3.2.d.).

Settlement rate varied greatly among larval types and to a lesser extent between current patterns. At all retention levels it was considerably higher in brooding than spawning corals and in currents with non-directional flow than with strongly directional flow (except when 100% of the larvae were retained, in which case the currents did not affect settlement) (Figures 3.2.a. and 3.2.b.). These results are similar to those found in *Chapter 2*, and were mainly due to the differences in total larval mortality among larval types and current conditions. Total larval mortality was lower in brooded larvae because of their shorter pre-competent and competent periods. Similarly, losses from mortality were lower in non-directional currents because larvae were more likely to meet a reef (generally the natal reef) earlier in these hydrodynamic conditions (see *Chapter 2*).

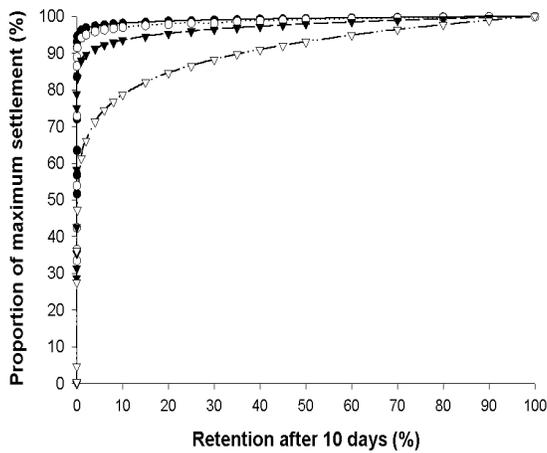
An increase in retention produced a larger increment in settlement rate in brooding than spawning corals. An increase from 0% to 100% water retention produced an increase in settlement rate of 375,000 and 529,000 larvae (per 10^6 produced) for brooders under non-directional and strongly directional currents respectively, compared to an increase of 253,000 and 354,000 larvae for spawners (Figure 3.2.b.). However, the increase in settlement proportion was larger in spawning corals. This increase was 48.3% and 66.5% for brooders without and with advection respectively, and 71.2% and ~100% for spawners (Figures 3.2.c. and 3.2.d.). Spawners under strongly directional currents increased their settlement rate from 2.8 larvae per million larvae released when no retention was present in the models to ~354,000 when 100% retention was used



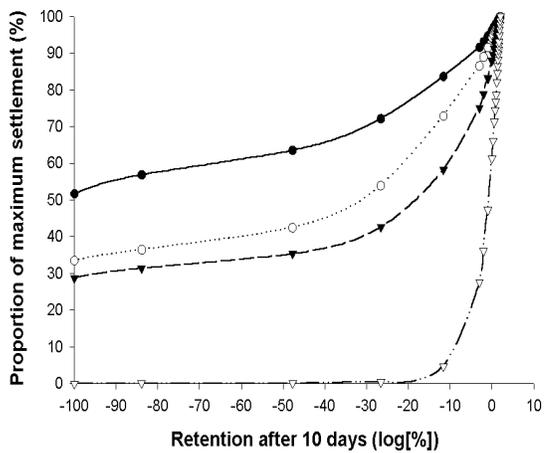
3.2.a.



3.2.b.

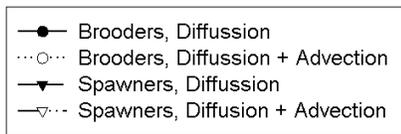


3.2.c.



3.2.d.

Figure 3.2. Effect of the level of water retention at the reefs on the larval settlement of a cohort. Settlement is displayed for each of the 4 larval type – current pattern combinations. (3.2.a.) Settlement rate (larvae settled per million larvae released), retention expressed linearly (%). (3.2.b.) Settlement rate (larvae settled per million larvae released), retention expressed in logarithmic scale (log[%]). (3.2.c.) Settlement proportion (proportion of maximum settlement), retention expressed linearly (%). (3.2.d.) Settlement proportion (proportion of maximum settlement), retention expressed in logarithmic scale (log[%]).

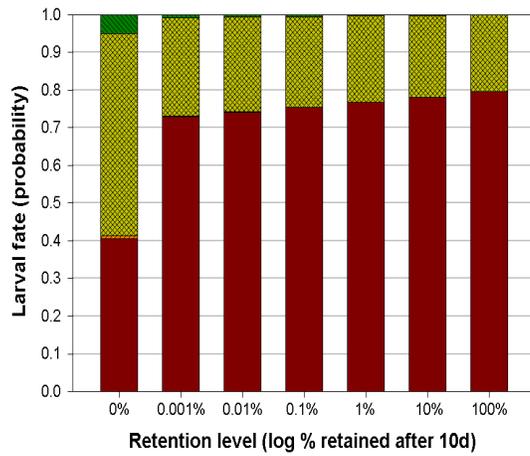


(Figures 3.2.a. and 3.2.b.). Note also that the effect of an increase in retention on settlement rate was more important as advection increased in the current (Figures 3.2.a. to 3.2.d.). Settlement rates for each larval type were lower with strongly directional currents, except at 100% retention when settlement rates were the same for all current patterns (when all larvae are being retained current patterns are irrelevant). Therefore, the increase in the effect of retention on settlement is greater the greater advection is in the currents.

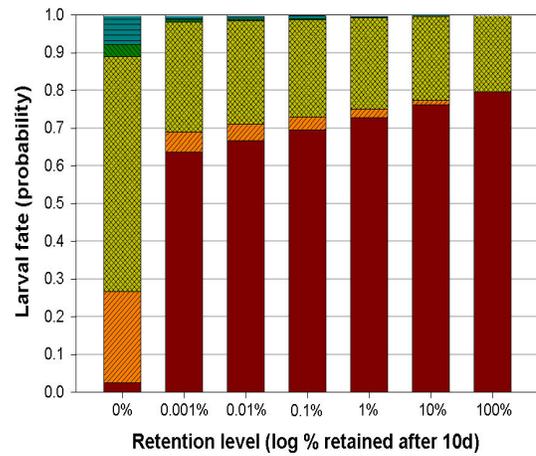
The increase in settlement rate with an increase in the level of water retention was translated into decreases in the rates of all the other possible fates of the larvae in a cohort (dying, ceasing competence, and getting lost out of the chart during the simulation). The largest decrease occurred in the mortality of the larvae, which was drastically reduced in all larval type – current pattern combinations (Figure 3.3.). The proportion of larvae becoming non-competent (i.e. post-competent) also diminished significantly in brooding corals with the increase in retention, as their larvae have short pre-competent and competent periods (Figures 3.3.a. and 3.3.b.). Finally, the small proportion of larvae lost out of the chart during the simulation also decreased, particularly for the larvae in a strongly directional flow (the only case where the loss was noticeable; Figures 3.3.b. and 3.3.d.).

3.3.B. Retention level and local vs. non-local settlement

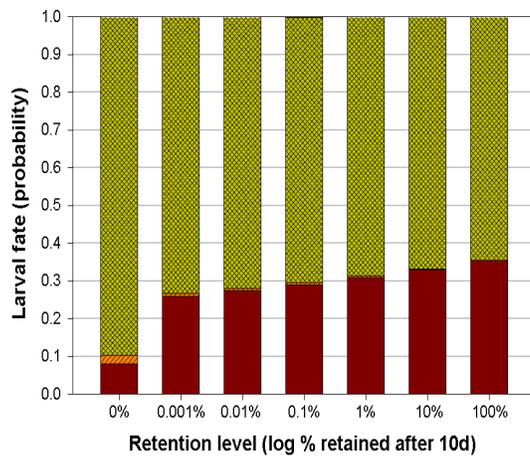
As predicted, increasing levels of water retention generally increased the proportion of larvae in a cohort that settled locally and decreased the proportion settling non-locally (Figures 3.3.a. to 3.3.d.). However, this was not strictly the case for spawners under a strongly directional flow, where the greatest proportion of non-local settlement occurred when low levels of retention were present (Figure 3.3.d.). For this larval type – current pattern combination, non-local settlement was almost negligible ($\sim 3 \cdot 10^{-6}\%$ of the larvae produced) in the absence of retention and highest ($\sim 0.7\%$) at 0.001% retention. Although this maximum value may seem modest, it corresponded to a 233,333-fold increase in non-local settlement relative to its value in the absence of retention. Furthermore, a non-natal settlement of 7,000 larvae per million produced can have significant ecological and particularly evolutionary implications. Following this maximum, non-local settlement gradually decreased with the increase in retention, but only became lower than in the absence of retention at levels close to 100% retention (Figure 3.3.d.).



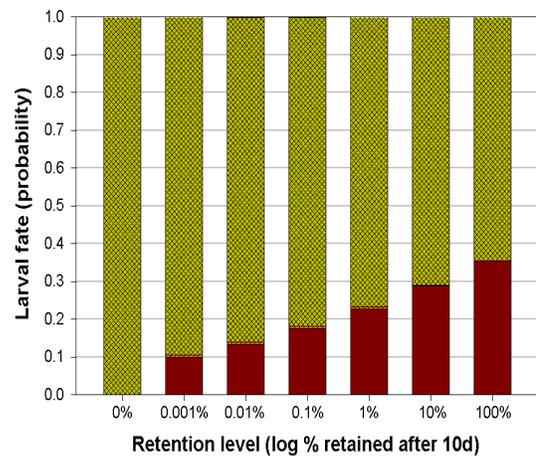
3.3.a. Brooders, non-directional flow



3.3.b. Brooders, strongly directional flow



3.3.c. Spawners, non-directional flow



3.3.d. Spawners, strongly directional flow

Figure 3.3. Effect of the level of water retention at the reefs on the fate of the larvae of a cohort. Retention is expressed as the proportion (%) of water particles retained at the reef after 10 days. (3.3.a.) Larvae of brooders in non-directional flow (diffusion only). (3.3.b.) Larvae of brooders in strongly directional flow (diffusion + advection). (3.3.c.) Larvae of spawners in non-directional flow (diffusion only). (3.3.d.) Larvae of spawners in strongly directional flow (diffusion + advection).



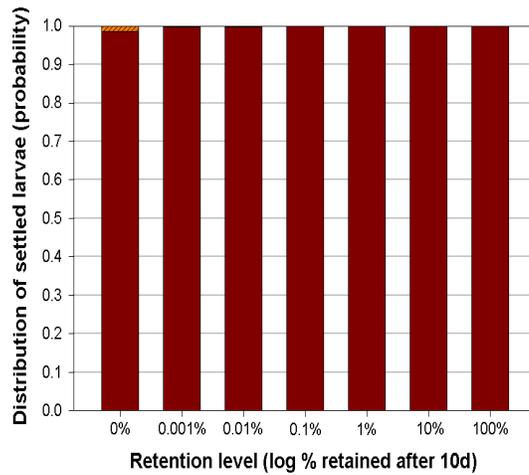
Nevertheless, the proportion of settlers settling non-locally (i.e. non-local settlement relative to total settlement, rather than to the total number of larvae produced) decreased with increasing levels of retention for all larval type – current pattern combinations (Figures 3.4.a. to 3.4.d.). In other words, although in spawners under strongly directional flow the proportion of larvae in the cohort settling non-locally increased with the initial increases in water retention, this increase was much smaller than the increase in the proportion of the cohort settling locally. In fact, in all the larval type – current pattern combinations, the largest decrease in non-local settlement (relative to total settlement) always occurred at these levels of retention (i.e. 0% to 0.001%). At 10% retention virtually all settlement was local (Figures 3.4.a. to 3.4.d.).

The increase in total settlement rate with the increase in the level of water retention was almost exclusively due to an increase in local settlement (only in spawners under strongly directional flow, non-local settlement contributed to the overall increase in settlement rate during the initial increases in water retention). Therefore, the main causes for the increase in local settlement with the increase in retention level were effectively those presented for the increase in total settlement rate (see *Section 3.3.A.*), a dramatic decrease in larval mortality accompanied by a decrease in the proportion of larvae becoming post-competent in brooders.

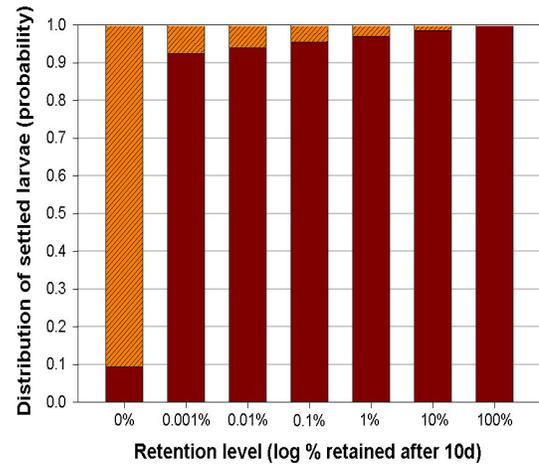
3.3.C. Retention level and connectivity among reefs

3.3.C.1. Evolutionary-scale connectivity

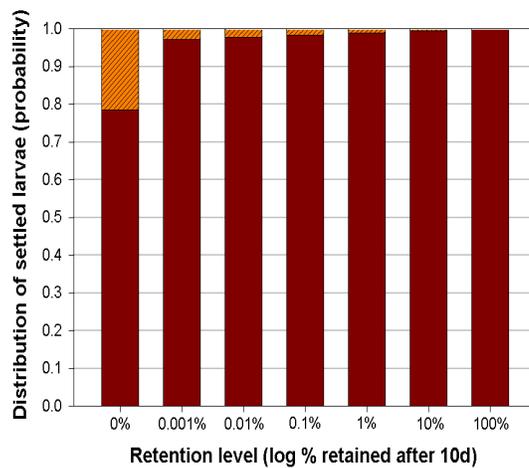
In general, connectivity at an evolutionary-scale behaved as predicted. That is, it decreased with increasing levels of water retention (Figures 3.5.a and 3.5.b.). Nevertheless, the decreases were generally very small until unrealistic levels of water retention (greater than 90%) were used (Figures 3.5.a and 3.5.b.). Notably, genetic connectivity by the larvae of spawning corals under currents with a strongly directional flow increased substantially at very low levels of retention (from ~10 reefs being connected on average at 0% retention to ~15 reefs at 0.001%, Figure 3.5.b.) and peaked when retention was set to levels between 4% and 8% (~18 reefs connected on average, Figure 3.5.a.). These larvae were mostly washed away from their natal reef and even from nearby reefs when retention was absent due to their long pre-competent periods. When retention of water at the reefs was present, not only did the larvae become trapped in their natal reef circulation but also on the circulation of other reefs, and connectivity



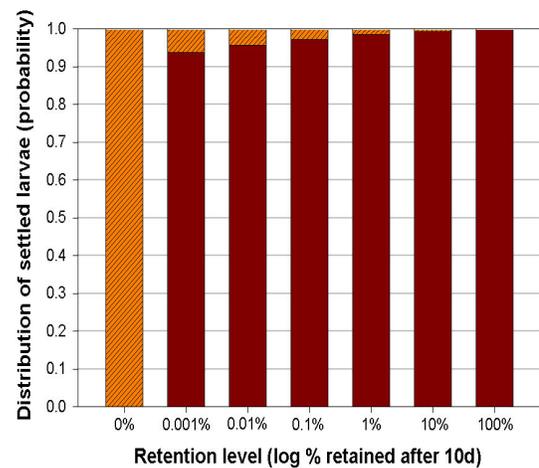
3.4.a. Brooders, non-directional flow



3.4.b. Brooders, strongly directional flow



3.4.c. Spawners, non-directional flow



3.4.d. Spawners, strongly directional flow

Figure 3.4. Effect of the level of water retention at the reefs on the spatial distribution of the settled larvae of a cohort. Retention is expressed as the proportion (%) of water particles retained at the reef after 10 days. (3.4.a.) Larvae of brooders in non-directional flow (diffusion only). (3.4.b.) Larvae of brooders in strongly directional flow (diffusion + advection). (3.4.c.) Larvae of spawners in non-directional flow (diffusion only). (3.4.d.) Larvae of spawners in strongly directional flow (diffusion + advection).

	Settled on natal reef
	Settled on other reefs

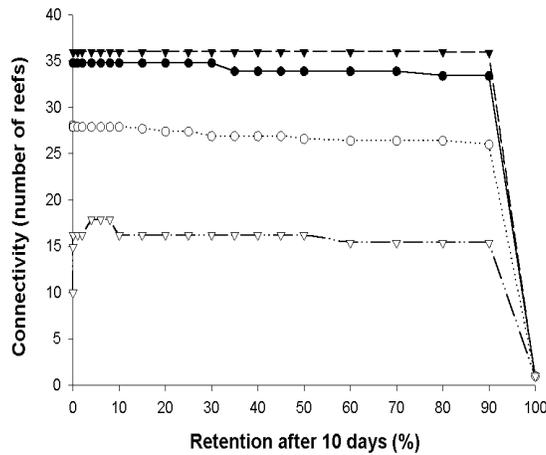
increased. When the retention level was 10% or higher, fewer larvae left the natal reef and connectivity decreased again.

3.3.C.2. Ecological-scale connectivity

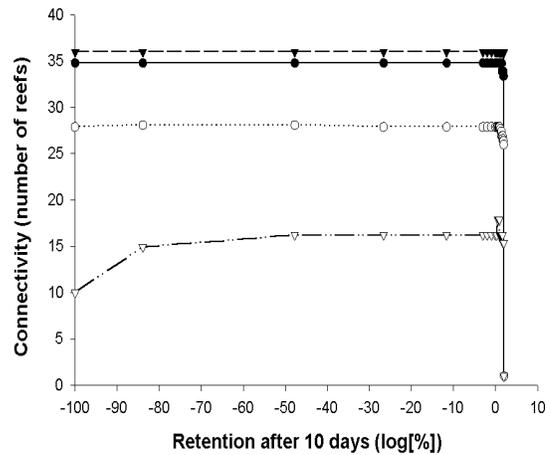
Connectivity at ecological scales was substantially reduced with the increase in retention when the current flow was non-directional (Figures 3.5.c. and 3.5.d.). Under these hydrodynamic conditions, in the absence of retention connectivity at an ecological-scale was relatively high (a reef was 'ecologically connected' to approximately 6 other reefs on average), but non-existent at medium-high retention levels (Figures 3.5.c. and 3.5.d.). The decrease in connectivity at an ecological-scale occurred at much lower levels of retention in brooders (initial decrease at $2.4 \times 10^{-27}\%$ and then a second decrease at 25% retention) than spawners (at 15% and 80% retention) (Figures 3.5.c. and 3.5.d.).

When the current flow was strongly directional there was also a decrease in connectivity of brooders at ecological scales with an increase in retention, although this decrease was smaller and occurred at higher retention levels than in non-directional currents (Figures 3.5.c. and 3.5.d.). Under these conditions, the brooded larvae released in a reef settled on average on ~ 6 reefs at 0% retention and on 2 reefs at 40% retention (including the natal reef, Figures 3.5.c. and 3.5.d.). Further increases in retention level did not decrease connectivity at ecological scales in brooders until very high levels of retention (over 90%) were reached (Figure 3.5.c.). In contrast, connectivity at ecological scales by the larvae of spawners was virtually none existent in the absence of retention and highest at very low levels of retention, peaking between $2.4 \times 10^{-27}\%$ and $2.4 \times 10^{-12}\%$ retention after 10 days (~ 2 reefs connected on average, Figure 3.5.d.). From there, connectivity decreased when retention was increased to 0.001%, but was not affected by further increases in the level of retention until values of over 90% retention were reached (Figures 3.5.c. and 3.5.d.). The causes for the initial increase in connectivity at an ecological-scale were analogous to those for the increase in connectivity at an evolutionary-scale (see *Section 3.3.C.1.*). The only difference being that the increase at an ecological-scale was smaller and occurred at lower retention levels because the number of larvae required to consider two reefs connected is higher at this level of connectivity.

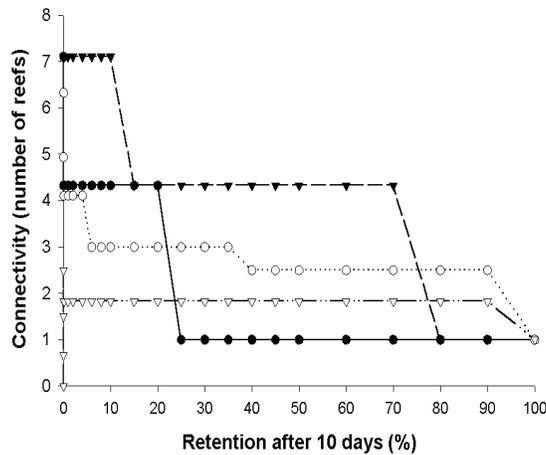
Notably, as a consequence of the above in the models for both larval types, ecological-scale connectivity was higher in non-directional currents than strongly directional ones at low retention levels, but this situation was reversed at higher



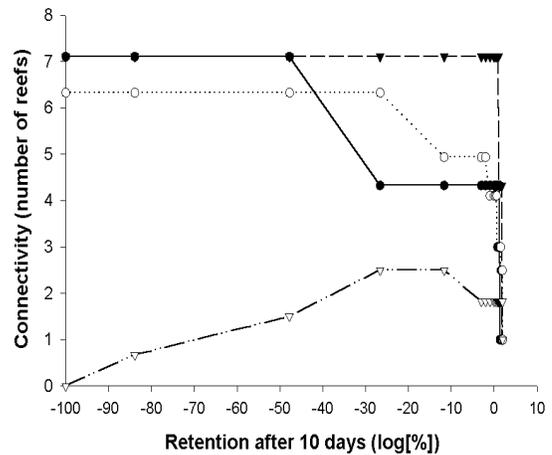
3.5.a. Evolutionary-scale connectivity, retention expressed linearly



3.5.b. Evolutionary-scale connectivity, retention expressed in logarithmic scale

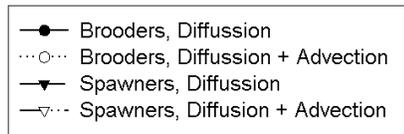


3.5.c. Ecological-scale connectivity, retention expressed linearly



3.5.d. Ecological-scale connectivity, retention expressed in logarithmic scale

Figure 3.5. Effect of the level of water retention at the reefs on the connectivity among reefs by the larvae of a cohort. Connectivity represents the number of reefs connected at different thresholds of larvae: > 0 larva (evolutionary-scale connectivity) and ≥ 1000 larvae (ecological-scale connectivity). (3.5.a.) Evolutionary-scale connectivity, retention expressed linearly (%). (3.5.b.) Evolutionary-scale connectivity, retention expressed in logarithmic scale ($\log[\%]$). (3.5.c.) Ecological-scale connectivity, retention expressed linearly (%). (3.5.d.) Ecological-scale connectivity, retention expressed in logarithmic scale ($\log[\%]$).



retention levels (Figures 3.5.c. and 3.5.d.). The reversal occurred at moderately high retention levels in brooders (~25% retention) and at very high levels in spawners (~80% retention).

3.3.D. Retention level and evenness of the larval input

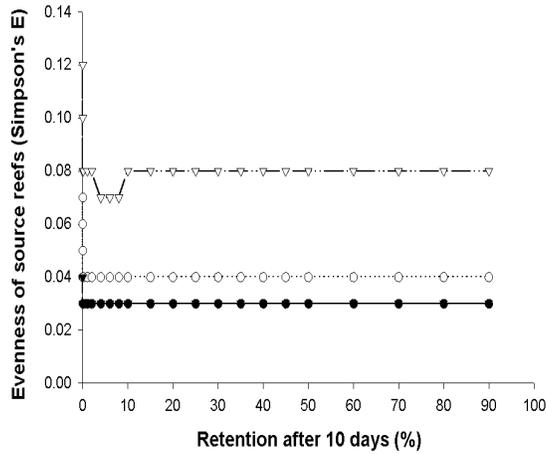
It was predicted that increasing levels of retention would decrease the evenness of the larval input to the reefs in terms of its reef sources because an increasing proportion of the settling larvae would originate locally. However, the simulations showed that the decrease in evenness generally only occurred after a certain level of retention had been reached, and that initial increases in retention had varying effects in each larval type – current pattern combination (Figures 3.6.a. and 3.6.b.).

In the absence of a strongly directional flow (diffusion only), the evenness of reef sources of the larval input to the reefs was very low even when no retention was present (Figures 3.6.a. and 3.6.b.). For brooders, under these hydrodynamic conditions evenness was so low that increases in retention level did not reduce its value. Under the same hydrodynamic conditions, the evenness of the larval input of spawning corals was also low but to a lesser extent, decreasing mildly when retention increased from 0% to very low retention levels ($2.4 \times 10^{-27}\%$). With the next increase in retention level (at $2.4 \times 10^{-12}\%$ retention) evenness decreased sharply to its lowest value, and further increases in retention did not alter its value (Figures 3.6.a. and 3.6.b.).

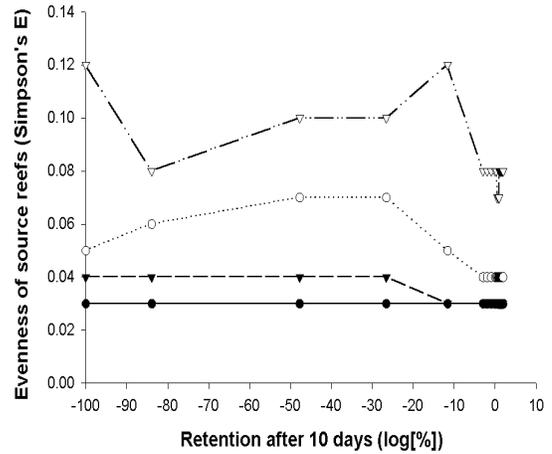
When the currents had a strongly directional flow, the evenness of reef sources of the larval input of both brooding and spawning corals increased initially at very low retention levels, and then decreased rapidly to its minimum, unaffected by further increases in retention level (Figures 3.6.a. and 3.6.b.). In brooders under these conditions, evenness peaked at $2.4 \times 10^{-27}\%$ retention and reached its lowest level at 0.001% retention. In spawners under the same hydrodynamic conditions, the increase in evenness was preceded by a very short and steep decrease, its peak occurring at $2.4 \times 10^{-12}\%$ retention (Figures 3.6.a. and 3.6.b.).

3.3.E. Retention level and diversity of the larval input

It was predicted that the diversity of the larval input to the reefs in terms of its reef sources would decrease with increasing levels of retention. Again, at very low and low retention levels no consistent pattern was found for the relationship between diversity

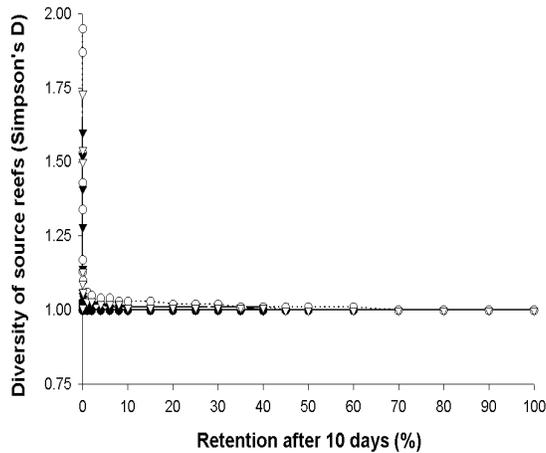
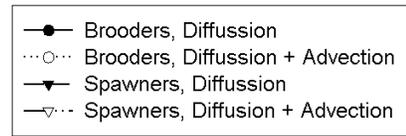


3.6.a.

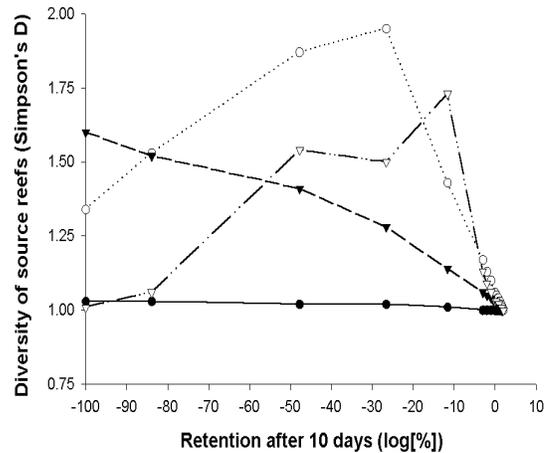


3.6.b.

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. (3.6.a.) Evenness of the larval input, retention expressed linearly (%). (3.6.b.) Evenness of the larval input, retention expressed in logarithmic scale (log[%]). Evenness values are based on the Simpson's evenness index (E), see *Chapter 2* and *Appendix IV* for details. (Evenness increases to 1 when retention is 100% (not shown)).

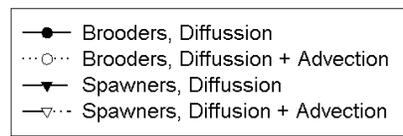


3.7.a.



3.7.b.

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. (3.7.a.) Diversity of the larval input, retention expressed linearly (%). (3.7.b.) Diversity of the larval input, retention expressed in logarithmic scale (log[%]). Diversity values are based on the Simpson's diversity index (D), see *Chapter 2* and *Appendix IV* for details.



and retention level, which varied greatly among larval type – current pattern combinations (Figure 3.7.b.).

In a non-directional flow the predictions held, and a decrease in the diversity of reef sources of the larval input was found even with the initial increases in retention level (Figure 3.7.b.). Once diversity reached a value of 1.0 (when effectively all recruitment was local) further increases in the level of retention did not alter its value. Under these current conditions the diversity of the larval input by brooders was very low even in the absence of retention (1.04), so its decrease with the increase in retention was very small (from 1.04 to 1.00) and short (from 0% to 0.001% retention). In the same hydrodynamic conditions the decrease in diversity in spawners was more substantial (from 1.6 to 1.0) and longer (from 0% to 40% retention).

In currents with a strongly directional flow, the prediction of a decrease in diversity of reef sources of the larval input with an increase in retention level also held, in general, for both brooding and spawning corals. However, under these conditions, the decrease in diversity was preceded by a rapid increase at very low retention levels (0% to $2.4 \times 10^{-27}\%$ in brooders and 0% to $2.4 \times 10^{-12}\%$ in spawners; Figure 3.7.b.). After this early rapid increase, diversity decreased considerably at low retention levels (Figure 3.7.b.). At medium-high levels of retention (~40%) diversity reached its minimum (1.0), with further increases in retention not affecting its value.

3.4. DISCUSSION

Of all the predictions tested, only the predictions of an increase in total and local settlement rate with an increase in the level of water retention at the reefs were supported in all cases. The other four predictions: (1) decrease in non-local settlement, (2) decrease in connectivity among reefs by larvae at evolutionary and ecological scales, (3) decrease in evenness and (4) reduced diversity of reef sources of the larval inputs to the reefs with increasing levels of retention, were supported except in some cases at very low or low levels of retention. At these levels the effect of small increases in retention on the studied variables varied greatly for each particular larval type - current pattern combination. Furthermore, at very low or low retention levels the behaviour of the variables generally contradicted the predictions when the currents had a strongly directional flow (i.e. when advection was clearly greater than diffusion). That is, non-

local settlement, evenness, diversity and particularly connectivity increased with increasing levels of retention. These are very significant results because these levels of water retention are comparable to those commonly found in the field (e.g. Black et al. 1991, Black 1993) and most populations of corals (and many other marine organisms) are located in areas subjected to currents with a clearly directional flow (e.g. Andrews and Pickard 1990, Wolanski 1994, and references within).

3.4.A. Consequences of the level of water retention in the models

3.4.A.1. Settlement rate and larval fate

In the absence of retention, larval settlement could be very low in the models, particularly when advection was strong and constant. The quantity of larvae settling depended on the amount of advection and diffusion in the background currents, which determined how quickly larvae were washed away from the reefs. The speed of background currents in coral reef systems typically ranges between 5 and 60 cm.s^{-1} , and is frequently between 10 and 30 cm.s^{-1} (e.g. Andrews and Pickard 1990). Their speed in the models ($\sim 17 \text{ cm.s}^{-1}$) fits in this range and is common, for example, in the central GBR (e.g. Wolanski 1994, and see *Chapter 4* and *Appendix III*). The spatial features (size, shape, and distribution) of the reefs and their interaction with the local hydrodynamics are also essential determinants of the recruitment of larvae transported by advection (e.g. Black 1993, and see also Chapter 7 in this Thesis). However, in the models both in this chapter and the previous chapter (where a wide range of reef topologies was used) when retention was absent and transport was mainly due to directional and constant currents, the larvae of spawning corals showed almost negligible settlement. Under these hydrodynamics conditions low settlement of spawners was caused mainly by the high levels of larval mortality that occurred as a consequence of the vast proportion of larvae dispersing away their natal (and nearby) reefs during their long pre-competent and competent periods. Using numerical modelling, Cowen and collaborators (Cowen et al. 2000) estimated that mortality and diffusion could reduce concentrations of larvae by up to nine orders of magnitude. In addition, in the models in this chapter a small proportion of larvae were unable to settle because they become post-competent before reaching another reef, particularly in brooders.

Even small increments in the level of water retention at reefs greatly increased settlement rates in the simulations. The increases in settlement rates were almost exclusively caused by increases in local settlement (only in spawners under strongly

directional flow non-local settlement contributed to the overall increase in settlement rate during the initial increases in water retention). While being retained at the natal (and nearby) reefs larvae could find suitable substrata for settlement and metamorphosis as soon as they became competent, rather than being transported offshore where a suitable substratum was less likely to be found, drastically reducing larval mortality and the proportion of larvae becoming post-competent.

The extremely low settlement rates obtained for spawners in the absence of retention in the models in this chapter are unlikely to be sufficient to sustain viable populations. This is in agreement with previous modelling studies, which found that if the reefs in the modelled reefal systems were not self-seeding coral cover declined in the systems except in those cases in which reef density in the system was high (Johnson and Preece 1992, Preece and Johnson 1993). Therefore, it is concluded that some level of larval retention must exist at the reefs for the persistence of populations of marine species with long-lived pelagic larvae. Moreover, the results of the models also indicate that only modest levels of water retention are required to significantly increase the recruitment (and thus the survival probability) of populations of marine species with a larval phase, particularly in species with long pre-competent and/or competent periods.

3.4.A.2. Non-local vs. local settlement

In the absence of retention and when strongly directional currents were used in the models not only local settlement was low, but also most of the brooded larvae and virtually all the spawned larvae settled non-locally. This finding is clearly contradicted by the results of genetic analysis of coral populations. These studies have found considerable genetic subdivision among coral populations, concluding that most recruitment by corals is very local and that populations rely mainly upon self-seeding for their maintenance (e.g. Ayre and Hughes 2000, Nishikawa and Sakai 2005). However, when the level of retention estimated for the typical reefs in the central GBR (~5-10% retention after 10 days, Black et al. 1991, Black 1993) was used in the models most settlement was local. This provides further evidence that some amount of larval retention must exist at the reefs.

3.4.A.3. *Connectivity among reefs by larvae*

At levels of retention likely to be found at the reefs (Black et al. 1991, Black 1993), connectivity at the evolutionary scale was high. A significant decrease in connectivity at the evolutionary scale was only evident when unrealistically high levels of retention were used (> 90% after 10 days). Connectivity at the ecological scale was considerably lower and decreased more quickly with the increase in retention, but even at moderately high levels of retention some connectivity among neighbouring reefs still remained with the background current speed used in the models. The high levels of connectivity at evolutionary scales and the low levels at ecological scales are consistent with genetic studies, which have estimated that although gene flow among reefs in the GBR is sufficient to maintain panmixis among distant populations most settlement is local (e.g. Stoddart 1986, Ayre and Hughes 2000, Nishikawa and Sakai 2005).

Moreover, in contrast to the original prediction, connectivity among reefs by the larvae of spawning corals initially increased (both at evolutionary and ecological scales) with increasing levels of retention when the currents had a strongly directional flow. Under these hydrodynamic conditions, when retention was absent spawners' connectivity was low at evolutionary scales and non-existent at ecological scales. Their evolutionary-scale connectivity peaked between retention levels of 2% and 8% after 10 days, and their ecological-scale connectivity was highest at very low retention levels (2.4×10^{-12} % retention). That is, at the retention levels estimated by Black (1991, 1993) for the typical reefs in the central GBR evolutionary-scale connectivity peaked and ecological-scale connectivity was only slightly lower than at its maximum in the models in this study (which used reef densities similar to those in the Central GBR). The cause of the rise in ecological scale connectivity in spawners was that larvae could get trapped in the retention circulation not only of their own natal reef but also of other reefs. This allowed larvae that encountered a reef during their pre-competent period to be retained until they became competent to settle. Also, larvae could be temporarily retained at their natal reef for varying lengths of time, arriving at the surrounding reefs at different stages of development. In this way, larvae that in the absence of retention arrived too early to nearby reefs could now reach them when they were ready or nearly ready to settle.

An important issue is to which extent larvae produced in reefs up-stream are captured in the circulation of reefs they encounter down-stream. Numerical models indicate that most incoming water flows around rather than enter the reefs down-stream,

as the water retained in the down-stream reefs is not available for replacement (Black 1993). This is particularly true for deep water (generally retention is at its maximum near the sea bed), but less so for surface water. Most coral larvae are positively buoyant initially, which may favour not only their dispersal after release but also their capture in the circulation of reefs down-stream. More data on the vertical positioning of coral larvae in the water column during their whole planktonic life is required to fully assess the effect of water retention at reefs on connectivity. Nevertheless, even if only a small proportion of the larvae produced up-stream is captured in the circulation of reefs down-stream connectivity by the larvae of spawners under strongly directional currents is likely to increase notably, particularly at an ecological-scale because in the absence of retention this connectivity was virtually negligible.

3.4.A.4. Evenness and diversity of reef sources of the larval input to the reefs

Ecological (e.g. Sammarco and Andrews 1988, 1989) and genetic (e.g. Ayre and Hughes 2000) studies indicate that dispersal by the larvae of spawning corals is greater than that of brooders. Based on these findings it could be assumed that the diversity of reef sources of the larval input of spawners is greater than that of brooders. In the models in this chapter, the sources of the larval input were more diverse for spawning corals than brooding corals when the currents lacked a strongly directional flow. However, when advection was included in the models and in the absence of retention the diversity of sources of the larval input of spawners was much lower than that of brooders; it was only when retention was present that their diversities were comparable (although spawners diversity remained slightly lower at most retention levels). The lower diversity of spawners than brooders in the models including currents with a strongly directional flow is a consequence of the long pre-competent periods of their larvae and the topology of the reefs in the chart used in the models. When their larvae encounter most of the reefs in the chart they are not competent to settle yet, and the reduced proportion of larvae that survives until competence only encounters a few reefs. In large reefal systems, such as the GBR, the larvae of spawners can encounter numerous reefs after they reach competence; however, even in these systems connectivity (particularly at an ecological-scale) and diversity of spawners would be low under strongly directional currents in the absence of retention as few larvae would settle on reefs near the natal one (due to their long pre-competent periods) and on the distant reefs (due to mortality and diffusion). Again, some retention seems to be

required for spawners to exploit the potential for dispersal provided by the long pre-competent and competent periods of their larvae.

3.4.B. Larval retention: implications and applications

3.4.B.1. Implications of larval retention

Local retention of larvae has important implications for the dynamics of marine populations (e.g. Williams et al. 1984, Doherty 1988, Willis and Oliver 1988b). For this reason, understanding retention is vital to understand the ecology and genetics of the organisms producing larvae (reviewed in Scheltema 1986, Strathmann et al. 2002). If all the larvae were dispersed away from their source, the population would operate as a completely ‘open’ system even at ecological time scales (e.g. Roughgarden et al. 1985, Warner and Hughes 1988, Caley et al. 1996). Recruitment would then be mainly driven by the mechanisms transporting larvae produced elsewhere, largely independent of local fertility (Roughgarden et al. 1985, Warner and Hughes 1988, Underwood and Fairweather 1989, Sale 1991, Caley et al. 1996). However, if all the larvae were retained, the population would be a completely ‘closed’ system regulated by local processes (Brogan 1994). The vast majority of the populations of most marine organisms are open to some extent, lying between the extremes of total dispersal and total retention, with the balance between these two processes changing in space (among populations) and time (within populations) (Sponaugle et al. 2002). Because different levels of local and non-local recruitment occur in different populations, some populations have, for instance, higher growth rates (Sammarco and Andrews 1988) and faster recovery from disturbance (e.g. Day and McEdward 1984, Connell 1997, Hughes and Tanner 2000) than others.

Dispersal also transports genes among populations. Gene flow shapes the genetic structure of the populations, consequently influencing processes like adaptation, speciation, and extinction (e.g. Brogan 1994, Palumbi et al. 1997). For example, in populations where the majority of the larvae are dispersed local adaptation is hindered, especially in species with short generation times (e.g. Loya 1976, Benyahu and Loya 1985). Rapid adaptation to local conditions can provide higher resistance to environmental disturbances, such as global warming (e.g. Hoegh-Guldberg 1999), decreasing the risk of local extinction. Reduced gene flow due to retention has, on the

other hand, been proposed as one of the causes for the surprisingly high rates of speciation in marine taxa with larvae with high dispersal potential (e.g. Palumbi 1994).

The results in this chapter indicate that only very small increases in retention are necessary to significantly modify the patterns of settlement and connectivity in coral metapopulations. This implies that even populations with modest levels of retention can attain important recruitment and growth rates. As a consequence, these fairly open populations could be regulated mainly by local processes. That is, populations do not need to be completely (or mostly) closed for local regulation to occur. Similarly, in these populations, despite the considerable levels of gene flow, a significant amount of recruits could be locally adapted.

3.4.B.2. Applications to management and conservation

Larval retention has significant implications for the design of marine reserves, management of fishery stocks, and conservation of marine biodiversity (e.g. Fairweather 1991, Strathmann et al. 2002). Some general guidelines relative to the implications of larval retention for the management and conservation of marine populations can be drawn from this and other studies. The conventional view is that if larvae are widely dispersed, local management may be ineffective and the establishment of networks of interdependent reserves is a better approach. In this case, the location of the reserves is critical (e.g. Swearer et al. 1999), and management efforts should concentrate on source and nursery habitats (e.g. Fairweather 1991) as they can contribute to the replenishment of populations downstream, beyond the borders of the reserves (e.g. Davis and Dodrill 1989). The geographic distribution of the populations in combination with the patterns of the currents flowing among them has been used to define connectivity regions or envelopes, which together with information on the planktonic duration of the larvae can be applied to the design of marine reserves (Roberts 1997). However, these envelopes represent the upper boundaries of connectivity, and if larvae are being retained in their natal populations these levels of connectivity will not be frequently realised. In this case, management initiatives are more likely to produce local benefits (Roberts 1997). The results in this chapter, nevertheless, indicate that only very small levels of retention are required to significantly increase local recruitment, still allowing numerous larvae to undergo dispersal and potentially connect local populations. Furthermore, very low or low levels of retention at the reefs down-stream can further increase connectivity and diversity (as

larvae can become trapped in their circulation). Therefore, it is possible, and perhaps even common, that the local management of a population could have both local and non-local effects. Incorrect assumptions about the typical dispersive levels of larvae may lead to erroneous management decisions, which can have severe implications for the populations (e.g. Carr and Reed 1993).

There are many other issues regarding larval retention that should be considered in the management of marine resources. In populations where recruitment limitation is common, it is critical to focus on protecting the zones where larval retention may occur, rather than concentrating efforts on the protection of adults (Warner et al. 2000); particularly if the populations are located in areas with a strongly directional flow, where larvae are commonly washed away from their natal reef and retention can have its biggest impact. After massive disturbance, if the populations are predominantly 'open', the species more likely to recover are those with extended pelagic larval phases and populations upstream from the disturbed area (e.g. Munro 1998). Conversely, if a species with short planktonic larval life has disappeared or is endangered in a poorly connected population, transplantation of individuals from another population may be the only viable approach (Tegner 1993). Modelling studies indicate that, independently of the intensity of disturbance, coral cover recovers more rapidly when water retention is present at the reefs (Johnson and Preece 1992, Preece and Johnson 1993). Moreover, these studies also found that in the absence of retention, coral cover may not recover after disturbance (i.e. it was maintained or further declined) when the damage was extensive and reef density low in the system. Therefore, under these circumstances it may also be crucial to concentrate management efforts on protecting the areas where larval retention takes place. In conclusion, before management plans are designed, a solid knowledge of the oceanographic conditions for retention, dispersal, and accumulation should be acquired. In addition, knowledge of the life history of the species in question, including the duration of the pre-competent and competent periods, mortality, and behaviour of the larvae is of prime importance.

3.4.C. Model Limitations

The model limitations presented in *Chapter 2* also apply to the models described in this chapter. Further limitations particular to the application of the models to the study of the effects of retention are presented below.

The values of the dispersal variables (i.e. settlement rate, connectivity, evenness and diversity) computed by the models refer to the specific charts (i.e. reefal systems) and mortality rate used in the simulations. Using other charts would produce quantitatively, and occasionally qualitatively, different effects of retention on the studied variables. Similarly, employing other mortality rates would produce quantitatively different effects of retention on the variables. Nevertheless, the general trends found in this chapter for the effects of retention on settlement, connectivity, evenness and diversity, should be maintained in most cases. For management applications, however, it is recommended to use implementations of the models specific for the relevant natural reefal system (i.e. spatially realistic models) with a range of mortality rates.

In the models larval mortality rate was kept equal in the reef and water cells. However, mortality of larvae is likely to be higher within than between reefs (see *Chapter 1, Section 1.3*). This kind of difference in mortality between the reefs and the open sea could not only reduce the effects of retention, but also constitute a significant selective pressure for the evolution of dispersal (i.e. selecting for off-reef development and dispersive life histories) in the larvae of marine organisms. More research is required to verify how generalised and extensive the differences in mortality are on spatial and temporal scales (particularly those occurring between the reefs and the open ocean) before they can be incorporated into the models.

The positions of the start, end, and inflexion points of the competence curves (e.g. peak and tail; Figure 3.1.) used in the models were based on the information available in the literature (see *Chapter 5* and references within). However, the height (i.e. proportion of larvae settling at each time) of these points were kept equal for both types of coral (Figure 3.1.) since variation among species was much more substantial than between both reproductive groups. As new data on the competence patterns of coral larvae becomes available, the models could be updated, adjusting the position and height of the inflexion points. Nevertheless, the revised competence curves are likely to be similar to those used in this chapter, and the effect of retention on the studied variables in the classical brooder and spawner should not differ significantly from those presented here (in fact, because rather conservative competence curves were used, the differences in the effect of retention between both reproductive groups would be expected to be larger rather than smaller).

3.4.D. Summary and Conclusions

Of the common predictions about the effects of an increase in the level of larval retention at the 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. The behaviour of these variables at low and more realistic retention levels depended on the specific conditions of the simulation (i.e. larval type – current pattern combination). In particular, when the currents had a steady and strongly directional flow (the common hydrodynamic conditions in coral reefs) the predictions were not met in many cases at these low retention levels.

Very small increases in the level of retention were enough to produce substantial increases in local and total settlement. To obtain settlement, connectivity and diversity values comparable to those found by ecological and genetic studies, some level of retention was required in the models for larvae with long pre-competent periods (spawners) in the presence of advection (directional flow). It was concluded, that a retention mechanism (hydrodynamic and/or behavioural) must exist, at least for this type of larvae at reefs subjected to constant and strongly directional background currents. Connectivity at ecological scales was in most cases notably reduced with retention, but some low levels of ecological-scale connectivity were maintained even at moderately high retention levels. However, retention only slightly reduced connectivity at an evolutionary scale, still allowing panmixis. Furthermore, retention could trap larvae not only at the natal reef, but also at other reefs. These non-natal reefs could retain the larvae until they become competent, allowing them to exploit their potential for dispersal. As a consequence, small levels of retention can also increase the number of larvae settling on reefs other than the natal one (i.e. non-local settlement) and the number of reefs where they settle (i.e. connectivity), especially when the larvae have long pre-competent periods.

Dispersal and retention are variable in space, time and among taxa. Despite this variability, both processes seem to be essential: retention maintaining viable local populations, and dispersal (and to a certain extent retention) maintaining connectivity among these populations. Retention has important implications for the ecology and evolution of many marine species, including the way in which populations are regulated. Dispersal, retention and accumulation must be considered in the design of marine reserves, management of fishery stocks, and conservation of marine

biodiversity. Multi-disciplinary studies, including the ecology of the species involved, the local hydrodynamics, numerical simulations and 'ground'-truthing should be conducted for each particular management project.

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

4.1. INTRODUCTION

The Great Barrier Reef (GBR) located off the tropical north-east coast of Australia, is the largest single collection of coral reefs ever known. It covers almost 350,000 km², extending approximately 2,600 km from latitudes 9°12'S to 24°30'S, roughly oriented from NW to SE (Figure 4.1.). Despite the relatively recent origin of the GBR in its present form (10,000 to 6,000 years ago; e.g. Mather and Bennett 1994, Veron 1986b), over 10% of the world's fish species (e.g. Pownall 1975) and more than 40% of the hermatypic corals species in the world (e.g. Veron 1995) inhabit the more than 2,500 reefs from which it is comprised. Due to its evolutionary history, biological diversity, and ecological importance, it is listed as a World Heritage Area (the largest of the world's 552 World Heritage Areas) and protected as a Marine Park (e.g. Wachenfeld et al. 1998).

In this chapter, I explore the patterns of settlement, connectivity, and diversity of the larvae of brooding and spawning corals on the GBR, and the mechanisms causing them, using spatially realistic models (see *Section 4.1.B.* for a detailed description of the aims of this chapter). Being such an extensive system, the GBR shows important spatial variation in physical and biological conditions that are critical for the production, dispersal, and settlement of coral larvae. For convenience, the GBR is often arbitrarily divided latitudinally into 5 sectors or regions (from North to South): *Torres Strait Sector* (9°12'S to 11°S); *Northern Sector* (11°S to 16°S); *Central Sector* (16°S to 20°S); *Southern Sector* (20°S to 22°30'S); and the *Capricorn-Bunker Groups Sector* (22°30'S to 24°30'S). Representations of the physical (i.e. topologic and hydrodynamic) conditions found in the GBR sectors were included in the models. Reviews on the physical geography and oceanography of the GBR are presented in *Appendices II* and *III* respectively, while the specific geographic and current settings used in the models are described in the *Materials and Methods Section*. The climatic and biological patterns found latitudinally along the GBR are essential for the interpretation and discussion of the results, and to understand the motivation for this chapter. Therefore, next I will briefly

review these patterns, finalising the introduction with a description of the particular aims of the research presented in this chapter.

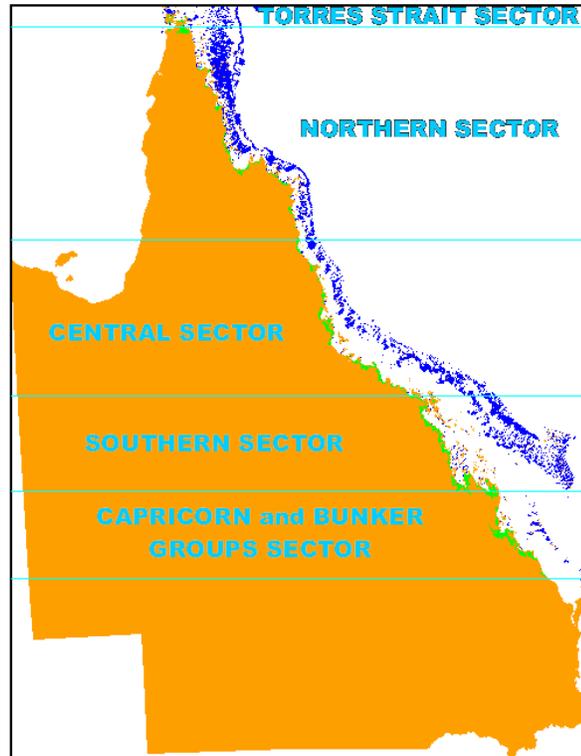


Figure 4.1. Map of the GBR and its sectors. Land-types are colour-coded. *Orange*: land (including mainland, coastline, islands and cays); *Green*: mangrove areas; *Blue*: reefs. Only part of the Torres Strait sector is included (see Methods).

