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Modelling marine connectivity in the Great Barrier Reef and exploring its ecological implications

Doctoral dissertation presented by

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in partial fulfilment of the requirements for the degree of

Doctor in Engineering Science

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Louvain-la-Neuve, August 2015

Acknowledgements

Back in the autumn of 2010 when I first arrived in Louvain-la-Neuve, I could never have imagined where the next four and a half years were to take me. I have learnt a huge amount during this time, and feel privileged to have been a part of the SLIM project. I am deeply grateful to Professors Emmanuel Hanert and Eric Deleersnijder for giving me the opportunity to join their team; without their trust and belief in me none of this work would have been possible. Their continual and energetic support, especially during the administrative tribulations which reared their head after my arrival, was always reassuring to have; I hope that I have been able to repay their trust.

The scientific guidance I received during the course of my project was vital in helping me to formulate coherent ideas and carry them out; I have been very fortunate to have benefited from the expertise of many people. First and foremost I am very grateful to Emmanuel for being a constant source of ideas, energy and optimism, and for always taking the time to read and discuss my work in all its minutiae. In addition to guiding me towards interesting research topics, his advice and corrections helped me to greatly improve the quality of my research and publications, and his continual support made my most ambitious targets always feel within reach. I am also very grateful to Eric for the advice, encouragement and guidance which he imparted to me during my time here, for his detailed corrections, and for our many varied and interesting discussions.

All the ideas in the world are useless, however, if you are unable act upon them, and it is thanks to the SLIM team that I was able to learn the skills I needed to implement my ideas. In particular, I am greatly indebted to Jonathan Lambrechts, whose mastery of SLIM is second only to his generosity in sharing his knowledge with anyone in need. Jonathan guided me through my first adventures with SLIM, imparted me with the expertise I needed to use and develop the model, and spent a countless amount of time helping me fix and improve my code. He also proved to be an ideal travelling companion on our unforgettable forays into the Australian outback!

Similarly I would like to extend a warm thanks to Tuomas Kärnä, whose office I shared during my first 2 years in Louvain-la-Neuve, and who also showed me the ropes with SLIM, C++, Python, Linux and generally anything computer-related. I am equally grateful to the various past and present members of the SLIM team for creating a friendly environment and for extending their help and advice whenever needed, especially Benjamin, Anouk, Olivier, Bruno, Philippe, Valentin and Sebastien. Likewise I would like to extend my thanks to the members of our small “SLIM-GBR users group”, particularly Matthieu and Jolan. In addition to teaching me the virtues of GIS, Jolan was also a fantastic companion during the adventures we shared together in Sydney and Townsville. Finally, I am also indebted to Vincent Traag for his help and collaboration in using his community detection code.

The purpose of any model is to study real problems, and modelling the Great Barrier Reef would not have been possible without the help of Professor Eric Wolanski. In addition to providing ideas and advice at the start of my Ph.D project, he helped me enormously when I arrived in Australia for the first time, making me feel at home away from home, and encouraging me to collaborate with scientists of other disciplines. I am very grateful to him for the kindness and generosity he showed me. I would also like to thank Dr. Fernando Andutta for his advice, enthusiasm and warm hospitality. I would also like to extend my thanks to the scientists I have collaborated with in Townsville, notably Dr. Thomas Bridge and Dr. Joana Figueiredo, both of whom were invaluable in providing me with ideas, inspiration and enthusiasm, who trusted me with their time and data, and whose advice

and professionalism were of great help.

This section would not be complete without mentioning my family. Every house needs strong foundations, and my achievements are built on the foundations laid by my parents, who created the ideal conditions for me to study and achieve my goals, and encouraged me to value intellectual endeavours. Finally, throughout the highs and lows of working on this thesis, it is thanks to Alessia that I have remained (relatively) sane, and happy. In addition to putting up with the countless late nights and weekends I spent tapping away at my laptop with great understanding, her support and energy have been a vital source of strength throughout these past years.