4.1.A. Climatic and biological latitudinal patterns on the GBR

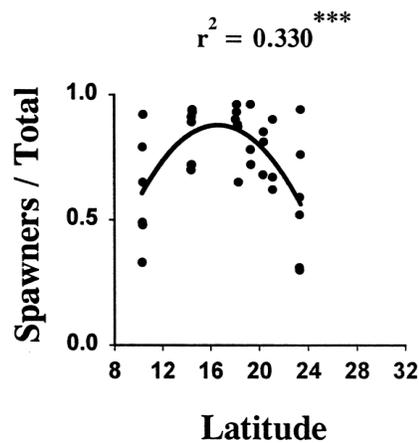
Climate ranges from warm tropical to sub-tropical in the approximately 15° of latitude encompassed by the GBR. Some of the most important climatic patterns in the GBR are the latitudinal gradients in the mean and variance of temperature. Average annual mean sea surface temperature (SST) decreases from over 27°C in the north to $\sim 24^{\circ}\text{C}$ in the south, and the annual range of SST increases from $3\text{--}4^{\circ}\text{C}$ in the north to $\sim 6^{\circ}\text{C}$ in the south (Lough 2001). An abnormality in the temperature gradient occurs occasionally (particularly from February to May) between latitudes 14°S to 15°S , where the continental shelf is at its narrowest and there is greater mixing of the warm shallow shelf waters and the deeper and cooler Coral Sea waters (see *Appendix III*). This generally results, in lower temperatures in this area than those occurring to the north and south (e.g. Endean 1982). Similarly, the change in other climatic variables is not strictly

gradual. For example, mean annual rainfall and river run-off are highest at 17°S, and as a consequence surface salinity in the lagoon is lowest in the central sector, increasing towards the north and south (e.g. Pickard et al. 1977). Moreover, many geological, geographic and hydrodynamic variables also display significant spatial variation along the GBR (see *Appendices II and III*) and their latitudinal patterns differ, further contributing to the formation of a mosaic of physical conditions in the GBR.

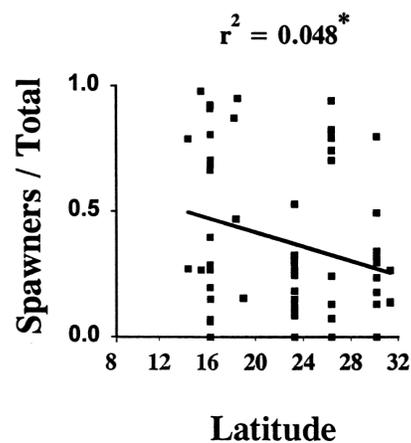
Differences in physical conditions provide diverse habitats and selection pressures to the communities inhabiting them, which may affect the distribution and abundance of the species (e.g. Brown 1995, Brown and Lomolino 1998). For example, with increasing latitude species richness generally decrease (e.g. Gaston 2000). In the GBR, however, species richness of both hard (Veron 1994) and soft (Fabricius and De'ath 2001) corals is highest between latitudes 14°S and 18°S, declining slightly toward the north and sharply towards the south. Similarly, hard coral cover (Hughes et al. 1999, Fabricius and De'ath 2001) and adult density (Hughes et al. 1999, 2000) are highest in the Central sector of the GBR. This pattern of abundance reflects the distribution pattern of the more ubiquitous broadcast spawning corals (Hughes et al. 1999). Despite this, coral cover by spawners although variable (2-fold difference) was not significantly different among sectors (Hughes et al. 1999). In contrast, coral cover by brooders did vary significantly among sectors (3-fold difference, Hughes et al. 1999). Nevertheless, in both types of coral the greatest variation in coral cover occurred among sites within reefs (see Hughes et al. 1999).

Hughes and collaborators also investigated coral recruitment along the GBR in 1995 and 1996 (Hughes et al. 1999, 2000 and 2001). They found that spatial variability in recruitment in the GBR occurs mostly at large (among sectors, 250-500 km away) and fine (sites within reefs, 0.5-3 km away; and among replicate panels, just a few cm. away) scales, while it was much lower at intermediate (among reefs, 10-15 km away) scales (Hughes et al. 1999). These spatial patterns were maintained both years, despite large variability in the number of recruits each year (3-fold difference). Total recruitment peaked in the Northern and Central Sectors, declining markedly to the south and more slowly to the north (Hughes et al. 2002a). However, there were important differences in settlement patterns between both reproductive groups. Spawning corals dominated overall recruitment, as sampling was centred in the 8 weeks surrounding the late spring mass spawning events. Therefore, the pattern of recruitment of spawners was very similar to that of overall recruitment, although with slightly more abrupt decreases

in recruitment both to the north and south. Brooded recruits, on the other hand, declined linearly from the Torres Strait Sector to the Capricorn-Bunker Groups Sector, but to a lesser extent than spawners. As a result, brooder recruits were dominant in the southern part of the GBR and in the sub-tropical reefs to its south (Figure 4.2.a.), conforming with previous observations (Figure 4.2.b.) (Harriott and Simpson 1997, Banks and Harriott 1996, Dunstan and Johnson 1998). In combination, the recruitment patterns of both types of coral led to a gradual decrease in the proportion of spawners in the overall coral recruitment from the North-Central Sectors to the southernmost parts of the GBR both in Hughes and collaborators large-scale study (Figure 4.2.a.) and in a meta-analysis of multiple small-scale recruitment studies (Figure 4.2.b.) (Hughes et al. 2002a). A smaller decrease in the proportion of spawners in the overall recruitment from the North-Central Sectors to the Torres Strait Sector was also observed in the large-scale study (Figure 4.2.a.). Hughes and collaborators found that the large-scale spatial and temporal variation in the density of spawning coral recruits was not significantly related to the differences in adult abundance (1999), but rather linked to adult fecundity (spatial and temporal variation in adult fecundity explained over 70% of the variation in recruitment by spawning acroporids, Hughes et al. 2000).



4.2.a.



4.2.b.

Figure 4.2. Variation in the proportion of spawner recruits in the total recruitment in the Great Barrier Reef. (4.2.a.) Results from a single large-scale recruitment study. (4.2.b.) Results of a meta-analysis of multiple small-scale recruitment studies (250 data points from 21 studies). (Modified from Hughes et al. 2001).

4.1.B. Aims of the study

This chapter has three main aims:

- (1) To investigate the variation in: settlement rate, proportion of local and non-local settlement, connectivity among reefs by larvae, and evenness and diversity of reef sources of the settled larvae of brooding and spawning corals along the GBR. For this, larval dispersal is modelled within 6 zones located at varying latitudes of the GBR, where recruitment has been previously studied. In the models in this section, settlement is dependent exclusively on physical factors (topology and background currents) for easy comparison among zones (i.e. biological variables, such as coral cover and fecundity, are not included in the models).
- (2) To assess the main mechanisms producing the latitudinal recruitment patterns of brooding and spawning corals in the GBR. In this case, the spatially realistic models of larval dispersal in the 6 zones in the GBR include varying levels of both physical and biological information. All models include representations of the zones' local topology and background currents (as for *Aim 1*), plus different combinations of the following information: coral cover, coral fecundity, and water retention level at the reefs. The information required by the models to reproduce the observed recruitment patterns in the GBR is presumed to be related to the mechanisms driving the production of these patterns in the field.
- (3) To explore the level of variation among reefs within zones in: settlement rate, proportion of local and non-local settlement, connectivity among reefs by larvae, and evenness and diversity of source reefs of the settled larvae of brooding and spawning corals. The investigation of the level of variation in these variables among nearby reefs is important for management purposes and to evaluate the risk of extrapolating the results found in field studies undertaken in a single location.

4.2. MATERIALS and METHODS

The general design, inputs, outputs, functioning and rules of the models are similar to those presented in previous chapters (see *Chapter 2* for a detailed description). Nevertheless, both the elaboration of the input files (given their spatial realism reproducing zones of the GBR) and the data analysis are considerably more complex than in previous chapters. Also, more types of models were used, since the coral cover and fecundity of the zones was included in some of the simulations. The differences among the models used in this chapter and those described previously are presented in detail below. In all cases, the competent periods of the larvae of brooding and spawning corals were represented non-linearly (see *Chapter 3*, Figure 3.1.), and a daily larval mortality of 0.3 was used (instantaneous mortality rate, $M = 0.357$).

4.2.A. Model Inputs

4.2.A.1. Spatial representations: Charts

Six charts, representing six zones located at different latitudes of the GBR, were used as inputs to the models (Figure 4.3.a.). The zones depicted each of the 6 sets of reefs used in the large-scale study of coral recruitment in the GBR by Hughes et al. (1999) and their surroundings within an area of 1.5° of latitude x 1.5° of longitude (Figure 4.3.b to 4.3.g., Table 4.1.). Each sector of the GBR was represented by one zone, except for the larger central sector that included two zones (Table 4.1.). Approximately only the uppermost third of Zone 1 actually belongs to the Torres Strait Sector, while the rest lies in the Northern Sector (Figure 4.3.a.). This constraint was imposed by the availability of spatial information (see below), Zone 1 being located as far north as possible within the available data.

Spatial information on the GBR was originally obtained from Dr. Adam Lewis (Great Barrier Reef Marine Park Authority) in the form of two ARC/INFOTM coverages. These coverages represented the coastline of Queensland (Australia) extending from $\sim 10^{\circ}30'S$, $142^{\circ}E$ (top-left corner) to $\sim 25^{\circ}S$, $153^{\circ}40'E$ (bottom-right corner) (Figure 4.3.a.). The two coverages were overlapped into one. The resulting coverage was checked and corrected for discrepancies and errors. The 12 land-types in the new coverage were reclassified into the 4 land-types compatible with the dispersal models:

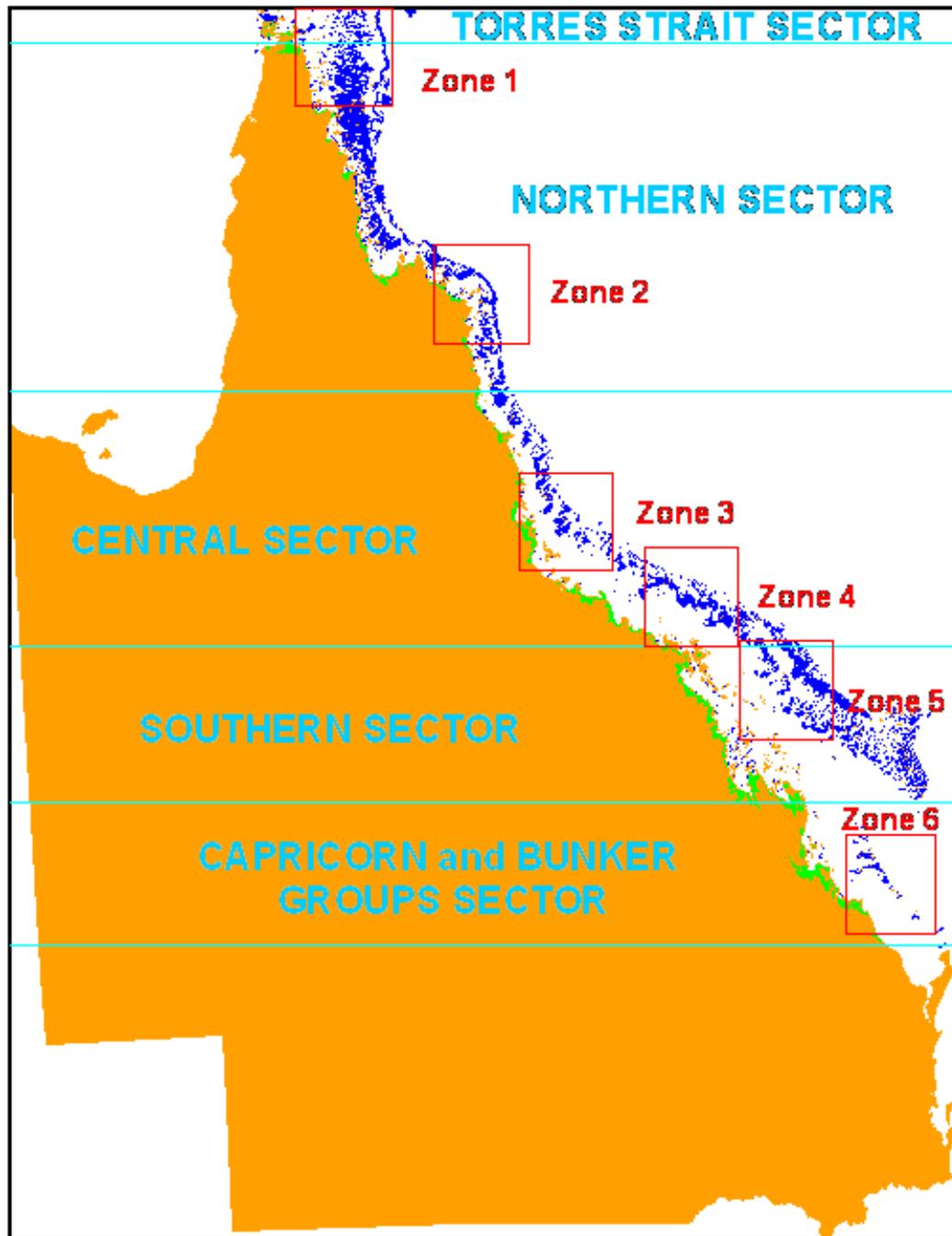
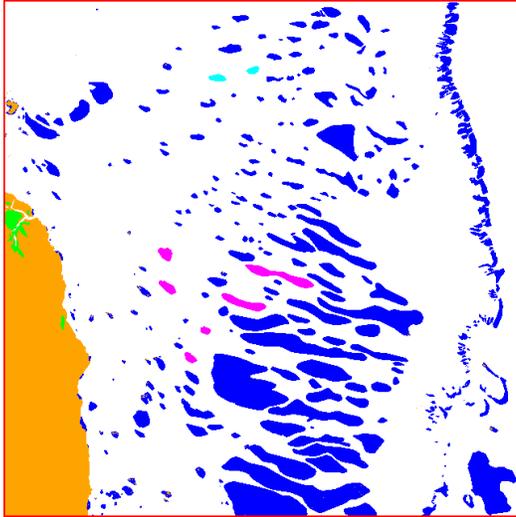
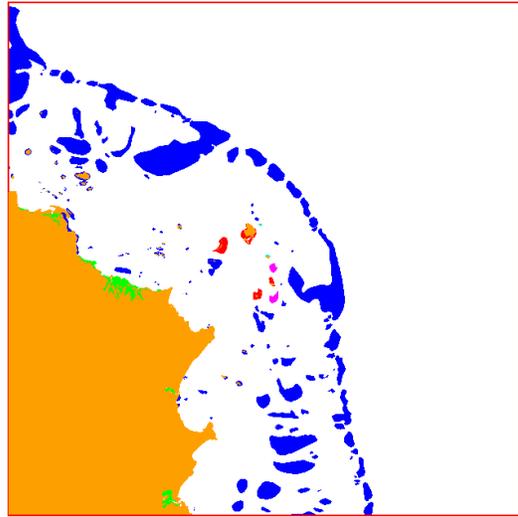


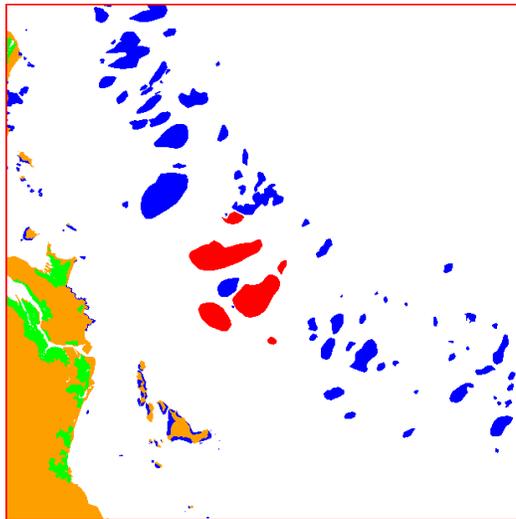
Figure 4.3. Maps of the GBR and the 6 zones used in the models (4.3.a. in this page; 4.3.b.-4.3.g. in next page). The land-types are colour coded. *Orange*: land (including mainland, coastline, islands and cays); *Green*: mangrove areas; *Dark Blue*: reefs; *Red*: reefs selected in the large-scale recruitment study by Hughes (1999, 2000 and 2001) and the results' analysis in this chapter. *Magenta*: reefs used in the results' analysis in this chapter but not in Hughes's study. *Turquoise*: reefs included in Hughes's study but not used in the results' analysis in this chapter. Only part of the Torres Strait sector is included. (4.3.a.) Map of the GBR, its sectors and the position of the zones used in the models. (4.3.b.) Zone 1 (Torres Strait – Far North zone, in Torres Strait and Northern sectors). (4.3.c.) Zone 2 (Lizard Island zone, in Northern sector). (4.3.d.) Zone 3 (in Central sector). (4.3.e.) Zone 4 (in Central sector). (4.3.f.) Zone 5 (Pompey Complex zone, in Southern sector). (4.3.g.) Zone 6 (Capricorn and Bunker Groups zone, in sector named after these groups of reefs).



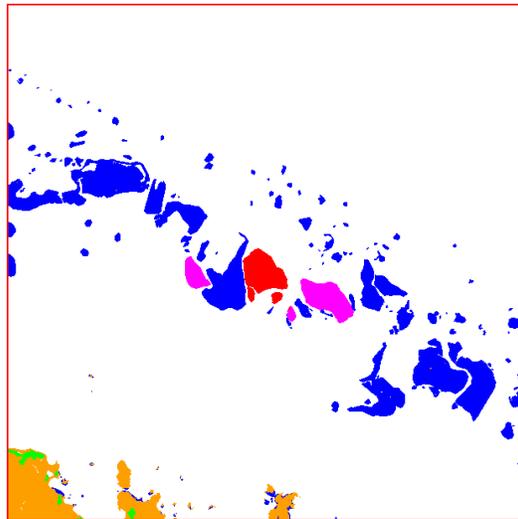
4.3.b. Zone 1



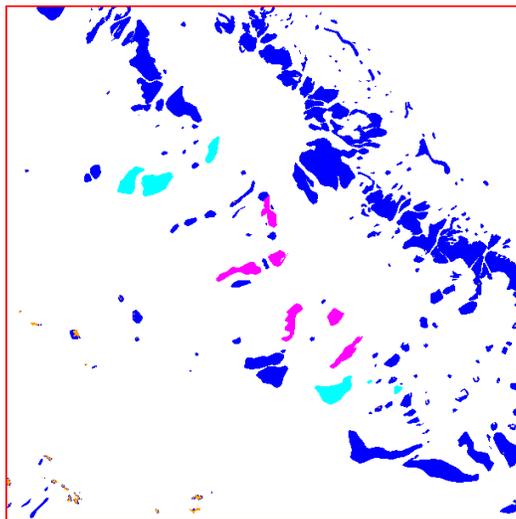
4.3.c. Zone 2



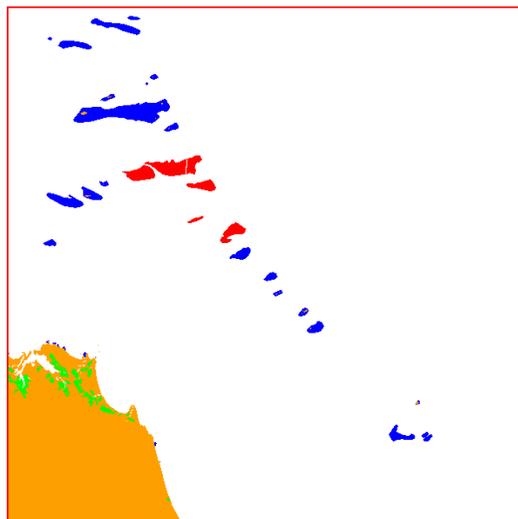
4.3.d. Zone 3



4.3.e. Zone 4



4.3.f. Zone 5



4.3.g. Zone 6

Table 4.1. Location of the Great Barrier Reef zones represented by the charts used as data input to the models in *Chapter 4*. *Sector*: sector where the modelled zone belongs. *Shell Position*: location of the modelled zone (zone top-left corner given first and then bottom-right corner). *Study Reefs*: 6 reefs within each zone used in the results analysis (U/N= Unnamed). (See *Section 4.2.A* for details).

Zone	Sector	Shell Position (Simulation)	Study Reefs (Analysis)
1	TORRES STRAIT	10 ⁰ 30'S, 142 ⁰ 15'E 12 ⁰ 00'S, 144 ⁰ 45'E	Christmas (11-025), U/N (11-030), U/N (11-034), Collette (11-037), U/N (11-042), U/N (11-050)
2	NORTHERN	14 ⁰ 00'S, 144 ⁰ 45'E 15 ⁰ 30'S, 146 ⁰ 15'E	Lizard Island (14-116), MacGillivray (14-114), Eyrie (14-118), North Direction Island (14-143), South Direction Island (14-147), Rocky Islets (14-132)
3	CENTRAL	17 ⁰ 30'S, 146 ⁰ 06'E 19 ⁰ 00'S, 147 ⁰ 36'E	U/N (18-022), Britomart (18-024), U/N (18-025), Trunk (18-027), Bramble (18-029), Rib (18-032)
4	CENTRAL	18 ⁰ 30'S, 148 ⁰ 00'E 20 ⁰ 00'S, 149 ⁰ 30'E	Cobham (19-074), Wallaby (19-071), Net (19-097), Martin (19-075), Showers (19-076), Fairey (19-109)
5	SOUTHERN	20 ⁰ 00'S, 149 ⁰ 39'E 21 ⁰ 30'S, 151 ⁰ 09'E	Southampton (20-299), Gable (20-305), Chauvel (20-307), U/N (20-351), Pompey (20-352), U/N (21-061)
6	CAPRICORN and BUNKER GROUPS	23 ⁰ 00'S, 151 ⁰ 30'E 24 ⁰ 30'S, 153 ⁰ 00'E	Sykes Reef (23-054), Heron Island (23-052), Wistari (23053), One Tree Island (23-055), Lamont (23-076), Fitzroy (23-077)

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 (See *Section 4.2.B* and *Appendix II*).

Sector	Latitude	Main References	Other References
TORRES STRAIT	9 ⁰ 12'S - 11 ⁰ S	Wolanski and Thomson (1984)	Wolanski and Ruddick (1981) Wolanski et al. (1992) Wolanski (1994)
NORTHERN	11 ⁰ S - 16 ⁰ S	Wolanski and Ruddick (1981) Wolanski and Thomson (1984)	Wolanski (1994)
CENTRAL	16 ⁰ S - 20 ⁰ S	Andrews (1983a and 1983b) Williams (1984) Andrews and Furnas (1986)	Kelly and Andrews (1985) Wolanski and Pickard (1985)
SOUTHERN	20 ⁰ S - 22 ⁰ 30'S	Griffin et al. (1987) Middleton et al. (1994)	Pickard et al. (1977) Middleton (1983)
CAPRICORN and BUNKER GROUPS	22 ⁰ 30'S - 24 ⁰ 30'S	Middleton (1983) Middleton and Cunningham (1984)	Middleton et al. (1994)

‘emerged land’, ‘mangrove area’, ‘reef’, and ‘inter-reefal water’ (see *Chapter 2*). A ‘reef-id’ field was created and used to assign a unique numerical code to each of the reefs in the coverage according to the spatial position it occupies within the GBR. The ‘land-type’ and ‘reef-id’ fields were combined into a single field, ‘land-class’, in which unique codes were used to represent: emerged land, mangrove area, inter-reefal water, and each individual reef.

Mercator transverse projections of the coordinates delimiting the 6 zones of interest in the GBR were used to create coverages representing the empty rectangles that outline these zones. The GBR coverage was then cut onto (‘identity overlap’ operation) these rectangles to create 6 smaller coverages depicting each of the zones of interest. Finally, a grid was created from each of the 6 zone coverages. Each of the cells in the grid represented an area of 1,000 m x 1,000 m, and contained a single value. The value of each cell represented its major ‘land-class’. These grids constituted the 6 charts used as inputs for the coupled lattice dispersal models.

4.2.A.2. *Physical Oceanography*

A literature review was conducted in order to create the representations of the physical oceanography for each sector of the GBR used in the models (Table 4.2., see also *Appendix III*). Water movements provided by tides and weather-band circulation were not included in the models, which only focussed on steady large-scale background currents.

Current sets (depicting the probabilities of a particle of water moving in 8 cardinal directions or remaining stationary in each iteration) and speeds were used to represent the hydrodynamic conditions provided by background currents in each sector of the GBR (see *Chapter 2* for a detail description of current representations). Two hydrodynamic conditions were used per sector, one for spawners and one for brooders (Table 4.3.). The former depicts the typical conditions present in the sector during the months when the mass spawning events occur in the GBR (October-December), after the SE trade winds weaken and before the monsoon winds and rains appear in full intensity (see *Appendix III*). The latter represents the conditions found in the sector averaged over the year (see *Appendix III*), as brooding corals generally release larvae through most of the year (see *Chapter 1, Section 1.2.B.*). For each of the two reproductive types of coral, dispersal with and without retention was modelled (Table 4.3.).

Table 4.3. Current sets used in *Chapter 4*. They represent the hydrodynamic conditions found in the 6 modelled zones of the GBR averaged over the whole year (for brooders) and at the time of the mass-spawning event (for broadcast spawners).

Reproductive Type	Retention	Zone	Currents Directions (C : N : NE : E : SE : S : SW : W : NW)	Currents Speed (cm.s ⁻¹)
BROODERS	No	1	0.040000 : 0.320000 : 0.145000 : 0.025000 : 0.100000 : 0.235000 : 0.050000 : 0.025000 : 0.060000	8.50
		2	0.030000 : 0.080000 : 0.040000 : 0.030000 : 0.300000 : 0.210000 : 0.110000 : 0.090000 : 0.110000	9.00
		3	0.030000 : 0.040000 : 0.030000 : 0.100000 : 0.400000 : 0.200000 : 0.110000 : 0.040000 : 0.050000	14.00
		4	0.030000 : 0.040000 : 0.030000 : 0.100000 : 0.400000 : 0.200000 : 0.110000 : 0.040000 : 0.050000	14.00
		5	0.030000 : 0.040000 : 0.030000 : 0.100000 : 0.400000 : 0.200000 : 0.110000 : 0.040000 : 0.050000	17.75
		6	0.010000 : 0.030000 : 0.010000 : 0.040000 : 0.250000 : 0.040000 : 0.010000 : 0.120000 : 0.490000	25.50
	Yes	1	0.976000 : 0.008000 : 0.003625 : 0.000625 : 0.002500 : 0.005875 : 0.001250 : 0.000625 : 0.001500	8.50
		2	0.976000 : 0.001979 : 0.000990 : 0.000742 : 0.007422 : 0.005196 : 0.002722 : 0.002227 : 0.002722	9.00
		3	0.976000 : 0.000990 : 0.000742 : 0.002474 : 0.009897 : 0.004948 : 0.002722 : 0.000990 : 0.001237	14.00
		4	0.976000 : 0.000990 : 0.000742 : 0.002474 : 0.009897 : 0.004948 : 0.002722 : 0.000990 : 0.001237	14.00
		5	0.976000 : 0.000990 : 0.000742 : 0.002474 : 0.009897 : 0.004948 : 0.002722 : 0.000990 : 0.001237	17.75
		6	0.976000 : 0.000727 : 0.000242 : 0.000970 : 0.006061 : 0.000970 : 0.000242 : 0.002909 : 0.011879	25.50
BROADCAST SPAWNERS	No	1	0.060000 : 0.270000 : 0.135000 : 0.045000 : 0.090000 : 0.210000 : 0.065000 : 0.045000 : 0.080000	6.50
		2	0.010000 : 0.060000 : 0.030000 : 0.010000 : 0.360000 : 0.240000 : 0.120000 : 0.080000 : 0.090000	12.00
		3	0.010000 : 0.010000 : 0.010000 : 0.050000 : 0.500000 : 0.250000 : 0.150000 : 0.010000 : 0.010000	20.00
		4	0.010000 : 0.010000 : 0.010000 : 0.050000 : 0.500000 : 0.250000 : 0.150000 : 0.010000 : 0.010000	20.00
		5	0.010000 : 0.010000 : 0.010000 : 0.050000 : 0.500000 : 0.250000 : 0.150000 : 0.010000 : 0.010000	22.50
		6	0.015000 : 0.025000 : 0.015000 : 0.050000 : 0.300000 : 0.050000 : 0.015000 : 0.110000 : 0.420000	17.50
	Yes	1	0.976000 : 0.006894 : 0.003447 : 0.001149 : 0.002298 : 0.005362 : 0.001660 : 0.001149 : 0.002043	6.50
		2	0.976000 : 0.001455 : 0.000727 : 0.000242 : 0.008728 : 0.005818 : 0.002909 : 0.001939 : 0.002182	12.00
		3	0.976000 : 0.000242 : 0.000242 : 0.001212 : 0.012123 : 0.006061 : 0.003636 : 0.000242 : 0.000242	20.00
		4	0.976000 : 0.000242 : 0.000242 : 0.001212 : 0.012123 : 0.006061 : 0.003636 : 0.000242 : 0.000242	20.00
		5	0.976000 : 0.000242 : 0.000242 : 0.001212 : 0.012123 : 0.006061 : 0.003636 : 0.000242 : 0.000242	22.50
		6	0.976000 : 0.000609 : 0.000365 : 0.001218 : 0.007310 : 0.001218 : 0.000365 : 0.002680 : 0.010235	17.50

4.2.B. Model Types

Six types of models were used in the simulations. In the first, all reefs in all zones of the GBR were assumed to have equal coral cover and adult fecundity. That is, the reproductive output of each reef was proportional to its area (as in previous chapters). This type of model is useful for investigating the effects of the intrinsic physical features of each zone (i.e. topology of the reefs and hydrodynamic conditions) on larval settlement and reef connectivity. Specifically, it was used to investigate the differences in patterns of larvae dispersal (and their effects) among GBR zones (Aim 1) and among reefs within zones (Aim 3). It was also one of the six models used to explore the possible mechanisms behind the recruitment patterns described for the GBR (Aim 2) (see *Section 4.1.A.* and references within).

Model types 2 and 3 included further information on the state of reefs in each sector. In model type 2 coral cover varied among sectors and between spawning and brooding corals within sectors (Table 4.4.). In model type 3 both coral cover and adult fecundity varied among sectors and coral types (Table 4.4.). Coral cover and fecundity were constant for all the reefs within a sector in all model types. Information on differences in coral cover and fecundity among sectors of the GBR was obtained from Hughes et al. (2000). Model types 4 to 6 were similar to types 1 to 3 respectively, but they also included water retention at the reefs. A level of 8% retention of water particles after 10 days was used, based on the estimates for the typical reefs in the central GBR by Black et al. (1991, 1993) (see *Chapter 3*). Model types 3 and 6 (in which both coral cover and adult fecundity varied among sectors) were used only for broadcast spawners, as information on the variation in fecundity among sectors in the GBR was not available for brooding corals.

Table 4.4. Coral cover and adult fecundity in the 6 zones of the GBR used in *Chapter 4*. The values in the table represent the cover and fecundity for each zone and larval type relative to the zone-larval type combination with the largest value, which is assigned a value of 1. Modified from Hughes et al. (1999, 2000, 2001).

Zone	Coral Cover		Adult Fecundity
	Brooders	Spawners	Spawners
1	0.18	1.00	0.360
2	0.16	0.79	0.924
3	0.13	0.91	1.000
4	0.47	0.96	0.820
5	0.39	0.87	-
6	0.26	0.79	0.608

Sixty simulations were run, corresponding to the combinations of: 6 reef zones and 2 reproductive types (brooders vs. spawners) with 4 model types for brooders and 6 for spawners.

4.2.C. Data Analysis

Only the values of six reefs in the centre of the zones used in the simulations were included in the analysis, since reefs offset from the centre are likely to be strongly connected to reefs not included in the chart making them unsuitable for the analysis (see *Section 4.4.2. Model Limitations*). Where possible these reefs were the same as those used by Hughes and collaborators (1999, 2000, and 2002a) in their large-scale study of recruitment in the GBR, to which the modelling results were compared. This was not possible in zones 1 and 4. The reefs sampled by Hughes and collaborators in the Torres Strait sector are close to the northern-most edge of zone 1, and no G.I.S. data was available north from this zone (Figure 4.5.b.). In zone 4, three of the reefs included in the field study were in the northern part of the chart and the remaining three in the southern part (Figure 4.5.e.). Hence, six different and more central reefs were chosen for the data analysis of both of these zones.

4.2.C.1. Aim 1: Patterns of larval dispersal and their effects in six zones of the GBR

The following variables were investigated: settlement rate, proportion of local and non-local settlement, connectivity among reefs by larvae, and evenness and diversity of reef sources of the settled larvae. These variables were calculated in a similar way to previous chapters (see *Chapter 2* for a detailed description), but with some minor differences. Firstly, the results from each simulation were the average for the 6 study reefs rather than for the whole chart. When using the whole chart, the input and output versions of the variables had the same value (see *Chapter 2* and *Appendix I*); however, in this chapter they could differ. For example, the average number of reefs that the study reefs received larvae from (input evolutionary-scale connectivity) could be different to the average number of reefs to which they exported their own larvae (output evolutionary-scale connectivity). For clarity only the results for the input versions of the variables are presented in this chapter. Secondly, the settlement rates were expressed as the number of larvae settled per km² of reef. In previous chapters the reefs were in most

cases theoretical and had equal size, thus settlement rates could be simply expressed per reef. In the models in this chapter, the reefs differed in size so the larval inputs to the reefs were weighted by the number of cells (each of 1 km²) in each receptor reef.

Two levels of connectivity were used in this chapter. They were defined as: (a) ‘evolutionary-scale connectivity’, where any amount of larvae dispersed between two reefs is enough to consider them connected (threshold > 0 larva), and (b) ‘ecological-scale connectivity’, where at least 1000 larvae must be dispersed between the reefs to consider them connected (threshold \geq 1000 larvae) (see *Chapter 2* and *Appendix IV*).

Relationships among reefs were further explored using what I will call ‘rank-contribution diagrams’, a variation on the rank-abundance diagrams (e.g. Begon et al. 1990). This type of plot provides a complementary and more integrated examination of the relationships among reefs than the connectivity, evenness, and diversity indices provide on their own. They depict the proportion of the average larval input to the 6 study reefs contributed by each of the other reefs in the zone against the rank of their contribution (see Figure 4.8.).

4.2.C.2. Aim 2: Mechanisms underlying the latitudinal recruitment patterns on the GBR

The six types of models described in *Section 4.2.B.* were used to investigate which mechanisms may be influencing the latitudinal recruitment patterns in the GBR. The predictive power of the settlement rates obtained with each type of model relative to the published recruitment values (Hughes et al. 1999) was evaluated using regression analysis. Because the published recruitment data was presented by zone rather than individual reef, settlement rates were averaged per zone (i.e. mean settlement rate of the six study reefs in each zone) before conducting the regression analyses. In model types 1, 2, 4 and 5, regressions were performed for both brooding and spawning corals; while in model types 3 and 6 they were conducted only for spawners due to the lack of information on the fecundity of brooders, necessary to construct their models. Finally, the proportion of spawners in the total settlement in each zone was calculated and graphed for model types 1, 2, 4 and 5.

4.2.C.3. *Aim 3: Patterns of larval dispersal among reefs within zones*

The final aim of this chapter consisted of a brief estimate of the level of variation in the studied dispersal variables (see *Section 4.2.C.1.*) among nearby reefs within zones. This was achieved by graphically comparing the values of the variables obtained for the 6 study reefs within each zone. Only some selected examples are presented and discussed.

4.3. RESULTS

4.3.A. *Aim 1: Patterns of larval dispersal in zones of the GBR*

4.3.A.1. *Settlement rates*

Settlement patterns of brooded and spawned larvae differed greatly among zones (Figure 4.4.). In zone 1, characterised by slow currents with variable direction, the number of larvae settled per km² was low, especially for spawners (Figure 4.4.). Despite this, total settlement in this zone was considerable given the large number and size of its reefs (Figure 4.3.a.). In zone 2, where currents change direction depending on the position of the bifurcation of the South Equatorial Current (SEC) and reefs are generally small (Figures 4.4. and 4.3.b., see *Appendix III*), settlement rate was low for both brooders and spawners. The current flow in zones 3, 4 and 5 is relatively fast and more predictable than in the other zones, generally parallel to the continental shelf in a SE direction. In zone 3, where reefs are not very numerous but large (Figure 4.3.c.), settlement rate was high for both brooding and spawning corals (Figure 4.4.). In zone 4, the study reefs are large, but many others are quite small (Figure 4.3.d.). There was a particularly large variation in settlement rate between the two larval types in this zone; they were very high (highest among all simulations) for brooders and very low (second lowest among all simulations) for spawners (Figure 4.4.). In zone 5, where reefs are numerous and relatively large (Figure 4.3.f.), settlement rate was intermediate for brooders and high (highest among all zones) for spawners. Zone 6 has middle-sized reefs and variable currents that resulted in a relatively high settlement rate for brooding corals, while its very low reef density led to an intermediate settlement rate for spawners (Figures 4.3.g. and 4.4.).

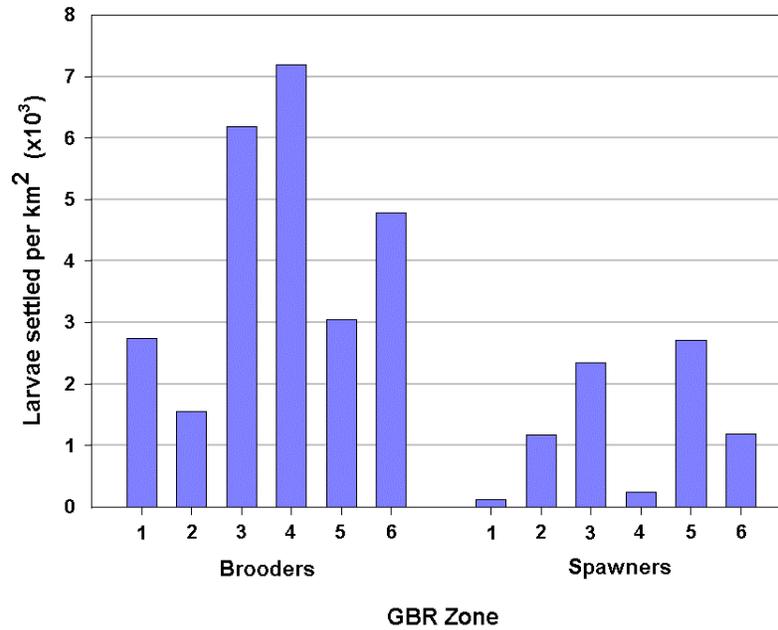


Figure 4.4. Average settlement rates (larvae settled per km² of receptor reef) for the 6 study reefs in each of the 6 zones of the GBR provided by model type 1. Models include: geographic (reefs location and size) and hydrodynamic (currents direction and speed) data, but no retention and no differences in coral cover and fecundity among zones.

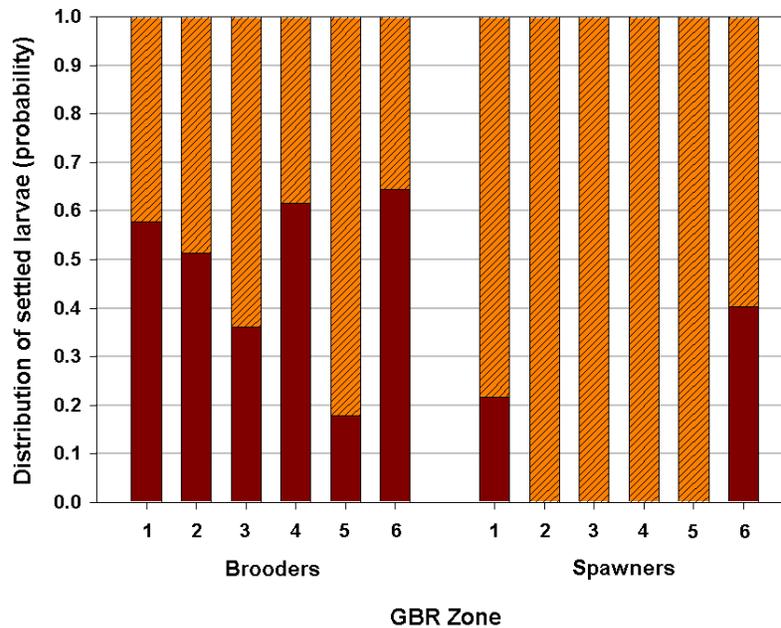


Figure 4.5. Average origin (local vs. non-local) of the settled larvae for the 6 study reefs in each of the 6 zones of the GBR provided by model type 1. Models include: geographic (reefs location and size) and hydrodynamic (currents direction and speed) data, but no retention and no differences in coral cover and fecundity among zones. Bars represent the average proportion of the settled larvae that originated locally and non-locally.

4.3.A.2. *Origin of settled larvae: local vs. non-local settlement*

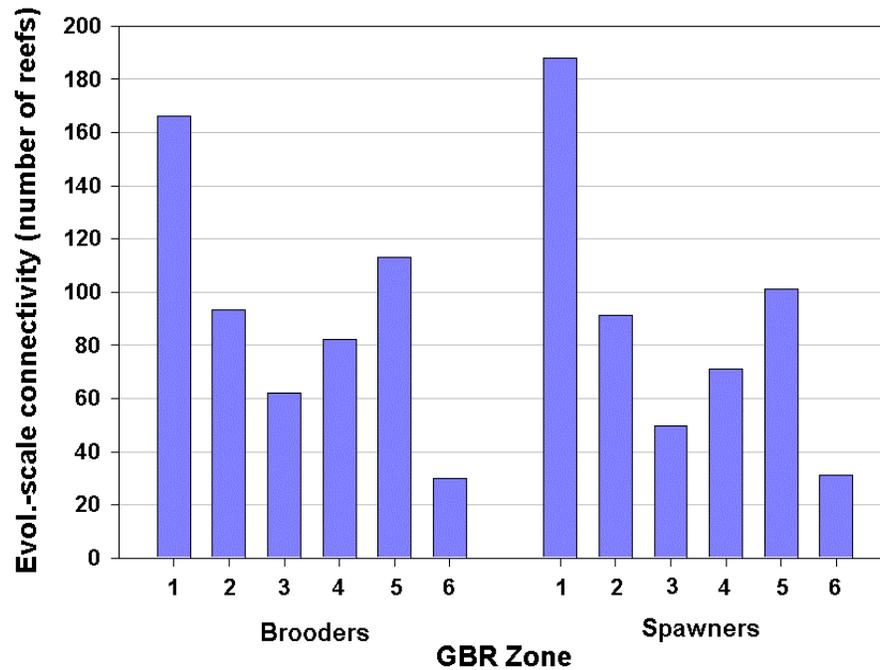
Local settlement was high for brooding corals in zones 1, 2, 4, and 6, reaching over 50% of the total settlement despite retention not being included in the models (Figure 4.5.). The causes for this high local settlement of brooding corals differed among zones, and are similar to those mentioned in the previous section (4.3.A.1.). Firstly, currents in zones 1, 2 and 6 are not very directional, and in the first two zones they are also weak (Table 4.3.). Secondly, the size of the study reefs is relatively large in zones 1 and 6, and very large in zone 4 (Figure 4.5.). Local settlement for brooding corals was lowest in zone 5 (Figure 4.5.) where currents flow relatively fast and constant in a SE direction (Table 4.3.), and the study reefs are small and spread out (Figure 4.3.f.).

Local settlement, as expected, was much lower for spawning corals in all zones (Figure 4.5.). In fact, it was negligible in zones 2, 3, 4 and 5. In zone 1, where currents are slow and varying in direction (Table 4.3.), ~20% of the larvae produced by spawners settled locally. This proportion increased to ~40% in zone 6, where the flow is not very directional and the density of reefs is lowest (Table 4.3., Figure 4.5.).

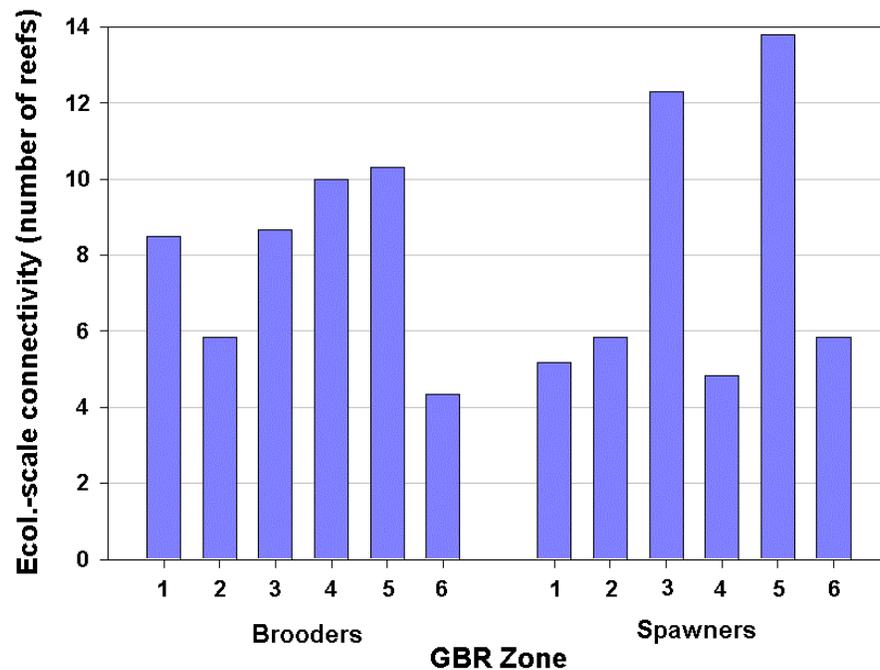
4.3.A.3. *Relationships among reefs*

4.3.A.3.a. *Connectivity at an evolutionary-scale*

Patterns of evolutionary-scale connectivity in the 6 zones of the GBR were very similar for brooding and spawning corals (Figure 4.6.a.), determined mainly by the number of reefs the zones (in evolutionary-scale connectivity and the number of reefs in the zones were strongly correlated, $r = 0.977$ and 0.987 for brooders and spawners respectively). Evolutionary-scale connectivity was higher for spawners than brooders in zones 1 and 6, similar in zone 2, and lower in zones 3, 4 and 5. These last three zones contain currents with a strongly directional flow to the SE, thus few of the larvae produced by spawning corals are found upstream of their source reefs by the end of their long pre-competent period, and hence very little settlement occurs in this area. Furthermore, during their long pre-competent period the larvae of spawners suffer high mortality. Brooded larvae, on the other hand, have short pre-competent periods so that by the time they are ready to metamorphose and settle more larvae can be found upstream of the source reef because a higher proportion of them are still alive and have not been washed downstream yet.



4.6.a.



4.6.b.

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. Models include: geographic (reefs location and size) and hydrodynamic (currents direction and speed) data, but no retention and no differences in coral cover and fecundity among zones. A reef is considered connected to another when it receives a certain threshold of larvae from it. (4.6.a.) Evolutionary-scale connectivity (threshold: > 0 larva). (4.6.b.) Ecological-scale connectivity (threshold: ≥ 1000 larvae).

4.3.A.3.b. *Connectivity at an ecological-scale*

In general, zones with less constant flow (zones 1, 2 and 6) had a lower connectivity at ecological-scales than those with a more directional flow (zones 3, 4 and 5) (Figure 4.6.b.). In the former, although larvae could reach many reefs they did not do so in large amounts. The exception to this pattern were spawners in zone 4, for which ecological-scale connectivity was low (lowest of all zones for this reproductive group of corals). In fact, zone 4 seems to behave atypically in many ways (see below).

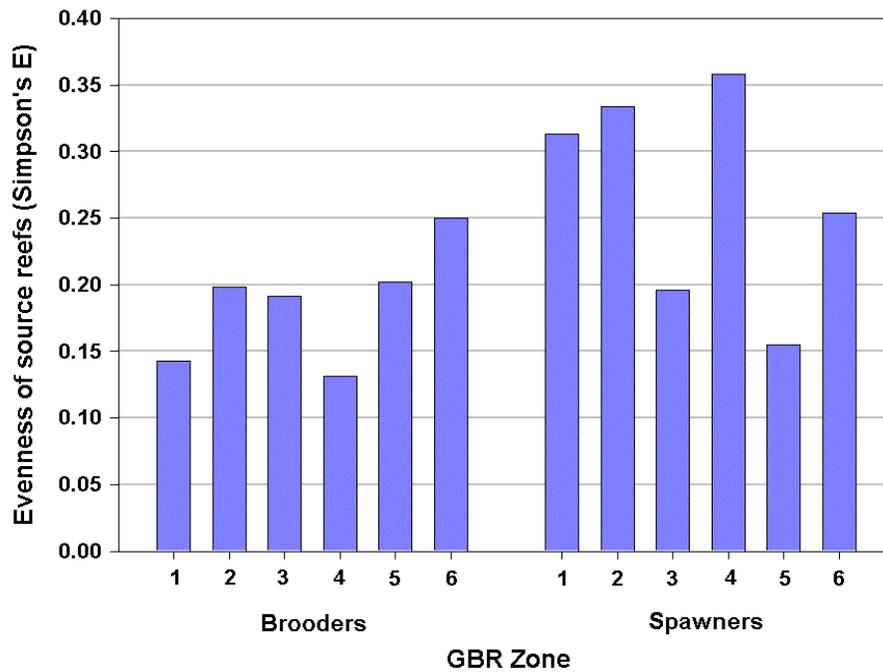
The patterns of connectivity were very different for brooders and spawners in most of the zones (Figure 4.6.b.). In general, spawners had higher ecological-scale connectivity than brooders (higher in zones 2 and 6; and much higher in zones 3 and 5). However, this pattern was reversed in zones 1 and 4. These zones are characterised by numerous reefs and very high reef densities (in the full extent of the chart in zone 1 and around the 6 study reefs in zone 4).

4.3.A.3.c. *Evenness of larval input*

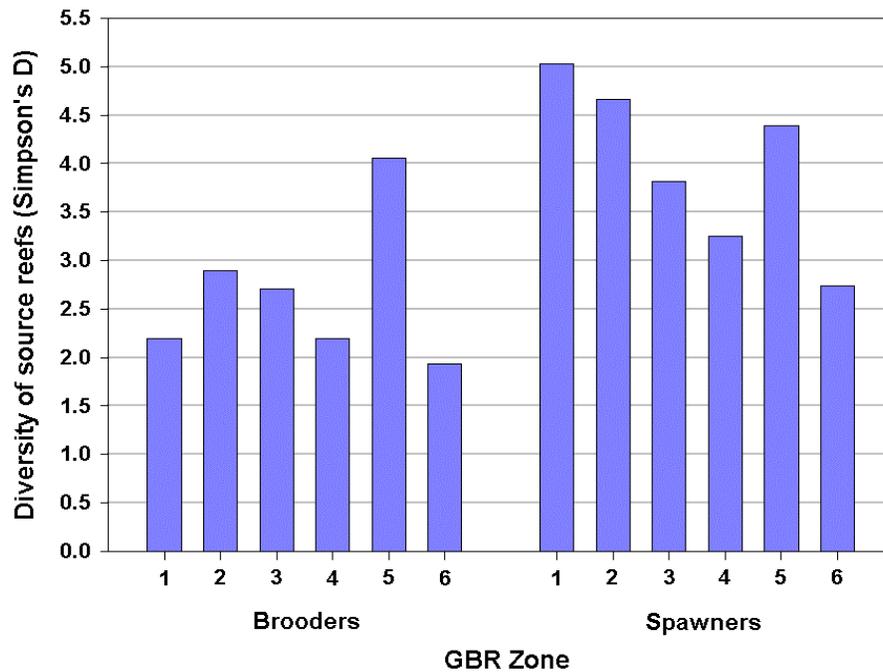
Patterns of evenness of reef sources of the larval input in the six zones were also substantially different for brooders and spawners (Figure 4.7.a.). Evenness was generally higher for spawners than brooders because of the higher proportion of local settlement in brooders (Figure 4.5.) due to their shorter pre-competent and competent periods. For spawners, evenness was high in the zones with variable and weak flow (zones 1, 2, and 6) and also in zone 4. For brooders, evenness was high in zones 2 and 6 for the same reasons, and in zone 5 where the reefs are numerous and reef density is high (Figure 4.3.f.). Although in zone 1 reefs are very abundant and the current direction is variable, the evenness of sources for brooders was low because most of the larvae settled locally as a result of the currents slow flow and the short pre-competent periods of this type of larvae.

4.3.A.3.d. *Diversity of larval input*

Diversity of reef sources of the larval input was also higher for spawners than brooders (Figure 4.7.b.) because a lower proportion of their settlement occurred locally. For both, brooders and spawners, diversity was very high in zone 5 and lowest in zone 6. This was mainly a consequence of the number of reefs and their resulting connectivity in these zones, high in zone 5 and very low in zone 6 (see Figures 4.3.f., 4.3.g. and *Appendix III*). In zone 4, diversity was also low for brooders and spawners



4.7.a.



4.7.b.

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. Models include: geographic (reefs location and size) and hydrodynamic (currents direction and speed) data, but no retention and no differences in coral cover and fecundity among zones. (4.7.a.) Evenness of reef sources of the larval input to the study reefs (Simpson's E index). (4.7.b.) Diversity of reef sources of the larval input to the study reefs (Simpson's D index).

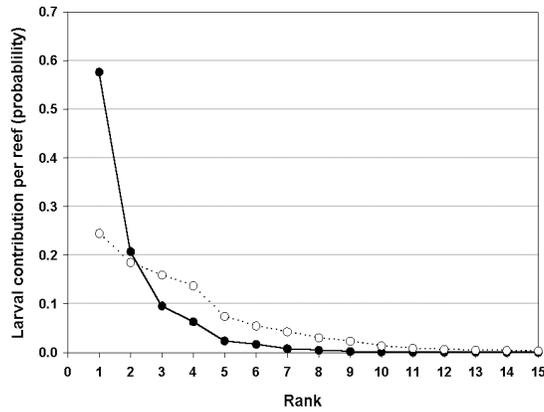
(Figure 4.7.b). In this case the limiting factor was different for each larval type, low evenness for brooders (Figure 4.7.a.) and low connectivity for spawners (Figure 4.6.b.). In the remaining zones, the diversity of the larval input differed greatly between brooders and spawners; it was high for spawners, but low to intermediate for brooders. In zones 1 and 2, this was mainly a reflection of the important differences in the patterns of evenness of reef sources of the larval input between brooders and spawners (Figures 4.7.b., 4.7.a. and *Section 4.3.A.4.a.*). In zone 3, on the other hand, connectivity patterns contributed most to the differences in diversity of sources of the larval input between both types of corals (Figures 4.7.b, 4.6.b. and *Section 4.3.A.3.b.*).

4.3.A.3.e. Rank-contributions plots

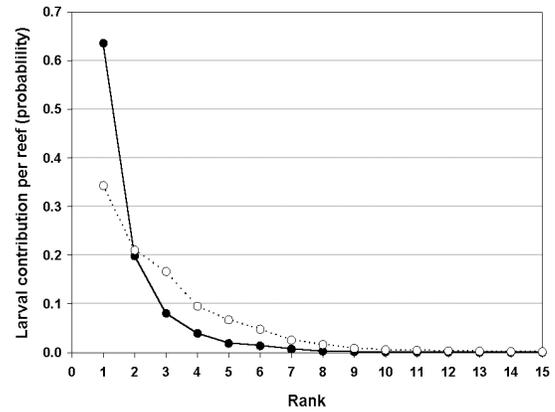
In this type of plot the lowest ranked point (the left-most point) represents the proportion of the input that comes from the most important reef source of larvae, typically the natal reef. Self-seeding was greater for brooders than spawners in all zones (Figure 4.8.), and particularly high (over 55%) for the former in the zones where the currents are less directional (zones 1, 2, and 6) (Figures 4.8.a., 4.8.b. and 4.8.f.). In zones 1, 3, and 5 the number of connected reefs (intercept of the rank-contribution line with the abscissa) was high; intermediate in zone 2, and in zone 4 for brooders; low in zone 4 for spawners; and very low in zone 6 (which has very few reefs). Evenness of the larval contribution of the reef sources (the horizontality of the rank-contribution line) was greater for spawners than brooders in all zones. The differences in evenness between larval types were small in zones with a strongly directional flow (3, 4 and 5) and larger in zones with a more variable flow (1, 2 and 6) (Figure 4.8.).

4.3.B. Aim 2: Mechanisms contributing to the latitudinal recruitment patterns on the GBR

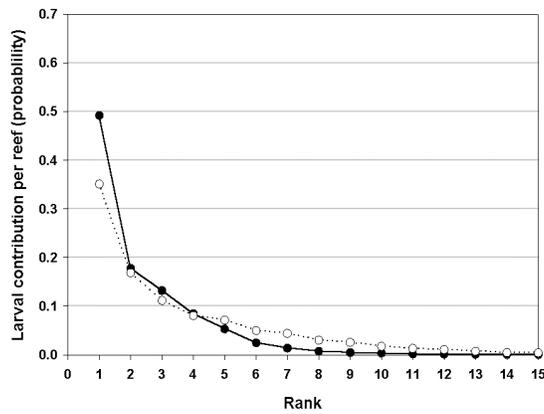
For brooders the relationships between the settlement rates observed in the field and those predicted by all model types were described by a negative slope (rather than the slope of ~ 1 expected if the models would correctly reproduce the field recruitment patterns) (Figures 4.9.a., 4.9.c., 4.10.a., and 4.10.c.). In general, the zones could be clustered into two sub-groups: one in the top-left of the diagrams, which contained zones 4, 5 and 6; and one in the bottom-right including zones 1 and 2 (the position of zone 3 varied among model types). This indicates that in the northern-most parts of the



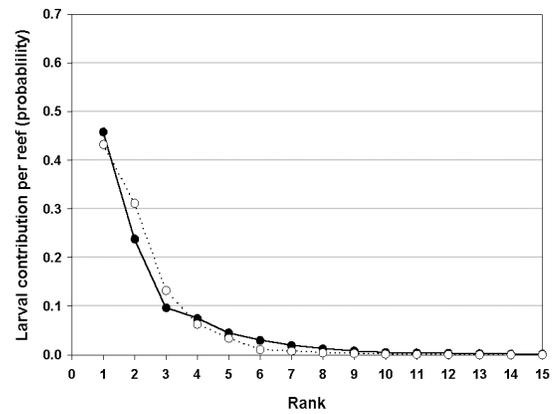
4.8.a. Zone 1



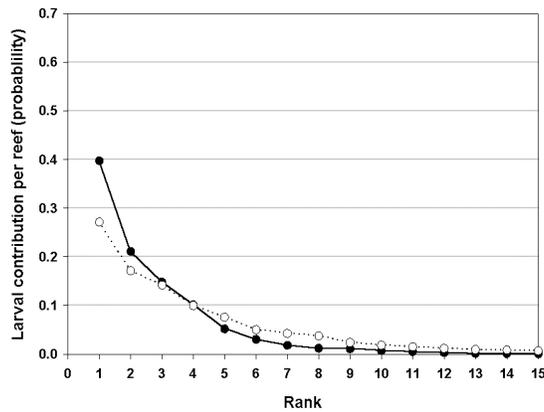
4.8.b. Zone 2



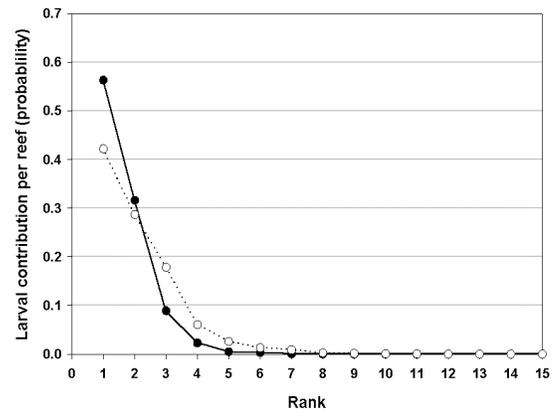
4.8.c. Zone 3



4.8.d. Zone 4

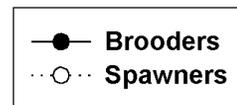


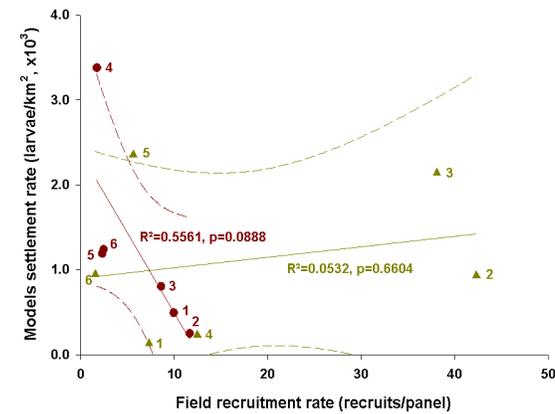
4.8.e. Zone 5



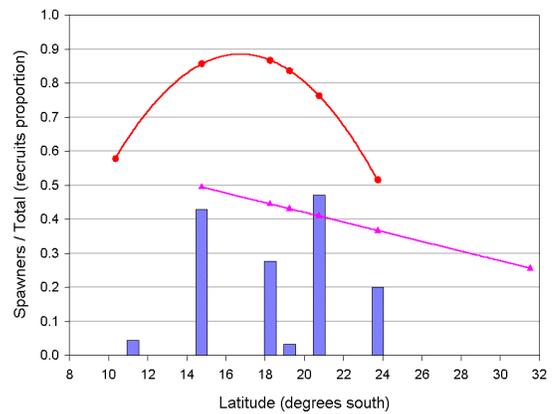
4.8.f. Zone 6

Figure 4.8. Rank - Contribution graphics for the 6 modelled zones of the GBR provided by model type 1. Models include: geographic (reefs location and size) and hydrodynamic (currents direction and speed) data, but no retention and no differences in coral cover and fecundity among zones. The average proportion of the larval input to the 6 study reefs contributed by each of the other reefs in their zone is plotted against the rank of this input (see Section 4.2.C.2.). The most abundant larval input is plotted first, then the next most common and so on. For clarity only the first 15 ranked reefs were represented, as reefs with a higher rank hardly contributed any larvae to the total settlement. Based on Rank-Abundance diagrams (e.g. Begon et al. 1990).

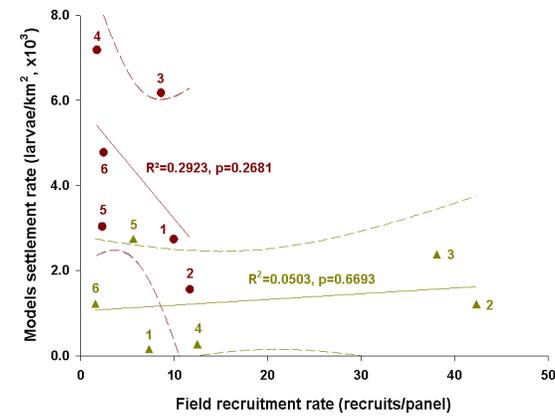




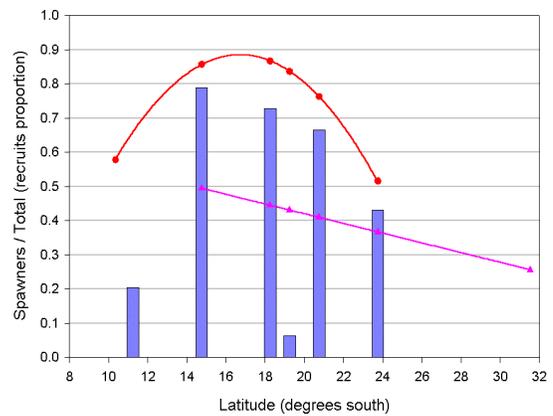
4.9.a.



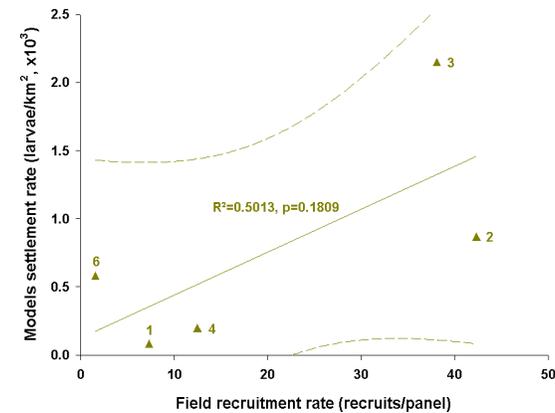
4.9.b.



4.9.c.



4.9.d.



4.9.e.

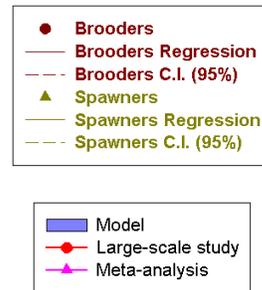


Figure 4.9. Comparison between settlement results in the models without retention and field recruitment data. (4.9.a.) Relationship between model type 1 results and field data. (4.9.b.) Proportion of total settlement produced by spawners in model type 1. (4.9.c.) Relationship between model type 2 results and field data. (4.9.d.) Proportion of total settlement produced by spawners in model type 2. (4.9.e.) Relationship between model type 3 results and field data (only run for spawners). Models include: *type 1*: geographic and hydrodynamic information; *type 2*: geographic, hydrodynamic, and coral cover information; and *type 3*: geographic, hydrodynamic, coral cover and fecundity information. On the right, legend for figures 4.9.a., 4.9.c., and 4.9.e.

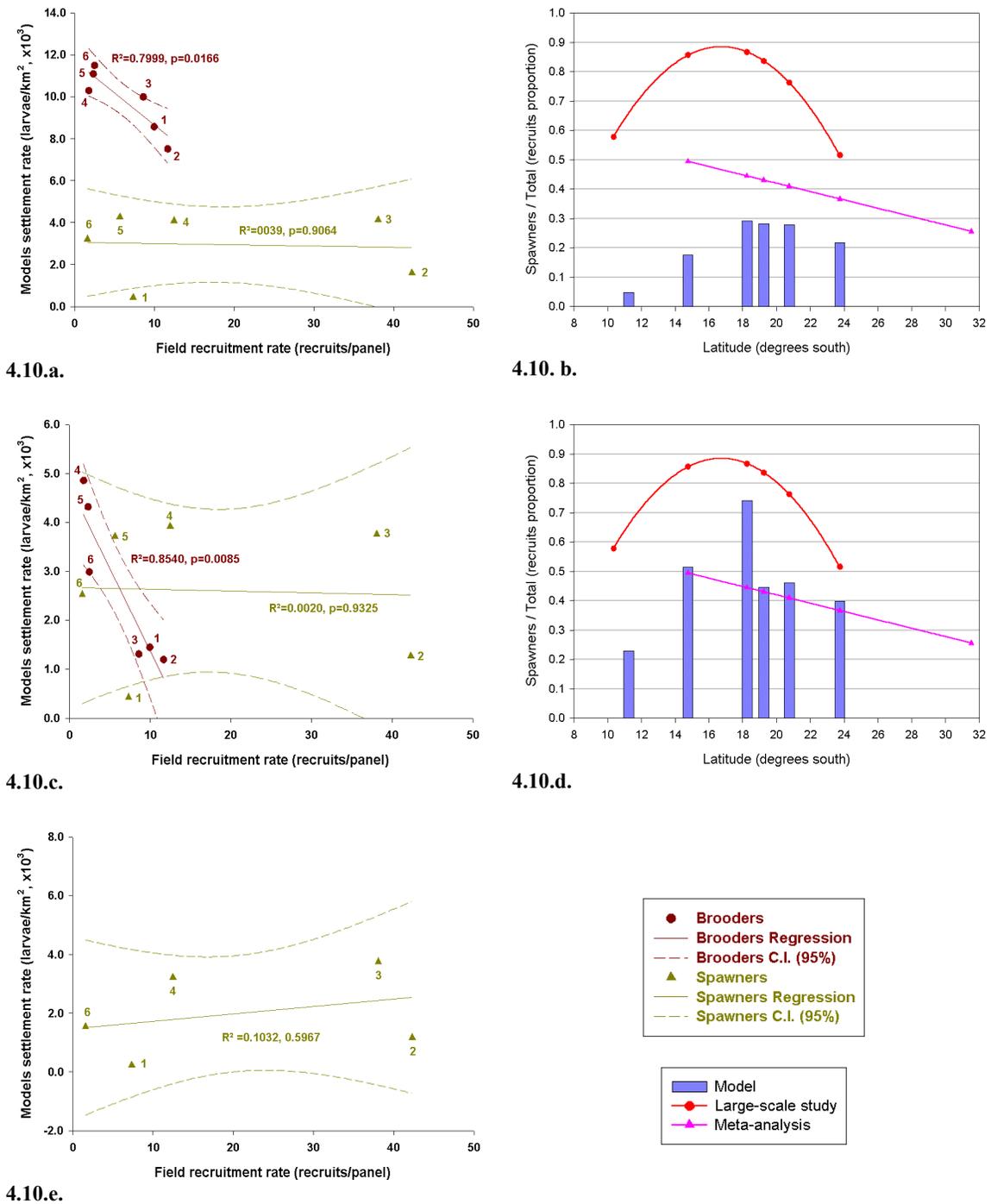


Figure 4.10. Comparison between settlement results in the models with retention and field recruitment data. (4.10.a.) Relationship between model type 4 results and field data. (4.10.b.) Proportion of total settlement produced by spawners in model type 4. (4.10.c.) Relationship between model type 5 results and field data. (4.10.d.) Proportion of larvae produced by spawners in total settlement in model type 5. (4.10.e.) Relationship between model type 6 results and field data (only run for spawners). Models, as well as retention, include: *type 4*: geographic and hydrodynamic information; *type 5*: geographic, hydrodynamic, and coral cover information; and *type 6*: geographic, hydrodynamic, coral cover and fecundity information. On the right, legend for figures 4.10.a., 4.10.c., and 4.10.e.

GBR settlement rates for brooders were consistently lower in the models than in the field. In fact, settlement in the models presented a bell shape with the north end displaying the lowest values, while a continuous latitudinal decrease is found in the field. Therefore, none of the model types run for brooders predicted accurately the coral recruitment patterns observed in the field, all underestimating settlement in the northern GBR. Unfortunately, information on the fecundity of brooders was unavailable and the most complete model types could not be run for them (model types 3 and 6).

Model type 1 included only information on reef topology and background currents (*Section 4.2.B*). The variation in settlement rate with latitude obtained for spawners using model type 1 did not match their variation in recruitment found in the field ($R^2=0.05$, $p=0.67$) (Figure 4.9.a.). The latitudinal variation in the proportion of larvae produced by spawners in the total settlement did not follow any predictable pattern (Figure 4.9.b.), also contrasting with the findings by the field studies.

Model type 2 included additional information about the coral cover in each zone. For spawners, its results were very similar to those obtained using model type 1 ($R^2=0.05$, $p=0.66$) (Figure 4.9.c.). The pattern of the latitudinal variation in the proportion of spawners in the total settlement (Figure 4.9.d.) resembled that observed in the field (Figure 4.4.a.). However, the values for zone 4 were too low to fully conform to the shape of the curve (zone 4 behaved atypically for many other dispersal variables, see *Section 4.3.A*), and the peak in the proportion of spawners occurred slightly north compared to the field data (13°S - 17°S in the models vs. 14°S - 18°S in the field).

In model type 3, the coral fecundity of the zones was also included. This type of model produced by far the best fit to the recruitment pattern observed for spawners in the field (Figure 4.9.e.). However, despite all zone values falling within the 95% confidence interval of the regression (Figure 4.9.e.), the relationship was still not significant ($R^2=0.50$, $p=0.18$).

Model types 4-6 are similar to types 1-3, but they also included water retention at the reefs. In general, when retention was added to the models, the fit between recruitment data in the field studies and settlement rates in the models weakened for spawners, in part because the settlement rates became more similar among zones (Figures 4.9. and 4.10.).

Model type 4 produced a very poor fit between settlement in the models and recruitment in the field for spawners ($R^2=0.04$, $p=0.91$) (Figure 4.10.a.). The plot representing the proportion of spawners in the total recruitment vs. latitude conformed

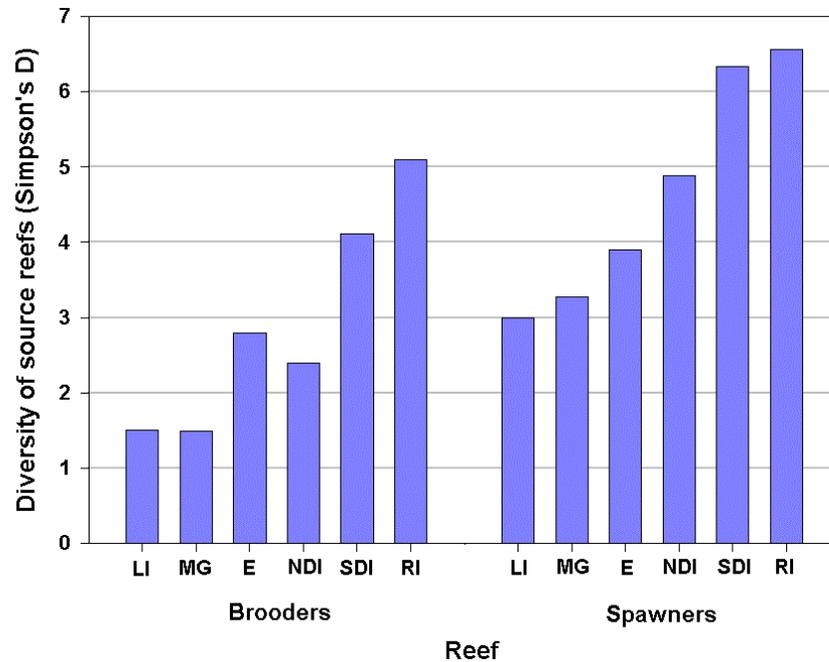
to the general shape of a curve (Figure 4.9.d.). Nevertheless, compared to the curve obtained from the field studies, it was flatter (especially in its second half) and peaked further south (between latitudes 18°S-20.5°S).

Model type 5 also produced a very poor fit for spawners ($R^2=0.00$, $p=0.93$) (Figure 4.10.c.). The shape and position of the curve representing the latitudinal variation in the proportion of spawners in the total settlement was similar to the one derived from the field data, with the exception of a smaller decline in the southern GBR between latitudes 21°S and 24°S (Figures 4.4.a. and 4.10.d.).

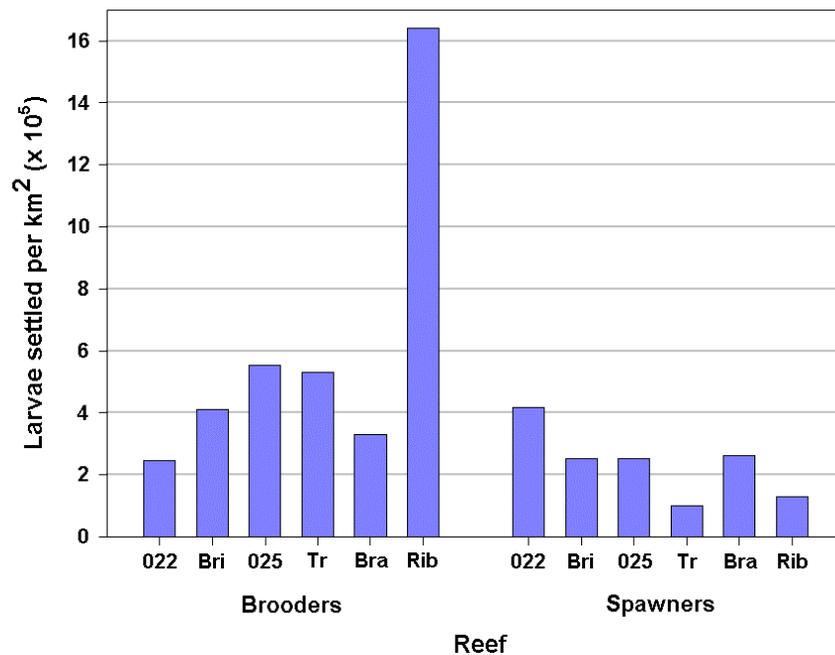
In model type 6, although the fit between the models and observations improved for spawners, it remained very weak ($R^2=0.10$, $p=0.60$). The pattern of latitudinal variation in the proportion of spawners in the total settlement could not be investigated using model type 6 since the simulations for brooding corals could not be run using this type of model.

4.3.C. Aim 3: Patterns of larval dispersal among reefs within zones

There was substantial variation in all the computed dispersal variables among the study reefs within the zones despite their close proximity to each other. For example, in zone 2 the diversity of the larval input predicted for the reefs of Lizard Island was much lower than for the nearby Rocky Islet reefs (less than a third in brooders and less than half in spawners; Figure 4.11.a.). Furthermore, the patterns of variation among reefs within zones were not always consistent between brooded and spawned larvae in the models. For instance, in zone 3 brooded larvae were predicted to have a much higher settlement rate in Rib reef than in the other five study reefs (Figure 4.11.b). In fact, this was one of the few true sink reefs in the models, where settlement was higher than larval production (see *Appendix IV*). For spawners, on the other hand, settlement rate on Rib reef was predicted to be the lowest of the six study reefs in zone 3 (Figure 4.11.b.).



4.11.a.



4.11.b.

Figure 4.11. Level of variation in the modelled dispersal variables among the 6 study reefs within zones. (4.11.a.) Diversity of reef sources in the larvae settling in zone 2 (LI = Lizard Island Reefs, MG = MacGillivray Reef, Ey = Eyrie Reef, NDI = North Direction Island Reef, SDI = South Direction Island Reef, RI = Rocky Islets Reef). (4.11.b.) Settlement rates (larvae settled per km² of receptor reef) in zone 3 (022 = Unnamed Reef 18-022, Bri = Britomart Reef, 025 = Unnamed Reef 18-025, Tr = Trunk Reef, Bra = Bramble Reef, Rib = Rib Reef). Both simulations were run using model type 1.

4.4. DISCUSSION

4.4.A. Patterns of dispersal among and within sectors in the GBR

4.4.A.1. Settlement rate

Although the models used in this chapter were deterministic, even the simplest, including only the physical description of the zones (i.e. topology and background currents), produced significant spatial variation in settlement rate both among zones and reefs. When differences in the state of the reefs (i.e. coral cover and fecundity) were included in more complex models, the variation in settlement rate further increased. Similarly, field studies have found that recruitment by many marine organisms with a dispersive larval phase is highly variable in space and time, including molluscs (Barnes 1956), fishes (Milicich 1994) and corals (Hughes et al. 1999). This high recruitment variability in the field is attributed to variation in processes occurring before (i.e. abundance and fecundity of the adults, e.g. Hughes et al. 2000), during (i.e. mortality, competence patterns and behaviour of the larvae, and transport mechanisms, e.g. Boicourt 1982, Grosberg 1982, Gaines et al. 1985, Underwood and Fairweather 1989, Milicich 1994) and after (i.e. larvae settlement behaviour and post-settlement mortality, e.g. Highsmith 1980, Goreau et al. 1981, Doherty 1991) dispersal. Some authors argue that due to the stochastic nature of these processes (particularly those occurring during dispersal) recruitment is not only variable, but also generally unpredictable (e.g. Houde 1987, Doherty and Williams 1988, Underwood and Fairweather 1989).

However, the models as well as producing important spatial variation in settlement rates, reproduced many of the patterns of the variation found in the field (Hughes et al. 1999, Hughes et al. 2002a); including: greater settlement variability for brooders at small spatial scales and for spawners at large spatial scales, and the latitudinal settlement patterns of spawners and brooders (although in the latter only in the bottom two thirds of the GBR, see *Section 4.4.B.1*). Therefore, it is likely that a substantial part of the large spatial and temporal variation in the recruitment rates observed in the field is not random, and settlement rates may be predictable to a certain extent if sufficient physical and biological information was available at the relevant spatial and temporal scales.

Settlement patterns for brooders and spawners were not necessarily similar at zone and reef levels in agreement with field studies (Hughes et al. 1999). This further

indicates the complexity in the management and conservation of marine populations with a dispersive larval phase, and the need for management projects specific to the organism and area of interest (see *Chapters 2 and 3*).

4.4.A.2. Relationships among reefs

Even in the models not including retention, the levels of local settlement were notable in all zones for brooders, and in zones 1 and 6 for spawners. However, they appeared lower than the levels found by genetic studies of corals in the GBR, particularly in broadcast spawners (e.g. Benzie 1994, Ayre and Hughes 2000). To obtain comparable levels of local settlement and connectivity in the models some level of water retention at the reefs was required (see *Chapter 3*). This is in agreement with the prediction of water retention for periods that may exceed the pre-competent period of the larvae of brooding and spawning corals by hydrodynamic models of the reefs in the central GBR (Black et al. 1991, Black 1993).

Evolutionary-scale connectivity was much higher than ecological-scale connectivity. In fact, for both coral types evolutionary-scale connectivity seemed to be mainly determined by the number of reefs present within each zone (at the mortality rate of 0.3 day^{-1} used in the models). These results are in agreement with the findings of genetic studies of corals in the GBR, which concluded that although most recruitment is local, long distance dispersal is very important over evolutionary time-scales (Ayre and Hughes 2000).

In general ecological-scale connectivity was higher in zones with a constant directional flow. When current flow was variable more reefs could be reached by larvae (i.e. higher evolutionary-scale connectivity), but fewer reefs received significant amounts of larvae from a given reef source (i.e. lower ecological-scale connectivity). The spatial patterns of connectivity at ecological-scale were quite different for brooding and spawning corals in most zones. It is generally assumed that brooding species have restricted dispersal based on their shorter larval life-spans (but see Richmond 1988). In the models, ecological-scale connectivity was lower for brooders in most zones. However, in zones 1 (with the highest reef density) and 4 (with very high reef densities around the 6 study reefs) ecological-scale connectivity was higher for brooders. This could be a result of the high reef density of these zones, and the higher mortality experienced by the larvae of spawners during their longer pre-competent period.

Nevertheless, the diversity of the larval input in terms of its reef sources, a combination of the connectivity and the evenness values, was higher for spawners than brooders in all model types.

4.4.B. Mechanisms contributing to the latitudinal recruitment gradients in the GBR

4.4.B.1. Latitudinal recruitment gradients in brooders and spawners

Most model types showed settlement peaks in the central GBR for both brooders and spawners. These peaks were generally centred in zone 4 (latitudes 18.5°S to 20°S) for brooders and zone 3 (latitudes 17°S to 18.5°S) for spawners.

Field studies, however, indicate a steady decrease in recruitment rates of brooders from north to south along the GBR (e.g. Harriott and Simpson 1997, Dunstan and Johnson 1998, Hughes et al. 2002a). That is, all model types underestimated settlement rates for brooders in the northernmost zones (1 and 2) of the GBR. This discrepancy could be due to the existence of latitudinal gradients in the GBR not included in the models, such as those in temperature, bathymetry, and substratum consistency (see *Section 4.1.A.* and *Appendix II*). These gradients can affect the fecundity and other aspects of the life history of corals. For example, release of brooded planula by corals typically occurs during longer periods of the year in the northern GBR than in the southern GBR (Kojis 1986, Harrison and Wallace 1990, see also Tanner 1996a). If the differences in settlement among zones in the field were due to differences in fecundity, the models including fecundity should be able to reproduce the recruitment patterns in the GBR. Unfortunately, fecundity information was not available for brooders. Nevertheless, despite the discrepancies between the models and field data in the northern GBR, the topology of the reefs and hydrodynamic processes were sufficient to reproduce the continuous decrease in settlement from the central to the southernmost zones in all model types.

As in the models, field studies have found a recruitment peak for spawning corals, though it is located further north, between latitudes 14°S and 18°S (Hughes et al. 2001). This area also has the highest species diversity of hard and soft corals on the GBR (e.g. Veron 1995, Fabricius and De'ath 2001), and is near the position where the SEC contributes large water masses to the GBR. Hence, some authors have linked the high recruitment rates of spawners and coral species richness of the area with the input of

larvae due to the SEC (e.g. Fabricius and De'ath 2001, but see Hughes et al. 2001). Although the area where the settlement peak for spawners occurred in the models can also receive the direct influence of the SEC (the exact SEC point of insertion varies seasonally and has been recorded as far south as 18.3°S, e.g. Pickard et al. 1977, Burrage et al. 1994, Wolanski 1994), this current and its possible larval contribution were not included in the models. Significantly, the topology of the reefs and the background currents in the zones were enough to produce the settlement peak observed in the field.

The inclusion of fecundity in the models dramatically increased their predicting power about the settlement patterns of spawning corals in the GBR, indicating that fecundity is an essential factor in determining these patterns. Field data also indicates that the main factor determining latitudinal variation in recruitment by spawners in the GBR is the regional and temporal variation in their fecundity (Hughes et al. 2000). In this study, fecundity alone explained ~72% of the variation in recruitment by spawning acroporids (the most common spawning coral family in the GBR), and once that fecundity was accounted for statistically there was no further effect of latitude on the large-scale patterns of recruitment of spawners in the GBR. However, even the results of the models including fecundity did not produce a significant fit to the field data. This could be due, at least in part, to the scarce number of data points (5 zones) available and the consequent low statistical power of the analyses. The models may also require more detailed hydrodynamic and/or biological data, or more significantly the inclusion of some other important factors contributing to the recruitment patterns of spawning corals in the GBR, such as additional environmental conditions (e.g. bathymetry, and substratum consistency). Post-settlement mortality could be another candidate to explain the lack of a stronger fit between the field and models; nevertheless, it is unlikely to have been significant in the field study because the settlement panels were deployed for only two months and they had few signs of predation or competitive interactions (Hughes et al. 1999).

4.4.B.2. Latitudinal gradient in the proportion of spawners in the total settlement

In the absence of any information about the state of the reefs the models could not reproduce the latitudinal variation in the proportion of spawners in the total settlement observed in the field (Hughes et al. 2002a, and see Section 4.1.1.). The models including the intrinsic physical features of the zones (reefs topology and background

currents), coral cover, and water retention at the reefs produced the closest fit to the observed patterns in the field. However, the decrease in the proportion of spawners in the total settlement from the central to the southern-most GBR in the best fitting model was less steep than in the field. That is, the increase in latitude produces a greater decrease in the recruitment of larvae by spawners (relative to the recruitment by brooders) in the field than in the models.

Latitudinal differences in environmental conditions not included in the models could also account for the greater effect of latitude in the proportion of spawners in the total settlement in the field than in the models. Temperature can significantly affect larval development (e.g. Hoegh-Guldberg and Pearse 1995), with a decrease in temperature leading to a reduction in development rate and consequently an increase in the duration of the pre-competent and competent periods. Longer pre-competent periods are likely to be translated into higher absolute larval mortalities and thus into lower settlement rates. This latitudinal effect of temperature on larval development and settlement is likely to be greater in spawners than brooders because of their longer pre-competent periods, which could contribute to explain the greater decrease in the proportion of spawners in the total settlement with latitude occurring in the field. It has also been suggested that brooding may be the optimal strategy for local recruitment under conditions of low larval survival (Szmant 1986). These environmental and subsequent recruitment differences can lead to preferential survivorship of brooding corals resulting in a process of 'species sorting' (sensu Vrba and Eldredge 1984, Vrba and Gould 1986). In support of this idea seems the fact that most corals in the cool and turbid waters of the eastern Pacific (e.g. Glynn and Wellington 1983, Veron 1994) and West Africa (e.g. Laborel 1974, Jackson 1986) are brooders (although in the former region coral reproduction is mainly asexual, e.g. Scott et al. 1988, Richmond and Hunter 1990). Similarly, some species that spawn through most of their ranges, brood or both spawn and brood in the sub-optimal conditions found in the margins of the ranges (e.g. Sakai 1997). A transition from reefs dominated by spawners at lower latitudes to brooder-dominated at higher and cooler latitudes, analogous to that observed in the GBR, also occurs in the Ryukyu Island chain in the Northern Hemisphere (24-32°N) (Hayashibara et al. 1993, Morse et al. 1996, Hughes et al. 2002a). In fact, greater resilience to marginal environmental conditions by brooding corals seems to have occurred recurrently in past geological times. For example, the closure of the Tethys sea (e.g. Kenneth 1982, Adams et al. 1986) and the opening of the Drake Passage between

South America and Antarctica originated the circum-antarctic deep circulation (e.g. Kennen 1982) around the Oligocene/Miocene boundary, leading to important upwelling of deep, cold, turbid and nutrient-rich water in the Caribbean (e.g. Edinger and Risk 1995). These changes in environmental conditions resulted in the local extinction of approximately half of the Caribbean coral fauna during the Early Miocene, preferentially affecting spawning corals (~ 71% of the spawning genera and 27% of the brooding genera became locally extinct, Edinger and Risk 1995). Environmentally caused differences in recruitment between both coral reproductive types could also be mediated, at least partially, by differences in fecundity. The models including fecundity produced the best fit to the field recruitment observations in spawners, but this hypothesis could not be tested due to the lack of data on the spatial patterns of fecundity of brooders in the GBR.

4.4.C. Model Limitations

The model limitations presented in *Chapters 2* and *3* also apply to the models described in this chapter. Additional limitations arise from the information handling methods used in this chapter to produce the data input files for the models, and our incomplete knowledge of the biology of corals in the GBR. The limitations specific to this chapter are discussed below.

Some error was introduced when the G.I.S. polygon coverages were transformed into grids to produce the charts representing the zones. In this process a value was assigned to each cell according to its dominant land-type. Some reefs can be over-represented in the chart if they constitute the most abundant land-type of a cell. More frequently reefs are under-represented (if they overlap several cells) or even not represented at all (if they are small). Therefore, there are some discrepancies in the total area of the reefs and the number of reefs per sector between the models and the real world, which introduce some error in the settlement and connectivity (particularly at evolutionary scales) values computed by the simulations. This limitation could be ameliorated using a smaller cell size and increasing the number of cells in the charts; however, this would greatly increase the computational cost (memory and time) of the simulations. Furthermore, the cell size was equal for each zone, and led to similar reductions in the number of reefs and reefal area in all the charts (Table 4.5.); thus this limitation should not greatly affect the comparison among zones.

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.

Zone	Polygon Coverage		Chart Representation		Difference (%)	
	Reefs Number	Reefal Area (km ²)	Reefs Number	Reefal Area (km ²)	Reefs Number	Reefal Area (km ²)
1	423	3477.40	268	3341	36.64	3.92
2	180	1333.09	103	1293	42.78	3.01
3	143	1262.16	81	1201	43.36	4.85
4	188	1757.52	100	1680	46.81	4.41
5	280	2145.56	142	2040	49.29	4.92
6	46	403.07	31	383	32.61	4.98

Although the study reefs were centred in each zone, it is likely that in the field they receive larvae from outside the zone (i.e. from reefs more than 80-85 km away). It is not feasible to run simulations using charts that contain areas greater than those already included in the modelled zones to assess this larval contribution for three main reasons. (1) There are no G.I.S. coverages for the reefs in some of these areas (no descriptions were available north of zone 1, and these were of limited extent east and south of zone 6). (2) Using charts representing larger areas would imply greater extrapolation error in the models, as the coral cover and fecundity values used for all the reefs in a zone were the average of those observed in a field study in 6 reefs located in the centre of the zone (Hughes et al. 1999) and the currents within the zones can differ greatly from those in the areas surrounding them (particularly north of zones 3 and 6, south of zones 1 and 2, and east of all zones). (3) Increasing the number of reefs in the simulations can have a significant cost in computer resources (i.e. memory and time). Nevertheless, an estimation of the contribution of larvae to the study reefs by reefs outside the charts was conducted by running additional simulations. In these simulations larvae were released in 8 theoretical reefs adjacent to the charts (located to the N, NE, E, SE, S, SW, W, and NW of the chart). In general, the proportion of larvae released in these reefs that settle on the study reefs was low due to larval mortality, diffusion, and the presence of intermediate reefs (Table 4.6.). In brooders this proportion was virtually negligible, as their larvae are unlikely to reach the study reefs before the end of the competent period. In spawners the contribution of larvae to the study reefs from reefs located to the northwest and/or north of zones 2, 3, 4, and 5 was relatively large in the models not including retention due to transport by the SEC. However, when retention was included

in the models (reproducing the most common situation in the GBR) the only important contribution to the study reefs was that by the reef located directly north of zone 4. Furthermore, the contribution by reefs farther away from the border of the charts would be smaller. Therefore, the problem posed by the limited size of the charts and the contribution of larvae by reefs not included in them introduces some error in the estimates for evolutionary-scale connectivity, but the error in the estimates for the remaining dispersal variables is mostly trivial.

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*. *Ret.* = Retention, *Reprod.* = Reproductive type. *Top number in cells:* Average contribution to the 6 study reefs, *Bottom number in cells (in brackets):* Maximum contribution to any of the study reefs. In *bold:* Cases where the maximum contribution is greater than 1×10^{-6} (i.e. ≥ 1 larva settling in a study reef per 10^6 produced in the source reef).

Zone	Ret.	Reprod.	N	NE	E	SE	S	SW	W	NW
1	No	Brooders	0 (0)	0 (0)	0 (0)	0 (0)	2.4x10 ⁻²² (1.4x10 ⁻²¹)	0 (0)	0 (0)	0 (0)
		Spawners	1.4x10 ⁻²⁴ (8.5x10 ⁻²⁴)	0 (0)	3.5x10 ⁻²⁹ (2.1x10 ⁻²⁸)	1.0x10 ⁻³⁵ (6.1x10 ⁻³⁵)	3.5x10 ⁻¹² (2.0x10 ⁻¹¹)	1.8x10 ⁻³⁷ (1.1x10 ⁻³⁶)	7.6x10 ⁻²⁵ (4.6x10 ⁻²⁴)	0 (0)
	Yes	Brooders	0 (0)	0 (0)	0 (0)	0 (0)	1.7x10 ⁻²⁵ (1.0x10 ⁻²⁴)	0 (0)	0 (0)	0 (0)
		Spawners	8.8x10 ⁻³⁵ (5.3x10 ⁻³⁴)	0 (0)	1.3x10 ⁻³⁸ (7.5x10 ⁻³⁸)	1.9x10 ⁻⁴⁴ (1.1x10 ⁻⁴³)	1.0x10 ⁻¹⁴ (5.9x10 ⁻¹⁴)	0 (0)	9.8x10 ⁻³⁰ (8.9x10 ⁻²⁹)	0 (0)
2	No	Brooders	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
		Spawners	1.3x10⁻⁶ (3.2x10⁻⁶)	4.1x10 ⁻³³ (2.4x10 ⁻³²)	5.3x10 ⁻³⁰ (2.4x10 ⁻²⁹)	0 (0)	0 (0)	0 (0)	2.3x10 ⁻⁴¹ (1.3x10 ⁻⁴⁰)	9.3x10 ⁻¹⁴ (5.5x10 ⁻¹³)
	Yes	Brooders	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
		Spawners	1.3x10 ⁻⁷ (4.4x10 ⁻⁷)	4.7x10 ⁻³⁷ (2.7x10 ⁻³⁶)	3.3x10 ⁻³² (2.0x10 ⁻³¹)	0 (0)	0 (0)	0 (0)	2.0x10 ⁻⁴² (1.2x10 ⁻⁴¹)	2.5x10 ⁻³¹ (1.5x10 ⁻³⁰)
3	No	Brooders	7.2x10 ⁻¹⁵ (4.3x10 ⁻¹⁴)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	5.1x10 ⁻²² (3.0x10 ⁻²¹)	1.1x10 ⁻¹⁶ (4.4x10 ⁻¹⁶)
		Spawners	1.9x10⁻⁷ (1.0x10⁻⁶)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.4x10 ⁻²⁹ (8.4x10 ⁻²⁹)	2.0x10⁻⁴ (1.2x10⁻³)
	Yes	Brooders	2.4x10 ⁻¹⁷ (1.4x10 ⁻¹⁶)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.9x10 ⁻²³ (1.2x10 ⁻²²)	9.6x10 ⁻²⁰ (5.8x10 ⁻¹⁹)
		Spawners	7.0x10 ⁻⁸ (4.0x10 ⁻⁷)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4.2x10 ⁻³⁰ (2.5x10 ⁻²⁹)	7.9x10⁻⁵ (4.7x10⁻⁴)
4	No	Brooders	1.3x10 ⁻¹⁹ (7.7x10 ⁻¹⁹)	0 (0)	3.7x10 ⁻³³ (2.2x10 ⁻³²)	0 (0)	0 (0)	0 (0)	6.4x10 ⁻²¹ (3.8x10 ⁻²⁰)	7.6x10 ⁻²⁰ (4.6x10 ⁻¹⁹)
		Spawners	8.2x10⁻⁵ (4.9x10⁻⁴)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2.3x10 ⁻³⁵ (1.4x10 ⁻³⁴)	9.9x10⁻⁶ (6.0x10⁻⁵)
	Yes	Brooders	3.2x10 ⁻²¹ (1.9x10 ⁻²⁰)	0 (0)	4.3x10 ⁻³⁷ (2.6x10 ⁻³⁶)	0 (0)	0 (0)	0 (0)	3.7x10 ⁻²⁴ (2.2x10 ⁻²³)	3.5x10 ⁻²⁸ (2.1x10 ⁻²⁷)
		Spawners	2.1x10⁻⁵ (1.3x10⁻⁴)	2.9x10 ⁻³⁷ (1.8x10 ⁻³⁶)	0 (0)	0 (0)	0 (0)	0 (0)	3.1x10 ⁻³⁶ (1.9x10 ⁻³⁵)	5.4x10 ⁻¹¹ (1.9x10 ⁻¹⁰)
5	No	Brooders	5.7x10 ⁻¹⁰ (3.4x10 ⁻⁹)	0 (0)	3.3x10 ⁻³¹ (2.0x10 ⁻²⁹)	0 (0)	0 (0)	0 (0)	1.8x10 ⁻²⁴ (1.1x10 ⁻²³)	4.1x10 ⁻¹² (2.3x10 ⁻¹¹)
		Spawners	7.8x10⁻⁵ (2.8x10⁻⁴)	0 (0)	2.9x10 ⁻⁴¹ (1.8x10 ⁻⁴⁰)	0 (0)	0 (0)	0 (0)	2.3x10 ⁻⁴¹ (1.3x10 ⁻⁴⁰)	1.6x10⁻⁶ (9.4x10⁻⁶)
	Yes	Brooders	2.8x10 ⁻¹³ (1.7x10 ⁻¹²)	0 (0)	8.3x10 ⁻⁴² (5.0x10 ⁻⁴⁰)	0 (0)	0 (0)	0 (0)	5.7x10 ⁻²⁵ (3.4x10 ⁻²⁴)	6.3x10 ⁻¹⁵ (2.8x10 ⁻¹⁴)
		Spawners	3.1x10 ⁻¹⁰ (1.8x10 ⁻⁹)	5.2x10 ⁻³⁸ (3.1x10 ⁻³⁷)	8.9x10 ⁻⁴⁵ (5.3x10 ⁻⁴⁴)	0 (0)	0 (0)	0 (0)	1.1x10 ⁻⁴¹ (6.4x10 ⁻⁴¹)	9.9x10 ⁻⁹ (5.9x10 ⁻⁸)
6	No	Brooders	4.2x10 ⁻²⁸ (2.5x10 ⁻²⁷)	0 (0)	9.2x10 ⁻¹⁸ (5.2x10 ⁻¹⁷)	5.0x10 ⁻¹² (3.0x10 ⁻¹¹)	1.2x10 ⁻⁴² (2.8x10 ⁻⁴²)	0 (0)	2.4x10 ⁻³⁹ (1.4x10 ⁻³⁸)	4.4x10 ⁻²¹ (1.6x10 ⁻²⁰)
		Spawners	3.4x10 ⁻¹⁸ (2.0x10 ⁻¹⁷)	0 (0)	2.0x10 ⁻¹¹ (8.6x10 ⁻¹¹)	7.7x10 ⁻¹³ (4.4x10 ⁻¹²)	1.7x10 ⁻²⁷ (8.6x10 ⁻²⁷)	0 (0)	2.5x10 ⁻²⁹ (1.5x10 ⁻²⁸)	1.9x10 ⁻¹⁴ (9.5x10 ⁻¹⁴)
	Yes	Brooders	1.0x10 ⁻³¹ (6.0x10 ⁻³¹)	0 (0)	1.1x10 ⁻¹⁸ (6.4x10 ⁻¹⁸)	5.6x10 ⁻¹⁵ (3.3x10 ⁻¹⁴)	1.2x10 ⁻⁴³ (3.2x10 ⁻⁴³)	0 (0)	8.8x10 ⁻⁴³ (5.3x10 ⁻⁴²)	2.0x10 ⁻²⁵ (1.1x10 ⁻²⁴)
		Spawners	1.1x10 ⁻¹⁹ (6.5x10 ⁻¹⁹)	0 (0)	4.2x10 ⁻¹³ (1.9x10 ⁻¹²)	1.8x10 ⁻¹⁴ (1.0x10 ⁻¹³)	9.7x10 ⁻²⁹ (4.6x10 ⁻²⁸)	0 (0)	1.5x10 ⁻³⁰ (9.0x10 ⁻³⁰)	6.2x10 ⁻¹⁶ (3.7x10 ⁻¹⁵)

The size of the 6 study reefs differed within and among zones. Because larger reefs can produce and receive more larvae, differences in reef size among zones are likely to generate differences in settlement rate (although this was partially overcome by expressing settlement in relation to the reef's production), diversity of sources of the larval input, and especially connectivity. Whenever possible, reefs of varying sizes were chosen for the analysis, but in some cases the average size of the study reefs was considerably different than in the other zones. In these cases, however, a large reefal area is a common characteristic of the reefs in the zone, and must be included in the analyses. In general, the selected reefs constitute a good representation of the range of reef sizes in the zone.

The models included the hydrodynamics generated by background currents, but the effect of tides and weather-band currents were not considered. These currents could have modified the advection of water by background currents in the models. Their principal effect would have been to increase diffusion, generally resulting in an increase in connectivity (at least at an evolutionary scale). This effect would have been more pronounced for brooded larvae (typically released year round) than in spawners (typically released in the spring-early summer, during a period of neap tides and relatively calm atmospheric conditions) (Harrison et al. 1984, Harrison and Wallace 1990).