This thesis was carried out under the project “Taking up the challenges of multi-scale marine modelling”, funded by the Communauté Française de Belgique under contract ARC 10/15-028. I would like to extend my sincere thanks to them for allowing me to carry out this thesis and for supporting scientific research. Finally, I thank the members of my thesis jury for their useful comments which served to improve this manuscript.

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CHAPTER 1

INTRODUCTION

The Great Barrier Reef (GBR) is the world's largest and most complex coral reef ecosystem. Located on the continental shelf off Australia's north-eastern coast, roughly 2,600 km in length and up to 200 km wide (see Figure 1.1), the GBR is home to a vast array of marine species, including over 600 species of coral and 1600 species of fish. As such, studying the interactions between its physical landscape and the living organisms which inhabit it has been a key focus of research in marine science (Cowen et al. 2007; Wolanski et al. 2003). Given the alarming rates of decline in the health of many species in the GBR (De'ath et al. 2012; Sweatman et al. 2011), understanding this relationship, and how marine life may respond to future environmental changes, has become increasingly urgent.

The water currents flowing through the GBR can act to transport marine organisms from one place to another, resulting in the exchange of individuals between populations in different habitats. This is known as *connectivity*, and is a fundamental process for the dynamics of many marine ecosystems (Cowen et al. 2007). Connectivity between habitats allows species to spread to new habitat patches (Gaylord and Gaines 2000; Trakhtenbrot et al. 2005), repopulate habitats which have been damaged by disturbances (e.g. bleaching events or tropical cyclones which can destroy large swathes of coral) (Cowen et al. 2006; Hughes and Tanner 2000) and also allows genetic mixing to occur between physically separate populations (Palumbi 2003; Trakhtenbrot et al. 2005). The net effect is to increase the *persistence* and *resilience* of these populations.

Connectivity in the GBR, as in many coastal marine ecosystems, mainly occurs through dispersal of larvae. Adult coral are physically attached to the reef surface and cannot migrate, and many reef fishes spend all of their lives in their home habitat or rarely stray far from it (Russ 2002; Shanks et al. 2003). During their earliest life stage however, most marine organisms exist as small free-floating larvae which can be dispersed by marine currents (Leis 1991). Depending on the strength and direction of the currents after they enter the water column, and on the biological characteristics of the larvae, they can potentially travel a wide range of distances from their natal habitat, from a few metres to hundreds of kilometres, before settling onto a suitable habitat (Cowen et al. 2006).

Despite the large research effort that has gone into understanding larval dispersal,

it is still a relatively poorly known ecological process (Levin 2006; López-Duarte et al. 2012). Larvae are notoriously hard to track in the ocean, due to their microscopic size and the relative vastness of the ocean, so it is not possible to physically track them using ships, divers or undersea robots. Diffusive processes act to rapidly dilute the concentration of larvae following their release, and their high mortality rates further diminish their numbers at any given location, rendering the use of aerial imaging to track their dispersal almost impossible (Cowen and Sponaugle 2009). Various empirical techniques have been used to try to infer information about larval dispersal indirectly (e.g. genetic methods, parentage analysis and artificial and natural tags); despite these efforts however we still lack detailed information about larval dispersal patterns, both in the GBR and in other coral reef ecosystems (Green et al. 2014).

Numerical modelling tools therefore have the potential to offer unparalleled insight into larval dispersal and population connectivity (Werner et al. 2007). By explicitly modelling the larval dispersal process, they can be used to estimate the potential for connectivity between separate populations over time- and length-scales which would be prohibitively large for empirical methods (Botsford et al. 2009b). Furthermore, they can be used to predict the impact of changes to the natural environment on connectivity, for instance an increase in water temperature or a change in water circulation patterns.