In the models, hydrodynamic conditions (current direction and speed, and diffusion level), coral cover and fecundity were kept equal for the whole area within each zone. Using a uniform current over the entire chart is equivalent to assume that the charts represent zones of the GBR sufficiently small for all the cells within the chart to experience similar currents (i.e. the background current encompass the whole area represented by the zone). In reality hydrodynamic and biological processes change in space and time (see *Section 2.4.F.2.*), thus incorporating spatial variability at this level would make the models more realistic. A limitation of coupled lattice models (particularly if they are spatially realistic as in this chapter) is that they can underestimate the dispersion speed of a proportion of the larvae being transported in the currents because the same level of diffusion is used in the whole chart, rather than greater at the edge than centre of the currents (see *Section 2.4.F.2.*). A number of techniques could be used to correct this problem (e.g. Kowalik and Murty 1993), and consequently refine the assumption that all cells experience similar currents. Nevertheless, because the aim of this study is not predictive but heuristic, this limitation

is not serious. Moreover, topographical and meteorological constraints are likely to result in greater spatial variability in hydrodynamic conditions. However, further studies on the physical oceanography of the GBR and especially the biology of the organisms inhabiting its reefs would be required to be able to include in the models this and many other aspects of the spatial and temporal variability in physical and biological processes in the GBR.

Although the study by Hughes and collaborators (1999, 2000, and 2002a) constitutes by far the largest recruitment sampling effort in the GBR to date, recruitment estimates at other latitudes (i.e. additional regression data points) would be required for a more reliable assessment of the mechanisms determining the recruitment patterns in this region. Additionally, the non-uniform distribution of the regression pairwise points (i.e. lack of homoscedasticity) affected the quality of the data analysis, particularly in brooders. The clustering of these points could be due to latitudinal environmental gradients not included in the models (see *Section 4.4.B.*), but additional information would be necessary to confirm this hypothesis. In particular, the most complete models could only be implemented for spawning corals, as data on the fecundity of brooders in the GBR was not available. Further studies would be required to identify the fecundity patterns of brooding corals in the GBR; however, the acquisition of this data is complex, as it requires repeated sampling throughout the year over a vast area.

4.4.D. Summary and Conclusions

Even the simplest of the deterministic models in this chapter produced important variation in settlement rates among reefs, zones, and coral types. Moreover, the models were able to reproduce many of the spatial patterns of variability in settlement and connectivity found in the GBR by field and genetic studies. For example, they accurately predicted: higher settlement variability for brooders at small spatial scales and for spawners at large spatial scales; much higher local-settlement for brooders, and higher connectivity for spawners in most zones; and the latitudinal settlement patterns of spawners and their proportion in the total settlement. However, in most cases the models producing the best predictions required significant amounts of information, including not only physical descriptions of the environment (i.e. reef topology, background currents, and retention levels at reefs), but also the state of the reefs (i.e. coral cover and fecundity). All models underestimated the settlement rates of brooders

in the northern GBR, but fecundity rates could not be included in the models for brooders as this data was not available.

Several important conclusions can be drawn from the results obtained in this chapter. Firstly, a significant part of the large spatial and temporal variation in recruitment found in the field may be related to the spatial and temporal variation in the factors determining dispersal, rather than to purely stochastic variation. This implies that settlement may be predictable to a certain extent, if sufficient physical and biological information is available. Secondly, in agreement with field studies (Hughes et al. 2000), the latitudinal patterns of fecundity are essential in determining the recruitment patterns in the GBR, at least in spawners. Thirdly, the large differences in settlement and connectivity patterns in space and among taxa found in the models and field (e.g. Hughes et al. 1999) suggest the complexity of the management of natural populations of marine organisms with a dispersive larval phase. Management plans and implementations involving this type of organisms should be specific in their aims and based on a sound knowledge of the species and processes occurring in the area to be regulated and its surrounds.

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

5.1. INTRODUCTION

For a species to expand its range, it must be able to (1) travel to a new area, (2) withstand potentially unfavourable conditions during its passage, and (3) establish viable populations upon its arrival (Brown and Lomolino 1998). Individuals of species capable of longer dispersal distances can bridge larger patches of unsuitable habitat, and can also contribute repeatedly to small populations in widely scattered locations rescuing them from local extinction ('rescue effect', Brown and Kodric-Brown 1977). The size of the geographic distribution range of a species is, therefore, potentially related to its dispersal capabilities. This prediction seems even more feasible in the marine realm, where physical barriers to dispersal are less common and the environment is more homogeneous than in terrestrial environments.

In most marine animals, the adult phase is sessile or sedentary, and migration usually occurs only during the larval phase (see *Chapter 1*). The importance of larval dispersal in marine animals has long been acknowledged by biogeographers (e.g. Zinsmeister and Emerson 1979, Scheltema 1986). Because longer larval stages can be associated with greater dispersion, the idea that the duration of the pre-competent and competent periods is a main factor controlling the geographic distribution of tropical corals has also been predominant (e.g. Atoda 1947a, Richmond 1988, Veron 1995). In fact, for many species, both terrestrial and marine, geographic range size has been correlated or assumed to be correlated with potential for dispersal, rather than average dispersal distance (Brown and Gibson 1983, Richmond 1990a, Sammarco 1991). Scheltema (1977) predicted that species with longer larval duration should have: (1) wider geographic ranges, (2) longer geological records, and (3) lower rates of speciation. In this chapter I explore the relationship between the potential for dispersal provided by the larvae of corals and the size of their geographic distribution ranges. Before describing the aims of this chapter in more detail, I next review the evidence for and against the relationship between dispersal potential and geographic range size in terrestrial and marine organisms.

5.1.A. Relationship between dispersal potential and geographic range size

In terrestrial environments, most studies have focused on vascular plants, relating the extent of the geographic range to the dispersal potential of the seed. Long distance dispersal of seeds by wind facilitates the crossing of geographic boundaries, providing the potential for increased ranges and reducing the chances of local endemism (Linder 1985, Bond 1988). A positive correlation between local endemism and short distance dispersal of the seeds has been found in South Africa (Linder 1985, Slingsby and Bond 1985, Cowling et al. 1992, McDonald et al. 1995) and the neotropics (Gentry 1988). Furthermore, seed dispersal mode (closely related to dispersal potential) has been estimated to be the most important trait determining endemism in the flora of the Cape Floristic Region (South Africa) (McDonald et al. 1995).

In terrestrial animals, studies investigating this relationship are limited. Evidence for the relationship between propensity to move (i.e. effective dispersal of the species) and geographic range size in birds seems equivocal. The size of the geographic range of birds has been found to be strongly correlated to the migratory tendencies of the species, but not to other measures of dispersal such as the distance between natal and breeding sites (Duncan et al. 1999). Furthermore, Duncan and colleagues (1999) estimated that two main determinants of the geographic range sizes of the birds of Britain and New Zealand are: (1) the species habitat abundance (greatly dependent on the variety of habitats that the species can exploit), and (2) life history traits associated with higher rates of population growth (high fecundity, fast development, and small body size). Thus, in birds other factors besides dispersal potential seem to be also essential in determining the size of the geographic range of the species.

In marine environments, Scheltema's predictions (see above) have been examined mainly in benthic gastropods. Research on extant species in this group generally agrees with the predictions. *Prediction 1 (species with longer larval duration have wider geographic ranges)*: There is a positive relationship between larval dispersal potential and geographic distribution area in the Indo-Pacific (IP) species of the genus *Conus* (Perron and Kohn 1985). *Prediction 2 (species with longer larval duration have longer geological records)*: Most modern benthic gastropod families with long-lived planktonic larva are the same as those found in the geological record (Scheltema and Williams 1983). *Prediction 3 (species with longer larval duration have lower rates of speciation)*: gastropod populations on the eastern and western Atlantic show an inverse relationship between the frequency with which their larvae are found in the plankton of

the open sea and their morphological differentiation (Scheltema 1971). Many other studies have used the relatively abundant and well preserved fossil record of benthic gastropods, generally confirming Scheltema's predictions (e.g. Shuto 1974, Hansen 1978, Jablonski 1986). However, in these studies species (both extant and extinct) generally belonged to only two categories according to the dispersal potential of their larvae: species with long planktonic development, and species with short or non-existent planktonic development. Greater variation in larval planktonic durations (ideally a continuum spectrum) is necessary for a proper assessment of Scheltema's predictions.

In coral reef fishes, the evidence for a relationship between larval dispersal potential and geographic range size is equivocal, with different studies producing strikingly contradictory results. Hughes and collaborators (2002b) found that the species of reef fishes with unusually small or large ranges in the IP are not a random draw of the total species pool. That is, some families of reef fishes are represented with more species than expected by chance alone and others with less in both the endemic and pandemic species pools. These departures are associated with the reproductive mechanism and larval development habitat of each family (all the over-represented families in the pandemic pool are broadcast spawners and all the under-represented are benthic spawners with an extended period of parental care). However, when only species with pelagic larval development are considered generally no clear relationship between pelagic larval duration (PLD) and range size is found, except at the extremes of PLD (Brothers and Thresher 1985, Ormond and Roberts 1997, Jones et al. 2002). In this case, the species with the longest PLDs also have the most extensive geographic ranges, whereas species with very short PLDs tend to have small ranges. In the study by Jones and colleagues (2002), including species of anemone fishes, angelfishes, butterflyfishes, damselfishes, groupers and snappers, variation in PLD explained only 8% of the variation in range size. Conversely, in a recent study including 28 families and all the tropical reef fish species with published PLDs to date, Lester and Ruttenberg (2005) found a significant but relatively weak relationship between PLD and range size in the IP, and no relationship in the Atlantic. The relationship in the IP was in great part due to the disproportionate contribution of the species with the largest ranges, which generally also had very long PLDs. The authors concluded that although PLD is not the primary determinant of range size, it can be important in certain topological circumstances (i.e. in large oceans with particular spatial distributions of habitat and dispersal barriers).

This study also found a negative correlation between PLD and species richness at the family level in the IP, in agreement with Scheltemas 3rd prediction. Some of the lack of relationship between PLD and geographic range size in these studies could be attributed to phylogenetic differences, but no relationship has been found within families for angelfishes (Thresher and Brothers 1985, Lester and Ruttenberg 2005), snappers (Zapata and Herron 2002), or surgeonfishes (Lester and Ruttenberg 2005). Conflicting results have been found for damselfishes (no relationship: Brothers and Thresher 1985, Wellington and Victor 1989, Victor and Wellington 2000, and positive relationship: Bonhomme and Planes 2000, Mora et al. 2003, Lester and Ruttenberg 2005), and wrasses (no relationship: Victor and Wellington 2000, and positive relationship: Mora et al. 2003, Lester and Ruttenberg 2005); while a so far undisputed positive relationship (although weak) has only been described in butterflyfishes (Jones et al. 2002). Therefore, the data for coral reef fishes is ambiguous, with a substantial part of it not in support of the relationship between PLD and range size. However, factors other than PLD (such as swimming capabilities, behaviour, and mortality of larvae) also contribute to the dispersal of larvae, but were not considered in the studies.

In corals, the relationship between dispersal potential of the larvae and geographic range size has received little attention. Jackson (1986) proposed that the relationship between larval life length and geographic range size is valid for most of the free-living aclonal taxa, but not among sessile organisms, clonal or aclonal. In the case of corals, he argued that the realised dispersal of their larvae is only relevant over short and medium distances. Jokiel (1984, 1990a) and Jackson (1986) attributed most long-distance dispersal and colonisation by corals to rafting of small colonies of adults attached to floating substrata. Nevertheless in corals, although most of the larvae in a cohort settle soon after they reach competence if a suitable habitat is encountered, a small proportion of the cohort is capable of delaying settlement and metamorphosis for significant lengths of time (see *Chapter 1, Section 1.2.2.*). This small fraction of larvae and the extent of the delay has been considered essential in determining the geographic distribution of coral species by other authors (Connell 1973, Wilson and Harrison 1998). In contrast with their findings for reef fishes, Hughes and collaborators (2002b) found that the number of species representing each coral family in the endemic species pool is very similar to that in the pandemic pool. However, large variation in PLD has been found within coral families and even within genus (e.g. Harrison et al. 1984, Baird 2001, see also *Table 5.3.*). Furthermore, the larvae of coral species can differ not only in the

duration of their larval stage but also in their competence patterns (Wilson and Harrison 1998, Baird 2001, see also *Figures 5.2. and 5.3.*), which provides even greater variation in dispersal potential among species. Thus, the relationship between dispersal potential of the larvae and geographic range extent is still lacking adequate testing in corals.

5.1.B. Aims of the study

The main aim of this study is to investigate the relationship between dispersal potential of larvae and size of geographic range in scleractinian corals. To study this relationship I use a suite of IP scleractinian corals, selected because they differ in the size of their geographic ranges and because their larval competence patterns are known, at least to a certain extent. The work in this chapter is sub-divided in 3 parts:

- (1) First, I examine the biogeography of 15 coral species (12 broadcast spawners and 3 brooders). I use 3 variables to describe the size of their geographic distribution: longitudinal range extent, latitudinal range extent, and area of the range.
- (2) Then, I estimate the potential for dispersal of the larvae of the 15 selected coral species, using spatially explicit models under two hydrodynamic conditions: absence and presence of water retention around the reefs. In the models, species differ exclusively in the competence patterns of the larvae (i.e. differences in larval behaviour or mortality were not included in the models). For the species where enough information is available I use two types of representations of the competence patterns of the larvae in a cohort: linear, and non-linear (see *Chapters 2 and 3, and Section 5.2.C.2.*). The comparison between both methods of representation is a secondary aim of this chapter. Retention is a variable factor in the models because its existence and significance has caused great controversy in the last 30 years within the scientific community. Yet, it has the potential to considerably alter the extent of larvae dispersal (see *Chapter 3*). The results of the simulations are analysed, and six variables related to the dispersal potential of the larvae are computed for each species.
- (3) Finally, I examine the predictive power of the 6 variables describing the dispersal potential of the larvae computed by the models in relation to the 3 biogeographic variables in the spawning species.

5.2. MATERIALS and METHODS

5.2.A. Species of coral used in the study

Fifteen species of scleractinian corals with distinctive larval competence patterns and geographic distributions were selected for the study. They included: five acroporids (*Acropora formosa*, *A. gemmifera*, *A. hyacinthus*, *A. millepora*, *A. valida*), six faviids (*Cyphastrea serralia*, *Goniastrea aspera*, *G. australensis*, *G. favulus*, *G. retiformis*, *Platigyra daedalea*), one mussid (*Acanthastrea lordhowensis*), and three pocilloporids (*Pocillopora damicornis*, *Seriatopora histrix* and *Styllophora pistillata*). The acroporids, faviids, and mussids in this study are typically broadcast spawners, while the pocilloporids are brooders (Fadlallah 1983, Harrison and Wallace 1990, Richmond and Hunter 1990, *G. aspera* also broods in Okinawa - Sakai 1997, and *P. damicornis* also spawns in western Australia - Ward 1992). All species inhabit the same ocean, the IP, to reduce the variation in the extent of distribution ranges derived from differences in geography, such as ocean size or bathymetry. The IP was selected for two reasons: (1) it is the ocean for which the larval competence patterns of more species have been studied, and (2) it is the largest uninterrupted tropical marine realm on earth, providing the greatest variation in geographic range sizes among species (Figure 5.1.).

5.2.B. Geographic range sizes

The geographic range sizes of the studied species were described using 3 variables: range area (in km²), and the maximum longitudinal and latitudinal extent of the ranges (in degrees). Information on the biogeography of the species was obtained from a coral biogeography database (Hughes et al. 2002b). This included the areas and the longitudinal and latitudinal limits of the species' ranges. From these data, the maximum longitudinal and latitudinal extents of the ranges were calculated.

5.2.C. Potential for dispersal of larvae

Spatially explicit models were used to investigate the potential for dispersal provided by the larvae of the 15 chosen species. The general design of the models, input formats, coupled lattice functioning and rules, output formats, and data analysis were similar to those described in Chapter 2. The specific details of the models used in this chapter are presented below. Given their importance for this chapter, special attention is

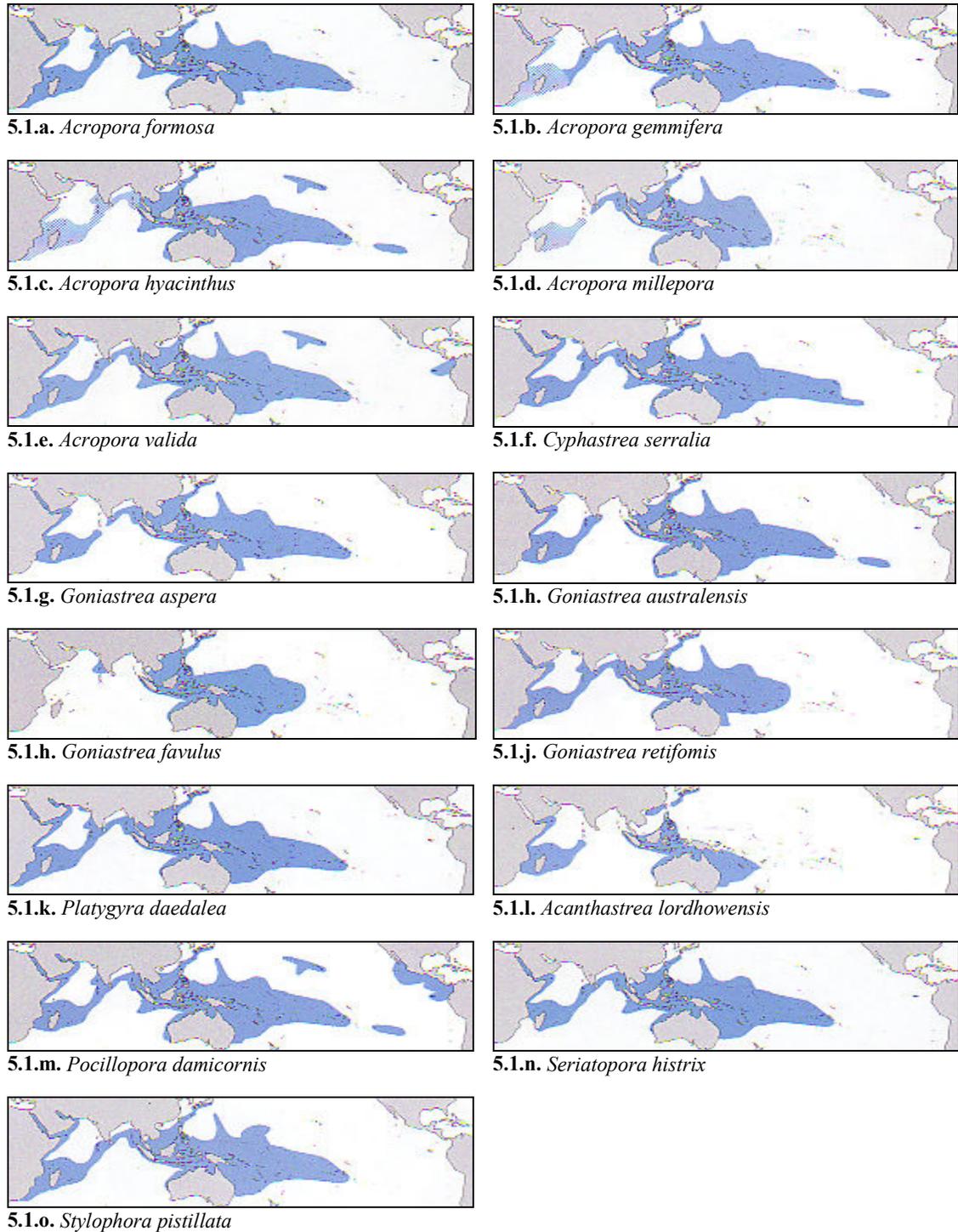


Figure 5.1. Geographic ranges of the 15 species of corals whose competent periods were used in the models. 5.1.a. to 5.1.l.: Broadcast spawner species. 5.1.m. to 5.1.o.: Brooder species. *Dark Blue*: general region where the species has been recorded (although it may not be found in some locations within the region); *Light blue*: areas where the species may occur, but some taxonomic uncertainty exists (due to rarity or the presence of a near species-level geographic variant). (Modified from Veron 2000).

devoted to the competence patterns of the larvae and their representation in the models (Section 5.2.C.2.).

5.2.C.1. Dispersal environment

A chart (spatial representation of the ocean, land, and reefs) consisting of 180 x 180 (32,400) cells of which 100 were assigned to be of reef land-type was used in the models (Table 5.1.). Each cell represented an area of 8 x 8 km. Therefore, the chart represented a square area with sides measuring 1,440 km and its diagonal ~2,036.5 km, comprising more than 2 million km². These dimensions, although large, are only a fraction of the extent of the IP. They were chosen because they are sufficient to discriminate the potential for dispersal among the larvae included in the study, some of them with very long pre-competent and competent periods (see Section 5.2.C.2.). In the models in this chapter, the reef cells can be understood like large reefs, or given their large size as reefal systems (complexes of patchy reefs). They were randomly distributed in the chart, but at least one cell apart from each other to clearly differentiate among them. This provides extensive variation in the distances among pairs of reef cells. The number of reef cells (100) was chosen as a compromise between obtaining a wide range of distances among pairs of reefs and the limitations imposed by computational resources. The reef density (percentage of reef cells in the chart grid) was 0.31%. An edge of 10 ‘water’ cells (180 km) was added around the described chart in order to reduce the edge-effect problem inherent to coupled lattice design (see Chapter 2), so the actual chart used in the models had a dimension of 200 x 200 (40,000) cells.

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

Input Type	Variants
Chart	FIXED: 100 reef areas of 64 km ² uniformly distributed cells in a 180x180 grid (reef density ≈ 0.31%) and 10 cells rim around grid (effective size = 200 x 200 cells)
Current Pattern	FIXED: Advection + Diffusion
Retention	No Retention
	Retention with Diffusion (8% after 10 days)
Life History	12 Broadcast Spawners
	3 Brooders
Larval Competence	Linear: Broadcast Spawners, Brooders
	Non-linear, 1 Pattern: Brooders
	Non-Linear, 2 Patterns (Retained, Dispersed): Broadcast Spawners

As in *Chapters 2 and 3* the current's speed was set to 605 m.h^{-1} ($\sim 17 \text{ cm.s}^{-1}$ or $\sim 14.5 \text{ km.day}^{-1}$). At this speed, a larva moving in a straight line would take ~ 99.3 days to travel from the top row of cells to the bottom one, and one being transported diagonally across the chart in the fastest possible way would take ~ 140.5 days. Only in one of the species in the study the competence patterns used in the models had pre-competent and competent periods that in combination lasted longer than 100 days. (110 days for *A. valida*, see *Section 5.2.C.2*). Furthermore, there are infinite possible routes between any two reef cells, and only a small proportion of the larvae in the cohort follows the shortest possible path (this proportion being smaller the farther apart the two reef cells are). The currents used in the models simulated transport by both advection and diffusion simultaneously, as occurs in the real world. Advection was arbitrarily chosen to occur towards the South, although the direction is irrelevant because the chart represents an idealised distribution of reefs or reefal areas in the ocean. Two different current sets were used, one including retention of water at the reefs and the other where retention was almost negligible (*Table 5.2*). Retention was implemented with diffusion; that is, the larvae were not retained perpetually in reefs, but gradually diffused away (see *Chapter 4*). Retention was set to a level where 8% of the larvae were retained after 10 days, corresponding to the value estimated for a typical reef on the central GBR (Black et al. 1991, Black 1993).

Table 5.2. Current sets used in the models. The sets represent dispersal by both advection and diffusion, with and without water retention in the reefs. The 9 numbers in the “*Current Set*” column represent the probability of a water particle remaining in its present position (‘centre cell’, C) or moving to each of the 8 adjacent cells cited clockwise from North to North-West (N to NW).

Retention	Transport Mechanism	Currents Set (C:N:NE:E:SE:S:SW:W:NW)
Absent	Advection + Diffusion	0.05000:0.03800:0.03800:0.03800:0.19000:0.38000:0.19000:0.03800:0.03800
Present	Advection + Diffusion	0.84503:0.00620:0.00620:0.00620:0.03099:0.06199:0.03099:0.00620:0.00620

Daily mortality rate was set to 0.1 for both the larvae being retained and dispersed. Mortality was set to a relatively low rate for two reasons: (1) to allow a large proportion of the larvae achieve most of their potential for dispersal, and (2) because the curves used to represent the competent periods in a cohort (see *Section 5.2.C.2.b*) already include

endogenous mortality (i.e. due to larval senescence), although not exogenous mortality (e.g. due to predation).

5.2.C.2. *Competence patterns of the larvae*

Depending on the amount of information known about the pre-competent and competent periods of the larvae, these periods were represented in two different ways in the models: linearly or non-linearly. The linear representation is a more simplified depiction of the competence patterns, but could be derived for all the species included in the study. The non-linear representation describes more accurately the competence patterns of the larvae. Furthermore, in this representation the data within each larval type (i.e. brooders and spawners) were obtained from a single author using standardised techniques, thus reducing error when comparing dispersal potentials among species. Unfortunately, representations of this type could only be constructed for 5 of the spawning species (see *Section 5.2.C.2.*). Since both the number and accuracy of the data points (i.e. competence patterns of individual species) are important for this study, the two representation types were used for spawners (see *Section 5.2.D.*). In brooders, non-linear representations could be constructed for all the species in the study, so only this type of representation was used.

5.2.C.2.a. *Linear representation of the larval competence patterns*

In this type of representation, only two data points are used to describe the competent patterns of a cohort: the beginning and end of the competent period. That is, all larvae in the cohort are assumed to become competent simultaneously and have the same competent period duration. Therefore, all the larvae that meet suitable substratum during their competence settle. The timing and duration of the competent periods used in the models were obtained from laboratory studies available in the literature (Table 5.3.). If more than one study was available for a species the values most commonly observed or those from the most detailed study (if there was no agreement among studies) were chosen.

Table 5.3. Reproductive type and competence patterns for the species used in the models in Chapter 5. “Competence Start”: values in *square brackets* represent the time when competence was first checked for and observed (but it is not known how much earlier it had started); values in *curved brackets* represent information that was not available in the cited paper, but was estimated based on the values found for other species in the same family. “Longevity”: maximum number of days that larvae have been observed alive in experiments. “References”: references from where the values were obtained.

Species	Reproductive Type	Competence Start	Competence End	Longevity	References
<i>Acropora formosa</i>	Spawner	5	20	23	Harrison et al. 1984
<i>Acropora gemmifera</i>	Spawner	[4]	34	60	Baird 2001
<i>Acropora hyacinthus</i>	Spawner	7	36	91	Harrison et al. 1984
<i>Acropora millepora</i>	Spawner	[4]	60	110	Baird 1998, 2001
<i>Acropora valida</i>	Spawner	[4]	110	130	Baird 1998, 2001
<i>Cyphastrea serralia</i>	Spawner	(5)	26		Wilson and Harrison 1998
<i>Goniastrea aspera</i>	Spawner	6	23	60	Abe 1937; Harrison et al. 1984
<i>Goniastrea australensis</i>	Spawner	6	56		Wilson and Harrison 1998
<i>Goniastrea favulus</i>	Spawner	6	22		Harrison et al. 1984
<i>Goniastrea retiformis</i>	Spawner	[4]	36	60	Baird 2001
<i>Platygyra daedalea</i>	Spawner	[4]	34	60	Baird 2001
<i>Acanthastrea lordhowensis</i>	Spawner	11	78		Wilson and Harrison 1998
<i>Pocillopora damicornis</i>	Brooder	0.5	9	212	Atoda 1947a; Harrigan 1972
<i>Stylophora pistillata</i>	Brooder	0.5	6		Atoda 1947b
<i>Seriatopora histrix</i>	Brooder	0.5	4		Atoda 1951

5.2.C.2.b. Non-linear representation of the larval competence patterns

In reality, the competent periods of the larvae in a cohort are not synchronised, and different proportions of larvae are available for settlement and metamorphosis at various times. In general, the great majority of larvae become competent at similar times but they cease competence gradually, so a decreasing proportion of larvae is available for settlement and metamorphosis over increasingly longer times (e.g. Wilson and Harrison 1998, Baird 2001). The non-linear representation is based on detailed competence studies, which follow the settlement behaviour of a cohort over time, and estimate the proportion of larvae competent to settle at different time intervals.

Competence patterns found in the laboratory for the larvae of spawners are different when they are reared either in the presence or absence of a suitable substratum. In the latter case, aliquots are transferred from an aquarium with no substratum into another with available substratum at different times, forcing the larvae to delay settlement and metamorphosis. The competence patterns obtained with both types of experiments were used in the models for 5 broadcast spawners species (3 acroporids: *A. gemmifera*, *A. millepora* and *A. valida*; and 2 faviids: *G. retiformis* and *P. daedalea*). The competence patterns observed when suitable substratum was present in the rearing aquaria were used

for the larvae retained at their natal reef (see *Chapter 3* for more details), and the patterns observed when no substratum was offered were used for the larvae being dispersed away from their source reef (Figure 5.2.). The larvae produced by many brooders do not require conditioned substratum to settle and metamorphose. They frequently settle onto the glass or plastic walls of aquaria or culture bottles where they are being reared (e.g. Atoda 1947a, Baird 2001), so only one type of competence experiment is possible. Therefore, a single competence pattern type was used in the models for the brooding species (Figure 5.3.).

The data used for the elaboration of the competence curves (representing the cohorts' settlement frequencies over time) in the non-linear representation models was based on laboratory studies conducted by Baird (1998, 2001) for broadcast spawners and by Atoda (1947a, 1947b, 1951) for brooders. For spawners, the competence curves for the cohorts reared in the absence of substratum were available, while those for the cohorts reared in its presence were derived from Baird's (2001) cumulative curves of competence. For brooded larvae, the competence curves were constructed from the settlement values presented by Atoda (1947a, 1947b, 1951). Similar competence curves to those used in this study for *S. histrix* and *S. pistillata* have been obtained by Baird (2001); however, the competence patterns of the larvae of *P. damicornis* vary greatly among laboratory experiments (competence ends after: 9 days in Atoda 1947a, 18 days in Edmonson 1929, and 103 days in Richmond 1988, and larvae have been observed alive for up to 212 days in Harrigan 1972). The competence patterns described by Atoda (1947a) were used because: (1) sufficient information was available to construct a competence curve (rather than just a linear representation), and (2) in this way all the data for brooders was collected by the same author (using the same methodology). The choice of this competence curve does not affect the main aim of this study because only the spawning species were used to investigate the relationship between larval dispersal potential and extent of geographic range (while the brooding species were only used in additional side tests, see *Sections 5.2.C.3., and 5.4.C.*).

The competence curves used in the models for spawners also differed from those presented by Baird (2001), in that the starting point of the curve was not approximated to 0 (i.e. time of fecundation), but to the time when the larvae became mobile (Figure 5.2). The time at which motile larvae were first found in the cohort was used as the starting point of the competence curves for the larvae retained at their natal reef (36 h for the acroporids and 14.5 h for the faviids, Figure 5.2.), while the time at which the

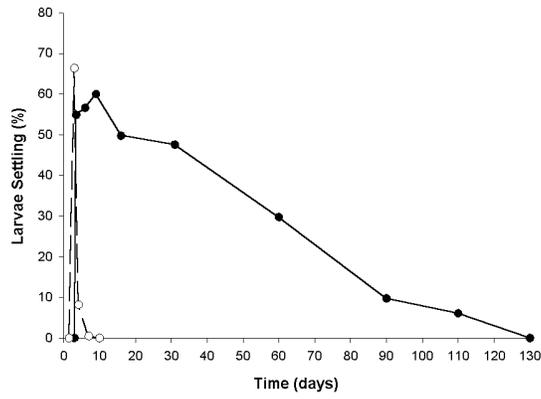


Fig. 5.2.a. *Acropora valida*

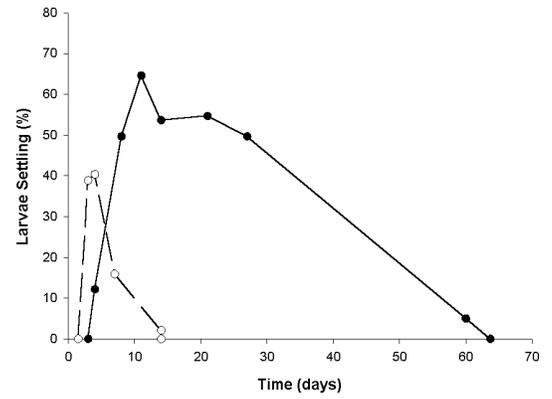


Fig. 5.2.b. *Acropora millepora*

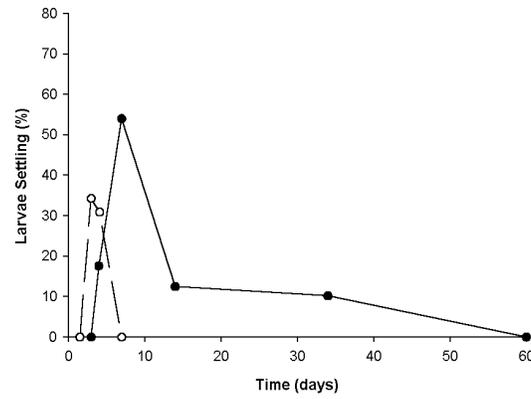


Fig. 5.2.c. *Acropora gemmifera*

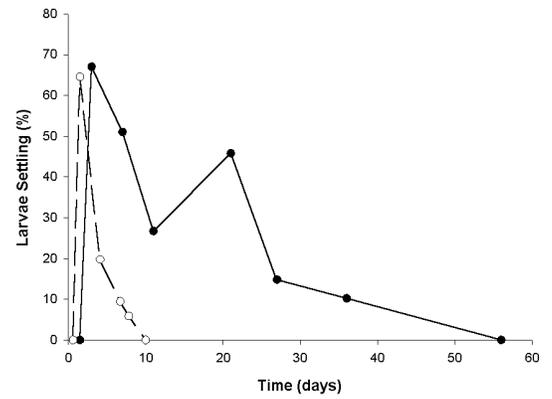


Fig. 5.2.d. *Goniastrea retiformis*

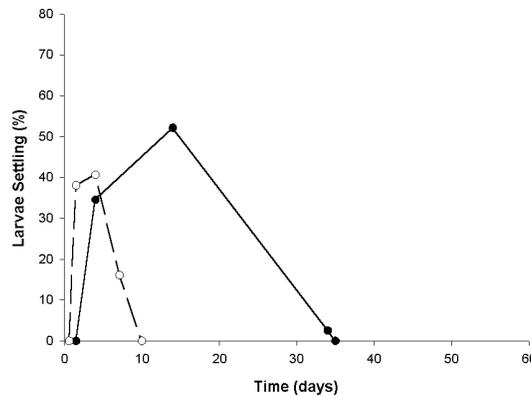


Fig. 5.2.e. *Platygyra daedalea*

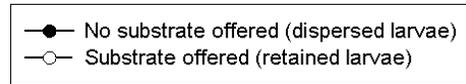


Figure 5.2. Competence patterns of the larvae of the five broadcast spawning coral species used in the non-linear models. Modified from Baird (1998, 2001).

whole cohort was found to be motile was used as the starting point of the competence curves for the larvae dispersed (72 h for acroporids and 36 h for faviids, Figure 5.2.). These times were chosen based on the assumption that larval development is slower in the absence of settlement cues. In brooding corals, larval embryogenesis is already completed and most larvae are mobile on release, although their movement may be limited. Therefore in the models for brooders, the competent period was set to begin upon release, with only a very small proportion of the cohort being competent in these early stages (Figure 5.3.).

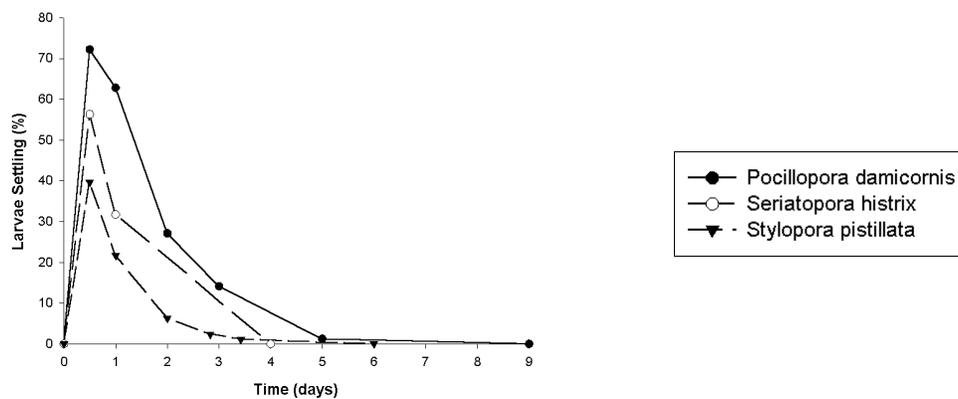


Figure 5.3. Competence patterns of the larvae of the three brooding coral species (substratum offered) used in the non-linear models. Based on data from Atoda (1947a, 1947b, 1951).

5.2.C.3. Data analysis

The analysis of the output data by the models was similar to that described in *Chapter 2*. In this chapter, only six of the dispersal variables computed by the program are presented. These were chosen because they may be relevant in determining the geographic range size of the species. They include: 2 settlement variables (total proportion of settlers - local and non-local - and proportion of non-local settlers in the total larval production); connectivity at evolutionary and ecological scales (i.e. using >0 and ≥ 1000 larvae as the thresholds to consider two reefs connected); and evenness and diversity of the larval input to the reefs in terms of its reef sources (see *Chapter 2* and *Appendix IV*).

5.2.D. Relationship between potential for dispersal and geographic range size

The predicting power of the 6 variables representing the potential for dispersal obtained with the models (proportion of larvae settling, proportion of larvae settling in reefs other than natal, connectivity at evolutionary and ecological scales, and evenness and diversity of the larval input) in relation to the 3 biogeographic variables (area, longitudinal extent and latitudinal extent of the species ranges) was investigated as follows. For each of the 18 possible combinations, a scatterplot was graphed to explore the shape of the relationship, and the coefficient of determination (R^2) and significance (p) of the corresponding regression model were computed. Four sets of this type of analysis were carried out, combining 2 hydrodynamic conditions (with and without water retention at the reefs) and 2 competence pattern representations (linear and non-linear). Therefore, in total 72 (3 biogeographic variables x 6 potential for dispersal variables x 4 sets of models) relationships were examined.

Only the broadcast spawning species were included in this part of the study for two reasons. Firstly, the methods used in the rearing and settlement of the larvae of brooding corals differ largely from those used in spawner corals, precluding direct comparison of the results obtained in both reproductive groups (see *Section 5.2.C.2.6.*). Secondly, competence patterns have been described in detail for very few species of brooding corals (only 3), preventing the independent analysis of the relationship between the dispersal and biogeographic variables within this group of corals.

5.3. RESULTS

5.3.A. Geographic ranges

The studied species differed considerably in the size of their geographic ranges (Figures 5.1. and 5.4.). *Acropora millepora* and *Goniastrea favulus* have relatively restricted distributions, limited to the Indian and Western Pacific oceans. *Acropora valida*, *A. hyacinthus*, *Cyphastrea seralia* and *Pocillopora damicornis* are pandemic in the IP, extending from East Africa to the Central or Eastern Pacific. The remaining 9 species have intermediate distribution range sizes. In general, species differed substantially in the area (Figure 5.4.a.) and longitudinal extent (Figure 5.4.b.) of their ranges, but varied relatively little in the latitudinal extent of their ranges (Figure 5.4.c.).

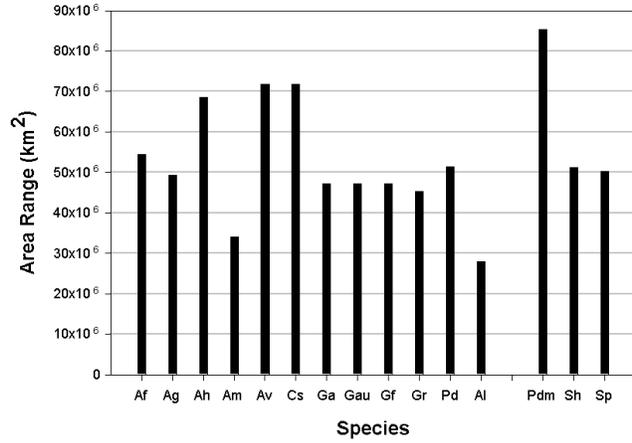
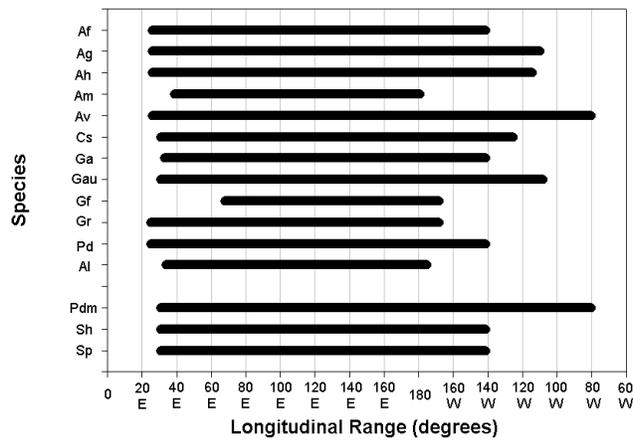


Fig. 5.4.a.



SPAWNERS:
 Af = *Acropora formosa*
 Ag = *Acropora gemmifera*
 Ah = *Acropora hyacinthus*
 Am = *Acropora millepora*
 Av = *Acropora valida*
 Cs = *Cyphastrea seralia*
 Ga = *Goniastrea aspera*
 Gau = *Goniastrea australensis*
 Gr = *Goniastrea retiformis*
 Pd = *Platygyra daedalea*
 Al = *Acanthastrea lordhowensis*

BROODERS:
 Pd = *Pocillopora damicornis*
 Sh = *Seriatopora hystrix*
 Sp = *Stylophora pistillata*

Fig. 5.4.b.

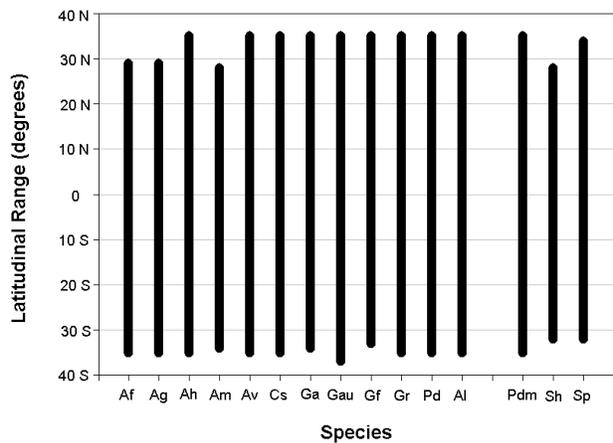


Fig. 5.4.c.

Figure 5.4. Variation in the geographic range sizes of the coral species used in the models. (5.4.a.) Range areas. (5.4.b.) Extent of the longitudinal ranges. (5.4.c.) Extent of the latitudinal ranges.

5.3.B. Potential for dispersal provided by the larvae

5.3.B.1. Broadcast spawners, linear representation

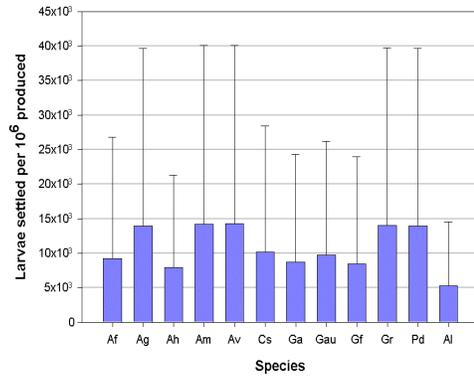
The models predicted that species with short pre-competent periods (*A. gemmifera*, *A. millepora*, *A. valida*, *G. retiformis* and *P. daedalea*) have greater settlement rates. When retention of larvae at reefs was included in the models, settlement rate increased in all species (Figures 5.5.a. and 5.6.a.), particularly in species with shorter pre-competent periods (e.g. 7.5 fold increase in *A. valida* vs. 3 fold in *Acanthastrea lordhowensis*). The increase in settlement with the increase in retention was mainly due to the rise in settlement on natal reefs. However, non-local settlement also increased, as dispersed larvae could become trapped in the circulation of non-natal reefs (see Chapter 3).

The species with longer competent periods (e.g. *A. valida* and *Acanthastrea lordhowensis*) showed higher connectivity among reefs (Figures 5.5.c., 5.5.d., 5.6.c. and 5.6.d.). The differences in connectivity among species were larger at an evolutionary scale (Figures 5.5.c. and 5.6.c.) than at an ecological scale (Figure 5.5.d. and 5.6.d.). When retention was included in the models connectivity at an evolutionary scale did not vary substantially (Figures 5.5.c. and 5.6.c.), but at an ecological scale it decreased becoming more similar among species (Figures 5.5.d. and 5.6.d.).

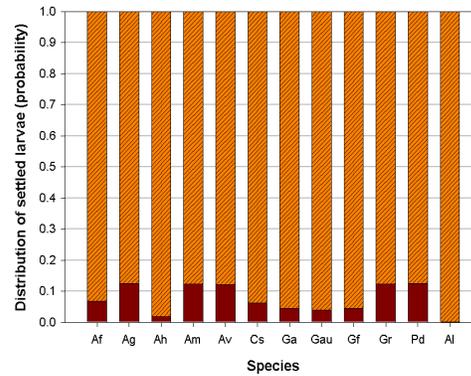
The evenness of reef sources of the settling larvae was very similar among all the species (Figures 5.5.e and 5.6.e.). In the absence of retention, there was no clear relationship between evenness and the length of the pre-competent or competent periods (Figure 5.5.e.). When retention was included in the models, evenness decreased in all species, but especially in those with short pre-competent periods (Figure 5.6.e.). The patterns of diversity of reef sources of the larval input were similar to those of ecological-scale connectivity among reefs (Figures 5.5.f., 5.5.f., 5.6.d., and 5.6.f.).

5.3.B.2. Broadcast spawners, non-linear representation

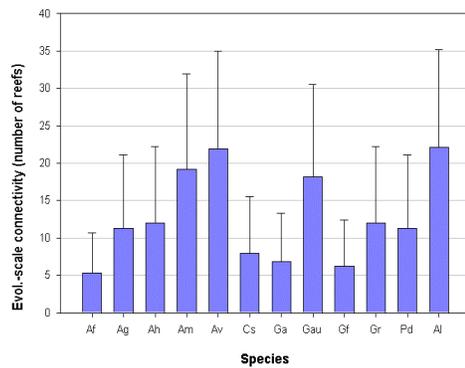
The results obtained in the simulations where a non-linear representation of the competent period of the larvae was used differed from those computed using linear representations, especially those in relation to settlement rate. Settlement rates were very similar in the 5 species used in both representation types when the linear representation was used because their pre-competent periods were equal (Figures 5.5.a. and 5.6.a.). However, the non-linear representation produced different results for all



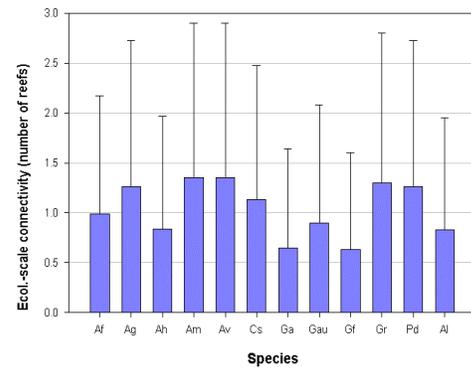
5.5.a.



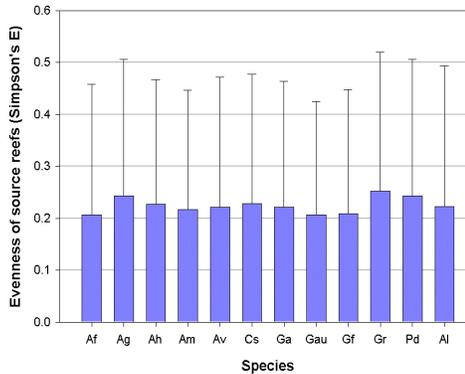
5.5.b.



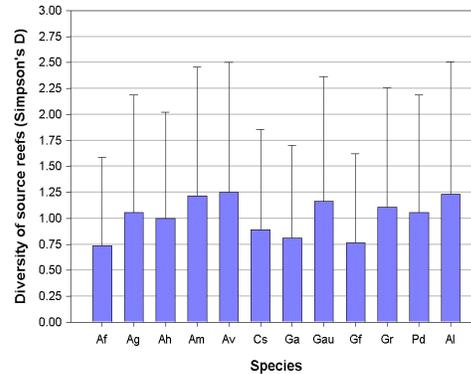
5.5.c.



5.5.d.



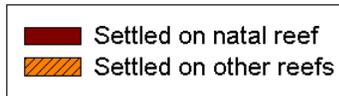
5.5.e.



5.5.f.

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. (5.5.a.) Settlement rate. (5.5.b) Proportion of larvae settling locally and away from natal reef.

(5.5.c) Connectivity among reefs at 0 larva threshold. (5.5.d) Connectivity among reefs at 1000 larvae threshold. (5.5.e) Equitability of larval reef sources (Simpson's E index). (5.5.f) Diversity of larval reef sources (Simpson's D index). Species codes: Af = *Acropora formosa*, Ag = *A. gemmifera*, Ah = *A. hyacinthus*, Am = *A. millepora*, Av = *A. valida*, Cs = *Cyphastrea serralia*, Gs = *Goniastrea aspera*, Gau = *G. australensis*, Gf = *G. favulus*, Gr = *G. retiformis*, Pd = *Platygyra deadalea*, Al = *Acanthastrea lordhowensis*. Error bars represent variation (expressed as standard error) among reefs in the chart. On the right: legend for figure 5.5.b.