Modelling larval dispersal and connectivity remains a challenging topic in itself however. The patchy and fragmented nature of coral reef ecosystems renders them particularly challenging to model due to their often intricate topography, and nowhere is this more the case than in the GBR (Wolanski et al. 2003; Wolanski and Spagnol 2000). Models of larval dispersal need to resolve water currents down to the scale of hundreds of metres, to account for small-scale flow features susceptible to influencing dispersal, whilst encompassing an area potentially hundreds or thousands of kilometres in length, for a period of up to weeks or months (Burgess et al. 2007; Graham et al. 2008) – a very computationally demanding task. Furthermore, dispersal of larvae is strongly influenced by larval biology as well as the hydrodynamic environment, and failure to properly account for the main biological processes can lead to erroneous estimates of dispersal potential (Connolly and Baird 2010; Lacroix et al. 2013).

The results of numerical modelling studies of connectivity could be used to inform marine management strategies. For instance, knowing which populations are well-connected (i.e. which populations receive many larvae from many other populations) – and which populations are more isolated – could allow more effective placement of *Marine Protected Areas* (MPAs) (White et al. 2013). MPAs are marine reserves within which damaging anthropogenic influences (e.g. fishing and tourism) are limited. If they had prior knowledge of larval dispersal patterns, marine managers could use MPAs to protect habitats with high potential to export larvae to surrounding habitats (Almany et al. 2009; Drew and Barber 2012; Hughes et al. 2005), as well as ensuring that separate MPAs are also well connected with each other, thus increasing the resilience of the MPA network itself (Christie et al. 2010; Kininmonth et al. 2011). At present however, connectivity is not accounted for in marine management strategies in the GBR due to a lack of detailed information on larval dispersal (Jones et al. 2009a), a situation common to many coral reef ecosystems around the world (Drew and Barber 2012).

The aim of the study presented in this thesis is to develop and use numerical modelling tools to simulate the dispersal of coral larvae through the GBR, and in doing so to gain new insights into the connectivity network linking the different reefs of the GBR. The ultimate objective is to produce information which could be used to inform marine

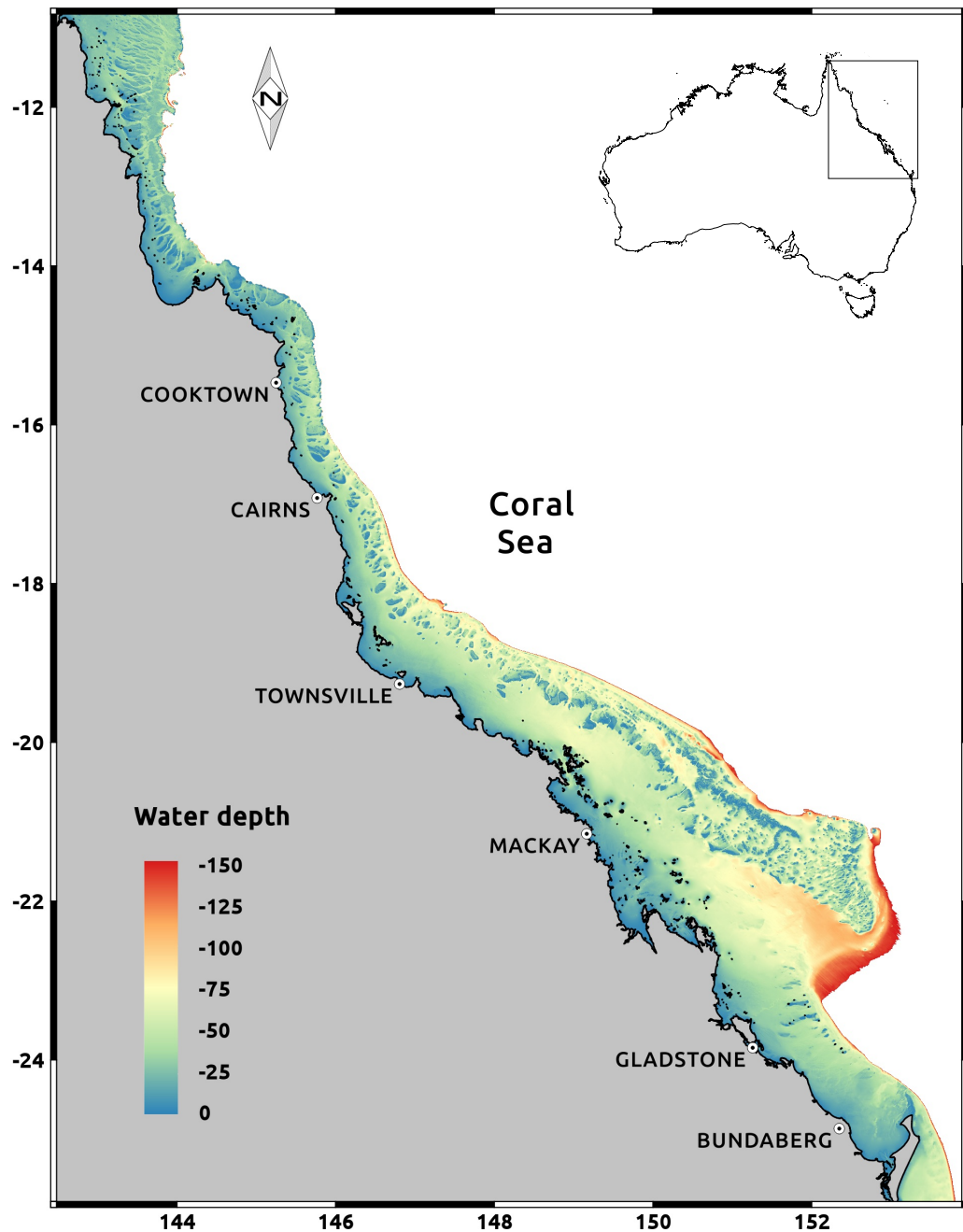


Figure 1.1: Bathymetric map of the Great Barrier Reef's continental shelf, down to the 150 m isobath. Land mass is in grey, and the positions of selected coastal towns are shown. The boundary to the East is with the Coral Sea.

management strategies. To this end, the specific goals of this study are:

1. To set up a realistic numerical model of larval dispersal and connectivity over large parts of the GBR.
2. To explore the use of network science tools to extract useful information from the output of this model, which could be used for marine management.