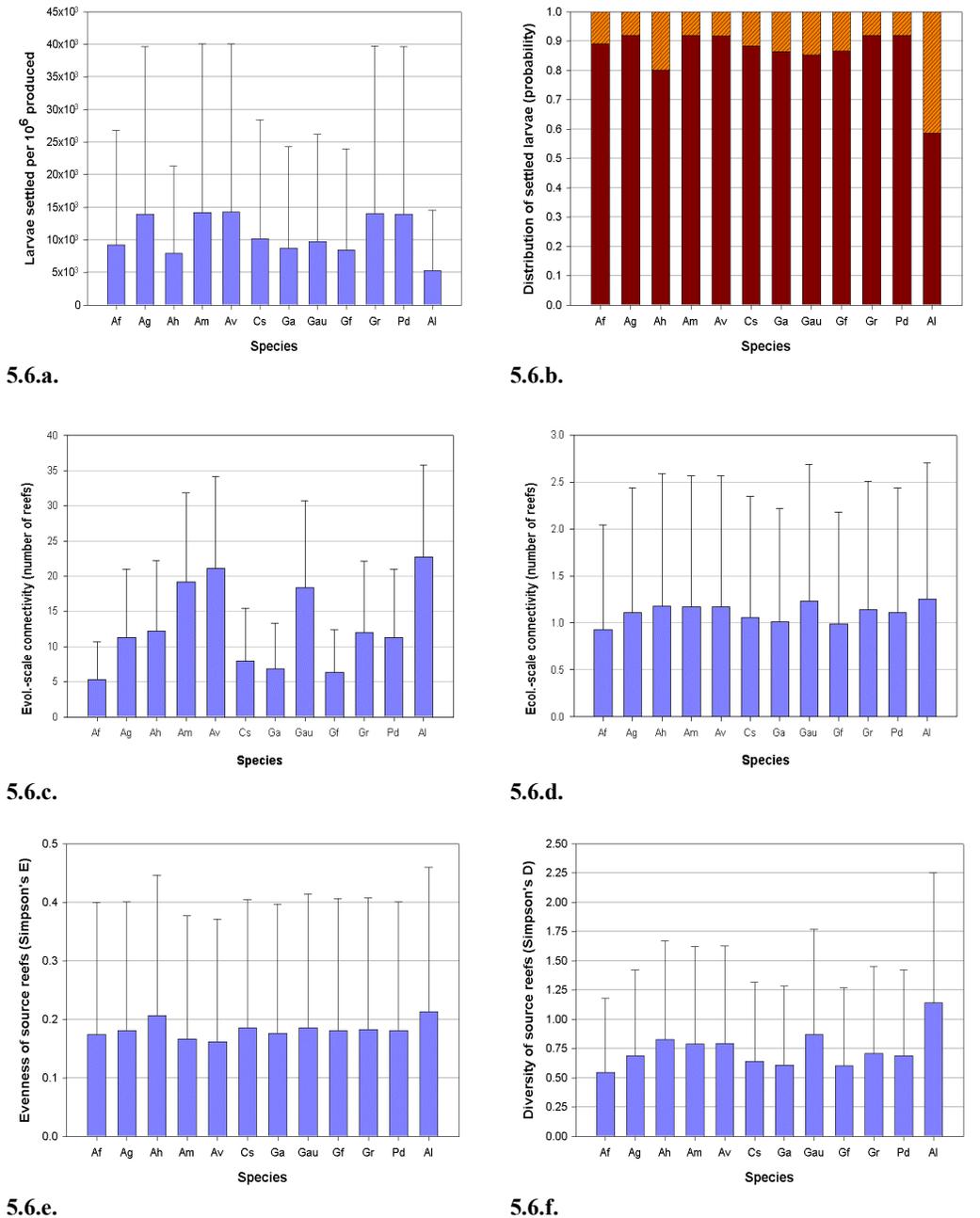


Figure 5.6. Simulation results for the larval dispersal of broadcast spawners in the presence of retention using a linear representation of the competent periods. (5.6.a.) Settlement rate. (5.6.b) Proportion of larvae settling locally and away from natal reef. (5.6.c.) Connectivity among reefs at 0 larva threshold. (5.6.d.) Connectivity among reefs at 1000 larvae threshold. (5.6.e.) Equitability of larval reef sources (Simpson's E index). (5.6.f.) Diversity of larval reef sources (Simpson's D index). Species codes: Af = *Acropora formosa*, Ag = *A. gemmifera*, Ah = *A. hyacinthus*, Am = *A. millepora*, Av = *A. valida*, Cs = *Cyphastrea serralia*, Gs = *Goniastrea aspera*, Gau = *G. australensis*, Gf = *G. favulus*, Gr = *G. retiformis*, Pd = *Platygyra deadalea*, Al = *Acanthastrea lordhowensis*. Error bars represent variation (expressed as standard error) among reefs in the chart. On the right: legend for figure 5.6.b.

species, because each of them varied in the shape of its competence curve. When no retention was used in the simulations, the highest settlement rate was by *G. retiformis*, followed by *A. valida* and *P. daedalea* with similar values, then *A. gemmifera*, and finally *A. millepora* (Figure 5.7.a.). The order differed when retention was present. In this case, the most successful cohort settling was also *G. retiformis*, but the most unsuccessful was *A. valida*, the second most successful species settling in the absence of retention (Figure 5.7.a.).

In the absence of retention, the proportion of larvae that settled locally relative to the total settlement was higher when using the non-linear representation. This was because in the non-linear representation the early peak in the competence curves (see Section 5.2.C.2. in *Methods*) implies that a much larger proportion of larvae in the cohort is competent to settle soon after the pre-competent period ends (when larvae are still close to the natal reef) than later in larval life (Figures 5.5.b., 5.6.b., 5.7.b. and 5.2.). Retention increased the proportion of larvae settling on the natal reef, as was the case in the linear representation of competence, but this increase was larger with the non-linear representation for all the species (Figures 5.5.b., 5.6.b. and 5.7.b.). Furthermore, in the non-linear representation retention altered the patterns of the distribution of settlers (local vs. non-local) across species (Figure 5.7.b.). For example, local settlement was lowest for *A. millepora* in the absence of retention, but intermediate in its presence.

The species ranking of connectivity among reefs was identical in the linear and non-linear representations both at an evolutionary-scale (*A. valida* > *A. millepora* > *A. gemmifera* > *G. retiformis* > *P. daedalea*) and at an ecological-scale (*A. millepora* ~ *A. valida* > *G. retiformis* > *P. daedalea* > *A. gemmifera*) (Figures 5.5.c., 5.5.d, 5.6.c., 5.6.d., 5.7.c. and 5.7.d.). However, the connectivity values differed more substantially among species in the non-linear representation than in the linear representation (Figures 5.5.c., 5.5.d, 5.6.c., 5.6.d., and 5.7.c.). As in the linear representation, connectivity values differed more among species at an evolutionary- than ecological-scale (Figures 5.7.c. and 5.7.d.). Retention increased connectivity among reefs because the larvae can become trapped at reefs other than the natal one (Figures 5.7.c. and 5.7.d., see Chapter 3). Nevertheless, the increase in connectivity with retention was small at an evolutionary-scale (Figure 5.7.e.) and very small at an ecological-scale (Figure 5.7.g.). With retention, connectivity among reefs also became more similar for all species (Figures 5.7.e. to 5.7.g.).

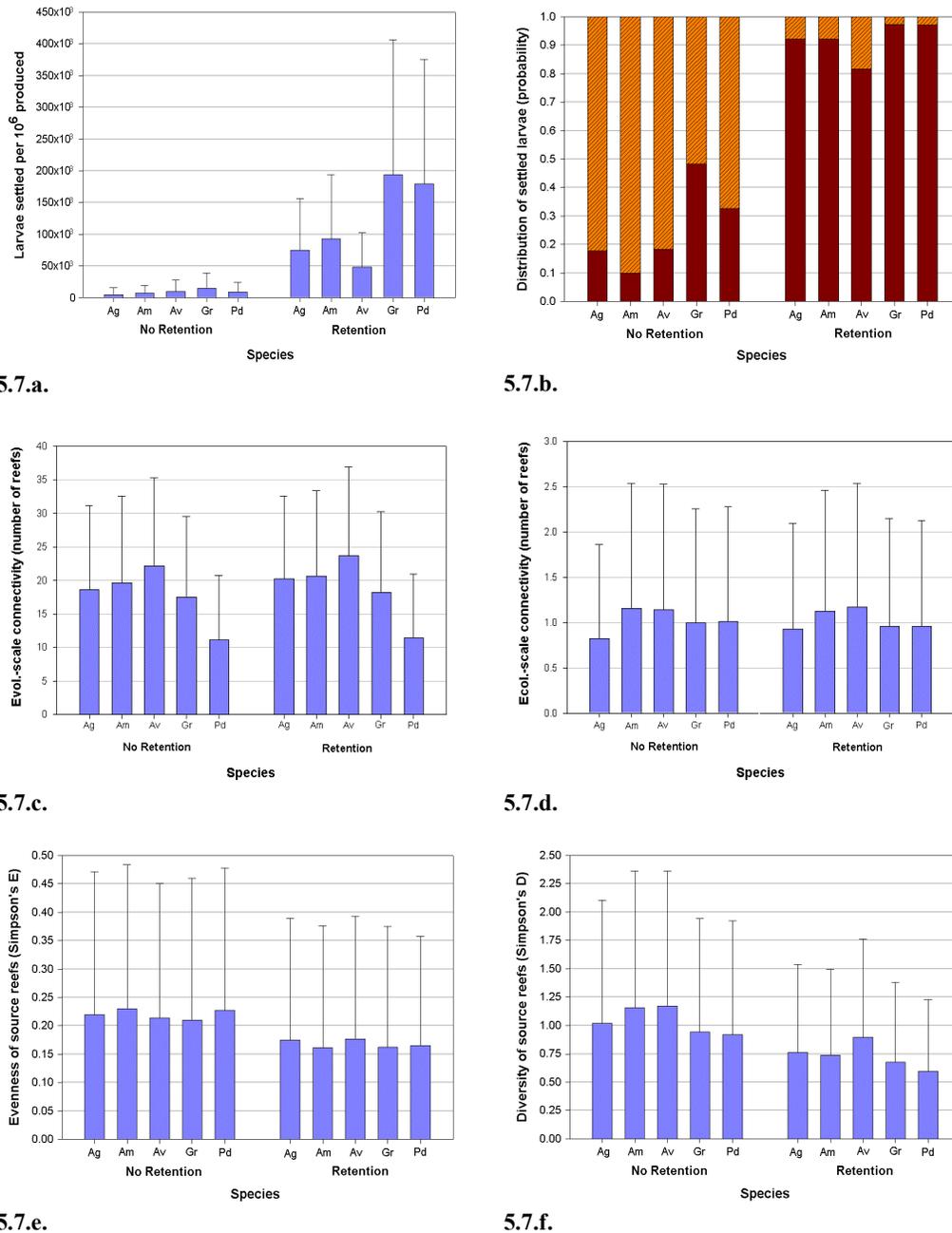
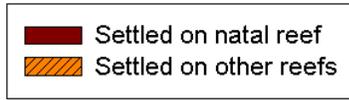


Figure 5.7. Simulation results for the larval dispersal of broadcast spawners in the absence and presence of retention using a non-linear representation of the competent periods. (5.7.a.) Settlement rate. (5.7.b) Proportion of larvae settling locally and away from natal reef. (5.7.c) Connectivity among reefs at 0 larva threshold. (5.7.d) Connectivity among reefs at 1000 larvae threshold. (5.7.e) Equitability of larval reef sources (Simpson’s E index). (5.7.f) Diversity of larval reef sources (Simpson’s D index). Species codes: Af = *Acropora formosa*, Ag = *A. gemmifera*, Ah = *A. hyacinthus*, Am = *A. millepora*, Av = *A. valida*, Cs = *Cyphastrea serralia*, Gs = *Goniastrea aspera*, Gau = *G. australensis*, Gf = *G. favulus*, Gr = *G. retiformis*, Pd = *Platygyra deadalea*, Al = *Acanthastrea lordhowensis*. Error bars represent variation (expressed as standard error) among reefs in the chart. On the right: legend for figure 5.7.b.



The patterns of evenness of sources of the settling larvae varied between the linear and non-linear representations. For example, in the absence of retention *G. retiformis* had the highest evenness among all species with the linear representation, but the lowest with the non-linear representation, whereas *A. millepora* showed the lowest evenness with the linear representation and the second highest with the non-linear one. The diversity of the larval input to the reefs showed similar patterns to those of connectivity, and to those obtained using the linear representation (Figure 5.7.f). Retention reduced evenness and diversity, and changed their patterns among species (Figures 5.7.e. and 5.7.f).

5.3.B.3. Brooders, non-linear representation

Settlement rates were much higher in brooders than spawners (Figures 5.5.a., 5.6.a., 5.7.a. and 5.8.a.). The highest settlement rate was exhibited by *P. damicornis*, followed by *S. histrix* and *S. pistillata*. This order is a consequence of the corresponding shapes of the larval competence curves (Figure 5.3.), rather than the duration of the pre-competent period (equal for all species). When retention was included in the models, settlement rate increased greatly in all 3 species, but the pattern among species was maintained (Figure 5.8.a.). In brooders, the increase in settlement rate provided by retention comes exclusively from an increase in local recruitment, and contrary to spawning corals non-local settlement decreased. In fact, non-local settlement was very small for all the brooded larvae even when no retention was present (0.11% to 0.75% of the total settled larvae), and virtually non-existent (0.05% to 0.24%) when retention was included (Figure 5.8.b.). The proportion of non-local settlers was mainly related to the shape and length of the larval competence curve (as the 3 species have the same pre-competent period length) (Figure 5.3., Table 5.3.), with *P. damicornis* having the highest proportion and *S. pistillata* the lowest (Figure 5.8.b.).

Connectivity among reefs was in all cases (i.e. for all species, hydrodynamic condition and connectivity threshold combinations) much lower in brooders than broadcast spawners (Figures 5.6.c., 5.6.d., 5.7.c., 5.7.d., 5.8.c. and 5.8.d.). Among the brooding species connectivity differed notably at an evolutionary scale (Figure 5.8.c.), and was similar at ecological scales (Figure 5.8.d.). Connectivity among reefs at an evolutionary scale was related to the length of the competent period. The highest connectivity at this scale was displayed by *P. damicornis*, and then *S. pistillata* closely followed by *S. histrix* (Figures 5.8.c. and 5.8.d., Table 5.3.). However, connectivity at

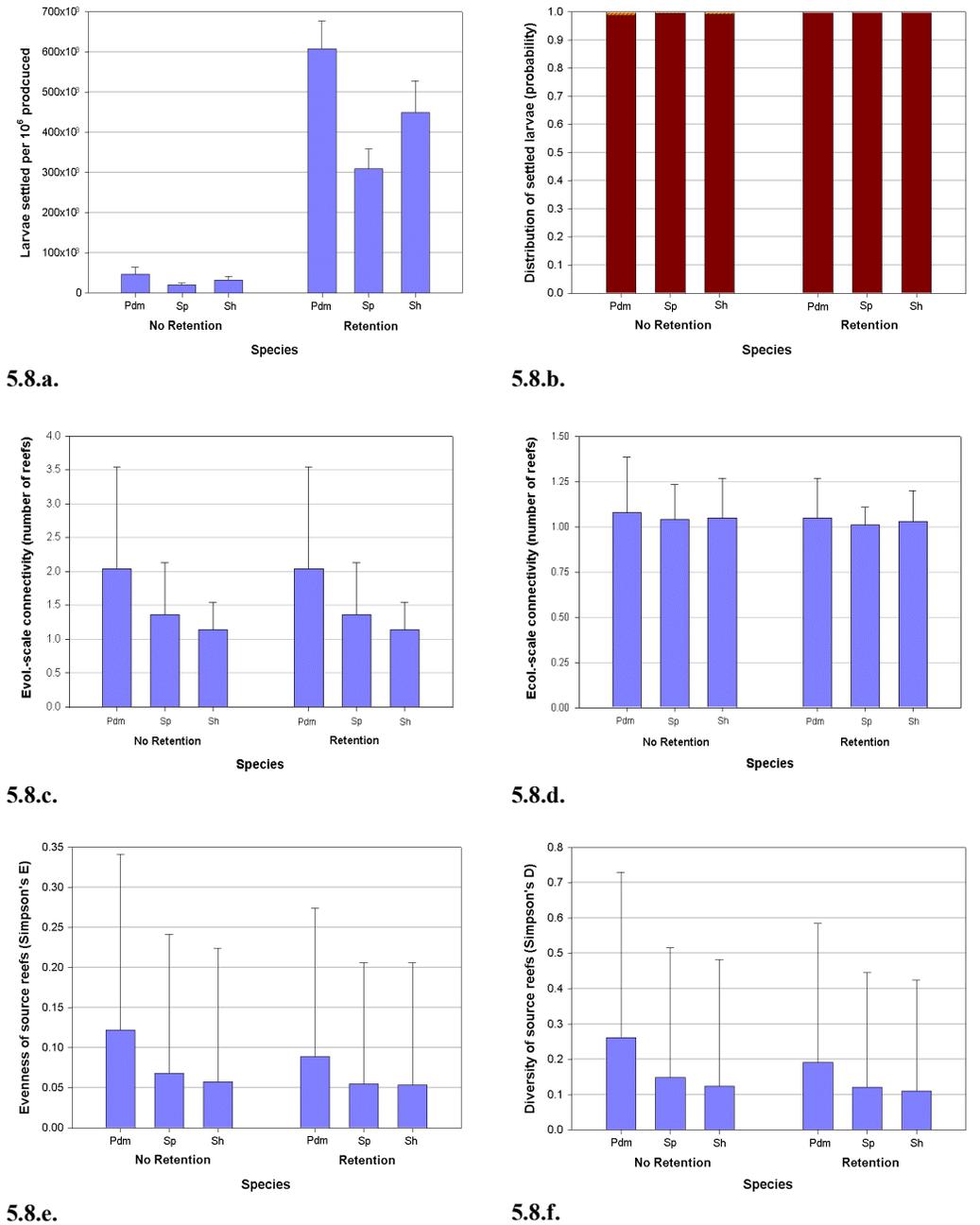
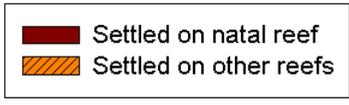


Figure 5.8. Simulation results for the larval dispersal of brooders in the absence and presence of retention using a non-linear representation of the competent periods. (5.8.a.) Settlement rate. (5.8.b) Proportion of larvae settling locally and away from natal reef. (5.8.c) Connectivity among reefs at 0 larva threshold. (5.8.d) Connectivity among reefs at 1000 larvae threshold. (5.8.e) Evenness of larval reef sources (Simpson’s E index). (5.8.f) Diversity of larval reef sources (Simpson’s D index). Species codes: Af = *Acropora formosa*, Ag = *A. gemmifera*, Ah = *A. hyacinthus*, Am = *A. millepora*, Av = *A. valida*, Cs = *Cyphastrea serralia*, Gs = *Goniastrea aspera*, Gau = *G. australensis*, Gf = *G. favulus*, Gr = *G. retiformis*, Pd = *Platygyra deadalea*, Al = *Acanthastrea lordhowensis*. Error bars represent variation (expressed as standard error) among reefs in the chart. On the right: legend for figure 5.8.b.



ecological scales, although similar among the 3 species, was lowest for *S. pistillata* (Figure 5.8.d.). This occurs because the tail of the competence curve of *S. pistillata* although longer is much thinner (i.e. a lower proportion of larvae is competent to settle) than the tail of the curve of *S. hystrix* (Figure 5.3.). Retention hardly affected connectivity at an evolutionary scale (Figure 5.8.c.), but slightly decreased it at an ecological scale (Figure 5.8.d.).

The evenness and diversity of the larvae recruited on the reefs were also mainly determined by the duration of the larval competent period (Figures 5.8.e. and 5.8.f., Table 5.3.). The values computed for evenness, diversity and their variation among reefs were largest for *P. damicornis*. The values for *S. pistillata* and *S. hystrix* were similar, the latter being the smallest. The diversity of the larval input to the reefs was considerably lower in the brooding than the spawning species (Figures 5.6.f, 5.7.f. and 5.8.f.). Retention decreased both evenness and diversity in similar proportions in all species (Figures 5.8.e. and 5.8.f.).

5.3.C. Relationship between larval dispersal potential and geographic range size

In only one of the 72 possible combinations between the variables describing the potential for dispersal of the larvae and the size of the geographic ranges of the spawning species (see *Section 5.2.D.*) the regression models revealed a significant relationship (Table 5.4.). This was the relationship between mean evenness of sources of the larval input to the reefs when the non-linear representation of the competent periods and water retention at the reefs were used in the models and the longitudinal extent of the range ($R^2 = 0.898$, $p = 0.014$) (Table 5.4.D. and Figure 5.11.).

5.4. DISCUSSION

5.4.A. Variation in range sizes of corals in the Indo-Pacific

The longitudinal extent and area of the geographic ranges of the 15 species of scleractinian corals in the study varied substantially. However, the variation in the latitudinal extent of their ranges was small. This is not surprising as there is a significant

Table 5.4. Relationship among biogeographic variables and the dispersal variables obtained with the models for broadcast spawning corals. (5.4.A.) Linear representation of the larval competent period and no retention. (5.4.B.) Linear representation of the larval competent period and retention. (5.4.C.) Non-linear representation of the larval competent period and no retention. (5.4.D.) Non-linear representation of the larval competent period and retention. *Columns:* biogeographic variables (*Area* = area of the range, *Long. Extent* = longitudinal extent of the range, *Lat. Extent* = latitudinal extent of the range). *Rows:* dispersal variables (*Total Settlement (%)* = Percentage of the larvae released that settled during the course of the simulation, *Non-local Settlement (%)* = Percentage of the larvae released that settled on reefs other than natal during the course of the simulation, *Ecological Connectivity* = Connectivity among reefs using '> 0' larva as connectivity threshold, *Evolutionary Connectivity* = Connectivity among reefs using '≥ 1000' larvae as connectivity threshold, *Evenness* = Evenness of sources of the settled larvae, *Diversity* = Diversity of sources of the settled larvae (see Section 5.2. for details and Chapter 2). *Cells: Top Row* = coefficient of determination (R^2), *Bottom Row* = significance (p).

5.4.A. Linear Representation, No Retention.

	Area	Long. Extent	Lat. Extent
Total Settlement (%)	0.0208 0.6548	0.0668 0.4173	0.0878 0.3496
Non-Local Settlement (%)	0.0313 0.5826	0.0798 0.3737	0.0768 0.3831
Evolutionary Connectivity	0.0684 0.4116	0.0233 0.6361	0.0260 0.6165
Ecological Connectivity	0.0208 0.6550	0.0930 0.3348	0.0761 0.3855
Evenness	0.0037 0.8505	0.0219 0.6464	0.0183 0.6753
Diversity	0.0615 0.4371	0.0374 0.5469	0.0244 0.6276

5.4.B. Linear Representation, Retention.

	Area	Long. Extent	Lat. Extent
Total Settlement (%)	0.0276 0.6060	0.0478 0.4947	0.1299 0.2498
Non-Local Settlement (%)	0.1954 0.1502	0.2151 0.1289	0.0000 0.9970
Evolutionary Connectivity	0.0870 0.3520	0.0158 0.6973	0.0278 0.6046
Ecological Connectivity	0.0474 0.4965	0.0349 0.5612	0.1321 0.2455
Evenness	0.0279 0.6038	0.0176 0.6809	0.1813 0.1676
Diversity	0.1530 0.2086	0.0006 0.9375	0.1049 0.3045

5.4.C. Non-Linear Representation, No Retention.

	Area	Long. Extent	Lat. Extent
Total Settlement (%)	0.0157 0.8408	0.0330 0.7698	0.5510 0.1508
Non-Local Settlement (%)	0.1544 0.5129	0.0001 0.9846	0.4460 0.2180
Evolutionary Connectivity	0.0627 0.6846	0.0705 0.6660	0.0945 0.6149
Ecological Connectivity	0.0060 0.9013	0.0546 0.7051	0.0060 0.9019
Evenness	0.2521 0.3887	0.1792 0.4775	0.3047 0.3347
Diversity	0.0383 0.7525	0.0229 0.7810	0.1894 0.4639

5.4.D. Non-Linear Representation, Retention

	Area	Long. Extent	Lat. Extent
Total Settlement (%)	0.1462 0.5253	0.2853 0.3538	0.2057 0.4429
Non-Local Settlement (%)	0.2676 0.3720	0.1838 0.4714	0.0110 0.8670
Evolutionary Connectivity	0.0760 0.6535	0.0969 0.6102	0.998 0.6045
Ecological Connectivity	0.0831 0.6382	0.0104 0.8702	0.0133 0.8534
Evenness	0.6025 0.1227	0.8979 0.0143	0.0087 0.8812
Diversity	0.3297 0.3114	0.3530 0.2908	0.0156 0.8415

temperature gradient associated with latitude (e.g. Brown and Lomolino 1998, Cox and Moore 2000), and the growth and reproduction of hermatypic corals have strict requirements for this environmental variable (e.g. Wells 1957, Nybakken 1993, Huston 1994). Suitable conditions for most scleractinian coral species are only found between latitudes 35°N and 35°S , a much narrower band than the longitudinal extent of the IP (260° , between longitudes 20°E and 80°W). The similarity in the extent of the latitudinal ranges in the study is a consequence of the species occupying the majority of this suitable latitudinal range.

5.4.B. Variation in larval dispersal potential of corals in the Indo-Pacific

As in previous chapters, settlement rate was mainly dependent on the length of the pre-competent period, while connectivity among reefs by larvae was primarily related to the length of the competent period. Short pre-competent periods allow the larvae to settle earlier, shortening the time larvae are exposed to the decimating environmental mortality that occurs during dispersal (e.g. Thorson 1950, Day and McEdward 1984, Young and Chia 1987, Rumrill 1990). Furthermore, short pre-competent periods also imply that the larvae will not be dispersed far away. Larvae that settle on their natal or adjacent reefs are more prone to find the conditions they are adapted to, potentially reducing post-settlement mortality (e.g. Warner 1997, Strathmann et al. 2002). Long competent periods, on the other hand, contribute to increase the chances of larvae encountering reefs within a wide range of distances, resulting in higher connectivity. Long pre-competent periods can also increase the distance between connected reefs, but do not necessarily increase connectivity, especially at ecological levels, as absolute larval mortality increase and very few larvae (or none) may settle on the natal and neighbouring reefs.

The shape of the competence curve is also crucial in determining settlement and connectivity. The linear representation of the competent periods yielded similar settlement rates for species with comparable pre-competent periods. However, with the non-linear representation settlement was not only more local but also quite different among species as it depended on the height and position of the cohort's competence peak too. Likewise, the linear representation produced similar connectivity values when the lengths of the pre-competent and competent periods of the species were comparable. However, with the non-linear representation differences in the tail of the competence curves produced distinct connectivity values for each species. Furthermore, the non-

linear representation also produced different connectivity patterns (i.e. species rankings) at different connectivity levels.

Retention increased settlement in both spawning and brooding corals, but the causes of the increase were slightly different in both reproductive groups. In both cases the greater settlement rates were mainly caused by an increase in settlement of larvae on their natal reefs. In fact, in species with long pre-competent periods unless retention was included in the models, local settlement was very low or null. In brooding corals, when retention was included in the models the already minimal non-local settlement became almost negligible. Conversely, in broadcast spawning corals an increase in non-local settlement also occurred when retention was present in the models, as larvae were also trapped in the circulation around the reefs they dispersed to (see *Chapter 3*). As a consequence, retention also contributed to a small increase in the connectivity among reefs of the spawning species, especially at an evolutionary scale, while it hardly had any effect on the connectivity of the brooding species. Because of their longer pre-competent and competent periods the larvae of spawners can encounter more reefs than the larvae of brooding corals. When retention is present, this potential can be translated into increased non-local settlement and connectivity because larvae that encountered the reefs too early in the absence of retention can then be retained until they are able to settle and metamorphose (see *Chapter 3*).

Additional simulations run using larger-scale charts (i.e. representing smaller areas) and higher reef densities produced comparable settlement patterns to the models previously used. However, these models yielded more similar connectivity values among species because the dispersal capabilities of the species were not fully exploited. Likewise, when higher mortality rates were used, settlement and connectivity were more similar among species, as fewer larvae entered the competent period and even less reached the latter stages of this period. Therefore, although the larvae of distinct species may possess different dispersal capabilities, the environmental conditions may considerably reduce the degree to which their variation in dispersal potential is actually expressed.

5.4.C. Relationship between larval dispersal potential and geographic range size

If the dispersal potential of the larvae of coral species was the main factor determining the size of their geographic ranges, it would be expected that as reef density decreases (e.g. when moving east in the Pacific) fewer species would be able to connect the increasingly separated 'stepping stones' reefs (*sensu* Kimura and Weiss 1964, Veron 1995). In other words, the species that produce larvae with greater dispersal capabilities would have larger distribution ranges. Nevertheless, only one of the 72 possible regressions among the model dispersal and biogeographic variables for broadcast spawning corals produced a significant fit. This was the regression between the average evenness of reef sources of the larval input to the reefs when the models included a non-linear representation of the larval competence patterns and water retention at the reefs and the longitudinal extent of the geographic range of the species. Although the models including a non-linear representation and retention are likely to be the most accurate (see *Section 5.2.C.2.* and *Chapter 4*), a significant relationship between evenness and longitudinal range extent is surprising. Because dispersal theory assumes that the size of geographic range is dependent on the maximum potential for dispersal of the species (e.g. Connell 1973, Brown and Gibson 1983, Richmond 1990a, Sammarco 1991, Veron 1995), the model dispersal variables expected to show the strongest relationship with range size are the connectivity among reefs (at evolutionary and ecological scales), the proportion of non-local settlers, and the diversity of the larval input to the reefs. Statistically, at a 95% confidence level, nearly 4 (3.79) significant relationships would have been expected by chance alone. In fact, obtaining one significant relationship out of 72 possible corresponds to a confidence coefficient of almost 0.99 (0.9861) (i.e. ~99% probability that the relationship was significant by chance alone). Moreover, evenness was a poor predictor of longitudinal range extent in the remaining 3 model types (i.e. when a linear representation of the competent period or no retention were used), further suggesting that the relationship was significant by chance. In addition to randomness, the significant relationship found in this study between the evenness of sources of the settling larvae and the longitudinal extent of the geographic ranges could be due, at least in part, to the low number of species (5) included in the analysis.

Similarly, a study of the population genetics of 9 species of corals along the GBR concluded that gene flow (an estimate of the genetically effective number of migrants

per generation) was not a good predictor of the geographic range size of the species (Ayre and Hughes 2000). Interestingly, within each reproductive group the estimates of gene flow in this study show a tentative relationship with the values obtained in the models for the dispersal variables (Table 5.5.). Unfortunately, both studies (modelling of dispersal potential and estimation of gene flow) have only 3 species in common within each reproductive type (*P. damicornis*, *S. pistillata* and *S. histrix* for brooders; and *A. hyacinthus*, *A. millepora* and *A. valida* for spawners). In brooders, for which both linear and non-linear representations of the competent period could be constructed for all the species, the relationship between larval potential for dispersal and gene flow was much stronger when the non-linear representation was used (Table 5.5.A.), reinforcing the idea of this being a more precise representation. The relationship between the dispersal variables and gene flow seemed stronger in brooders than spawners. This could simply be due to particularities in the life histories of the species (e.g. *A. millepora* and *A. valida* showed evidence for extensive localised asexual reproduction in the genetic study) and/or the locations where the genetic study was carried out (e.g. the reef matrix in the GBR might be too dense, with numerous 'stepping-stone' reefs, to allow effective discrimination among the long dispersal potentials of the larvae of the spawning species in their gene flow estimates) (see also Ayre and Hughes 2000, 2004). Nevertheless, if only the curve representing the competence patterns obtained for the larvae reared in the presence of suitable settlement substratum was used in the models for spawners, the relationship between the larvae dispersal variables obtained in the simulations and gene flow became more obvious (Table 5.5.C.). This result suggests that in the GBR the majority of larvae of spawning corals either develop with competence patterns closer to those found in larvae reared in the presence of settlement cues than in their absence (which would imply that the reef matrix of the GBR provides abundant cues over all its extension) or more likely develop and settle on or near their natal reefs.

The environmental conditions used for rearing the larvae of spawners in the presence of suitable substratum and brooders, although not identical, were similar in that in both cases settlement substratum was available at all times to the larvae. The values of the variables describing dispersal potential computed by the models using the competence curves of these larvae (i.e. brooders and spawners reared exclusively in the presence of substratum) were combined to increase the sample size and allow the investigation of their relationship with gene flow using regression analysis. Of all the

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. Rows: potential for dispersal variables (*Total Settlement (%)* = Percentage of the larvae released that settled during the course of the simulation, *Non-local Settlement (%)* = Percentage of the larvae released that settled on reefs other than natal during the course of the simulation, *Evolutionary Connectivity* = Connectivity among reefs using '> 0' larva as connectivity threshold (criteria to consider two reefs as connected), *Ecological Connectivity* = Connectivity among reefs using '≥ 1000' larvae as connectivity threshold, *Evenness* = Evenness of origins of the larvae settled, *Diversity* = Diversity of origins of the larvae settled (see Section 5.2. for details and Chapter 2)) and gene flow (N_m). (5.5.A.) Brooding coral species. (5.5.B.) Broadcast spawning coral species, using 2 competence curves (representing presence and absence of substratum during rearing, see Section 5.2.C.2.) in the non-linear representation. (5.5.C.) Broadcast spawning coral species, using only 1 competence curve (representing presence of substratum during rearing, see Section 5.4.C.) in the non-linear representation. Competence could only be represented linearly for *A. hyacinthus*.

Table 5.5.A. Brooding corals. *P.d.* = *P. damicornis*, *S.h.* = *S. hystrix* and *S.p.* = *S. pistillata*.

BROODERS	LINEAR NO RETENTION			LINEAR RETENTION			NON-LINEAR NO RETENTION			NON-LINEAR RETENTION		
	<i>P.d.</i>	<i>S.h.</i>	<i>S.p.</i>	<i>P.d.</i>	<i>S.h.</i>	<i>S.p.</i>	<i>P.d.</i>	<i>S.h.</i>	<i>S.p.</i>	<i>P.d.</i>	<i>S.h.</i>	<i>S.p.</i>
Species												
Total Settlement (%)	4.69	4.47	4.19	29.20	29.13	29.04	4.77	3.17	2.04	60.75	44.99	30.95
Non-local Settlement (%)	0.96	0.75	0.51	0.26	0.20	0.13	0.06	0.03	0.01	0.02	0.01	0.00
Evolutionary Connectivity	1.73	1.07	0.69	1.73	1.07	0.69	2.04	1.14	1.36	2.04	1.14	1.36
Ecological Connectivity	0.72	0.61	0.57	0.62	0.57	0.54	1.08	1.05	1.04	1.05	1.03	1.01
Evenness	0.18	0.12	0.08	0.14	0.09	0.06	0.12	0.06	0.07	0.09	0.05	0.06
Diversity	0.43	0.28	0.19	0.33	0.20	0.14	0.26	0.12	0.15	0.19	0.11	0.12
Gene Flow (N_m)	31.00	1.40	2.50	31.00	1.40	2.50	31.00	1.40	2.50	31.00	1.40	2.50

Table 5.5.B. Broadcast spawning corals, using 2 competence curves in the non-linear representation. *A.h.* = *A. hyacinthus*, *A.m.* = *A. millepora* and *A.v.* = *A. valida*

SPAWNERS	LINEAR NO RETENTION			LINEAR RETENTION			NON-LINEAR NO RETENTION			NON-LINEAR RETENTION		
	<i>A.h.</i>	<i>A.m.</i>	<i>A.v.</i>	<i>A.h.</i>	<i>A.m.</i>	<i>A.v.</i>	<i>A.h.</i>	<i>A.m.</i>	<i>A.v.</i>	<i>A.h.</i>	<i>A.m.</i>	<i>A.v.</i>
Species												
Total Settlement (%)	0.79	1.42	1.42	4.20	10.71	10.71	-	0.69	0.99	-	9.29	4.86
Non-local Settlement (%)	0.78	1.25	1.25	0.84	0.87	0.87	-	0.62	0.81	-	0.73	0.89
Evolutionary Connectivity	12.02	19.20	21.97	12.16	19.15	21.15	-	19.64	22.11	-	20.62	23.68
Ecological Connectivity	0.84	1.35	1.35	1.18	1.17	1.17	-	1.16	1.14	-	1.13	1.17
Evenness	0.23	0.22	0.22	0.21	0.17	0.16	-	0.23	0.21	-	0.16	0.18
Diversity	1.00	1.22	1.25	0.83	0.79	0.79	-	1.16	1.17	-	0.74	0.89
Gene Flow (N_m)	4.80	24.80	12.30	4.80	24.80	12.30	4.80	24.80	12.30	4.80	24.80	12.30

Table 5.5.C. Broadcast spawning corals, using 1 competence curve. *A.h.* = *A. hyacinthus*, *A.m.* = *A. millepora* and *A.v.* = *A. valida*

SPAWNERS	NON-LINEAR NO RETENTION			NON-LINEAR RETENTION		
	<i>A.h.</i>	<i>A.m.</i>	<i>A.v.</i>	<i>A.h.</i>	<i>A.m.</i>	<i>A.v.</i>
Species						
Total Settlement (%)	-	0.73	0.70	-	14.83	15.76
Non-local Settlement (%)	-	0.00	0.00	-	0.00	0.00
Evolutionary Connectivity	-	2.56	1.61	-	2.56	1.61
Ecological Connectivity	-	0.61	0.54	-	0.59	0.53
Evenness	-	0.18	0.13	-	0.14	0.09
Diversity	-	0.44	0.29	-	0.33	0.20
Gene Flow (N_m)	4.80	24.80	12.30	4.80	24.80	12.30

dispersal variables, evolutionary-scale connectivity (the number of reefs connected by any amount of larvae) was expected to have the greatest predicting power about gene flow, as it was in fact calculated in the models as a surrogate for gene flow. Not only did evolutionary-scale connectivity show the strongest relationship with gene flow among all the dispersal variables, but it was also an almost significant predictor of the latter, its variation explaining nearly 76% of the variation in gene flow ($R^2=0.7596$, $p=0.0542$) in both models with and without retention (evolutionary-scale connectivity values are almost identical in both types of models) (Table 5.6., Figure 5.9.). This further indicates a relationship between dispersal potential of the larvae and gene flow, and reinforces the idea that in the GBR either settlement cues are abundant or larvae settle close to their natal reef. Consequently, realised gene flow seems related to the dispersal potential of the larvae, but neither of them primarily determines the geographic range of the coral species in the IP. Similarly in fishes, where the relationship between geographic ranges and larval duration is also unclear (see *Section 5.1.A.*), there is tentative evidence for a positive relationship between gene flow and duration of pelagic larval life, at least within families (Schulman and Bermingham 1995, Schulman 1998).

Geographic ranges are in continuous evolution since environmental conditions change endlessly (particularly at geological time-scales). To attain their present ranges, species have needed substantial periods that are likely to differ in length among species (i.e. species might have originated and/or experienced changes in the environmental conditions in their ranges at different times). The lack of relationship between dispersal potential and geographic range may be partially due to differences in “dispersion” (i.e. range expansion) time among the species in the study. However, there are numerous other factors that determine the biogeography of corals. Some of them, like the dispersal capabilities of the larvae, are intrinsic to each species. These include larval behaviour, as well as the life history and multi-dimensional environmental niche (*sensu* Hutchinson 1957) of the species. Other factors are related to the physical world that the species inhabit, such as: environmental conditions, historical events, and stochastic (e.g. chance dispersal) events. These factors are highly inter-related, combining differently in space, time, and each species. Relatively small differences (biological or historical) among otherwise similar species can have pervasive effects on the ecology of the species, which may be reflected in their spatial distributions (Brown 1995). Although the dispersal potential of the larvae can be an important factor determining the geographic

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*). (5.6.A.) Retention absent. (5.6.B.) Retention present. *Columns* = gene flow (N_{em}) and dispersal potential variables (*Total Settlement (%)* = Percentage of the larvae released that settled during the simulation, *Non-local Settlement (%)* = Percentage of the larvae released that settled on reefs other than natal during the simulation, *Evolutionary Connectivity* = Connectivity among reefs using '> 0' larva as connectivity threshold, *Ecological Connectivity* = Connectivity among reefs using '≥ 1000' larvae as connectivity threshold, *Evenness* = Evenness of origins of the larvae settled, *Diversity* = Diversity of origins of the larvae settled (see *Section 5.2* for details and *Chapter 2*)). *Cells: Top Row* = coefficient of determination (R^2), *Bottom Row* = significance (p).

Table 5.6.A. No Retention.

RETENTION ABSENT	Total Settlement	Non-Local Settlement	Evolutionary Connectivity	Ecological Connectivity	Evenness	Diversity
Gene Flow (N_{em})	0.0470	0.1305	0.7596	0.0423	0.5906	0.5395
	0.7260	0.5502	0.0542	0.7398	0.1289	0.1575

Table 5.6.B. Retention Included.

RETENTION PRESENT	Total Settlement	Non-Local Settlement	Evolutionary Connectivity	Ecological Connectivity	Evenness	Diversity
Gene Flow (N_{em})	0.0288	0.1824	0.7596	0.0467	0.5677	0.5052
	0.7848	0.4731	0.0542	0.7270	0.1414	0.1784

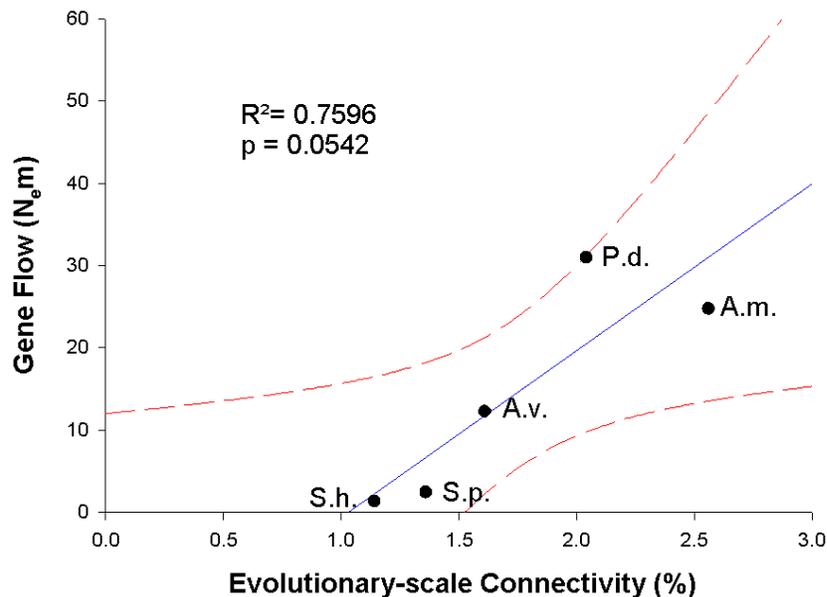


Figure 5.9. Relationship between the evolutionary-scale connectivity values computed by the models (using non-linear representations of the larval competent period) and the gene flows estimated in the GBR (Ayre and Hughes 2000) for 5 species of coral. P.d. = *Pocillopora damicornis*, S.h. = *Stylophora pistillata*, and S.p. = *Seriatopora histrix*, A.m. = *Acropora millepora* and A.v. = *Acropora valida*. Blue = regression fitted line, Red = 95% confidence interval, R^2 = coefficient of determination, p = significance.

ranges of coral species, other contributing factors mask its differential effect across species in the IP.

5.4.D. Study limitations

Constraints in the models and statistical analysis limited the investigation of the relationship between dispersal potential of the larvae and size of geographic range in this study. The models themselves were limited by the experimental data.

5.4.D.1. Experimental limitations

The results from different laboratory experiments may be difficult to compare, as many environmental conditions can affect the duration and patterns of the pre-competent and competent periods of the larvae in a cohort (Pechenik 1990). The competence data for the non-linear representation of spawners and brooders each come from a single author using the same methods for all species (see *Section 5.2.C.2.6.*), thus most of the environmental variability among experiments within reproductive types had been controlled for, facilitating comparisons among species. The data on the competence patterns used in the linear representation of spawners, on the other hand, were obtained from 4 different authors (see Table 5.1.). In these cases the environmental conditions and experimental protocols might have influenced the results. Temperature is one of the most important factors affecting the length of the pre-competent and competent periods, with lower temperatures extending their duration (e.g. Pechenik 1987, Hoegh-Guldberg and Pearse 1995, Zaslow and Benayahu 1996, Avila 1998). The competence studies for *A. lordhowensis* were carried out at 22 to 26°C (Wilson and Harrison 1998); this is 2 to 8 °C lower than the temperature at which the other experiments were carried out. The very long pre-competent (11 days) and competent (67 days) periods found for this species may be due, at least in part, to the low temperature at which the experiments were carried out.

The experiments from which the competence patterns used in the models were derived each employed larvae obtained from a single location. However, there is important geographic variation in the reproductive biology of corals. Of the species in the study, *G. aspera* both spawns and broods in Okinawa (Sakai 1997), while *P. damicornis* spawns in western Australia (Ward 1992). The brooded larvae of *G. aspera* settle soon after release (Sakai 1997), so they are unlikely to increase the dispersal

potential of the species and are therefore irrelevant to this study. On the other hand, the longevity and competence patterns of the larvae generated via spawning by *P. damicornis* have not been studied. Moreover, the competence patterns used for each species were derived from data obtained in a single experiment. When data from more than one experiment were available, the competence patterns obtained more commonly or by an author who studied multiple species were used (see *above* and *Section 5.2.C.2.*). In these cases the differences in competence patterns among experiments were small (Atoda 1947b, 1951, Baird 2001) except for the brooded larvae of *P. damicornis*, which have been described to settle 103 days after release (Richmond 1988) and live up to 212 days (Harrigan 1972). Both, the brooded and spawned larvae of *P. damicornis* may, therefore, have greater dispersal potential than that used in the models.

5.4.D.2. Model limitations

The model limitations presented in *Chapters 2 and 3* also apply to the models described in this chapter. Different combinations of reef charts (with different grid sizes, reef numbers, and reef densities) and larval mortalities were used in the models. The combination described in detail in the methods and results sections correspond to the set that produced the most discriminating results among species. Larger charts with smaller cells and reef densities could have been implemented, producing even more distinctive results among species. However, these simulations would have had a higher cost in computational resources (memory and time), and their results are likely to be qualitatively similar.

5.4.D.3. Statistical analysis limitations

The main limitation of this study was the low number of data points available for the statistical analysis of the relationship between larval dispersal potential and geographic range size in corals. Linear representations of the competence patterns could be constructed for 12 species, but non-linear representations could only be constructed for 5 species. Despite the non-linear being a superior representation and the use of standardised protocols in the settlement experiments (see *Sections 5.2.C.2.* and *5.4.B.*), the inclusion of more species with this type of representation would have been desirable. It is hoped that detailed descriptions of the larval competence patterns of more coral species will be available in the near future.

5.4.E. Summary and Conclusions

Both geographic ranges and dispersal potential of the larvae vary greatly among corals species. The lengths of the pre-competent and competent periods are the main factors determining the settlement rates of larvae and the connectivity among reefs respectively. Because of this, brooders have higher settlement rates and lower connectivity than broadcast spawners, although there are important differences among species within each reproductive type. Describing the competent period only by its starting and finishing times can be misleading. Competence patterns are better represented non-linearly as the height and position of the competence peak and tail are also crucial. Therefore, the use of non-linear descriptions of the larval competence patterns is recommended for models of larval dispersal, particularly those applied to management and conservation. Unfortunately, at present this type of representation is only available for a few species of corals.

The potential for dispersal of the larvae of coral species was a poor predictor of the size of their geographic ranges. Similarly, gene flow does not seem to be a good predictor of geographic range size in corals (Ayre and Hughes 2000). Notably, within each reproductive type (brooders and broadcast spawners) the patterns of gene flow observed in genetic studies and the dispersal variables computed by the models show a tentative positive relationship. Furthermore, when only the competence curves obtained in the presence of suitable substratum were used in the models and the dispersal results for both reproductive type were pooled together, evolutionary-scale connectivity was an almost significant predictor of gene flow. This also suggests that in the GBR either settlement cues may be abundant (presumably due to its large extension and reef density) or more likely larvae settle near their natal reef. Nevertheless, data on more species is required to confirm the relationship between the dispersal potential of the larvae and gene flow in corals. In conclusion, the dispersal potential of the larvae can be an important factor determining the geographic ranges of coral species, but the dispersal hypothesis per se cannot explain the size of the geographic ranges of corals in the IP. Differences in “dispersion” (i.e. range expansion) time among the species in the study (derived from differences in the time elapsed from their origin and/or the last environmental change in their ranges) may contribute to the lack of relationship between dispersal potential and geographic range size. However, the distribution of corals is influenced by many other factors, such as: behaviour of the larvae, life histories and multi-dimensional environmental niche of the species, and the occurrence of

historical and stochastic events. These factors mask the effect of the dispersal potential of the larvae in determining the geographic ranges of coral species in the IP.

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

6.1. INTRODUCTION

The Indian and Pacific Oceans (IP) form a vast aquatic realm that extends over 25,000 km at the equator. Together, they contain more than three-quarters of the tropical waters and approximately 85% of the coral reef area of the Earth (Cox and Moore 2000). The numerous coral reefs in the IP support a great diversity of marine life, including more than 600 species of zooxanthellate scleractinian corals (over 80% of the total number of species) and more than 3,000 species of coral reef fishes (~ 75% of all coral reef fish species and over 25% of all marine fish species).

6.1.A. Patterns of species richness in the tropical Indo-Pacific

Marine species are not distributed homogeneously across the tropical IP. In fact, one of the most striking patterns in marine biogeography is the presence of a high diversity centre in the Central Indo-Pacific (CIP), located in the triangular area that includes the Philippines, the Malay Peninsula, Indonesia, and New Guinea (e.g. Ekman 1953, Briggs 1974, Stoddart 1992, Paulay 1997). Moving away from this area, biodiversity gradually decreases in all directions. The decrease is greatest along the longitudinal axis, specially to the East of the diversity centre (towards the American west coast), and milder along the latitudinal axes (e.g. Veron 1995, Ormond and Roberts 1997). Similar patterns of species richness (SR) occur in the IP for: corals (e.g. Stehli and Wells 1971, Veron 1994), molluscs (e.g. Kohn 1985), echinoids (e.g. Mayr 1954), fishes (e.g. Ormond and Roberts 1997, Bellwood and Wainwright 2002), and seagrasses and mangroves (e.g. McCoy and Heck 1976). As a consequence, there exists a very high correlation between the number of species of corals and reef fishes in different regions of the IP (e.g. Harmelin-Vivien 1989, Ormond and Roberts 1997, Bellwood and Hughes 2001, Hughes et al. 2002b), and presumably among other taxonomic groups. The centre and gradients of diversity in the IP can be observed at family, genus, and species level within major taxa (e.g. Veron 2000). As we move deeper in the phylogeny (i.e. from families to species), the diversity centre becomes better defined (i.e. smaller) and the diversity

gradients become clearer. Moreover, similar diversity patterns may also occur at an even lower level of organisation, and parallel genetic diversity gradients seem to exist within-species in the IP (Nishida and Lucas 1988, Palumbi 1997). In this chapter I investigate the mechanisms of origin of the diversity patterns in the IP, in particular those related to the topology (i.e. spatial attributes and relationships) of the habitats of scleractinian corals. Therefore, next I present a brief review of the theories proposed to date to explain these patterns, concluding the introduction with a more detailed description of the aims of this chapter.

6.1.B. Theories proposed to explain the patterns of species richness in the tropical Indo-Pacific

The consistency of diversity patterns across taxonomic groups in the IP is usually considered as evidence for a common mechanism of origin of these patterns (e.g. Jokiel and Martinelli 1992, Ormond and Roberts 1997, Bellwood and Hughes 2001, Bellwood and Wainwright 2002). Nevertheless, there is little consensus about the mechanism causing the diversity patterns in the tropical IP, and hence major questions about the biogeography of the IP remain unanswered (e.g. Rosen 1988). Traditionally, four major theories have been proposed to explain the origin of the diversity hotspot in the CIP. These include the perception of this area as a:

- *Centre of species origin* (or *evolutionary source* or '*cradle*'). According to this theory, the centre of diversity is also the centre of origin of new species, which gradually disperse, colonising peripheral areas. The patterns of declining diversity in the IP would be a consequence of the differences in age of the species, dispersal potential of their propagules (larvae, seeds,...), and degree of isolation of the suitable substrata. This theory has been repeatedly proposed to explain the origin of the diversity patterns in the IP of: corals (Stehli and Wells 1971, Dana 1975), fishes (Allen 1975, McManus 1985, Myers 1989), and marine organisms in general (Ekman 1953, Briggs 1974, 1984, 1992, Zinsmeister and Emerson 1979). The following facts seem to support this theory: (1) there seems to be a decrease in the average age of coral genera as we move away from the centre of diversity (Stehli and Wells 1971, but see Vermeij 1978, Jokiel and Martinelli 1992, re-examined and supported in Veron 1995); (2) high levels of endemism have been described for some taxa in the centre of diversity (Fautin and Allen 1992, Veron 1995, 2000, but

see Fenner 2002, Hughes et al. 2002b, and Section 6.4.3.); and (3) the pelagic larval stage of most marine taxa have high dispersal abilities (e.g. Ekman 1953, although this can also support the 'centre of accumulation' theory). However, the 'centre of origin' theory cannot explain completely the patterns of diversity in the IP. For instance, speciation seems to have occurred in numerous locations all over the IP (see *below*). Rosen (1988) suggested that only sympatric speciation can occur in the centre of diversity, as allopatric speciation (the most common type of speciation) would be prevented by the low degree of isolation of the reefs in this area, therefore leading to low speciation rates. Nevertheless, most authors now believe that the history of tectonic, eustatic, climatic, and oceanographic (TECO) events in the geologically complex basins of the CIP have promoted speciation in the region (e.g. McManus 1985, Springer and Williams 1994). However, Potts (1985) postulated that sea-level fluctuations during the Plio-Pleistocene were too rapid to allow speciation in taxa with long generation times such as corals, in practice reducing their number of species in the area.

- *Centre of species accumulation.* In this theory, species originate mainly in peripheral areas of the IP, but over time currents transport propagules of these species, expanding their geographic ranges to include the CIP centre of diversity. This theory has also enjoyed wide support as an explanation for the diversity patterns in the IP of corals (McCoy and Heck 1976, Wallace 1997, Pandolfi 1992a), crustaceans (Ladd 1960), fishes (Kay 1990), sea-grasses and mangroves (McCoy and Heck 1976), and marine organisms in general (Newell 1971, Kay 1984, Pandolfi 1992b). The following facts seem to support this theory: (1) high levels of endemism (at least relative to the total number of species) and presumably speciation have been found in peripheral areas of the IP for corals (Wallace et al. 1991, Pandolfi 1992a), molluscs (Reid 1986), sea urchins (Palumbi 1997), and fishes (Ormond and Edwards 1987, Smith et al. 1987, Hourighan and Reese 1987); (2) the planktonic larval stage of most marine taxa affords high dispersal capabilities (e.g. Ekman 1953, but this can also support the 'centre of origin' theory); (3) the flow of the currents in the Pacific is mainly from East to West promoting transport to the CIP (e.g. Munk 1955, but see Section 6.1.5.), and there is direct evidence of transport of reef organisms by these currents (e.g. Jokiel 1984, 1990a, 1990b). However, this theory is also unable to adequately explain all patterns of diversity in

the IP. For example, it cannot account for the apparent decrease in the average age of coral genera with the increase in distance from the centre of diversity.

- *Centre of overlap.* This theory attributes the high diversity of the CIP to the confluence of several biogeographic provinces in this area, each contributing their own diversity. Although usually proposed in combination with other mechanisms of origin, this theory has been forwarded as one of the main contributors to the diversity patterns of marine organisms in the IP (e.g. Ekman 1953). The following facts seem to support this theory: (1) the centre of diversity is found at the boundary of the Indian Ocean and West Pacific biogeographic regions (Valentine 1973); (2) there is no evidence for extensive coral reefs in the area presently occupied by the centre of diversity prior to the early Miocene, when the Australian and SE Asian plates collided in the region (Wilson and Rosen 1998); and (3) vicariant divergence among populations in both oceans has been suggested for: sponges (Kelly-Borges and Valentine 1995), corals (Wallace 1997), molluscs (clams, Benzie 1998), crustaceans (crabs, Lavery et al. 1996), and fishes (Woodland 1983, Donaldson 1986, Blum 1989, McMillan and Palumbi 1995). However, these same facts can also support other theories. In this case TECO events, such as low sea levels in the Plio-Pleistocene, could have impeded or at least restricted gene flow between the Indian and Pacific Oceans (e.g. Potts 1983), and most species would have originated after, rather than before, the collision of the Australian and SE Asian plates. In fact, a problem with the 'centre of overlap' theory is that the age of many species in the CIP should be older than currently thought because in this theory much of the diversity would have arrived to the area in the early Miocene (Palumbi 1997, Bellwood and Wainwright 2002). A recent study of the distribution of genetic diversity among populations of the marine fish *Hippocampus trimaculatus* in SE Asia has revealed significant geographic (East-West) genetic divergence (Lourie and Vincent 2004). Some genetic divergence occurred between the basins of the Indian and Pacific oceans; however, most of the divergence was associated with Wallace's Line and consistent with a post-glacial (i.e. recent) colonisation of the Sunda Shelf. These results indicate that the genetic (and likely species) diversity patterns of marine organisms in SE Asia are the result of a complex history (see Section 6.1.C).
- *Centre of species refuge (or survival or 'museum').* In its most simple form, this theory postulates that diversity in the CIP is the vestige of a cosmopolitan and rich

distribution of marine organisms of broadly Cretaceous origin (McCoy and Heck 1976, Potts 1985). During the sea-level changes in the Cainozoic the persistence of shallow habitats in this region would have reduced the rates of local extinctions of marine species, whereas oceanic islands suffered repeated faunal losses during this period (Potts 1985, Myers 1989, Paulay 1996). Recently, the ‘centre of refuge’ theory has received renewed support largely because genus, species, and alleles originate by different mechanisms (e.g. Palumbi 1997) and therefore speciation per se cannot explain the presence of similar diversity patterns at different levels of organisation, while extinction can (Palumbi 1997, Bellwood and Wainwright 2002). This theory, however, presents a similar problem regarding the age of the coral species in the IP to that found in the ‘centre of overlap’ theory, as many of them should also be more ancient than presently thought. Furthermore, the ‘centre of refuge’ theory only provides an explanation for the maintenance of the level of SR in the CIP, and not for the origin of the species itself. Rosen (1984) proposed a variant of this theory known as the ‘Vicariance and Refuge Model of Coral Biogeography’, containing elements of both the ‘centre of accumulation’ and ‘centre of refuge’ theories. In this conceptual model, speciation would have occurred largely in the numerous reefal areas surrounding the centre of SR as a result of TECO events and isolation. These areas would have acted as ‘diversity pumps’ (sensu Valentine 1967), and the species that had extended their ranges to the centre of diversity would have successively avoided extinction caused by sea-level fluctuations. As a consequence, the CIP would have increased its number of species over geological times by acting both as a centre of accumulation and centre of refuge.

More recently, two theories involving aspects of the size and/or location of the geographic ranges of the species have been proposed to explain the high SR of the CIP. The first theory is based on the premise that with decreasing latitude the environmental tolerances and consequently ranges of the species narrow (Rapoport’s rule), leading to an increase in SR (Stevens 1989). Testing this theory has proved difficult due to statistical problems (Lyons and Willig 1997) and conflicting results have been obtained by studies of different marine organisms, regions, and/or authors (e.g. Rohde et al. 1993, Roy et al. 1994, Stevens 1996, Gaston et al. 1998, Taylor and Gaines 1999, Fortes and Absalao 2004). A recent statistically robust analysis has shown no support for Rapoport’s rule in the CIP for either corals or reef fishes; that is, the high SR of these

taxa in this low latitude region is not a consequence of the accumulation of species with small ranges (Hughes et al. 2002b). The second theory maintains that the high SR of the CIP is a result of its central position in its domain (the IP) and the ‘mid-domain effect’ (MDE). The MDE makes reference to the predisposition of SR to peak in the middle of the domains due to the geometric constraints existent in the placement of geographic ranges within their domains (i.e. because ranges cannot surpass the boundaries of their domains, the larger a range is the more likely it will be to include the middle of the domain, producing a SR peak in this zone). Some studies indicate that the MDE contributes to determine the SR patterns in the IP; however, there is little agreement on the scale of its contribution (e.g. Connolly et al. 2003, Bellwood et al. 2005). Moreover, neither of these two theories provides information on the spatial patterns and/or mechanisms of speciation and extinction in the IP.

Many variations and combinations of these and other theories have been proposed to explain the diversity patterns of reef organisms in the tropical IP (reviewed in Rosen 1988, Crame 1992, Veron 1995, Paulay 1997, see also Fraser and Currie 1996, Bellwood et al. 2005). The large number of theories and the disagreement among scientists is a consequence of the difficulty in testing them (e.g. Pandolfi 1992a). For instance, the ‘centre of origin’ and ‘centre of accumulation’ theories differ only in the direction in which species disperse (see Palumbi 1997).

6.1.C. Processes determining species richness patterns and the ‘Vortex Model’

Having a plethora of plausible explanations for the same diversity patterns lacks the elegance of a general theory (Ormond and Roberts 1997, but see Gaston 2000). Despite their differences, all four theories described above agree in that the diversity patterns found today in the IP are the result of a long and complex history, which comprised a number of events including vicariance speciation, dispersal, and extinction (Bellwood and Wainwright 2002). There are only two processes that can modify global diversity: speciation, and extinction (e.g. Brown 1995, Gaston 2000). At smaller spatial scales, shifts in the geographic ranges of the species can also alter diversity locally. Changes in the geographic range of a species can occur via dispersal (immigration/emigration) and by local extinction (e.g. Gaston 2000).

Jokiel and Martinelli (1992) included the 3 processes capable of altering SR (speciation, extinction, and dispersal) in a model developed to explain the origin of the diversity patterns found in the Pacific. The 3 processes were applied over a matrix of evenly spaced islands assumed to represent the Pacific. Initially, species were uniformly distributed across the islands (i.e. the same species occurred initially in all islands). Speciation and extinction occurred randomly, each of them with equal probability in all islands. Dispersal was also stochastic, but its probability among pairs of neighbouring islands was based on the prevailing surface circulation patterns in the Pacific. In the simulations where speciation and extinction rates led to an increase in the number of species over time, a gradient of decreasing SR from west to east was produced across the grid of islands representing the Pacific. The relative values of the speciation and extinction rates determined the number of iterations needed to obtain this pattern of SR, but the only mechanism included in the model to generate the SR pattern was the dispersal pattern among islands caused by the currents. For this reason, the authors named their model ‘Vortex Model of Coral Reef Biogeography’, and concluded that although other factors are important current pattern is the dominant factor that controls the distribution of species in the Pacific Ocean.

6.1.D. Limitations of the ‘Vortex Model’

The ‘Vortex Model’ (Jokiel and Martinelli 1992), despite the prominent role it assigns to dispersal, does not account for any topological description of the habitats among which dispersal occurs. However, significant topological differences occur across the IP. For example, the continental shelves are much wider in the eastern margin of Asia than on the western margin of the Americas, and volcanic islands are more common in the western than the eastern Pacific (e.g. Cox and Moore 2000). Not only is the abundance of shallow marine habitats heavily skewed towards the Indo-West Pacific, but in fact approximately 65% of the IP’s coral reefs (~55% of the world’s coral reefs) occur in South-East Asia (e.g. Muller 1995).

Moreover, the only transport mechanisms of taxa included in the ‘Vortex Model’ are the main modern surface currents, which include little return circulation from west to east (only via the Equatorial Counter Current, e.g. Munk 1955). However, counter currents, usually known as undercurrents, can also exist beneath surface currents (e.g. Garrison 2002), and are therefore necessary for an accurate representation of the ocean

circulation (e.g. Sponaugle et al. 2002). Undercurrents can be very large, their volumes sometimes approaching those of the surface currents above them. In the tropical Pacific, the Pacific Equatorial Undercurrent or Cromwell Current flows under the North Equatorial Current with an average speed of 5 km.h^{-1} at a depth of 100-200 m and width of 300 km, carrying a volume of water equivalent to approximately half the Gulf Stream. This undercurrent has been traced from New Guinea to Ecuador (over 14,000 km). Unfortunately, our understanding of the biology and behaviour of the larvae of most marine invertebrates (including their positioning in the water column) is not sufficient to assess the significance of this type of water transport. In addition, weather-band currents also contribute to the water circulation patterns in the oceans, adding complexity (e.g. Andrews and Pickard 1990). Particularly important in the IP are El Niño/Southern Oscillation (ENSO) events, which can reverse near-surface ocean circulation and move large masses of water (e.g. Wyrski 1985, Thurman and Trujillo 2002). These events open new dispersal routes and can increase the dispersal distances of the larvae of marine organisms, potentially enabling them to expand their geographic ranges (Richmond 1990b). During the past century, such events, although highly irregular in frequency, have occurred on average every 4 years, with 9 of them being strong or very strong (Hansen 1990, Thurman and Trujillo 2002). ENSO events typically persist for about a year, but some have lasted for more than 3 years (Garrison 2002). They are believed to have been an ongoing phenomenon during the interglacial periods that have occurred since the closure of the Panamanian Isthmus (Colgan 1990), which created the modern IP circulation patterns approximately 3.5 m.y.a. (Coates et al. 1992, Coates and Obando 1996). Therefore, ENSO events are frequent enough to be significant at evolutionary and biogeographic time-scales. Likewise, there is some controversy over the circulation patterns in the IP in past geological times, especially prior to the Quaternary, since tectonic events (e.g. Luyendyk et al. 1972, Kennett 1980, Barron and Peterson 1989, but see Schopf 1979) and climatic changes (e.g. McIntyre 1976, Stoddart 1976, Glynn and Wellington 1983) could have altered them significantly. They may have been more complex, variable, or simply different, than those occurring today and used in the Vortex Model.

6.1.E. Aims of the study

In this chapter I present a ‘Topological Model of IP Coral Reef Biogeography’. The same 3 processes capable of altering SR (speciation, extinction, and dispersal) included

in the ‘Vortex Model’ are included in the ‘Topological Model’, but in this case I also incorporate a description of the spatial attributes and relationships among the coral habitat areas amongst which dispersal occurs. The primary objective of the study is to assess the importance of habitat topology in the genesis of the species richness patterns in the Indo-Pacific. Because of this, in the model dispersal from the habitats source of larvae occurs exclusively by diffusion (i.e. the circulation patterns in the IP are not included in the model to allow for the evaluation of the individual contribution of topology to the SR patterns generated by the model). A secondary aim of the study is to use the ‘Topological Model of Coral Reef Biogeography’ as a null model against which to compare the SR patterns found in the IP. The differences found must be due predominantly to important factors or mechanisms not included in the ‘Topological Model’ (i.e. caused by factors other than habitat topology). Explanations for the differences are proposed and discussed.

6.2. MATERIALS and METHODS

The ‘Topological Model of IP Coral Reef Biogeography’ consists of 2 sub-models: a ‘Dispersal Sub-model’ and a ‘Biogeography (or Species Dynamics) Sub-model’. The ‘Dispersal Sub-model’ is similar to the models described in previous chapters. It was run preceding the ‘Biogeography Sub-model’ in order to compute the probabilities of dispersal among the areas of coral habitat in a spatially realistic representation of the IP, which were then used as data inputs in the 2nd sub-model. The ‘Biogeography Sub-model’ simulates the variation in SR over time as a consequence of speciation, extinction, and dispersal in the habitat areas in the IP representation. This sub-model is implemented as close as possible to the ‘Vortex Model of Coral Reef Biogeography’ (Jokiel and Martinelli 1992), from which it differs only in the topology of the habitat areas and the probabilities of dispersal among them.

6.2.A. ‘Dispersal Sub-model’

The dispersal process is the main difference between the ‘Topological’ and ‘Vortex’ Models of Coral Reef Biogeography. In the model developed by Jokiel and Martinelli, the dispersal of larvae occurred among theoretical reefs, which they called ‘islands’,

uniformly distributed (every 10° of latitude and 20° of longitude) in the Pacific Ocean (between latitudes 30°N to 30°S and longitudes 120°E to 120°W). The larvae released in each island could only disperse to the 4 closest neighbouring islands (situated to the North, East, South, and West), with probabilities that the authors assigned based on the generalised circulation patterns of the modern surface background currents in the Pacific described by Munk (1955). In the model presented in this chapter, dispersal of larvae can occur among any of the areas of coral habitat present in the spatially realistic representation of the IP. The probabilities of dispersal among each pair of habitat areas are calculated by the ‘Dispersal Sub-model’, and depend on the topology (e.g. size, shape, location, and distance) of the habitat areas, hydrodynamic conditions (speed and direction of the currents), and biology of the larvae (competence patterns and mortality rates).

The general design of the ‘Dispersal Sub-model’, including input formats, rules and functioning of the coupled lattice, and output formats, is similar to that described in *Chapter 2 and 3*. Their main differences lie in the input data sets used in the simulations, particularly in the ‘charts’ (spatial representations of the environment, see *Section 6.2.4.1*). The singularities of the input data sets used in this chapter are presented below (*Section 6.2.A.1*).

Mortality rate, length of the competent period, and current speed, were not included in the ‘Vortex Model’, but are required by the ‘Dispersal Sub-model’ of the ‘Topological Model’, making it more realistic. However, compared to previous chapters, the constraints imposed by the variables were relaxed (i.e. low mortality rates and long competent periods were used) to maximise dispersal. Maximising the likelihood of dispersal in the model accounts for the occurrence of rare (i.e. chance) highly dispersive events during the extended periods of time in which the geographic ranges of species are shaped. These highly dispersive events are likely to have a crucial contribution to the exchange of species and genes among isolated locations, and are therefore essential in determining the distribution of taxa (e.g. Cowen et al. 2006). Furthermore, relaxing the constraints imposed by the variables makes the ‘Topological Model’ differ to a lesser extent from the ‘Vortex Model’, and implies that dispersal is essentially driven by the topology of the habitat areas, the main factor of interest. All this facilitates the comparison with Jokiel and Martinellis’ model.

6.2.A.1. Charts: spatial representations of the environment

I digitised the main spatial features included in the area between latitudes 30⁰N to 30⁰S and longitudes 100⁰E to 70⁰W in a Mollweide's homolographic projection map of the IP oceans (equatorial scale 1:48,000,000) using CartaLinkTM software. This area comprises the tropical sections of the Pacific and western Indian Oceans, including the IP centre of diversity. It covers 70⁰ of longitude more than the model of Jokiel and Martinelli, which included only the Central Pacific, most of the Western Pacific, and some of the Eastern Pacific. The digitised map was exported to ARC/INFOTM, where it was edited and built as a G.I.S. coverage. The polygons were classified into 3 land-types (Figure 6.1.): 'land' (continents and major islands), 'shallow water' (≤ 100 m in depth), and 'deep water' (> 100 m in depth). The shallow water polygons were used as a surrogate for coral habitat. That is, it was assumed that there is a positive linear relationship between the extent of ocean shallower than 100 m and the area of substratum suitable for the production and recruitment of coral larvae in the IP.

The polygon coverage representing the IP was transformed into a grid representation, in which each cell depicted an area of 60 km x 60 km. A single land-type code was assigned to each cell using three different methods. In the first one, the land-type occupying the largest proportion of the cell was assigned as the cell-code. This method under-represents the land-types of polygons that are small in size and/or have irregular shapes, such as many of the 'land' and 'shallow water' areas in the IP models presented here (see *Discussion in Chapter 4*). The second method gives priority to the 'land' and 'shallow water' land-types. If any of these two land-types are present in the cell, the code representing the most common one is assigned to the cell. The code for 'deep water' is only assigned when none of the other two land-types are present. In the final method the following priority ranking was used (in descending order): 'shallow water', then 'land', and lastly 'deep water'. That is, if 'shallow water' was present in the area represented by the cell its code was assigned to the cell, and only if 'deep water' occupied the whole cell was its code assigned. The last two methods deliberately overestimate the abundance of the 'shallow water' and 'land' land-types. In these methods, it is assumed that these land-types are qualitatively more important than 'deep water', so they must be represented in the grid wherever they appear, even if quantitatively they cover only a small part of the cell. Finally, each of the cells containing a 'shallow water' code was re-coded into a unique code. In this way, each of

the cells representing an area of habitat in the model could be individually distinguished.

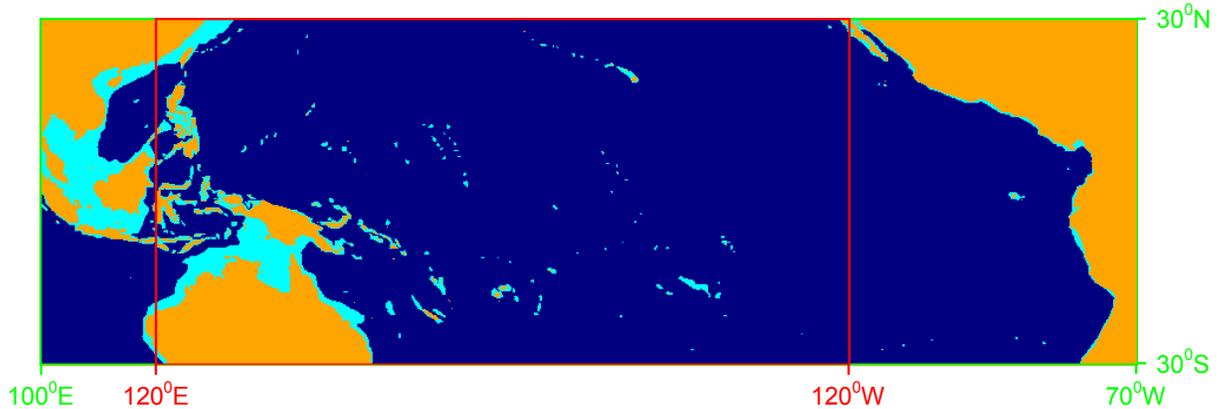


Figure 6.1. Digitised map of the Indo-Pacific used in the simulations in *Chapter 6*. Land-types: *Navy blue* = deep water, *turquoise* = shallow water, *magenta* = emerged land. Areas: *red box*: area included in the ‘Vortex Model of Coral Reef Biogeography’, *green box (whole picture)*: area included in the ‘Topological Model of Coral Reef Biogeography’.

6.2.A.2. Currents

Diffusion with equal probability in any direction was the only transport mechanism of larvae included in the models. Transport by advection provided by background currents was not included to avoid confounding the dispersal patterns originated by the topology of the habitats with the patterns resulting from directional transport. Uniform diffusion in all directions was implemented by making the probabilities of a water particle moving to each of the neighbouring cells equal in the currents set used to represent water flow in the model (Table 6.1., see *Chapter 2*). Retention within each cell was included, but set to a relatively low level (column ‘C’ in Table 6.1.) in order to maximise dispersal (see above).

For convenience, the speed of the diffusion flow was set to 0.5 cells.d^{-1} ($\sim 36.2 \text{ km.d}^{-1} \sim 1.50 \text{ km.h}^{-1} \sim 42 \text{ cm.s}^{-1}$), meaning that each iteration in the simulations corresponds to 2 days in the real world. This speed, although not uncommon among the currents of the IP (e.g. Pickard et al. 1977, Andrews and Pickard 1990), is higher than the speeds used in previous chapters in order to maximise dispersal.

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. *Column headers* indicate the cell position that the water particle will occupy in the following iteration (C = Central, N = North, NE = North-East, E = East, SE = South-East, S = South, SW = South-West, W = West, NW = North-West), and the *numbers* denote the probability of transport occurring in the corresponding direction.

Current Directions (probability)									Current Speed (cm.s-1)
C	N	NE	E	SE	S	SW	W	NW	
0.1	0.1125	0.1125	0.1125	0.1125	0.1125	0.1125	0.1125	0.1125	42

6.2.A.3. Pre-competent and competent periods of the larvae

Although coral species differ in their competence patterns and therefore dispersal potential (see *Chapter 5* and references within), the same competence patterns were used for all the species in the simulation. Specifically, the competence patterns of the broadcast spawning coral *Acropora valida* described by Baird (2001) were used for all the species in the simulations (Figure 6.2.). The larvae produced by *A. valida* can remain competent to settle for at least 110 days (see *Chapter 5*), which provided ample dispersal opportunities among the areas of habitat present in the models.

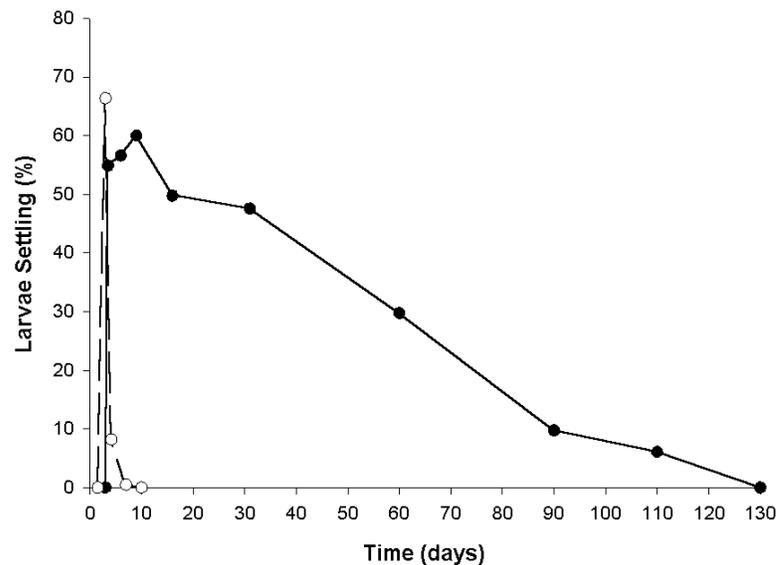


Figure 6.2. Competence patterns of the larvae of broadcast spawning coral *Acropora valida*, used in the models in *Chapter 6* (modified from Baird 2001).

● No substrate offered (dispersed larvae)
○ Substrate offered (retained larvae)

6.2.A.4. Fixed parameters

Three different larval mortality rates were used in the simulations: 0.1, 0.2, and 0.3 (instantaneous mortality (M) = 0.1054, 0.2231, and 0.3566 respectively). Because not all the substratum present in shallow water areas is suitable for the settlement and production of coral larvae, the larval output (combined value of coral cover and fertility) per km^2 of substratum was reduced from 10^6 larvae. km^{-2} in the models described in previous chapters to 10 larvae. km^{-2} in the models in this chapter. Nevertheless, these values are merely indicative, as the interest of this study is to compute the probabilities of larval dispersal between habitat areas (and the values of these probabilities relative to each other), and not the total number of larvae actually dispersing among habitat areas.

6.2.B. 'Biogeography Sub-model'

The 'Coral Reef Biogeography Sub-model' was designed to be as similar as possible to the 'Vortex Model of Coral Reef Biogeography' of Jokiel and Martinelli (1992). The objective of this sub-model was to simulate the variation in the number of species over time in each area of coral habitat in the IP. Variation in SR in the 'Biogeography Sub-model' occurred as consequence of 3 processes: extinction, mutation, and dispersal among habitat areas. These processes were implemented using standard Monte Carlo techniques (e.g. Manly 1997). This simply consisted of drawing random numbers and comparing them to set values representing the probability of a species becoming locally extinct, mutating, or dispersing to another habitat area (see below). In the 'Vortex Model' these three probabilities were set before the simulation started, with the probability of dispersal being arbitrarily assigned based on a general model of the modern IP surface currents. In the 'Biogeography Sub-model', the three probabilities were also set before the simulation started, but the probabilities of dispersal among habitat areas were based on the calculations by the 'Dispersal Sub-model'. Each habitat area was initialised with the presence of the same 10 species. Then, each species in each habitat area was sequentially exposed to the 3 SR modifying processes during each of the iterations of the simulation. These processes were implemented as follows:

1. *Extinction*: At the beginning of each simulation a value is entered for the probability of a species becoming extinct (EXTPROB in Jokiel and Martinelli's terminology).

The same EXTPROB value was used for all species, habitat areas, and iterations of

the simulation. During the simulation a random number between 0 and 1 is drawn and compared to EXTPROB for each species, habitat area, and iteration. If the drawn number is smaller than EXTPROB, the species is removed from the corresponding habitat area (i.e. it becomes locally extinct). Species can recolonise a habitat area via dispersal from another habitat area where the species is present.

2. *Mutation*: At the beginning of each simulation a value is entered for the probability of a species mutating into a different species (MUTPROB in Jokieli and Martinelli's terminology). The same MUTPROB value was used for all species, habitat areas, and iterations of the simulation. During the simulation a random number between 0 and 1 is drawn and compared to MUTPROB for each species, habitat area, and iteration. If the drawn number is smaller than MUTPROB, speciation occurs and a new species is added to the corresponding habitat area. When a species mutates into a new one it does not disappear from the area where it mutated. The sub-model design does not allow for a species to both mutate and become extinct in the same area and iteration (i.e. extinction occurs first). Only one new species can be formed per mutation event, and the same species can only be created once (i.e. each time a species mutates it produces a new species).
3. *Dispersal*: the 'Dispersal Sub-model' was used to estimate the probability of larvae dispersing among areas of habitat (see above *Section 6.2.A.*). During the simulation for each species, habitat area, and iteration, a random number between 0 and 1 was drawn and compared to the values contained in a modification of the second database produced by the 'Dispersal Sub-model' (Figure 6.3. and see *Chapter 2*). The values contained in this database are the computed probabilities for the possible fates of the larvae dispersing from each area of habitat. These fates include: dispersing to each of the habitat areas in the chart, dying, becoming non-competent, falling into a mangrove area (always null, as mangrove areas were not included in the models in this chapter), or becoming lost out of the chart (Figure 6.3.). These probabilities are mutually exclusive and add to 1. In order to allow comparison with the drawn values, several transformations were made to this database (Figure 6.3.). Firstly, the probabilities of the larvae dying, becoming non-competent, and falling into a mangrove area were combined into a new probability value. This combined probability was named 'effectively death' probability, because all of the combined probabilities prevent the larvae from successfully settling, which eventually lead to the death of the larvae. Secondly, because the proportion of larvae becoming lost out

of the simulation area is irrelevant for the processes occurring in the ‘Biogeography Sub-model’ its value was ignored and the probability values representing the remaining possible fates of the larvae (i.e. dispersing to each habitat area and becoming ‘effectively death’) were increased proportionally to add to 1. Finally, the values in the new set of probabilities representing the fate of the larvae produced in each habitat area were transformed into cumulative probabilities. Each of the values drawn for the dispersal process during the simulation was compared sequentially to the cumulative probabilities for the relevant habitat area (i.e. the habitat area from which larvae may disperse) in the transformed database until a higher value was found. The position of this value in the database was used to determine the fate of the dispersing species in the simulation (Figure 6.3.).

The absolute values of EXTPROB and MUTPROB, and in most occasions their relative values, varied among simulations. The simulations were generally run for 200 iterations. In each iteration the identity of the species present in each area of habitat was recorded.

6.2.C. Data Analysis and Results Presentation

In each simulation the probability values drawn during the extinction, mutation, and dispersal processes were saved in 3 files. The randomness of these values was validated using scatter and density plots, and they were found to be adequate random samples in all cases.

To investigate the evolution of SR in the chart, the data outputs of the simulations in each iteration were summarised into number of species per habitat area, and these summaries were inspected graphically every 20 iterations. An analysis of the sensitivity of the ‘Topographic Model’ to the larval mortality, MUTPROB, and EXTPROB values, and the transformation method used to convert the IP coverage into grids (see *Section 6.2.A.1.*) was conducted. The results of the ‘Topological Model’ were compared with those obtained by the ‘Vortex Model’ and with the coral SR patterns observed in the IP.

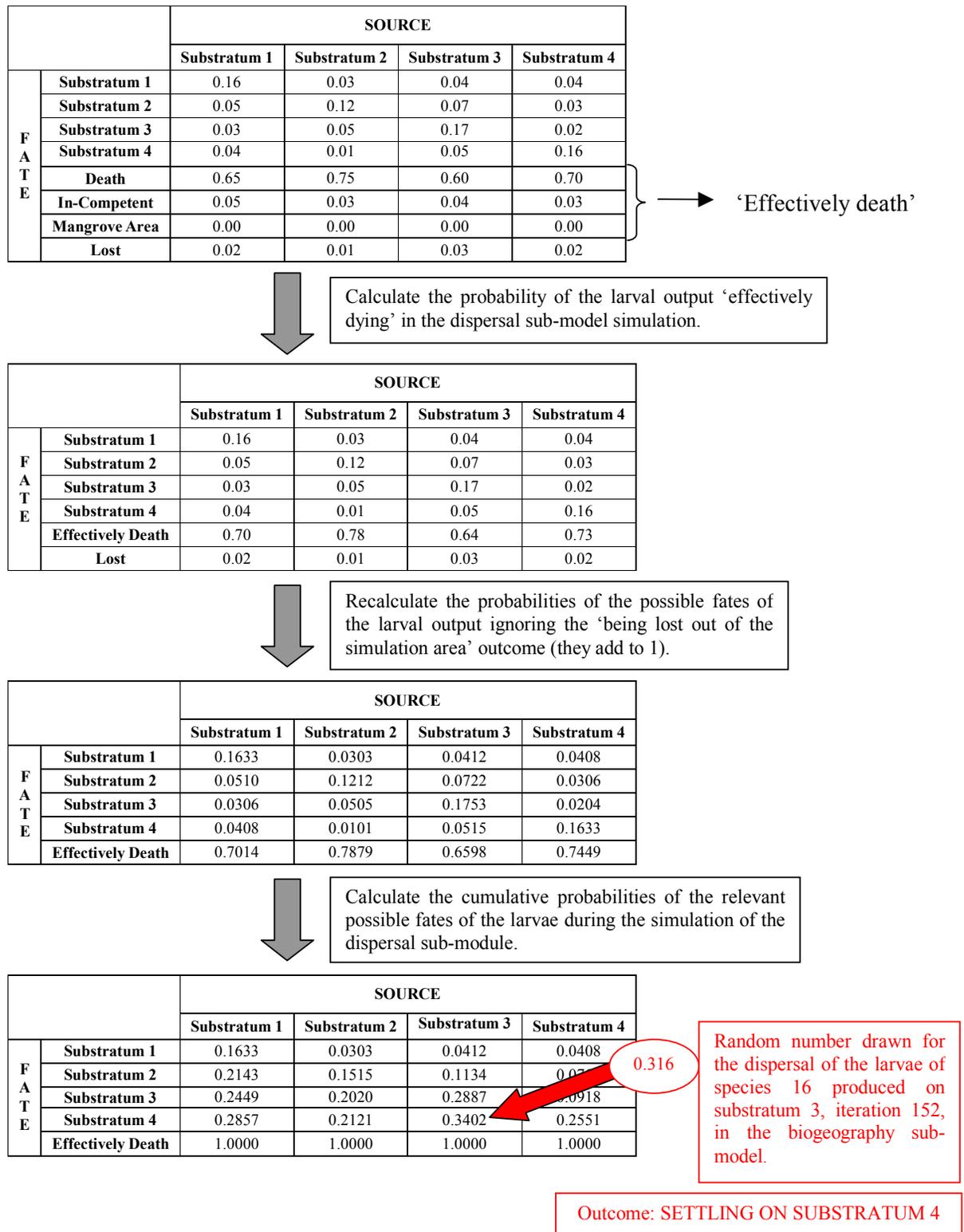


Figure 6.3. Information flow and use in the 'Topological Model of Indo-Pacific Coral Reef Biogeography'. In *black*: Example of the construction of the database containing the cumulative probabilities representing the fate of the dispersing larvae from the 2nd output database in the 'Dispersal Sub-model'. In *red*: Example of the computation of the outcome of a dispersal event in the 'Biogeography Sub-model'.

6.3. RESULTS

6.3.A. Species richness patterns generated by the ‘Topological Model of Coral Reef Biogeography’

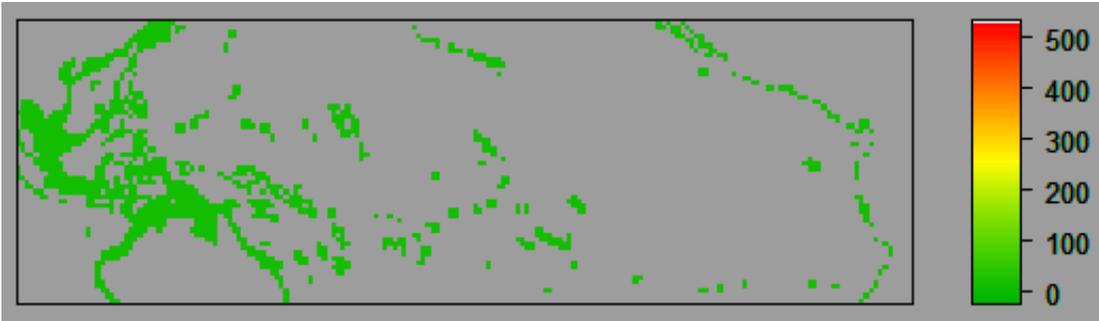
Most simulations generated a SR hotspot centred over the Indonesian Archipelago (Figures 6.4. and 6.5.). This process was slow at first because the initial number of species was low with a uniform distribution across all habitat areas (10 species were present initially on each habitat area). As the number of species in the habitat areas increased, the development of the SR patterns in the IP became increasingly faster. In the simulations, the centre of SR first originated between east Borneo and Sulawesi (Figure 6.4.h.), but rapidly spread to include the Philippine, Indonesian, and New Guinean archipelagos (Figures 6.4.i. and 6.4.j.). Once the centre was formed, SR generally increased first in the Malay Peninsula and the north coast of Australia (Figure 6.4.k.), and then progressively more slowly and to a lesser extent in the SE Asian coast, the east and west coasts of Australia, and through the Western and Central Pacific (Figure 6.4.l.).

Occasionally, in some simulations random extinction temporarily led to abnormally low SR in some areas of the centre of diversity. Nevertheless, when diversity in the centre was depressed it recovered quickly due to immigration of species from habitat areas within the centre and/or its surroundings (i.e. Malay Peninsula, SE Asia, northern Australia, and the Western Pacific) and to a lesser extent by speciation. Some of the areas neighbouring the centre of diversity occasionally also suffered a species depression for a few iterations. However, given sufficient time these areas also recovered, due mainly to immigration of species from the centre of SR.

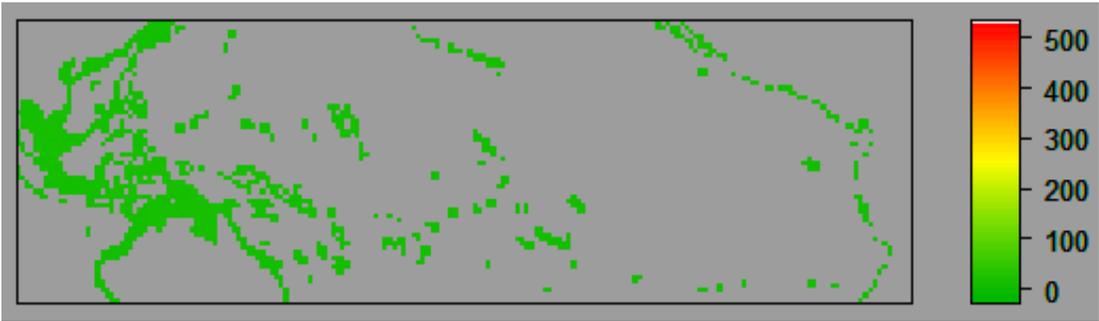
6.3.B. Sensitivity analysis

The three transformation methods used to convert the IP coverage into grids (see *Section 6.2.A.1.*) produced SR gradients similar to those found in the real world. The first method, in which the most abundant land-type in the area represented by a cell was assigned as its cell-code, yielded the poorest approximation. The other 2 methods, where ‘shallow water’ and ‘land’ were given priority over ‘deep water’, produced similar results.

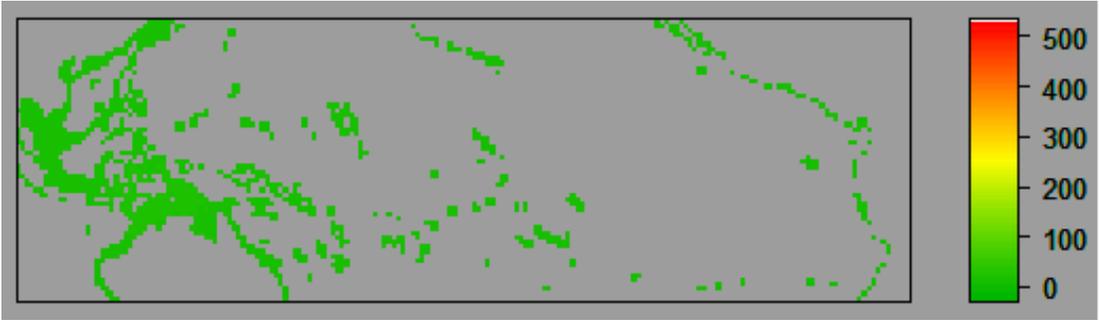
The sensitivity analysis indicated that altering the values of the parameters in the models generally does not prevent the appearance of some kind of SR gradient from the



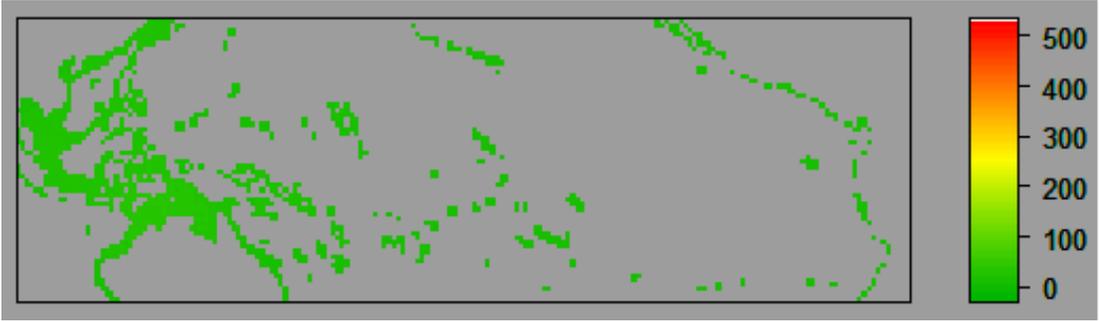
6.4.a. Iteration 0. Ten species everywhere.



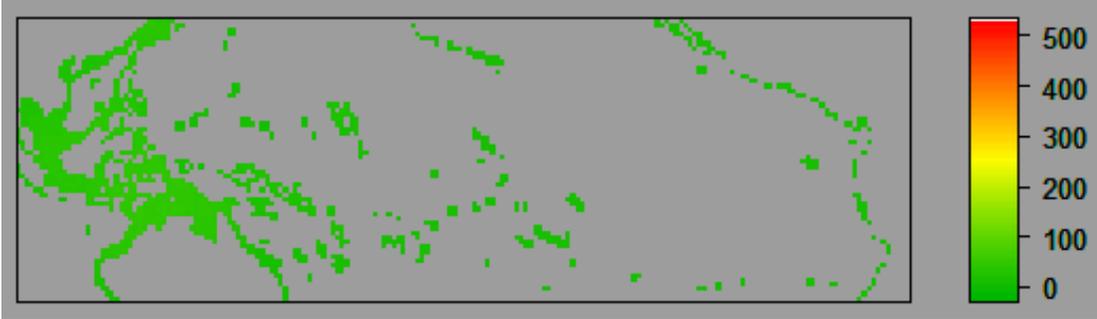
6.4.b. Iteration 10



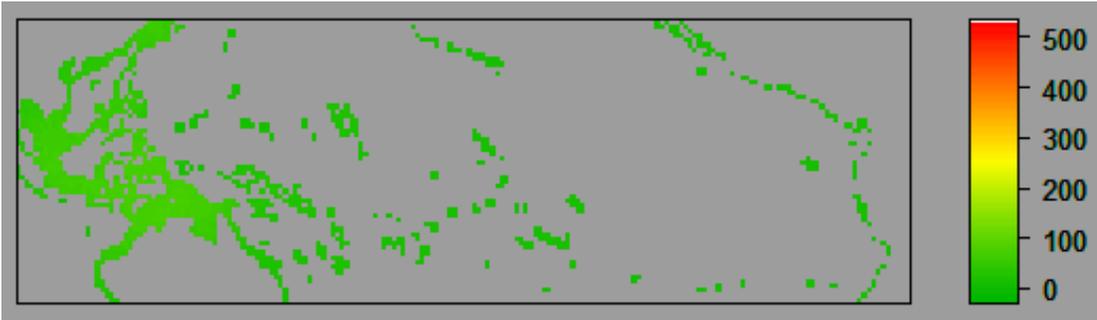
6.4.c. Iteration 20



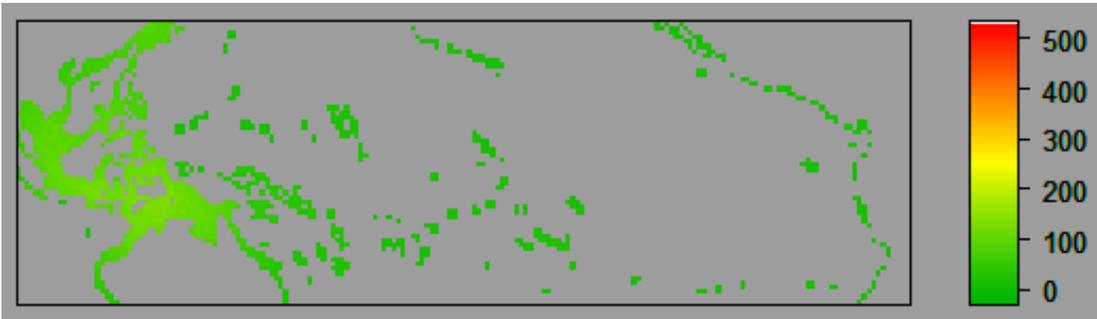
6.4.d. Iteration 30



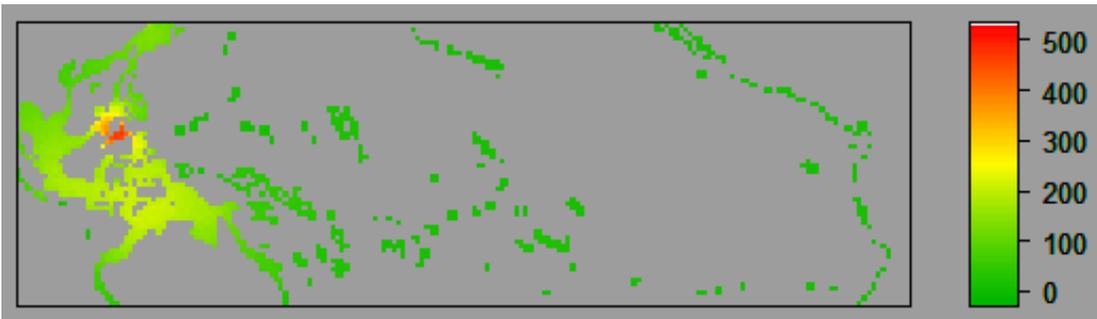
6.4.e. Iteration 40



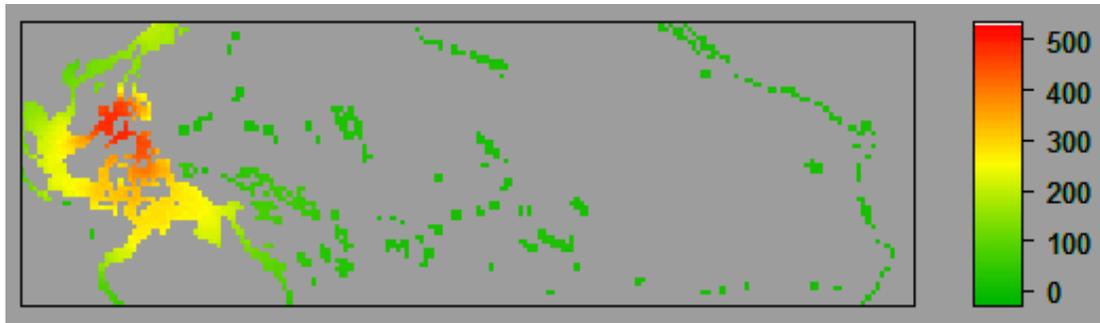
6.4.f. Iteration 50



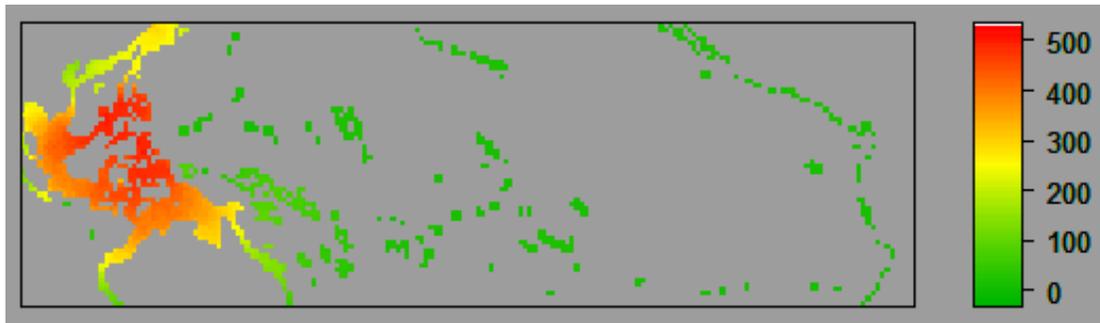
6.4.g. Iteration 60



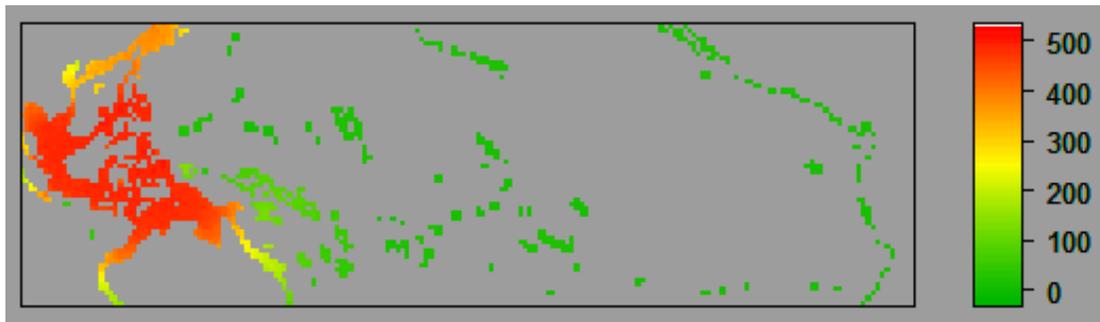
6.4.h. Iteration 70



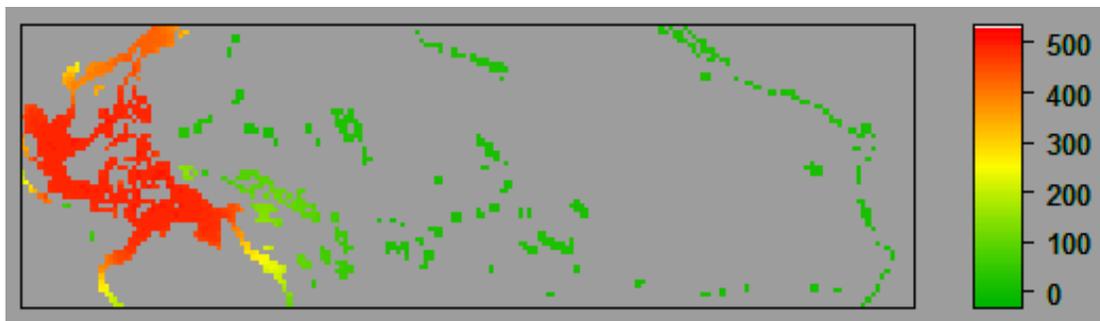
6.4.i. Iteration 80



6.4.j. Iteration 90



6.4.k. Iteration 100



6.4.l. Iteration 200

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.