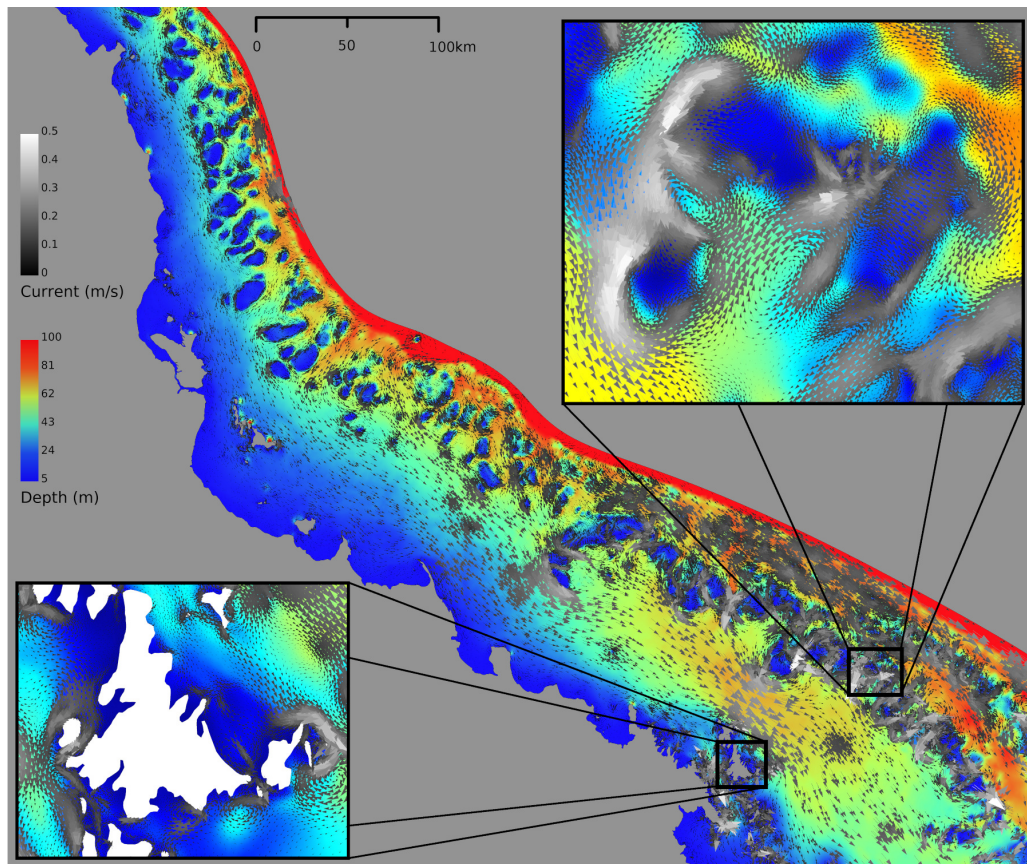


Figure 1.2: Depth-averaged currents (arrows) averaged over the period 22 November – 27 December 2010, as obtained using the SLIM ocean model, overlaid onto the bathymetry (in colour) of the central GBR. The intricate bathymetry leads to complex water circulation patterns at both small and large scales, with strong horizontal current gradients and a large number of secondary circulation features in the wakes of reefs and islands.

3. To use the model to make quantitative estimates of the inter-reef connectivity network for coral in the GBR and explore the physical processes driving larval dispersal.
4. To evaluate how connectivity patterns are liable to change in the future under the effects of climate change.

In the next section of this chapter I will briefly describe the features of the numerical model of larval dispersal which is the subject of this study. I will finish the chapter by outlining what is contained in the subsequent chapters of this thesis. Glossaries of ecological and hydrodynamical terms used in this thesis are included at the end of this chapter; terms listed in this glossary are printed in *italics* when they are first encountered in the text. A list of acronyms and abbreviations used in this thesis is also included at the end of this chapter.

1.1 A multi-scale, integrated biophysical modelling approach: motivation, challenges and objectives

Modelling the dispersal of coral larvae through the world's most complex coral reef ecosystem, the Great Barrier Reef, poses a number of challenges. The set of tools used to carry out this modelling, and interpret the results, must therefore be carefully chosen. The modelling process can be decomposed into three basic stages:

1. Modelling the hydrodynamics of the GBR's coastal ocean.
2. Modelling the dispersal of coral larvae through the GBR, using the hydrodynamics (water currents and elevation) calculated in stage 1.
3. Analysing the connectivity networks generated in stage 2, and extracting information relevant for marine management and conservation.

Taken together, stages 1 and 2 are known as a *biophysical model* of larval dispersal, as they involve explicitly simulating the hydrodynamics in the region and the physical transport of larvae through it (the “physical” part), as well as the most important biological processes (the “bio” part) taking place on the larvae during their dispersal.

In order to understand the requirements for a biophysical model of larval dispersal in the GBR, it is useful at this stage to look at the physical features which define the region¹. The GBR is not a single continuous feature, but is composed of over 3,000 reefs and islands, varying in size from ~ 0.01 to ~ 100 km². These are occasionally found in isolation, are sometimes scattered sparsely and separated by wide expanses of sea, but more often are located in large, dense clusters and separated by narrow, meandering passages or channels, as shown in the bathymetric map in Figure 1.1 (Wolanski et al. 2003). This results in horizontal water currents with high variability in space (as can be seen in Figure 1.2), and in time, with strong tidal and wind-driven currents present (Pickard et al. 1977; Wolanski 1994).

Tidal currents are significant in most of the GBR, and the tidal eddies formed in the wakes of reefs and islands are known to have an important effect in restricting the dispersal of larvae away from their natal reef (Burgess et al. 2007), a phenomenon clearly illustrated in Figure 1.3. The presence of strong inter-reef tidal currents in the domain is known to steer large-scale residual circulation away from reef-dense areas, so small-scale flow around reefs can potentially affect large-scale circulation through the coastal ocean (Wolanski and Spagnol 2000). The strong winds blowing over the relatively shallow coastal ocean lead to a well-mixed water column for most of the year across the whole GBR (Luick et al. 2007; Middleton and Cunningham 1984; Wolanski 1983).