Western to the Eastern Pacific. In the ‘Vortex Model’, the values of MUTPROB and EXTPROB needed to be relatively similar to achieve an increase in SR over time. In this model, when MUTPROB values were low relative to EXTPROB no SR pattern was produced, and when they were high the habitat areas became overwhelmed with species before a pattern could be established. In the ‘Topological Model’, however, the values of these two probabilities could differ more substantially. In addition, in the ‘Topological Model’, the balance between MUTPROB and EXTPROB not only determined the total number of species present in each area (for a given number of iterations) and the speed at which the diversity centre developed, but could also influence the shape and extension of the centre (see *Section 6.3.3.*). Similarly, larval mortality rate could affect the model results. Low larval mortality rates increased the chances of transport in the ‘Dispersal Sub-model’. This was generally translated into faster and wider range expansions of the newly formed species, and consequently smoother species gradients in the outcomes of the ‘Biogeography Sub-model’.

6.3.C. Differences between the species richness patterns found in the field and models

Although the results of the models closely resembled the patterns of SR found in the IP, some notable differences also occurred. As mentioned above, whilst the centre of diversity was usually centred over the Indonesian Archipelago, its exact location, extent, and shape varied among simulations. In some simulations the centre occupied only the Indonesian Archipelago, in most simulations it also included the Philippines and New Guinea, while in some others it expanded from the Malay Peninsula to north Australia (Figures 6.4.k. and 6.4.l.).

The SR of the eastern (e.g. French Polynesia) and sometimes middle-southern (e.g. Samoa, Tonga, and Fiji) parts of the Central Pacific were more similar to the SR of the Eastern Pacific in the models than in the real world (Figures 6.4.l. and 6.5.). In contrast, SR in the Arafura Sea, between New Guinea and Australia, was higher than in the real world (Figure 6.4.l.).

In the models, SR in the GBR gradually decreased from north (i.e. Torres Strait sector) to south (i.e. Capricorn-Bunker Groups sector). In reality, SR of scleractinian corals in the GBR increases gradually from the Torres-Strait (~ 300 species) to the Central sector (343 species), and decreases more rapidly from the Central sector to the

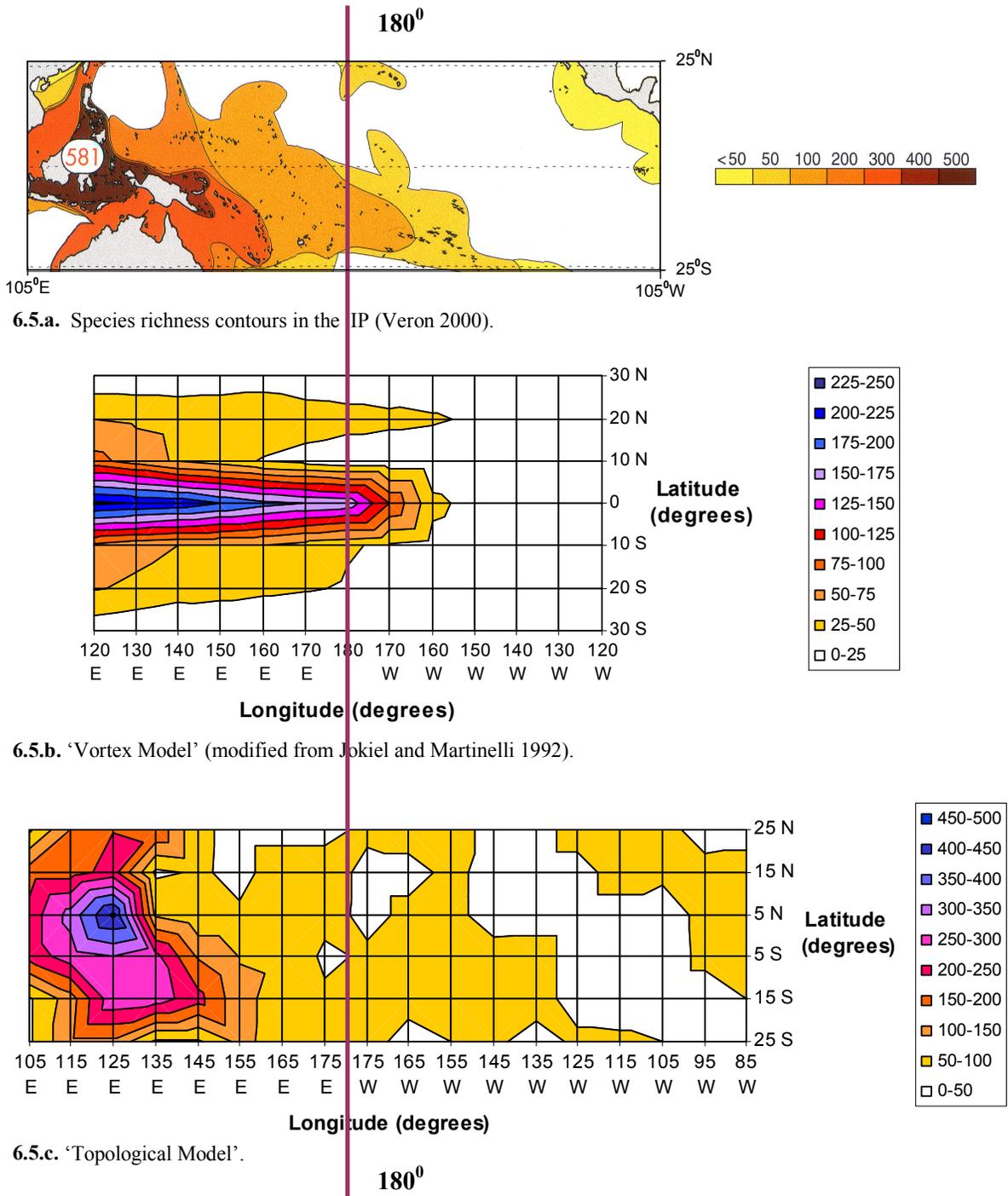


Figure 6.5. Comparison between the species richness patterns found in the IP and the results produced by the 'Vortex' and 'Topological' Models of Indo-Pacific Coral Reef Biogeography. (6.6.a.) Species richness contours in the IP (Veron 2000). (6.6.b.) Species contours after 120 iterations using the 'Vortex Model'. Simulation parameters: MUTPROB = 0.01, EXTPROB = 0.02 (modified from Jokiel and Martinelli 1992). (6.6.c.) Species contours after 200 iterations using the 'Topological Model'. Method 2 was used to assign the land-type value contained in the grid cells. Simulation parameters in the 'Dispersal Sub-model': Mortality 0.1 day⁻¹; and in the 'Biogeography Sub-model': MUTPROB = 0.0001, EXTPROB = 0.01. *Brown vertical line:* reference line at longitude 180°.

Capricorn-Bunker Groups (244 species) sector (Veron 1995). A similar pattern has been found for soft corals (Fabricius and De'ath 2001).

6.4. DISCUSSION

The 'Topological Model of Coral Reef Biogeography' developed in this chapter produces a good approximation to the present patterns of coral SR in the IP. Furthermore, the 'Topological Model' produces a better fit than the 'Vortex Model' (Jokiel and Martinelli 1992). In the 'Vortex Model' colonisation of species is driven by current patterns, while in the 'Topological Model' it is mainly driven by the spatial attributes and relationships of the areas of coral habitat. Therefore, contrary to Jokiel and Martinelli (1992), I conclude that current pattern (direction, speed, and variability) may not be the dominant factor shaping the geographic distribution of tropical inshore species. The topology of the species' habitats (shape, area, and distribution) appears to be at least as important as the hydrodynamics of the region.

6.4.A. Evidence in support of the 'Topological Model of Coral Reef Biogeography'

Ecological studies have long observed an association among SR patterns and many aspects of habitat topology. The relationship between SR and extent of habitat area is strong and consistent (e.g. Rosenzweig 1995, Brown and Lomolino 1998, Gaston 2000, Roos et al. 2004, and references within). Schoener (1976) described it as "one of community ecology's few laws". Larger patches are likely to provide higher structural complexity and habitat heterogeneity at varying spatial scales, which in turn can support a greater number of species (e.g. Brown and Lomolino 1998, and references within). Furthermore, because regional diversity contributes to a certain extent in defining the structure of local assemblages (e.g. Brown 1995, Gaston 2000), local diversity is also dependent on the size of the total available habitat at larger scales. This is particularly true for coral reefs, where interactions among species do not seem sufficient to limit local richness, and coral communities are regionally enriched with no evidence of saturation (Cornell and Karlson 1996, Karlson and Cornell 1998, Hugueny and Cornell 2000, Karlson et al. 2004). In fact, the SR of corals and fishes on tropical reefs has been found to be strongly correlated to the extent of habitat area both at local and regional

scales (e.g. Ormond and Roberts 1997, Bellwood and Hughes 2001, Bellwood et al. 2005). Similarly, the degree of spatial isolation can affect the level of SR supported by the habitat, as less isolated populations frequently experience higher connectivity, thereby being ‘rescued’ from extinction more often (e.g. MacArthur and Wilson 1963, 1967, Brown and Kodric-Brown 1977). This relationship has also been confirmed for corals and reef fishes by numerous studies (e.g. Fraser and Currie 1996, Karlson and Cornell 1998, Findley and Findley 2001).

The well-established relationship between SR and habitat topology may merely indicate the important role of the latter in maintaining the former. However, the mechanisms maintaining SR do not need to be the same than those creating it (e.g. Vermeij 1978, Rosen 1984, Gaston 2000, Bellwood and Wainwright 2002). Habitat topology can only be the cause of a rise in global SR if it increases speciation and/or decreases global extinction (e.g. Rosenzweig 1995, 1999). Larger habitat areas can support larger populations. Genetic studies indicate that larger populations can accumulate and maintain higher genetic diversity, even if they are of more recent origin (e.g. Palumbi 1997), and demographic models have shown that the probability of extinction increases non-linearly with decreasing population size (e.g. Goel and Richter-Dyn 1974, Leigh 1975, Goodman 1986, Pimm 1991). Palaeontological evidence also indicates the significant role of habitat topology in the origin of the patterns of SR of marine organisms; diversity of benthic communities being repeatedly higher during the geological periods in which shallow seas, and therefore habitat areas, were more extensive on the continental plates (e.g. Raup 1972, 1976, Rosen 1984, Wilson and Rosen 1998, Bellwood and Wainwright 2002). Moreover, historical habitat area (with its corresponding promotion of speciation and inhibition of extinction) is also likely to have been important in the origin of the present SR patterns in the IP (e.g. Rosenzweig 1995, Wiens and Donoghue 2004).

6.4.B. Potential evidence against the ‘Topological Model of Coral Reef Biogeography’

A common criticism to the ‘centre of origin’ theory is that the patches of habitat in the centre of diversity do not seem to be sufficiently isolated from each other to provide the conditions required for allopatric speciation, the most common type of speciation (e.g. Rosen 1988, Jokiel and Martinelli 1992). Although in the ‘Topological Model’

speciation occurs with equal probability throughout the IP, a great proportion of it occurs in the CIP given its large reefal area, and thus this criticism could also be applied to this model. Nevertheless, it now seems evident that TECO events have created periods of geographic isolation among patches of habitat in this area many times (e.g. McManus 1985, Thompson and Goldstein 2005). Barriers providing isolation do not need to be 'hard' (e.g. emerged land), and can instead be 'soft' (e.g. cold currents) (e.g. Bellwood and Wainwright 2002). Furthermore, environmental changes can also create filters or selective barriers (e.g. isolation by distance due to sea level change), preventing dispersal of some species but not others (e.g. Rosen 1984, Brown and Lomolino 1998, Rocha et al. 2002). Therefore, the conditions for allopatric speciation could have been repeatedly present in the CIP (e.g. McManus 1985, Springer and Williams 1994), and in fact evidence suggests that at least in some of these periods speciation was rapid (e.g. Palumbi 1994). In addition, the existence of mechanisms leading to reproductive isolation of populations other than geographic isolation has become increasingly accepted (e.g. Knowlton et al. 1992, Knowlton and Jackson 1994, Palumbi 1994, Via 2001), and they are now thought to be a more rapid way of speciation (i.e. sympatric speciation) than allopatric speciation (e.g. Kondrashov and Mina 1986, Kondrashov 1998, McCune and Lovejoy 1998, Coyne and Orr 1999).

Endemic species were believed to be an important contributor to the SR in the centre of diversity (e.g. Veron 1995, 2000). However, many species previously thought to inhabit exclusively the centre of diversity have gradually been found in other locations. It is now believed that the number of endemic coral species is low in most regions of the IP (with the exception of the Red Sea and Hawaii), and as a result the proportion of endemics in the centre of diversity is very low (<1%), with endemism hardly contributing to the SR of the region (Fenner 2002, Hughes et al. 2002b). This could also be considered as evidence against the 'Topological Model' given the high proportion of species originated in the CIP in this model. However, high endemism areas are not only the result of high speciation rates, but also of low dispersal rates. In fact, Rosen (1984) suggested that the key factor in the production of coral endemics is the relative isolation of the populations. Species may be readily formed in the centre of diversity and its low endemism could be simply due to the facility of the centre to export the newly formed species to other locations, whereas the high endemism in the Red Sea and to a lesser extent in the Hawaiian Islands would largely arise from their greater isolation.

Other potential criticisms of the ‘Topological Model’ are whether the durations of the isolating TECO events were long enough to allow speciation, and whether sufficient time has passed since these events occurred to redistribute the newly formed species. Although the best documented TECO events are the glacio-euctasy periods that occurred in relatively recent geological times during the Plio-Pleistocene, comparable TECO events have occurred repeatedly since the appearance of large and complex habitat areas in SE Asia during the Miocene. In addition, recent genetic studies have shown that at least some species in the IP have a much more recent origin than previously thought (e.g. McMillan and Palumbi 1995, Palumbi 1996, 1997, Palumbi et al. 1997, Kooistra et al. 2002). Furthermore, the time required for the development of the present SR patterns in the IP depends not only on the time required for speciation to occur, but also on the time needed for the new species to disperse and colonise their modern ranges. This time can be significant, depending on the connectivity of the location of origin and the dispersal potential of the new species. In this sense, the ‘Topological Model’ may have an advantage, as it is the model in which less species are required to disperse and colonise new areas.

6.4.C. Comparison of the ‘Topological Model’ with other theories including habitat topology

Several conceptual models and field studies that address the patterns of SR in the IP suggest that habitat topology plays a significant role in the genesis of these patterns (e.g. McCoy and Heck 1976, Rosen 1984, Bellwood and Hughes 2001, Bellwood et al. 2005). To explain the origin of the patterns of SR in the IP many of these works use a combination of mechanisms operating in concert, generally including elements of the four traditional theories and occasionally the MDE theory (see *Section 6.1.B.*). Frequently in them, particular features of the areas of coral habitat and/or currents are needed to explain the formation of the centre of SR in the CIP. For example, some ‘centre of refuge’ models propose features for the habitats in the centre of SR that would make them more resilient to TECO events, and most ‘centre of accumulation’ models assume that the direction of the currents is constant over time and across depths.

In the ‘Topological Model of Coral Reef Biogeography’ the CIP also functions simultaneously as a ‘centre of origin’, a ‘centre of accumulation’, and a ‘centre of refuge’. However, in this model, the topology of the habitats was sufficient for the CIP

to fulfil all these functions. The numerous and large areas of coral habitat in the centre of diversity originated and dispersed numerous new species to other areas in the IP (i.e. acting as a ‘centre of origin’). Species produced outside the centre of diversity colonised the habitat areas in this region (i.e. acting as a ‘centre of accumulation’). Finally, the species in the habitat areas located in the centre of diversity became extinct less frequently, and if extinct they recolonised more rapidly and often than the species in other areas (i.e. increased ‘rescue effect’, Brown and Kodric-Brown 1977). Both low extinction and high re-colonisation contributed to make these areas act as effective refuges (i.e. acting as a ‘centre of refuge’). Moreover, the MDE did not play a role in the generation of the high SR in the CIP in the models, since this region was not centred in the chart (as the chart did not include the whole Indian Ocean) (see *Section 6.2.A.1.*). This does not imply that the MDE on the origin and/or maintenance of the SR patterns in the IP is trivial, but highlights even further the importance of habitat topology for these processes.

6.4.D. The ‘Topological Model of Coral Reef Biogeography’ as a null model

Although the ‘Topological Model of Coral Reef Biogeography’ yielded results similar to the patterns of SR in the IP, some differences between both were found. These differences are presumed to be due predominantly to factors other than habitat topology. Below, I discuss the most evident discrepancies between the SR patterns found in the models and the real world, and their possible causes.

6.4.D.1. Central Indo-Pacific

The size and exact location of the centre of SR differed among simulations (see *Section 6.3.C.*). This discrepancy was generally caused by differences among simulations in the relative values of the mutation and extinction rates, and in larval mortality rate. However, the extent of the centre of diversity could also differ among simulations with equal parameters, indicating the importance of chance events in determining patterns of SR.

6.4.D.2. Central and Eastern Pacific

SR in the Eastern Pacific and Central Pacific are more similar in the models than in real life. In the real world, the EP is not only more depauperated of species, but also the species composition of its assemblages differs significantly from those in the rest of the

Pacific Ocean (Bellwood and Hughes 2001). In other locations of the Pacific Ocean the local pool of species is close to a random sample of the global species pool, while in the EP faviids are over-represented and acroporids are under-represented (Bellwood and Hughes 2001). These deviations seem to be related to environmental factors not included in the models, such as low water temperature and high turbidity, which limit the growth and reproduction of corals in the EP (e.g. Dana 1975). In these sub-optimal conditions, faviids appear to be more resilient than acroporids (e.g. Brown and Howard 1985, Hughes and Connell 1999).

6.4.D.3. *Arafura Sea*

SR in the Arafura Sea was higher in the models than in the real world. Shallow substrata are common between New Guinea and Australia, leading the models to predict a high SR for this region. Suitable coral habitat area is, however, much more sparse in this sea due to abundant river run-off and the presence of unfavourable substratum (see *Section 6.4.E.*), in practice limiting the SR of the region.

6.4.D.4. *Great Barrier Reef*

The SR patterns produced by the models for the GBR differ quite notably from those found in the real world. In the field, there is an increase in SR from the Torres Strait sector to the Central sector, followed by a larger decrease from the Central sector to the Capricorn-Bunker Groups sector, for both hard (Veron 1995) and soft (Fabricius and De'ath 2001) corals; while in the models SR gradually decreased from north to south. Over the large expanse of the GBR ($\sim 15^{\circ}$ of latitude and over 2,500 km) many factors not included in the models that can significantly modify SR vary (see *Chapter 4* and *Appendix II*). These factors include: climate (e.g. temperature, wind, and rain patterns), bathymetry, substratum type, salinity, and hydrodynamic regimes (e.g. tidal, weather-band, and background currents). In particular, the decrease in temperature that occurs with increasing latitude has been proposed to shape the latitudinal patterns of SR in numerous other systems (e.g. Rohde 1992, Roy et al. 1998, Roy et al. 2000). The latitudinal gradient in temperature, however, should reinforce rather than distort the SR gradient predicted for the GBR by the models. Because the Central sector often receives large volumes of water from the southern IP via the South Equatorial Current (SEC) (e.g. Munk 1955), it has been suggested that the SR peak in the Central sector is related

to the contribution of larvae by this current (e.g Fabricius and De'ath 2001). However, the Northern sector receives large masses of water from the SEC more frequently than the Central sector (see *Appendix III*) and has lower SR than the latter sector. In the models in Chapter 4, reef topology (rather than shallow substratum topology) in combination with background currents was sufficient to produce a settlement peak in the Central sector, thus these factors may also contribute to the high SR of this sector. Nevertheless, the causes of the high SR of the Central sector remain uncertain and further research is needed to determine them.

Differences in SR between the models and the real world in other areas also have no obvious explanations and may require further analysis and/or research. Nevertheless, the 'Topological', 'Vortex', and 'MDE' Models of Coral Reef Biogeography are not mutually exclusive, and combinations of them could be used as null models against which the SR patterns in the IP can be contrasted. In these cases, the differences with the patterns found in the real world would be attributable to factors other than habitat topology, currents patterns, and/or geometric constraints in the placement of geographic ranges within their domains.

6.4.E. Model limitations

The 'Dispersal Sub-model' is subjected to the limitations previously cited in *Chapters 2 and 3*. Cartographic errors in the production of the map of the IP and digitising errors in its conversion to charts (see *Section 6.2.A.1.*) can also limit the accuracy of this study. However, the aims of this chapter are not to predict exact SR values at particular times and/or locations, but to investigate the origin of the patterns of SR in the IP. For this use, the limitations introduced by these types of errors are likely to be insignificant. More important are the inaccuracies derived from the assumption of a linear relationship between the extent of shallow substratum (≤ 100 m.) and coral habitat in the tropical IP. Coral reefs in the IP generally occur in substrata shallower than 50 m, which are not necessarily uniformly distributed within the 100 m depth contours. Furthermore, in some areas abundant shallow substratum may not equate to suitable habitat due to environmental constraints. For example, the area south of New Guinea is affected by abundant river run-off, and cold turbid waters frequently occur in the EP. This limitation is likely to affect more importantly the use of the 'Topological

Model' as a null model than its application in the investigation of the origin of the SR patterns in the IP. Nevertheless, the implementation of a 'Topological Model' incorporating the 50 m depth contours or ideally the reefs themselves as coral habitats is desirable.

In the 'Biogeography Sub-model', speciation and extinction rates were constant in space (i.e. in all cells representing coral habitat) and time (i.e. in all iterations). Although genetic analysis suggests that speciation has occurred throughout the Pacific (Palumbi 1997), events leading to speciation are more likely to occur at particular locations (e.g. those with a certain degree of isolation) and times (e.g. following TECO events) (e.g. Ridley 1996, Brown and Lomolino 1998). For example, connectivity and gene flow between the Pacific and Indian Oceans have been much more limited at periods of low sea (Potts 1983), with these two oceans effectively acting as two distinct biogeographic provinces (Valentine 1973, Bellwood and Wainwright 2002). Similarly, punctual episodes of mass-extinction, usually followed by periods of rapid diversification, have been implicated in the evolution of marine systems (e.g. Boucot 1983, Bellwood and Wainwright 2002). Nevertheless, the 'Topological Model' produced SR patterns similar to those presently found in the IP, indicating the importance of the spatial attributes and relationships of the reefs in originating these patterns. Although in the models, speciation and extinction rates did not vary in space, their effects did, as the rates at which new species expanded their ranges and locally extinct species recolonised varied largely depending on the topology of the suitable habitats.

6.4.F. Summary and Conclusions

The 'Topological Model of Coral Reef Biogeography' produces a good approximation to the present patterns of SR in the IP even though dispersal is modelled to occur exclusively by diffusion. Moreover, this approximation is better than that produced by the 'Vortex Model'. It was concluded, that current pattern (direction, speed, and variability) may not be the dominant factor determining the distribution of tropical inshore species, and that the topology of coral habitats (shape, area, and distribution) is at least as important. Numerous ecological, biogeographic, and genetic studies have also indicated the important role of habitat topology in generating and maintaining SR patterns, and several conceptual models proposed to explain the origin of the patterns of SR in the IP have included habitat topology (or some aspect of it). In

many of these models, some particular properties of the CIP (e.g. properties leading to the ‘origin’ or ‘survival’ of species, and its position in the centre of its domain) and/or the currents it receives (e.g. their direction leading to the ‘accumulation’ of species) are assumed for the development of a centre of SR in this region. However, in the ‘Topological Model’ the spatial attributes and relationships of the areas of coral habitat in the IP are sufficient to reproduce their patterns of SR. In this model, although speciation and extinction rates do not differ in space, their effects do as a result of the topology of the habitats. This allows the CIP to act simultaneously as a ‘centre of origin’, a ‘centre of accumulation’, and a ‘centre of refuge’. Therefore, it seems necessary to incorporate habitat topology into biogeographical and ecological theory as well as into the design of management projects (particularly in those of regional-scale). In fact, the ‘Topological Model’ can be used as a null model, against which the patterns of SR observed in the field can be compared. Nevertheless, the ‘Topological’, ‘Vortex’, and ‘MDE’ Models of Coral Reef Biogeography are not mutually exclusive, and mixed models could be used as null models. The results in this chapter have important implications for the conservation of marine biodiversity. Human activity often leads to degradation, reduction, and fragmentation of coral habitats, significantly modifying their topology. Because of the close relationship between SR and topology in the IP coral reefs, their local and regional diversity can be seriously threatened by this activity. Therefore, human actions should be evaluated, regulated, and monitored, particularly in key and sensitive locations.

Chapter 7: **GENERAL DISCUSSION**

In this thesis, I investigated the effects and determinants of coral larvae dispersal using spatially explicit and spatially realistic models (see *Chapter 2* and *Appendix IV*). The thesis is conceptually divided into three parts. *Part 1* is mainly theoretical, while the models in *Parts 2* and *3* included empirically obtained data. These data consisted of a combination of realistic representations of the following information inputs: topology of reefs, direction and speed of currents, competence patterns of larvae, and both abundance and fecundity of adults. *Part 1* (*Chapters 2* and *3*) explored the effect of factors determining larvae dispersal on settlement rate, connectivity among reefs by larvae, and the evenness and diversity of sources of the larval input to reefs (Figure 7.1.). In *Part 2* (*Chapter 4*) spatially realistic models of the dispersal of larvae on the Great Barrier Reef (GBR) were used to investigate settlement patterns in the region and explore the mechanisms determining them (Figure 7.1.). *Part 3* (*Chapters 5* and *6*) investigated the relationships between larvae dispersal and biogeography of corals (Figure 7.1.).

In this chapter, I briefly revise the main findings in the five data chapters in this thesis, presenting them in a broader context, considering their interrelationships, implications, and applications. To conclude the chapter, I present and discuss possible directions for further research, including both empirical and modelling work.

7.1. OVERVIEW AND DISCUSSION OF THE MAIN FINDINGS IN THE THESIS

7.1.A. *Chapter 2:* Larval types, currents patterns, and their interaction

In *Chapter 2* the effects of different combinations of larval types (classic brooder vs. classic spawner) and current patterns (non-directional flow vs. strongly directional flow) on settlement, connectivity, and evenness and diversity of the larval input to the reefs were investigated (Figure 7.1.). Despite their simplicity the models revealed complex dynamics, and contrasting results were found for different reproductive strategies, hydrodynamic conditions, and individual reefs. Furthermore, the interactions among

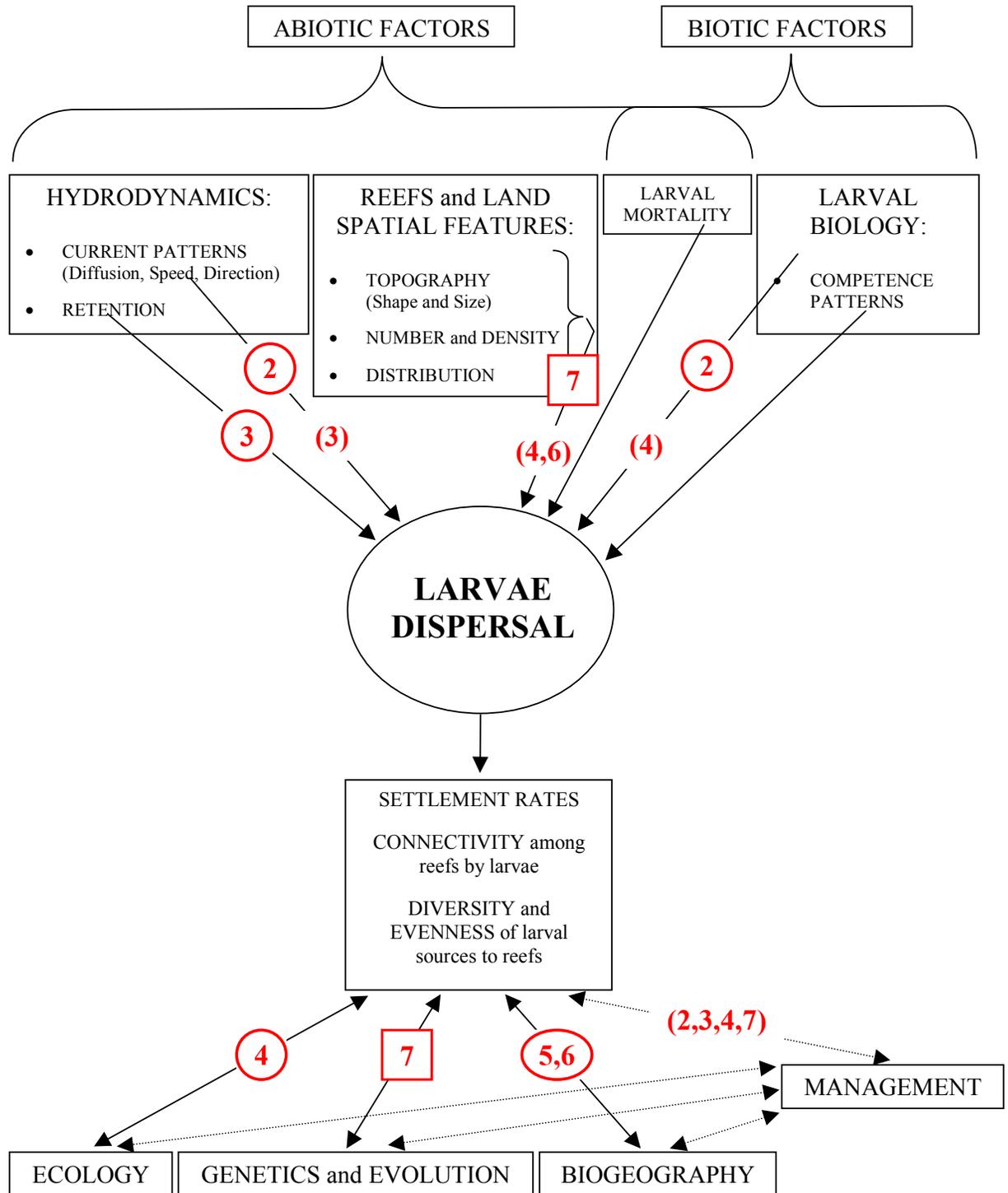


Figure 7.1. Mechanisms and implications of the dispersal of coral larvae and their investigation in this thesis. In red: chapter investigating the indicated relationship (circles denote that the relationship was the main aim of the chapter; parentheses that the relationship was investigated in the chapter, but is not the main objective; and squares that the relationship was discussed).

the investigated factors determining dispersal were also complex, with different current patterns producing different effects on each of the larval types. These results suggest the difficulty in applying global management solutions, and the need for management plans specific to individual problems, including the environmental conditions (e.g. hydrodynamics and reef topology) and species relevant to each case.

In the models settlement rates were higher for brooders than spawners because the larvae produced by spawners experienced higher mortality during their longer pre-competent and competent periods. Despite the theoretical settling advantage of brooding corals, spawning corals often dominate reefs throughout the world (e.g. Veron 2000, Bellwood and Hughes 2001), suggesting the importance of the benthic processes leading to mortality of recruits and/or adults in the regulation of coral reef assemblages. The pattern of the currents also contributed significantly in determining the settlement rate of larvae in the models (although not as much as larval type), in general with higher settlement occurring in non-directional currents than in strongly directional currents.

Current pattern, on the other hand, was the main determinant of the spatial distribution of settlers (i.e. local vs. non-local settlement) and of the connectivity among reefs by larvae. Stronger (i.e. more directional) currents dramatically increased the proportion of larvae settling non-locally in the models, especially for larvae with long pre-competent and competent periods in which local settlement became practically negligible. This suggests that, at least in the case of spawners, to obtain the levels of local recruitment estimated by genetic studies for the GBR (e.g. Ayre and Hughes 2000) some level of water retention must exist at the reefs (see also *Chapter 3*). Although advection increased non-local settlement, the number of reefs that the larvae settled on decreased (i.e. instead of settling on the natal and surrounding reefs larvae mainly settled on a few reefs further away). In concordance with genetic (e.g. Ayre and Hughes 2000) and ecological (e.g. Hughes et al. 2000) studies, evolutionary-scale connectivity was very high but ecological-scale connectivity was limited, especially when the current flow was strongly directional. In the models (with relatively dense reefal systems and not including retention) the traditional view that connectivity was higher in spawners than brooders (e.g. Harrison et al. 1984) only held in the absence of advection. Under strongly directional currents, although spawners presented much higher non-local settlement (relative to the total settlement) than brooders, the number of reefs connected by their larvae was lower. Furthermore, reefs and reefal systems with high evolutionary-scale connectivity did not necessarily have high ecological-scale connectivity and vice-

versa. Consequently, when mentioning connectivity it is essential to identify the taxa and scale of interest.

The differences between the effects of an increase in advection in the currents on settlement rate, proportion of local settlement, connectivity and evenness of the larval input, in brooders and spawners were quantitative. That is, in both reproductive groups more directional currents produced decreases in the first 3 variables and an increase in the latter, although with differing magnitude in brooders and spawners. However, the effect of an increase in advection in the currents on the diversity of sources of the larval input was qualitatively different in each larval type, diversity increasing in brooders and decreasing in spawners. This shows once more the complexity of the larval dispersal process and its multiple effects.

Moreover, settlement rate, connectivity, and diversity also varied notably among reefs. Variability among reefs was greater under strongly directional than non-directional flow, and for spawners than brooders. This further indicates the complexity of larval dispersal and the need of specific management plans for marine communities.

7.1.B. Chapter 3: Effect of larval retention on reefs

Chapter 3 investigated the effect of water retention at the reefs on settlement, connectivity, and evenness and diversity of the larval input, in brooder and spawner corals under varying current patterns (Figure 7.1.). Of the common predictions for the effects of an increase in retention, only the increases in total and local settlement were supported in all the larval type – current pattern combinations. The remaining predictions (reduction in non-local settlement, connectivity, evenness and diversity) were generally supported, except at low or very low levels of retention. However, these lower levels of retention are more realistic. At low retention levels the behaviour of the variables differed greatly depending on the conditions (i.e. current pattern-larval type combinations) in the simulations, but generally the predictions were not met when the currents had a strongly directional flow (the most common hydrodynamic situation). Under these conditions significant quantities of larvae were still being dispersed away from the natal reefs, while retention was sufficient to vastly increase non-local settlement, connectivity, evenness and diversity, by trapping larvae in the circulation of reefs other than natal until they were competent to settle.

Under constant directional currents and in the absence of retention, settlement and connectivity could be low, especially for larvae with long pre-competent and competent periods because of their prolonged exposure to mortality sources. To obtain results comparable to those estimated by ecological (e.g. Sammarco and Andrews 1988, 1989, Hughes et al. 2000) and genetic (e.g. Stoddart 1986, Ayre and Hughes 2000) studies, some level of larval retention at the reefs was required in the models. It was concluded, that some retention mechanism (hydrodynamic and/or behavioural) is necessary when the reefs are subjected to background currents with a relatively constant and strongly directional flow (the majority of the reefs), at least in the case of spawning corals (the most speciose and often the most abundant type of corals). Moreover, only very small increases in the level of retention are required to produce dramatic increases in local and total settlement.

In the simulations, reef density (4%) and current pattern (directional flow with a speed of $\sim 17 \text{ cm.s}^{-1}$) were similar to those of the central GBR. Notably, the level of retention estimated by previous modelling studies for the reefs in this area (8% after 10 days - Black et al. 1991, Black 1993) seemed optimal for spawners. According to the models, at this retention level recruitment rates in spawners showed a $\sim 10^5$ fold increase relative to those obtained in the absence of retention, reaching a value of $\sim 79\%$ of the maximum settlement rate (obtained when 100% of the water was retained at the reefs). Furthermore, this level of retention maximised genetic connectivity and produced relatively high ecological-scale connectivity (ecological-scale connectivity was much higher than in the absence of retention, and only slightly smaller than at its maximum value obtained at very low retention levels).

7.1.C. *Chapter 4: Dispersal of larvae on the Great Barrier Reef*

Chapter 4 used spatially realistic models to investigate settlement on 6 zones (located at different latitudes) of the GBR and the factors determining it, by comparing their predictions to the findings of empirical studies (Figure 7.1.). Field studies show that recruitment is variable in space, time, and among taxa (e.g. Barnes 1956, Milicich 1994, Hughes et al. 1999). Consequently, it is generally assumed that settlement is not only variable but frequently unpredictable (e.g. Houde 1987, Doherty and Williams 1988, Underwood and Fairweather 1989). Even the simplest of the deterministic models in this chapter produced important variation in settlement rates among zones, reefs within

zones, and larval types. Furthermore, the models reproduced many settlement and connectivity patterns previously found by field and genetic studies, including: greater settlement variability for spawners at larger spatial-scales and for brooders at smaller spatial-scales, much higher local-settlement for brooders, higher connectivity for spawners in most zones, and the latitudinal settlement patterns of spawners and their proportion in the total settlement (e.g. Hughes et al. 1999, Ayre and Hughes 2000). However, the models that best reproduced the field patterns required significant amounts of information, such as physical and biological data on the environment and state of the reefs. It was concluded, that a substantial part of the large variation in recruitment found in the field is related to variation in the factors included in the models, rather than to purely stochastic variation. Therefore, settlement patterns may be predictable to a certain extent if sufficient physical and biological information is available at the relevant spatial and temporal scales.

In the models, settlement peaked in the central GBR for both brooding and spawning corals, generally decreasing more steeply to the north than to the south. In the field, recruitment rates of brooders decrease steadily from north to south along the GBR (e.g. Harriott and Simpson 1997, Dunstan and Johnson 1998, Hughes et al. 2001), thus all types of models underestimated their settlement in the northern GBR. However, the most complete type of models could not be run for brooders, as data on their fecundity on the GBR was not available. The latitudinal patterns of recruitment of spawners in the GBR also display a bell shape, although its peak occurs farther north than in the models (Hughes et al. 2002a). The models that produced the best fit to the field patterns required the inclusion of data on the latitudinal fecundity patterns of spawners along the GBR. This is in agreement with field studies, which have found that the main factor determining latitudinal variation in recruitment by spawning acroporids (the most common spawning coral species on the GBR) is their regional and temporal variation in fecundity (Hughes et al. 2000). The models also reproduced the latitudinal variation in the proportion of spawners in the total settlement observed in the GBR, although the decrease in this proportion from the Central to the Southern-most GBR in the best fitting model was less steep than in the field. This and other discrepancies between the models and field observations may be partially due to the scarce number of data points (5 to 6 zones) available and the consequent low statistical power of the analyses. Nevertheless, the discrepancies are likely to also reflect the importance of environmental factors not included in the models, such as the decrease in temperature,

and the increase in depth and soft substratum abundance with latitude (see *Section 4.1.1.*, *Appendix II*, and references within). These gradients can affect to different extent in different taxa multiple life history aspects essential for the recruitment of new individuals to local-populations (such as the fertility of adults, and the survival of larvae and recruits).

7.1.D. *Chapter 5: Larval competent period and size of geographic range in corals*

Chapter 5 explored the putative relationship between the potential for dispersal of the larvae of scleractinian corals and the extent of their geographic range using spatially explicit dispersal models. The size of the geographic range of the 15 species in the study varied substantially (especially the longitudinal extent and area of their ranges, less so their latitudinal extent). The models using the competence patterns described for these species also produced large differences in the dispersal variables investigated (settlement rate, proportion of non-local settlement, evolutionary- and ecological-scale connectivity among reefs by larvae, and evenness and diversity of sources of the larval input). In general, variation in settlement rate was associated with the duration of the pre-competent period, while the variation in connectivity was related to the duration of both the pre-competent and competent periods. The shape of the competence curve (describing the proportion of a cohort of larvae available for settlement over time) was also essential in determining settlement and connectivity by larvae. The use of non-linear descriptions of the larval competence patterns (rather than just the beginning and ending times of the pre-competent and competent periods) is, therefore, strongly recommended in models of larval dispersal, particularly if they are to be applied to management and conservation. Unfortunately, currently competence curves are only available for a few species of corals.

Nevertheless, the variables that described the potential for dispersal of the larvae were poor predictors of the size of the geographic ranges of the coral species in the study. Similarly, a genetic study in the GBR concluded that gene flow (the genetically effective number of migrants per generation) is not a good predictor of geographic range size (Ayre and Hughes 2000). Notably, the estimates of gene flow in this study showed tentative positive relationships with some of the dispersal variables computed by the models. The relationships were stronger for brooders than spawners. Moreover, if

only the competence curves obtained in the laboratory for larvae reared in the presence of substratum were used in the models and the dispersal results for both reproductive groups were pooled together, evolutionary-scale connectivity was an almost significant predictor of gene flow. This further indicates a relationship between the dispersal potential of the larvae and gene flow, also suggesting that in the GBR settlement cues may be abundant (perhaps due to the large extension and density of its reef matrix) or more likely larvae settle close to their natal reef. However, more research is needed to confirm this relationship, as data on both gene flow and competence patterns (required by the models) were available for only 3 species within each reproductive group.

Although the dispersal potential of the larvae influence the geographic ranges of scleractinian coral species, the dispersal hypothesis per se cannot explain the size of the geographic ranges of corals in the Indo-Pacific (IP). The lack of relationship between dispersal potential and geographic range could be due, at least in part, to differences in the time of range expansion among the species in the study (derived from differences in the time elapsed from their origin and/or the last environmental change in their ranges). However, multiple other factors contribute to the biogeography of corals. These include: factors related to dispersal not included in the models (e.g. larval behaviour and rafting), the environmental niche (*sensu* Hutchinson 1957) and life history of the species, and factors related to the physical world that the species inhabit (e.g. environmental conditions, historical events, and stochastic events). These factors mask the effect of the dispersal potential provided by the larvae on the geographic ranges of coral species in the IP.

7.1.E. *Chapter 6*: Larval dispersal, habitat topology, and species richness in Indo-Pacific corals

Chapter 6 investigated the mechanisms by which the patterns of species richness (SR) in the Indo-Pacific may have originated using a computer model of the coral reef biogeography of the region. The model consisted of two sub-models: one representing dispersal, and the other representing the benthic phase of the species dynamics (integrating speciation, recruitment, and local extinction). Previous models have implemented dispersal based entirely on the predominant modern surface current patterns in the region, without considering the topology (i.e. spatial attributes and relationships) of the substrata ('Vortex Model of Coral Reef Biogeography', Jokiel and

Martinelli 1992). In the model in this chapter ('Topological Model of Coral Reef Biogeography'), however, dispersal occurred exclusively by diffusion and over a spatially realistic representation of the IP (including descriptions of the emerged land, and shallow and deep substratum areas). The 'Topological Model' provided a good approximation to the patterns of coral SR in the IP. Furthermore, the results produced by the 'Topological Model' were more similar to the SR patterns in the IP than those produced by the 'Vortex Model'. Therefore, contrary to Jokiel and Martinelli (1992), I concluded that current pattern (direction, speed, and variability) may not be the dominant factor shaping the geographic distribution of tropical inshore species. The topology of the habitats of the species (shape, area, and distribution) is at least as important as the hydrodynamics of the region.

Multiple ecological, genetic, and biogeographic studies have indicated the substantial role of habitat topology in generating and maintaining patterns of SR (e.g. Schoener 1976, Rosenzweig 1995, Brown and Lomolino 1998, Gaston 2000). Habitat topology (or some aspect of it) has also been included in several conceptual models proposed to explain the origin of the patterns of SR in the IP coral reefs (e.g. McCoy and Heck 1976, Raup 1976, Rosen 1984, Wilson and Rosen 1998, Bellwood and Wainwright 2002). In many of these models, some particular properties of the CIP (leading to the 'origin', 'survival' or 'geometrically constrained distribution' of species) and/or the currents it receives (leading to the 'accumulation' of species) are assumed for the development of a centre of SR in this region. In the 'Topological Model', however, the spatial attributes and relationships among habitats were sufficient for the CIP to act simultaneously as a centre of 'origin', 'accumulation', and 'refuge', and consequently develop a centre of SR. In this model, although speciation and extinction rates did not differ in space, their effect could, indicating the importance of the topology of the habitats. The 'Topological' model, alone or in combination with the 'Vortex' and 'Mid Domain' models, can be used as a null model, against which the actual patterns of SR in the IP can be contrasted. The differences between the patterns observed in the field and those produced in the simulations would then be due to factors not included in the models, and may require further study.

7.2. APPLICATIONS: CONSERVATION and MANAGEMENT

Corals and the myriads of organisms associated with them are presently endangered (e.g. Hughes et al. 2003). Human activity threatens around 58% of the coral reefs of the world (Bryant 1998) and the area they occupy is in steady decline (Wilkinson 2000). Furthermore, human impacts are so substantial that the extinction of marine taxa (at least at local scales) in these ecosystems are of real concern (e.g. Dulvy et al. 2003, Pandolfi et al. 2003). Under these circumstances, there is a clear need for active management, including measures directed to both protect existing reefs and restore damaged ones.

Traditionally most management efforts on coral reefs have been based on the abundance of adults of one or a few species, which populations are assumed to be predominantly 'open' (and thus, given sufficient time, always recoverable), and implemented locally. However, this approach presents important limitations, and a new management style seems to be emerging in recent times. The main guidelines of this new style are:

1. The present status of a reef may not be an adequate predictor of its dynamics (Hughes et al. 1999, Sale 1999). As a consequence, management based on adequate knowledge of the processes and mechanisms driving the dynamics of coral reefs will be more robust than that simply based on monitoring patterns of abundance (Hughes et al. 1999).
2. Until recently human impacts on reefs occurred mainly locally (e.g. traditional fishing and pollution); however, newer human threats take place over much larger areas (e.g. habitat loss and climate change). Moreover, recovery of a damaged reef is often highly dependent on the remaining reefal system (e.g. Johnson and Preece 1992). Therefore, management of coral reefs should consider the whole interconnected reefal system, and not just one or a sub-set of reefs as often done to date (e.g. Hughes et al. 2005, Pandolfi et al. 2005).
3. It seems now clear that the populations of many species inhabiting coral reefs are less open than previously thought (e.g. Hughes et al. 1999, Jones et al. 2005, Cowen et al. 2006), and in fact their dynamics are determined by processes occurring at various temporal and spatial scales (e.g. Sale et al. 1984, Fisk and Harriot 1990, Fahrig 1992, Cowen et al. 2006). Hence, plans for the conservation of coral reefs should include management actions at multiple scales (e.g. Hughes et al. 2005).

4. The fates of the numerous species inhabiting coral reefs are closely interrelated. Consequently, coral reefs should be managed as entire ecosystems (e.g. Pandolfi et al. 2005) or at least at the level of functional groups (Bellwood et al. 2004). That is, management plans should be aimed to improve (or at the very least protect) the resilience of the whole ecosystem, accounting for uncertainty and future change (e.g. Bellwood et al. 2004, Steneck 2006).
5. The most suitable and realistic approach to the management of coral reefs is to consider them as socio-ecological systems, acknowledging their biological, economical, cultural, and aesthetic values (e.g. Hughes et al. 2005). Therefore, the design of plans for the management of these ecosystems should involve a broad range of professionals, including marine ecologists, fisheries biologists, economists, and social scientists (e.g. Bellwood et al. 2004).

Models can be useful tools in this new style of management and conservation of coral reefs. In particular, the models presented in this thesis can contribute to the management and conservation of coral reefs in a number of ways. These potential contributions can be grouped in the following three broad areas:

1. The dispersal and retention processes occurring during the larval phase of the coral life cycle are an essential part of the dynamics of coral populations. Thus, understanding the origin and consequences of the patterns of larval dispersal and settlement is essential for the appropriate management of coral reef ecosystems (e.g. Man et al. 1995, Roberts 1997, Hughes et al. 1999). The models in this thesis provide insights into the effects that factors determining dispersal have on settlement and connectivity patterns, and their relationship with the ecology and biogeography of the species.
2. The particular scales of dispersal and retention, together with the patterns of larval connectivity among the reefs of an area have important implications for the design of marine reserves, conservation of marine biodiversity, and management of fishery stocks (e.g. Fairweather 1991, Roberts 1997, Strathmann et al. 2002). The spatially realistic models in *Chapter 4* and/or similar ones could be used in the design of specific conservation and management plans (see *Section 7.3.B*).
3. In the face of the destruction and degradation of large reefal areas occurred and predicted around the world, active restoration may be required as an integral part of management plans (Rosenzweig personal communication). Models similar to those

used in this thesis could also be used for the design and location of artificial reefs. Additional work conducted during the course of my Ph.D. candidature (to be presented elsewhere) investigated the effect of the topology of the reefs on larval settlement and connectivity among reefs (see *Section 2.2.B.1.*). The results of this work could be readily applied to restoration management initiatives. For example, results indicated that at low reef densities creating a few large artificial reefs will be a better option than placing many small reefs, and that grouping the reefs in a few clusters will be preferable to distributing them uniformly or randomly. However, if disturbances were frequent, a higher number of reefs and clusters would be required to spread the risk of damage among them.

In addition, five main general conclusions relevant to the management of natural resources can be drawn from the studies in this thesis:

1. The spatially realistic models in this thesis were able to reproduce to a certain extent the settlement patterns observed in the field, despite their high variability in space (*Chapter 4*). However, the best fitting models required a considerable amount of detail, including data on the topology of the reefs, hydrodynamics of the area, competence patterns of the larvae, and abundance and fecundity of the adults.
2. Even the simplest theoretical dispersal models in *Part I* of this *Thesis* were capable of producing very different results depending on the particular settings in the simulations (*Chapters 2, 3, and 5*). For example, settlement rates and connectivity patterns could vary largely among larval types, current patterns, and reefs. This is in agreement with the results of ecological and genetic studies (e.g. Barnes 1956, Milicich 1994, Hughes et al. 1999, Ayre and Hughes 2000). Moreover, in the models there were significant interactions among the factors determining the dispersal of larvae, and changes in the topology of the reefs (e.g. reef size, reef density) or hydrodynamic conditions (e.g. retention level at the reefs, advection strength) could have very different effects (both quantitatively and qualitatively) on distinct larval types.
3. Very small levels of water retention at the reefs can lead to dramatic increases in settlement without substantially reducing the connectivity among reefs or the diversity of their larval input. In fact, these levels of retention may even increase the connectivity of larvae with long pre-competent and competent periods (i.e.

spawners) when the currents have a strongly directional flow, as larvae can become trapped in the circulation of non-natal reefs (*Chapter 3*). Both retention and dispersal are crucial for life in coral reefs: retention maintaining viable local populations, and dispersal (and to a certain extent retention) maintaining connectivity among these populations. Dispersal, retention and accumulation must be, therefore, considered in the management and conservation of marine biodiversity.

4. There is a very close relationship between SR and habitat topology in coral reefs, at least in the IP (*Chapter 4*). This implies that human activities leading to the degradation, reduction, and/or fragmentation of reef habitat can have profound consequences for local and regional marine biodiversity (see also Bellwood and Hughes 2001, Bellwood et al. 2005). It is, therefore, essential to evaluate, regulate, and monitor these activities, particularly in key and sensitive locations.
5. Finally, a double corollary can be drawn from the complexity of dispersal and its effects found in this thesis and the empirical studies. Firstly, there is a significant risk in generalising the results obtained by field studies sampling a small number of reefs on a single occasion. Secondly, although spatially realistic models are undoubtedly useful tools in the design and evaluation of management plans, incorrect assumptions and/or over-simplifications may lead to inaccurate estimates of the typical levels of larvae dispersal, which can result in erroneous management decisions with severe implications for the populations (e.g. Carr and Reed 1993). For this reason, the models must be specific to each problem and include adequate information on the physical conditions of the area and the biology of the species to be managed. Management plans should incorporate multi-disciplinary studies on the local topology and hydrodynamic conditions, the ecology of the relevant species, numerical simulations, and conduct regular ‘ground’-truthing in the field.

7.3. SUGGESTIONS FOR FURTHER WORK

The models developed in this thesis were frequently limited by the lack of a complete understanding and detailed description of the physical and biological processes occurring within and among reefs. I start this section revising the areas in

which additional empirical (field and laboratory) research would most benefit the models, and then I suggest directions for future modelling work.

7.3.A. Empirical work

Perhaps the most significant limitation for the development of more reliable models of larval dispersal is the lack of understanding of the patterns of larval mortality in the sea. Research aimed to gain insights into the variation in larval mortality over time, space, and among taxa is strongly recommended. Other important aspects of larval biology requiring further investigation are the differences among individual species in their susceptibility to be passively or actively retained, and in their capabilities to detect settlement cues. In order to develop effective models, laboratory settlement experiments should aim to compile competence curves rather than simply indicate the beginning and end of the larval competent period, and also provide an estimation of the larval mortality rates in the study. Competent patterns in these experiments are estimated in larvae reared in the absence of most sources of nutrition. The amount of error introduced by such estimates is not evident, but it could be significant if the abilities of the larvae to assimilate external sources of energy differ largely among the species used in the simulations. Therefore, it is advisable to use conditions as close as possible to those found in the field while conducting settlement experiments.

Further limitations derive from the particular applications of the models. Although these were discussed in detail in the '*Model Limitations*' section within each data chapter, the most significant ones are revised below. In general, more detailed descriptions of the physical processes and the biology of the species in the models would improve the accuracy and reliability of the simulations. In particular, the models investigating the settlement patterns and the mechanisms driving them on the GBR (*Chapter 4*) would benefit from better descriptions of the hydrodynamics of the region and especially from the inclusion of data on the fecundity of brooding corals (presently unavailable). The models exploring the putative relationship between the potential for dispersal provided by the larvae of coral species and the extent of their geographic ranges (*Chapter 5*) would gain from detailed descriptions of the larval competence patterns of more species. This study could only be conducted for spawning corals due to the paucity of information on the competence patterns of brooders. Gene flow estimates for more of the species included in these models are required to confirm the relationship between the dispersal

variables and of gene flow in the GBR. Using reefal areas, rather than ocean floor shallower than 100m as an approximation for the former, could provide more unequivocal evidence for the importance of the topology of the coral habitats in the origin and maintenance of the patterns of coral species richness in the Indo-Pacific (*Chapter 6*).

7.3.B. Modelling work

The next step for the models in *Part I* of this *Thesis* (*Chapters 2 and 3*) should be to incorporate all coral life-history phases in the models; that is, the models should include both the pelagic larval phase and the benthic adult phase. In this type of model the pelagic phase sub-model would be analogous to the models described in *Chapters 2 and 3*, while the benthic phase sub-model could be implemented as a density function or using transition probability matrices (e.g. Tanner 1996b, 1997). Models including both life-history phases were used in *Chapter 6*, but their application to theoretical reefal systems, such as those in *Chapters 2 and 3*, would be particularly valuable. The integration of the larval and adult phases in the same study is essential to understand how they inter-relate and contribute to the ecology of marine species (e.g. Gaines and Bertness 1993, Gaines and Lafferty 1995). Models of this type could be used, for example, to investigate the effect of different life history traits (e.g. rate of asexual reproduction, age of first sexual reproduction, or adult mortality rate) on the dynamics of coral metapopulations, and the causes of demographic fluctuations that can lead to extinction at local- and regional-scales. The integration of both phases has been prevented in field studies mainly because the larval and adult phases operate in different spatial scales. However, in simulation models the scales can be multiple and the parameters can be controlled, facilitating the investigation of questions that address interrelated mechanisms acting at different scales in a single study.

Transforming these deterministic models that incorporate both life history phases into individually-based stochastic models would allow the investigation of more complex questions, but at a higher computational (memory and time) cost. During my Ph.D. candidature I developed an individually-based spatially explicit metapopulation model to investigate the evolution of dispersal in the larvae of marine invertebrates. This model will be used to examine the effects of carrying capacity, adult fecundity, larval mortality, and current pattern (directionality and speed), on the proportion of

dispersers in a cohort. The model could be extended to investigate the co-evolution of multiple dispersal traits. For example, the evolution of competence patterns of larvae (defined by at least two points in time, its beginning and ending) could be explored. In addition, the model could incorporate trade-offs associated with dispersal other than larval mortality, such as post-settlement mortality due to poorer adaptation to distant environments. This type of models could be used, for example, to test the common assumptions that isolated and/or degraded reefs are more likely to select for species with long planktonic durations, which in turn may have important consequences for the community structure at the reefs (e.g. Bellwood et al. 2004). Individually-based stochastic models could also be used to investigate the effects of dispersal and reproductive mode on the genetic structure of metapopulations by ‘introducing’ two copies of a gene (or more genes at higher computational cost) in the individuals (in both larvae and adults) and implementing sexual and asexual reproduction in the models.

Using greater detail in the hydrodynamic descriptions (e.g. tides, weather-band currents, and depth stratification) would also be desirable, especially in the spatially realistic models in *Chapter 4*. In this chapter, in particular, it would also be beneficial to include spatial and temporal variability in advection and diffusion in the models. The uniform flow used in the models can be understood as a background current wide enough to encompass the whole area represented by the chart. However in reality, the speed and direction of the currents and the level of diffusion change in space and time due to topographical and meteorological constraints. Similarly, diffusion is smaller in the centre than the edge of background currents, so larvae follow more similar routes and have more similar dispersion speeds (i.e. less under-dispersed larvae) in this area of the currents (see *Sections 2.4.F.2 and 4.4.C.*). Nevertheless, to include many of these aspects in the models a more complete knowledge of these processes in the GBR is required (see *Section 4.4.C.*). In fact, as new data on the physical and biological processes occurring within and among reefs are obtained, the models could be revised to accommodate this information and produce more accurate and reliable models (see *Section 7.3.A.*). Similarly, the dispersal sub-model of the models in *Chapter 6* (where dispersal is driven exclusively by diffusion over a spatially realistic representation of the IP) could be extended to also include a spatially realistic representation of the generalised circulation patterns of the background currents in the IP. Models of this type could be used to explore whether (and how) the inclusion of realistic topology and

realistic currents in the simulations can improve the predictions by either the Topological or Vortex models, particularly in the areas poorly predicted by the latter two models (see *Sections 6.3.C* and *6.4.D*). Additionally, combining this type of dispersal sub-model with a biogeography sub-model in which speciation leads to different larval competence patterns in different species and extinction takes place with non-uniform patterns (i.e. it can vary in space and time), could be used to examine why larval competence patterns vary so much among coral species in the IP. Likewise, more extensive sensitivity analyses of the key parameters (i.e. using more values and combinations of values for these parameters) would also be valuable, especially in the models directly compared to field data (*Chapters 4 to 6*).

From a more practical point of view, modifications of the models in this thesis could be used in the management and conservation of coral reefs in multiple ways. For example, models could be built to investigate the effect of habitat loss (by fragmentation and/or degradation) and disturbance in the connectivity, settlement, and dynamics of marine organisms with a larval phase. Likewise, models could be implemented to explore what and how factors contribute to the resilience of coral reefs to environmental change. Additionally, models could be developed to assist in the design of marine reserves (MR). MR are areas where fishing is forbidden (or at least regulated) to provide refuge for exploited and/or endangered species, and from which spill-over of individuals can help the replenishing or survival of nearby areas (often contributing to sustaining or even increasing local fisheries) (e.g. Russ 2002, Gell and Roberts 2003, Halpern and Warner 2003). Considerable controversy over the most adequate size, location, and management style of MRs has arisen recently (e.g. Botsford et al. 2001, McClanahan et al. 2006). At a larger spatial-scale, it is not clear whether it is more beneficial concentrating the available resources in protecting diversity hotspots, endemism hotspots, or other strategic locations (e.g. Berger et al. 2003). These issues could be examined using models similar to those in this thesis. However, more physical and biological information that is commonly available would be required for the development of reliable models of MRs specific to particular areas (e.g. Sale et al. 2005, Cowen et al. 2006).

7.4. CONCLUSIONS

Despite its importance (see *Chapter 1* and above) larvae dispersal has not received as much attention as processes occurring during the adult phase of marine organisms. There is, therefore, an urgent need to incorporate the larval phase and its dispersal into research programs, conceptual models, and management plans for marine organisms (e.g. Underwood and Fairweather 1989, Fairweather 1991, Gaines and Bertness 1993, Gaines and Lafferty 1995). Dispersal (specially passive dispersal) has traditionally been considered a highly stochastic process, but increasing evidence suggests that although probabilistic it is quite predictable (e.g. Sivilov 1961, Muller 1974, Lomolino 1994, Brown 1995, Brown and Lomolino 1998). Likewise, the abundance of coral larvae at settlement is highly variable in space and time (e.g. Barnes 1956, Milicich 1994, Hughes et al. 2000), but despite its complexity the dispersal of larvae is not a random process.

However, to fully understand the mechanisms and implications of larval dispersal and settlement both physical and biological processes must be considered as their interaction is crucial (e.g. Cowen et al. 2006, and this thesis). Coupled lattice models are a powerful formalism that allows the incorporation of processes occurring at different spatial and temporal scales. The spatially explicit and spatially realistic models implemented using this technique in this thesis allowed innovative approaches to meaningful biological questions. The results of these models provided significant and often novel insights into the factors determining the dispersal and settlement of larvae and their consequences.

Despite their conceptual nature (i.e. using theoretical reefal systems), the models in *Part I* revealed patterns with significant heuristic value. *Chapter 2* indicated that the effects of advection on the larvae of different types of coral (classical brooder vs. classical spawner) can differ not only quantitatively, but also qualitatively. This result suggests the complexity in the management of coral reef communities. *Chapter 3* revealed that even very small levels of water retention at the reefs can lead to a vast increase in larval settlement. Moreover, this chapter also produced some results challenging the common assumptions about the effects of retention on the settlement and connectivity by larvae. Low and/or very low levels of retention could actually increase non-local settlement, connectivity, and the evenness and diversity of the reef

sources of the larvae settling on the reefs in spawners in reefal systems where advection was relatively strong (the most common current conditions).

The models in *Parts II* and *III*, although limited by the amount of data available, proved useful for investigating the mechanisms leading to ecological, genetic, and biogeographic patterns observed in the field. The results in *Chapter 4* were in agreement with the findings by field studies indicating that patterns of fecundity are essential in determining patterns of larval settlement in the corals of the GBR. These results also suggested that some level of retention must be present at the reefs of the GBR, since the models including retention generally provided a closer fit to the field observations. However, all models underestimated the recruitment by brooders in the northern GBR, suggesting that factors not included in them also play an important role in this region. *Chapter 5* showed for the first time that, at least in the IP, the potential for dispersal provided by the larvae of coral species and the size of their geographic ranges are not correlated, indicating that additional factors have had a significant effect in moulding the distribution of corals in these oceans. Notably, a tentative relationship between estimates of gene flow in this area and some of the variables calculated by the dispersal models (chiefly evolutionary-scale connectivity) was found in this chapter, although more data is needed to confirm this relationship. *Chapter 6* contributed important new insights into the origin of the patterns of species richness in the IP. The results in this chapter indicate that contrary to previous suggestions current pattern (direction, speed, and variability) may not be the dominant factor shaping the geographic distribution of tropical inshore species in this region, and that in fact the topology of the habitats of the species (shape, area, and distribution) is at least as important.

The findings in this thesis have significant implications for the management and conservation not only of coral populations (see *Section 7.2.*), but coral reef ecosystems as a whole since corals, directly or indirectly, provide essential habitat and nourishment for the other species inhabiting coral reefs. Moreover, because the many of species inhabiting coral reefs have a dispersive larval phase, models similar to those used in this thesis can also be developed for them. Nevertheless, for particular management applications the models should be tailored to the relevant problems and contain sufficient information on the physical conditions and organisms in question.

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

Tables App.I.1. and App.I.2. display a complete list of the variables calculated by the ‘data analysis and summary’ module in the larvae dispersal models used in *Chapters 2 to 6*. These variables are contained in the 3rd database output of the models (see *Methods* in *Chapter 2* for details on the inputs, functioning, rules, and outputs of the core model, and the data analysis and summary module). Some of these variables have been described in detail in *Chapter 2 (Section 2.2.E.)*. Below I present a brief description of the complete set of variables and their sub-types, focusing on the variables not presented previously.

The variables in the 3rd output database can be classified into three broad types: larval fate variables (Table App.I.1.), variables describing the degree of connectivity among reefs by larvae, and variables related to the diversity of the larvae settling on the reefs (Table App.I.2.). The larval fate variables can be further classified into four sub-types: production, output, input, and success variables (Table App.I.1.), while both the connectivity and diversity variables can be classified into three sub-types: output, input, and difference variables (Table App.I.2.).

The variables in the difference sub-type are calculated by subtracting the value of the input variable from the corresponding value of the output variable (i.e. difference variable = output variable – input variable), and therefore they can be positive or negative. The variables in this sub-type are used to estimate if a reef is a source (positive difference) or receptor (negative difference) for a given variable. For example, a reef is a source for connectivity if it exports its larval production to more reefs than it receives its larval input from. The difference sub-type was not applied to the larval fate type, because the vast majority of the reefs produce more larvae than they receive (due to diffusion, mortality, and larvae ceasing competence during dispersal), and virtually no reef is a ‘sink’ in this sense (see *Appendix IV*). Nevertheless, the variables in the success sub-type can be used to compare the relative amount of larvae produced and recruited both at reef and reefal system (i.e. chart) level (Table App.I.2.).

Other variables not presented in *Chapter 2* include: computations of the evenness and diversity of the larval input and output of the reefs based on the Shannon’s Evenness and Diversity Indices (Table App.I.2.), variables in the production sub-type within the

larval fate type describing the amount of larvae released by each reef (Table App.I.1.), and variables expressing the larval fate in absolute numbers of larvae (previously presented only as probabilities) (Table App.I.1.).

Table App.I.1.: Larval fate variables.

Larvae fate	Production	Number of larvae produced per reef
		Proportion of the total larvae produced by each reef
	Output	Number of larvae settled on the natal reef by retention in the total larval output of a reef
		Number of larvae settled on the natal reef by dispersal in the total larval output of a reef
		Number of larvae settled on the natal reef in the total larval output of a reef
		Proportion of the total larvae produced by a reef settled on the natal reef by retention
		Proportion of the total larvae produced by a reef settled on the natal reef by dispersal
		Number of larvae settled on non-natal reefs in the total larval output of a reef
		Number of larvae settled in the total larval output of a reef
		Number of larvae dead while retained at the natal reef in the total larval output of a reef
		Number of larvae dead while dispersed away from natal reef in the total output of a reef
		Number of larvae dead in the total larval output of a reef
		Proportion of the total larvae produced by a reef dead while retained at the natal reef
		Proportion of the total larvae produced by a reef dead while dispersed away from natal reef
		Number of larvae that become non-competent in the total larval output of a reef
		Number of larvae fallen in mangrove areas in the total larval output of a reef
		Number of larvae lost outside the chart in the total larval output of a reef
		Proportion of the total larvae produced by a reef that settled on the natal reef
		Proportion of the total larvae produced by a reef that settled on non-natal reefs
		Proportion of the total larvae produced by a reef that settled
		Proportion of the total larvae produced by a reef that died
		Proportion of the total larvae produced by a reef that became non-competent
	Proportion of the total larvae produced by a reef that fell in mangrove areas	
	Proportion of the total larvae produced by a reef that was lost outside the chart	
	Input	Number of larvae settled in a reef that came from that reef
		Number of larvae settled in a reef that came from other reefs
		Number of larvae settled in a reef
		Proportion of the total larvae settled in a reef that came from that reef
		Proportion of the total larvae settled in a reef that came from other reefs
		Proportion of the total larvae recruited in the system that settled in a reef
Success	Proportion of larvae produced by a reef - Proportion of larvae settled at the reef	
	Larvae settled in a reef per million larvae produced by the reef	

Table App.I.2.: Connectivity and diversity variables.

Connect. among Reefs	Output	Richness (no.) of receptor reefs in larvae dispersed from a source reef at threshold > 0 larva
		Richness (no.) of receptor reefs in larvae dispersed from a source reef at threshold ≥ 1 larva
		Richness (no.) of receptor reefs in larvae dispersed from a source reef at threshold ≥ 1000 larvae
	Input	Richness (no.) of source reefs in larvae received by a sink reef at a threshold > 0 larva
		Richness (no.) of source reefs in larvae received by a sink reef at a threshold ≥ 1 larva
		Richness (no.) of source reefs in larvae received by a sink reef at a threshold ≥ 1000 larvae
	Difference	Output Richness - Input Richness, at a threshold > 0 larva
		Output Richness - Input Richness, at a threshold ≥ 1 larva
		Output Richness - Input Richness, at a threshold ≥ 1000 larvae
Diversity indices	Output	Simpson's Diversity Index (D) of receptor reefs of the larvae dispersed from a source reef
		Simpson's Evenness Index (E) of receptor reefs of the larvae dispersed from a source reef
		Shannon's Diversity Index (H) of receptor reefs of the larvae dispersed from a source reef
		Shannon's Evenness Index (J) of receptor reefs of the larvae dispersed from a source reef
	Input	Simpson's Diversity Index (D) of source reefs of the larvae received by a receptor reef
		Simpson's Evenness Index (E) of source reefs of the larvae received by a receptor reef
		Shannon's Diversity Index (H) of source reefs of the larvae received by a receptor reef
		Shannon's Evenness Index (J) of source reefs of the larvae received by a receptor reef
	Difference	Simpson's Output Diversity – Simpson's Input Diversity
		Simpson's Output Evenness - Simpson's Input Evenness
		Shannon's Output Diversity - Shannon's Input Diversity
		Shannon's Output Evenness - Shannon's Input Evenness

Appendix II: GEOGRAPHIC SETTING OF THE GREAT BARRIER REEF

Reefs within the GBR vary greatly in their topology (size, shape, and distribution), structure, geological history, and composition of their flora and fauna. Sizes of reefs range from approximately 0.01 to 100 km². Reefs are generally separated by inter-reefal waters forming channels, ranging from 100's of metres to 10's of kilometres in width. Most of the reefs (54% of the reefs and 94% of the reefal area in the GBR) are concentrated in a band, usually 50-60 km wide, near the edge of the continental shelf. Within this band the reefs are scattered irregularly, but usually form clusters. Although varying in size and shape, these outer shelf reefs typically are platforms reefs (knoll-like formations), and can be morphologically sub-classified into approximately: 30 dissected platform reefs, 30 deltaic platform reefs, 130 ribbon platform reefs, and 1300 common platform reefs (see below). Inner shelf reefs are usually found fringing continental islands or the mainland coast (26% of the reefs in the GBR) or forming patchy submerged reefs or shoals (20% of the reefs in the GBR). Although numerous, the reefs in the inner GBR are generally small and constitute only about 6% of the total area occupied by coral reefs. Because of its low reefal density the inner part of the GBR is known as the lagoon or channel. In this area extensive meadows of *Halimeda* algae can be found. In total, coral reefs constitute only about 6% of the GBR World Heritage Area. The remaining area consists of: continental slope (36%), inter-reefal areas (25%), and the GBR lagoon (33%) (Wachenfeld et al. 1998).

The continental shelf also varies in width and depth along the GBR. It is narrow, approximately 50 km, between latitudes 14⁰ to 15⁰ S, the narrowest point being about 36 km wide off Cape Melville (latitude 14⁰10' S). From this point the margin of the continental shelf diverges from the coastline, towards the north and south reaching a maximum width of 350 km in the Torres Strait region to the north and 412 km near Broad Sound (latitude 22⁰S) to the south (e.g. Jones 1977). Shelf depth increases progressively from the coastline to the shelf edge and from north to south. In fact, the latitudinal extent of the GBR is thought to be limited to the south by water depth and the predominance of soft substrates, rather than by water temperature (Veron 1995). Coral assemblages only occur in two areas south of the GBR: Elizabeth/Middleton reef group and Lord Howe Island. These are the southernmost coral reefs in the world, relicts of

Plio-Pleistocene reef development (Slater and Phipps 1977, Veron and Done 1979). For convenience, the GBR is commonly divided latitudinally into 5 sectors or regions (Figure 4.1.):

- *Torres Strait Sector* ($9^{\circ}12'S$ to $10^{\circ}41'S$): This sector is mainly located north of Cape York. The continental shelf is bound to the north by Papua New Guinea and the Papuan Trough into which it slopes gently, and to the east by the Queensland Trough (over 2000 m deep) into which it drops steeply. The shelf is about 100 km wide and very shallow (5-10 m in the northern half and rarely exceeding 15-20 m in the southern half). This region receives strong hydrodynamic influences from the Gulf of Carpentaria, Gulf of Papua, and the Coral Sea (which define its limits to the West, North, and East respectively) (see *Appendix III*). The reefs are set back several kilometres from the shelf edge. From latitude $9^{\circ}45'S$ the outermost reefs form a belt of typically elongated patches separated by shallow channels, constituting a protective barrier from wave action. The channels, product of the strong tidal currents, are straight between latitudes $9^{\circ}45'S$ and $10^{\circ}S$, and meander between latitude $10^{\circ}S$ and the end of this sector ($10^{\circ}41'S$). For this reason, the northern outer reefs are known as 'dissected reefs' and the southern as 'deltaic reefs'. The rest of the reefs in the region are common platform reefs. Platform reefs and shoals are particularly abundant in the northern and shallower part of this sector, which combined with the exposure of this region, produces strong currents. There is no lagoon in this sector, and there are few fringing reefs as there is no coastline and continental islands are scarce.

- *Northern Sector* ($10^{\circ}41'S$ to $16^{\circ}S$): The continental shelf is narrow, especially between latitudes $14^{\circ}S$ and $15^{\circ}S$, its maximum depth rarely exceeding 30 m. The shelf drops abruptly into the Queensland Trough like in the Torres Strait sector. The outermost reefs are located very close to the edge of the shelf. From latitudes $10^{\circ}41'S$ to $11^{\circ}40'S$ these reefs are deltaic reefs. From latitude $11^{\circ}40'S$ to the southernmost end of this sector the outer reefs are elongated with recurved ends and their main axis parallel to the margin of the shelf, generally measuring 5 to 20 km in length and 300 to 500 m in width. They are separated by narrow channels, forming a more continuous belt than the reefs further north, from

which they are known as 'ribbon reefs'. Platform reefs (ranging between 5 to 10 km maximum length) are scattered densely across most of the remaining shelf. The reefs lying closer to the coast are smaller in size (1 to 2 km maximum length) and have a more complex geomorphology (their assemblages can consist of shingle ridges, exposed limestone platforms, mangrove areas, and small islands).

- *Central Sector* (16⁰S to 20⁰S): The continental shelf margin gradually diverges from the mainland coast. Within the lagoon the maximum depth is seldom greater than 40 m and the sea floor is fairly flat. The edge of the continental shelf slopes gently to 100 m at the shelf break, where the floor of this and the more southern regions drop into the Coral Sea platform (less than 1000 m depth). Most of the reefs in this sector are found in the outer and middle shelf. In this and the Southern sector, the outer belt of ribbon reefs is not present and the reefs are set back several kilometres from the shelf edge. There are several large rivers in this area, which contribute to the development of a large, mostly reef-free lagoon. Some of the few inner platform reefs are large (up to 20 km maximum length), with several containing lagoons. Reefs gradually become sparser moving south from 16⁰S to 19⁰S, where reef density is lowest in the GBR. However, between 19⁰S and 20⁰S the reefs become more numerous again. The coast is rugged, with numerous shallow mangrove areas.

- *Southern Sector* (20⁰S to 22⁰30'S): This sector is bordered to the east by the Coral Sea platform and to the south by the Capricorn Channel where a deep tongue of water enters the region. The continental shelf is wide (maximum width of the GBR occurs at latitude 22⁰S) and deeper than in northern sectors (generally between 60 and 120 m, reaching a maximum of 145 m). The GBR lagoon is large, occupying both the inner and middle shelf, and although in this sector numerous rocky islands are found near the coast with associated fringing reefs, most reefs are situated in the outer shelf. From latitude 20⁰S to 21⁰10'S the reef matrix is densely packed with reefs varying in size and shape. Between latitudes 21⁰10'S and 22⁰30'S the reefs are more widely dispersed. A concentration of numerous small reefs occurs to the south of this region, just north of the Capricorn Channel; this is known as the Swain Reefs Complex.

- *Capricorn and Bunker Groups Sector* (22°30'S to 24°30'S): In this southernmost sector of the GBR the continental shelf is deep. Two small groups of reefs (about 30 reefs in total), the Capricorn and Bunker Groups, lie about 80 km from the main coastline. Their reefs are relatively large and generally associated with islands, in most cases sand cays carrying well-developed vegetation often including bushes and trees. These two groups are next to each other, but quite isolated from the reefs in the Southern sector and the few small fringing reefs situated next to the mainland in this sector.

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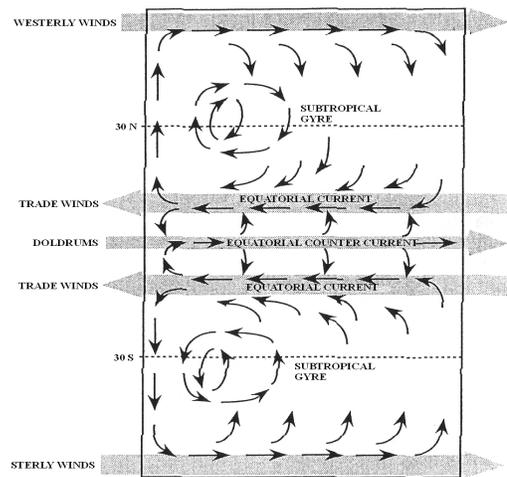
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Appendix III: PHYSICAL OCEANOGRAPHY OF THE GREAT BARRIER REEF

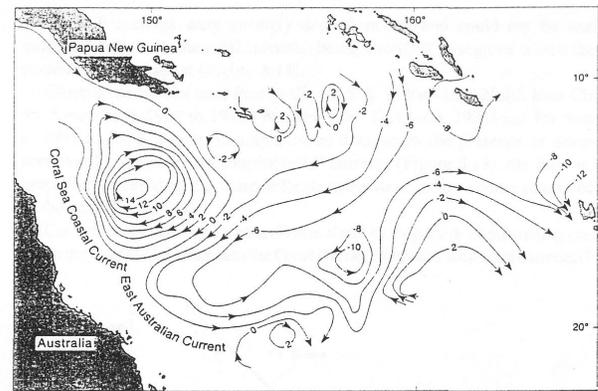
Currents on continental shelves can be classified into three groups according to the duration and frequency of their occurrence: a) Tidal currents: regular currents with near semi-diurnal frequencies (i.e. high and low tide occur within an ~12 hour period); b) Weather band currents: more variable currents with a periodicity of days to a month generated principally by wind stress; and c) Background (= drift, residual, or seasonal) currents: low-frequency, long-duration currents (e.g. Andrews and Pickard 1990). The currents in each frequency band have been recognised to influence differently the dynamics of coral reefs conglomerates: tidal currents flush individual reefs, weather-band currents flush reefs and supply meso-scale communication, while background currents provide connection at the scale of the continental shelf (Williams et al. 1984). Background currents are ecologically very important as they can transport nutrients and biota over very long distances (Andrews and Pickard 1990). They are large-scale, broad, slow currents forced by longshore pressure gradients produced by very-low frequency or steady wind stress and/or the Earth's rotation (e.g. Csanady 1984, Andrews and Pickard 1990). On the GBR, background currents are mainly driven by the South Equatorial Current (SEC) and seasonal wind regimes.

The SEC is the northern branch of the geostrophic counterclockwise gyre in the southern Indo-Pacific (IP) (e.g. Munk 1955, Figure AppII.1.a.). It flows westward, meeting the eastern Australian continental shelf in the western part of the Coral Sea in the northern half of the Great Barrier Reef (GBR), which leads to its division into two longshore currents that flow along the GBR slope and outer edge with associated recirculation gyres (e.g. Burrage et al. 1994, Wolanski 1994, Figure AppII.1.b.). The southern arm (poleward flowing) is called the East Australian Current (EAC) and the northern arm (equatorward flowing) is called the Coral Sea Coastal Current (CSCC) or Hiri Current (e.g. Pickard et al. 1977, Wolanski 1994). The bifurcation point generally occurs between latitudes 14°S and 15°S, but presents high seasonal variability and has been observed as far south as Mirmidon Reef at latitude 18.3°S (e.g. Pickard et al. 1977, Burrage et al. 1994, Wolanski 1994). This variability has profound implications on the current directions along and over the shelf. The speed of the EAC decreases with depth (e.g.: speeds of 55 cm.s⁻¹ at 27 m depth and 20 cm.s⁻¹ at 100 m depth were measured at

Myrmidon Reef, 18.3°S, Wolanski 1994). The speed of the current also varies with the wind speed, especially near the water surface. An equatorward undercurrent flows under the EAC, at depths of 300-900 m (Church and Boland 1983). The currents on the shelf-edge can induce upwelling of deep nutrient-rich water onto the continental shelf, due to their associated Ekman flux and/or fluctuation of their speeds (e.g. Middleton et al. 1994, Wolanski 1994). These deep water intrusions are more frequent in summer (Wolanski 1994).



ApIII.1.a.



ApIII.1.b.

Figure ApIII.1. Background currents influencing the water circulation in the GBR. (ApIII.1.a.) Simplified current scheme for the Pacific Ocean (from Jokiell and Martinelli 1992, adapted from Munk 1955). (ApIII.1.b.) Contours for the volume of transport in the top 1000 m of the Western Coral Sea at 2.5-Sv intervals (from Wolanski 1994, adapted from Andrews and Clegg 1989).

Strong south-east trade winds blow almost constantly during the dry winter months (from March to October) in the GBR region (e.g. Wolanski 1982, Wolanski and Bennett 1983). During the spring-early summer (October to December) the seasonal wind component is considerably reduced. Throughout the summer (December to February) the northern parts of the GBR are influenced by monsoonal north-westerly winds and rainfall. During January and early February the monsoon front usually extends to the northern parts of the central sector (as far as latitude 17.5°S, in the Cairns-Innisfail area). Over the rest of the GBR, variable and generally weak winds occur at this time of the year.

Tides create a semi-diurnal oscillatory flow in the waters of the GBR. Throughout the majority of the GBR this oscillation is orientated in a cross-shelf direction. During the flood tide, water builds up on the shallow continental shelf. The amplitude of this build up (tidal amplitude or range) varies according to the shelf width (with a maximum average tidal range of 11 m near Broad Sound at latitude 22°S -where the continental shelf is widest in the GBR-, and a minimum of 1.7 m in the Cairns area at latitude 17°S). Tidal currents can attain considerable velocities, especially in locations where tidal ranges are large, and reefs are densely packed and close to the continental shelf margin (such as the deltaic and ribbon reefs in the Torres Strait Sector and the Pompey complex in the Southern Sector). Tidal range also varies throughout the year. The biggest tides (spring tides) occur in December-February and in May-August exposing the reef flats in some locations at extreme low tide, and the smallest (neap tides) occur during October-November. The speed of the tidal currents is ~1.5 times its average during the spring tides and ~0.5 times during the neap tides.

The effects of the EAC and CSCC on the background currents are larger on the outer shelf than on the GBR lagoon, where background currents are more variable and dependent on the winds. Water exchange between the lagoonal and reefal areas of the GBR is limited. However, tidal excursions, coastal headlands, and climatic conditions can produce cross-shelf flows at some areas and times (Wolanski and Bennett 1983). Coral mass-spawning in the GBR occurs in spring-early summer (Harrison et al. 1984), coincident with periods of calm winds and neap tides. Therefore, during spawning background currents are less influenced by these factors and thus less variable at this time than during the rest of the year, especially in the central and southern sectors. Consequently, in general, advection is greater and diffusion smaller in summer than winter and in the outer than the inner shelf (e.g. Williams et al. 1984). However, the particular circulation around each reef is greatly complicated by the topography of the reef and continental shelf, the presence of other reefs upstream, and the tidal regimes (e.g. Wolanski 1994). Hydrodynamic conditions also change with bathymetry, as the effect of winds and the influence of coastal currents (EAC and CSCC) decrease with depth. Nevertheless, only in the bottom boundary layer of the continental shelf (less than 1 m from the bottom) current flow and consequently the conditions for dispersal are not extensive (e.g. net longshore drift 10 m above the bottom is around 10 cm.s⁻¹, Williams et al. 1984).

The specific hydrodynamic conditions in the GBR by sector (see Appendix II) are as follows:

- *Torres Strait sector:* In this sector current flow is weak and variable (Wolanski and Thomson 1984, Wolanski et al. 1992, Wolanski 1994). Numerous factors contribute simultaneously to the circulation in this sector. They include: the CSCC, the currents through the Great North East Channel and Torres Strait, winds, strong tidal currents, the presence of numerous reefs, the uneven bottom surface, and river runoff in the Gulf of Papua that results in strong salinity stratification (Wolanski et al. 1992, Wolanski 1994). The CSCC flows to the north-west, the currents in the Torres Strait display alternating flow to the east and west between the Gulf of Carpentaria and GBR waters, the large tides in the area produce a cross-shelf flow to the west, and the monsoon winds (December to February) blow to the south-east (Wolanski and Thomson 1984, Wolanski 1994). The large reefs (Warrior Reefs) and islands (Bank Islands) to the west of this region and the dense matrix of reefs to the east topographically steer the water flow with alternating northward and southward flows parallel to the continental shelf (Wolanski and Thomson 1984). The numerous reefs and turbulent bottom friction (much larger than in the central sector) damp the current flow (Wolanski and Thomson 1984). The large tides and horizontal velocities around the reefs on the edge of the continental shelf force upwelling of water and nutrients (Wolanski and Ruddick 1981).

- *Northern sector:* The physical oceanography of this sector is also complex. Net flow is equatorward in the northern part of this sector and poleward in the southern part (Wolanski and Thomson 1984, Wolanski 1994). Water circulation is profoundly influenced by the location of the bifurcation point of the SEC. Although the position of this point varies seasonally, in the absence of wind no evidence of southward drift has been found north of latitude 14⁰S (Wolanski 1994, but see Wolanski and Ruddick 1981). The circulation in this area is also significantly affected by wind regimes, especially nearshore where the southeasterly trade winds push the water northwestward (Wolanski and Ruddick 1981). As in the Torres Strait sector, bottom friction, reef density, and intense

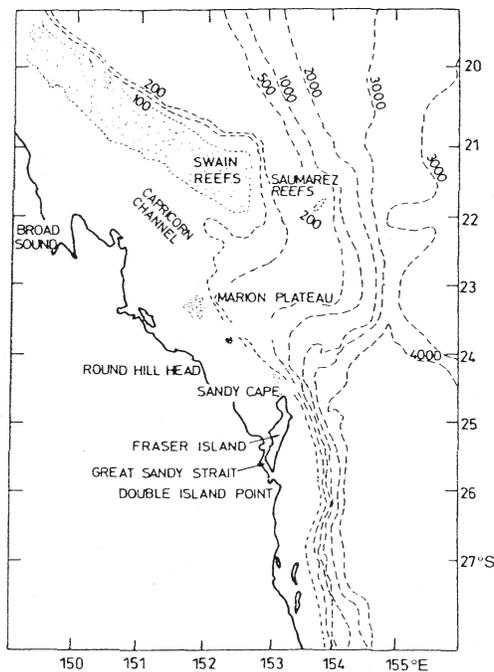
tidal currents modify and weaken the current flow, especially in the northernmost part of this sector (Wolanski and Thomson 1984).

- *Central sector:* The net flow of the background currents in the outer reefs is S-SE longshore, its speed decreasing gradually from the continental shelf edge to the lagoon edge (Andrews 1983a, 1983b). This flow is almost entirely unidirectional and constant in summer (Andrews 1983a, Williams et al. 1984), but slower and occasionally reversed in the more superficial layers during periods of strong trade winds in winter (Williams et al. 1984, Andrews and Furnas 1986). The net flow in the lagoon, although weaker than in the outer reef matrix, is also poleward when winds are absent; however, it is highly variable and alternates in direction throughout the year depending on the winds (Williams et al. 1984, Kelly and Andrews 1985, Wolanski and Pickard 1985). Localised tidal upwelling carries slope water over the shelf in this sector (Andrews 1983b).

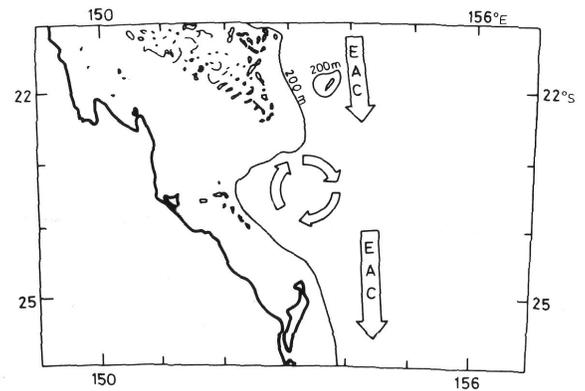
- *Southern sector:* The background currents also flow poleward longshore in this sector, with similar patterns and seasonal fluctuation than in the Central sector (Middleton 1983, Middleton and Cunningham 1984, Middleton et al. 1994). There is significant interaction between shelf and slope water masses, and transport of nutrients in this sector is important as the tidal inflow and the strongly flowing EAC produce considerable upwelling (Middleton et al. 1994).

- *Capricorn-Bunker Groups sector:* Daily currents are highly variable and over long periods of time circulation patterns are complex, but generally with a mean net flow north to north-westward (Griffin et al. 1987). Near the Capricorn Channel the continental shelf is narrow at the 100 m depth contour, but wider at greater depths, especially around the 500 m mark where it forms the Marion Plateau (Figure AppII.2.a.). The strong EAC flows around the Marion Plateau, rejoining the continental slope at Fraser Island where it reassumes its south-eastward direction, driving a large weak clockwise eddy over this sector of the GBR (Griffin et al. 1987, Middleton et al. 1994) (Figure App.II.2.b.). Nevertheless, this is not a permanent feature of the region; it occurs in pulses of usually 6 to 10 days, driven by fluctuations on the EAC (Middleton et al. 1994).

When the eddy is not present water generally circulates longshore SE-southward as in the Central and Southern sectors, but the flow is weaker than during the eddy events (Pickard et al. 1977, Middleton 1983, Griffin et al. 1987). The surface water may flow in a different direction or move slower than the eddy due to wind stress, but during winter the trade winds contribute to the northwestward net flow and eddy formation (Griffin et al. 1987). Upwelling and nutrient uplift from the upper slope to the outer shelf also appears to be common in this sector due to the tides (Middleton 1983).



ApIII.2.a.



ApIII.2.b.

Figure ApIII.2. Topography and hydrodynamics of the Capricorn - Bunker Groups sector (ApIII.2.a.) Bathymetric map of the region (modified from Middleton et al. 1994). (ApIII.2.b.) Circulation of the EAC and large weak clockwise eddy (modified from Griffin et al. 1987). Depth shown in metres.

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Appendix IV: GLOSSARY

The following definitions describe commonly used concepts and variables computed by the models in this thesis. The words shown in italics are terms that can be cross-referenced within the glossary.

Cell neighbourhood (= cell local neighbourhood) A fixed group of cells within a *cellular automaton*, usually in a set position relative to a reference cell. In the models in this thesis a 9-cell local neighbourhood was used, consisting of the reference cell and its 8 surrounding cells.

Cellular automata Modelling technique consisting in a digitised environment traditionally described by the following characteristics (although some may differ in particular cellular automata implementations):

- (1) it consists of an array of discrete spatial cells
- (2) each array is regular
- (3) each cell is identical
- (4) each cell takes a finite set of possible values
- (5) cells are computed (i.e. evolve or update) at discrete time intervals
- (6) all cells are updated each iteration
- (7) all cells are updated by fixed deterministic rules (rules cannot alter dynamically)
- (8) the rules of the evolution of a cell depend on its *local neighbourhood*
- (9) each cell's update relies on a fixed number of preceding rules.

The points above can be summarised by the mathematical expression:

$$a^{(t+1)}_i = O[a^{(t)}_{i-j}, a^{(t)}_{i-j+1}, \dots, a^{(t)}_{i+j}]$$

where a is a cell in the cellular automata which can take k different values (generally from 0 to $k-1$), O is the rule used to update the cell every certain time t (i.e. each iteration), i and j correspond to the relative positions of the cells in the lattice of sites, and the expression in square brackets is the *cell neighbourhood*.

Centre of accumulation hypothesis Theory proposed to explain the origin of the species richness patterns of marine taxa in the Indo-Pacific, and particularly in the

centre of diversity located in the triangular area including the Philippines, the Malay Peninsula, Indonesia and New Guinea. According to this theory, species originate mainly in peripheral areas of the Indo-Pacific, but over time currents transport propagules (i.e. larvae, seeds...) of the new species expanding their geographic ranges to include the centre of diversity. The patterns of declining diversity in the Indo-Pacific would be a consequence of the varying number of overlaying geographic ranges in different areas of the Indo-Pacific, which would be highest in the centre of diversity.

Centre of origin hypothesis Theory proposed to explain the origin of the species richness patterns of marine taxa in the Indo-Pacific, and particularly in the centre of diversity located in the triangular area including the Philippines, the Malay Peninsula, Indonesia and New Guinea. According to this theory, the centre of diversity is also the centre of origin of new species, which gradually disperse, colonising peripheral areas. The patterns of declining diversity in the Indo-Pacific would be a consequence of the differential dispersal abilities of the species propagules (i.e. larvae, seeds...) and the degree of isolation of suitable substrates.

Centre of overlap hypothesis Theory proposed to explain the origin of the species richness patterns of marine taxa in the Indo-Pacific, and particularly in the centre of diversity located in the triangular area including the Philippines, the Malay Peninsula, Indonesia and New Guinea. According to this theory, the high diversity of the Malaysian-Indonesian Archipelago arose from the confluence of several biogeographic provinces (at least 2, an Indian and a Pacific) in the area, each contributing its diversity. This theory has usually not been proposed as an exclusive mechanism of origin, but combined with other explanations.

Centre of refugia hypothesis Theory proposed to explain the origin of the species richness patterns of marine taxa in the Indo-Pacific, and particularly in the centre of diversity located in the triangular area including the Philippines, the Malay Peninsula, Indonesia and New Guinea. According to the simplest form of this theory, the high species richness in the Malaysian-Indonesian Archipelago is the vestige of a cosmopolitan and rich distribution of marine organisms of broadly Cretaceous origin. During the sea-level changes in the Plio-Pleistocene and earlier geological times, the persistence of shallow habitats in this Archipelago would have reduced the rates of local

extinctions of marine species, whereas oceanic islands suffered repeated faunal losses throughout these periods. In the centre of diversity, the areas acting as refuges would have been more abundant, larger, and/or occurred more frequently over time, than in other regions of the Indo-Pacific.

Charts Spatial representations of the physical environment used in the models in this thesis. Each chart consisted of a matrix of cells, in which each cell depicted a square area of varying size (depending on the model) and contained a code symbolising its *land-type*. Charts were used as moulds underlying the *cellular automata* models, providing them with spatial information required for their functioning.

Competence Developmental stage of the larvae of most marine invertebrates during which they are able to settle and metamorphose into a dividing polyp if suitable habitat is encountered.

- **Competent period** Stage in the larval phase during which the larva is competent to settle and metamorphose (extending from the end of the *pre-competent period* to either settlement or the beginning of the *post-competent period*). The duration of this period in the field is variable as larvae usually can delay settlement until stimulated by cues that typically indicate the presence of suitable habitat.
- **Pre-competent period** Stage in the larval phase extending from release (in brooders) and fertilisation (in spawners) until competence; this period is usually associated with continuous, rapid, and substantial morphological and physiological development, specially in spawning species.
- **Post-competent period** Stage in the larval phase extending from the cessation of competence until death. Generally, the larvae of marine invertebrates can prolong competence if suitable substrate is not found, but because settlement and metamorphosis are processes that require energy, during which larvae are unable to feed, there is a limit to the time that the larvae can delay settlement. If the energy level of a larva is reduced below a certain threshold, settlement and metamorphosis may not be possible, and the larva enters the post-competent period. Larvae in this period have been observed to experience: spontaneous settlement (i.e. in the absence of cues), abnormal metamorphosis, or the loss of their ability to settle and metamorphose resulting in degradation and ultimately death.

Connectivity Degree of relationship among populations in a metapopulation by immigration and emigration of individuals. In the models in this thesis it is computed as the number of reefs connected by a chosen threshold of larvae. Connectivity can be considered equivalent to richness, representing in this case richness or abundance of connected reefs.

- **Connectivity threshold** Minimum number of larvae that have to disperse in between two reefs to consider them as connected.
- **Ecological-scale connectivity** Degree of relationship among populations by amounts of individuals sufficient to influence the demography of the receptor population (i.e. significant at ecological time scales). In the models in this thesis it is computed as the number of reefs connected by a threshold of at least 1000 larvae.
- **Evolutionary-scale connectivity** Degree of relationship among populations by amounts of individuals sufficient to influence the genetics of the receptor population (i.e. significant at evolutionary time scales). In the models in this thesis it is computed as the number of reefs connected by a threshold of any amount (> 0) of larvae (i.e. there is a possibility of connection, although on average there may be less than one larva connecting the reefs per dispersal episode, as the reefs may only be connected occasionally rather than in all dispersal events).

Coupled lattice Generalisation of *cellular automata*. Coupled lattices differ from traditional *cellular automatas* in that cells can contain continuous values (i.e. their state is represented by continuous variables) and their state can be updated using more information than solely the state of the cells in the neighbourhood.

Coverage Unit of storage in Geographical Information Systems generally consisting in a single layer digital version of a map sheet (topological information) plus a database with the attributes of the objects included in the map (non-topological information). In this thesis the coverages represented reefal systems.

Diversity Mathematical index measuring the diversity of species in a community. It takes into account both species richness and the relative abundance of the species. The most commonly used indices are the Simpson Diversity Index (D) and the Shannon Diversity Index (H):

$$D = 1 / \sum P_i^2 \qquad H = - \sum P_i \ln P_i$$

where P_i = proportion of individuals (or biomass) that the i th species contributes to the total in the sample.

In this thesis it refers to the diversity of reef sources of the larvae settled on a reef (*larval output* diversity) or the diversity of reef receptors of the larvae released by a reef (*larval input* diversity). In the models both the Simpson and Shannon Diversity Indices were computed (substituting the proportion of individuals per species by the proportion of larvae per reef), but in this thesis only the results for the Simpson Index were included.

Edge-effect Problem presented when using *cellular automata* models caused by the difference in *local neighbourhoods* between the inner and outer cells in the lattice. Inner cells have the ‘standard’ neighbourhood (a 9-cells neighbourhood in the models in this thesis), while outer cells have smaller neighbourhoods (a 6-cells neighbourhood for the side cells and a 4-cells neighbourhood for the corner cells).

Evenness (= Equitability) Mathematical index measuring the evenness with which individuals are distributed among species in a community. The most commonly used indices are the Simpson Evenness Index (E) and the Shannon Evenness Index (J):

$$E = D / S \qquad J = H / \ln S$$

where D = Simpson Diversity Index, H = Shannon Diversity Index, and S = species richness in the sample.

In this thesis it refers to the evenness with which the larvae produced in a reef settle on their receptor reefs (*larval output* evenness) or with which the larvae settled in a reef were originated among their reef sources (*larval input* evenness). In the models both the Simpson and Shannon evenness indices were computed (substituting the proportion of individuals per species by the proportion of larvae per reef), but in this thesis only the results for the Simpson Index were included.

Land-type Categories representing the type of environment present within the cells of a *chart*. The following land-types were used in the models in this thesis: reef (marine substrate suitable for coral settlement and development), water (marine floor not suitable for coral settlement and development, effectively open water for the larvae), land (any emerged land, including: mainland, foreshore, islands, cays and rocks), and mangrove (areas occupied by mangroves).

Larval input Larvae settled on a reef (i.e. the reef is considered as a receptor).

Larval output Larvae produced by a reef (i.e. the reef is considered as a source).

Metapopulation Population of local populations connected by immigration and emigration processes, and thus where the dynamics of a single local population cannot be understood without considering the demography of the other local populations.

Rank-abundance diagram Graphical plot of the distribution of the abundances (i.e. relative abundance) of the species in a community. It provides a more complete description of the structure of a community than single-variable descriptors, such as species richness, diversity, or evenness.

Rank-contribution diagram In this thesis a graphical plot of the distribution of the larval contributions (i.e. relative contribution) from the reefs in a reefal system to a given reef (or set of reefs). It provides a more complete description of the structure of the larval input to the reef than single-variable descriptors, such as connectivity, diversity, or evenness. Thus enabling the examination in a single graph of the connectivity and evenness of a reef system, and showing not only whether recruitment is dominated by a few reefs, but also allowing identification of the main *source reefs*. This type of plot is a modification of the *rank-abundance diagrams* widely used in ecology.

Retention Retainment of water particles at a reef. In this thesis retention of water implied retention of larvae, as in the models larval biology of corals was represented by the competence patterns and mortality of the larvae, but not their behaviour (i.e. active horizontal or vertical movements by the larvae were not included).

- **Retention level** In this thesis defined as the percentage of water particles retained at a reef after 10 days.

Settlement Process in which the larva ends its pelagic life by attaching itself to a suitable substrate, usually followed by metamorphosis and growth.

- **Settlement rate** In the models in this thesis computed as the number of larvae settled per million of larvae produced.
- **Local settlement** Settlement of larvae on the natal reef.
- **Non-local settlement** Settlement of larvae on reefs other than natal.

Sink reef Commonly, reefs in which *larval input* (settlement) is greater than *larval output* (production), that is they receive more larva than they produce. However, because the production of larvae in the reefs is very large, and larval mortality and diffusion are significant, few reefs are true sinks and the term *receptor* is preferred (*see below*).

Spatially explicit models Sub-type of *spatially structured models* that incorporate the geometry of the set of sites (reefs in the models in this thesis) included in the models, accounting for spatial relationships such as the distances separating them and their relative positions.

Spatially realistic models Sub-type of *spatially structured models* that incorporates both the geometry (e.g. distances, relative positions) and the spatial and/or temporal heterogeneity (e.g. size, shape, carrying capacity, fecundity) of the sites (reefs in the models in this thesis) included in the models. They are the modelling alternative that provides the most accurate representation of spatial processes.

Spatially structured models Type of model in which the environment consists of a number of distinct sites or populations (reefs in the models in this thesis) linked by dispersal of individuals (larvae in the models in this thesis).

Species richness (= species abundance) Number of species present in a community.

Source reef (1.) Reefs as origin of larvae. **(2.)** Commonly, reefs in which *larval output* (production) is greater than *larval input* (settlement), that is they produce more larvae than they receive. Most reefs are sources in this sense, however the number of actual settlers in their larval output is drastically reduced by mortality and diffusion. **(3.)** In this thesis, source reefs are those where the output is greater than the input for a given variable computed by the models (i.e. settlement ratios, connectivity at different thresholds, evenness and diversity). For example, a reef is a source in terms of *settlement* when the number of settlers in their larval output is greater than in their larval input, and in terms of *evolutionary-scale connectivity* when it exports larvae to more reefs than it receives them from.

Receptor reef (1.) Reefs as recipients of settlement by larvae. **(2.)** In this thesis, receptor reefs are those where the input is greater than the output for a given variable computed by the models (i.e. settlement ratios, connectivity at different thresholds, evenness and diversity). For example, a reef is a receptor in terms of *settlement* when the number settlers in their larval input is greater than in their larval output, and in terms of *evolutionary-scale connectivity* when it receives larvae from more reefs than it export them to.

Zooxanthellae Microscopic photosynthetic mutualistic algae present in the tissues of adult and some larvae of corals (and other marine invertebrate groups).