Given the above scenario, it is imperative that our model be able to resolve flow down to the scale of reefs, both because of the important role played by small-scale tidal eddies near reefs in restricting larval dispersal, and because the flow around reefs can potentially affect the flow at the larger scale, so not properly resolving the former can lead to misrepresenting the latter. Given the well-mixed nature of GBR waters, modelling the flow in three dimensions is secondary in importance to achieving an acceptable resolution in the horizontal plane, at least for the purposes of resolving horizontal transport.

¹A more detailed analysis of the water circulation through the GBR can be found in Chapter 2.

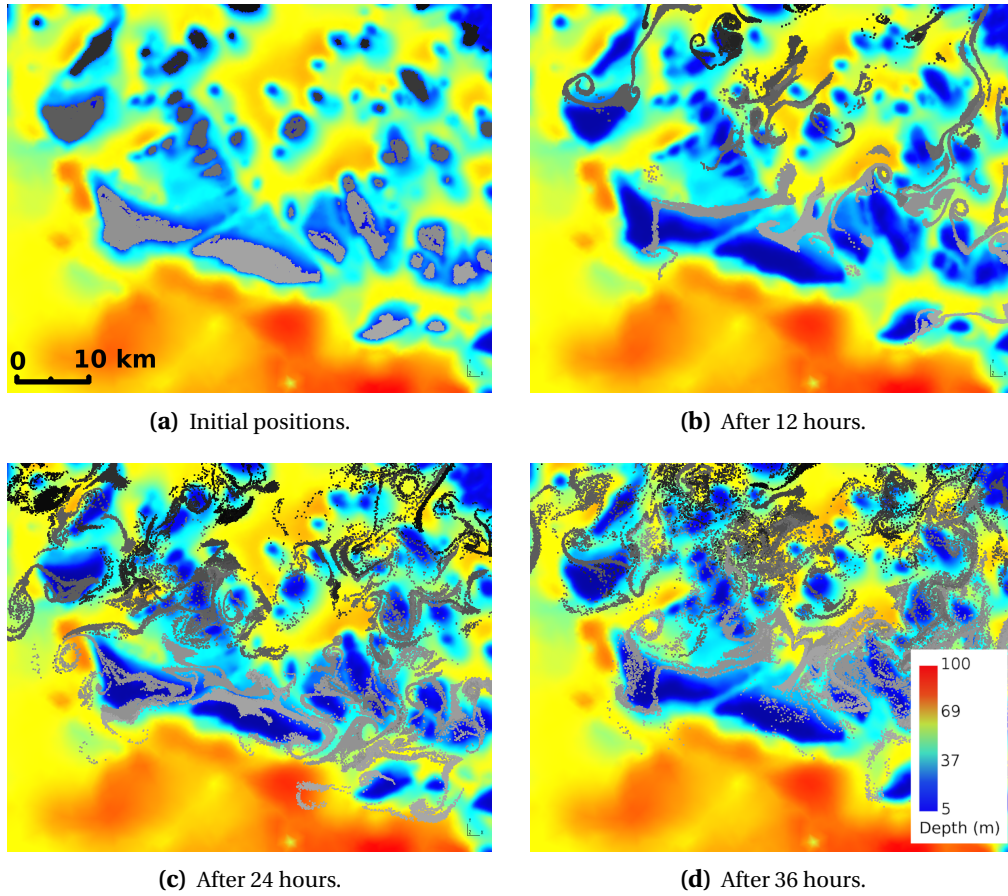


Figure 1.3: Snapshots showing the dispersal of *A. millepora* coral larvae around a group of reefs in the southern GBR, as simulated by the SLIM model. Figure 1.3(a) shows the initial positions of the particles, whilst Figures 1.3(b)-1.3(d) show particle positions after 12, 24 and 36 hours. Particles are coloured different shades of grey depending on the reef they were released over, and the bathymetry is shown in colour. The dominant currents were semi-diurnal tides (period of 12.4 hours). The presence of eddies in the wakes of reefs can be seen to be acting to retain larvae close to their natal reef. This illustrates the importance of accurately resolving reefs and reef passages.

This is borne out by the similar performance of 2D and 3D models in the region in estimating depth-averaged horizontal currents in previous intercomparisons (e.g. see Black et al. 1991; Lambrechts et al. 2008; Luick et al. 2007; Wolanski et al. 2003).

As the topography of the GBR is intrinsically multi-scale, with important physical processes occurring across a wide range of scales (Wolanski et al. 2003), unstructured mesh models offer a natural way to model the hydrodynamics of the region (Legrand et al. 2006). Using an unstructured mesh allows the model resolution to be varied in space, so it can be increased in areas where fine-scale flow is known to be important, such as near coastlines and reefs (Deleersnijder et al. 1992; Hamner and Hauri 1981; Wolanski et al. 1996), and kept much coarser in areas with a more uniform flow, in order to keep computational costs acceptable. The only previous attempt to apply unstructured mesh models to the GBR is by the SLIM project², which this thesis itself contributes to. In par-

²SLIM is the Second generation Louvain-la-neuve Ice-ocean Model; see www.climate.be/SLIM.

ticular, this study builds on the work of Lambrechts et al. (2008) in modelling the water circulation in the GBR. Whilst progress in the development of the 3D version of SLIM is ongoing (see Delandmeter et al. 2015; Kärnä et al. 2013), the computational costs remain prohibitive to model an area as large as the whole GBR. Given the overriding importance of having a high horizontal resolution, and given the well-mixed nature of GBR waters, this study uses the depth-integrated SLIM code to resolve the hydrodynamics on the GBR shelf.

In addition to simulating transport of larvae, an acceptable larval dispersal model must also account for the main biological processes involved during dispersal, such as larval mortality, competence acquisition and loss, release of larvae from reef habitats and settlement of larvae onto reef habitats (North et al. 2009). The approach followed in this study is to build a Lagrangian model of larvae capable of simulating these processes by incorporating the latest findings from published empirical studies of larval biology. This Lagrangian model is implemented into SLIM as an additional module to be run offline from the hydrodynamic code, and can potentially be used to study dispersal of larvae of a range of marine organisms, including coral, fish and seagrass.

The output of the larval dispersal model can be represented as a large connectivity network, as illustrated in a simplified way in Figure 1.4. The nodes in the network represent different reef habitats, and the lines linking the nodes (known as arcs), represent a transfer of larvae from one reef to the other. Two reefs are connected if larvae from one reef disperse to the other, and each connection is directed (i.e. acts from one reef to the other) and weighted (i.e. more larvae transferred result in stronger connections).

Clearly, the connectivity networks generated by the biophysical model can contain a huge amount of information. For the GBR, which contains over 3000 reefs, there are ~9 million potential connections to consider. Even taking a subset of the GBR containing 1000-2000 reefs means considering over a million potential reef-to-reef connections. A set of tools is needed to interpret this output if we are to draw useful conclusions. Two approaches are explored in this study: the first approach makes use of novel clustering tools from graph theory to identify spatial patterns in the network that are of ecological interest. These tools can be used to identify spatial clusters of highly-connected reefs over multiple scales. The second, simpler approach employed involves calculating a set of ecologically relevant connectivity statistics to characterise the network or subsets of it. Both sets of tools will be used to gain insights into connectivity patterns in the GBR.

1.2 Thesis structure

Following on from this introduction, **Chapter 2** presents an overview of the state of present knowledge of larval dispersal and connectivity, and of the physical mechanisms driving this process on the GBR, namely the water circulation. The principal drivers of the on-shelf circulation are discussed, specifically the tides, the wind and the inflow from the neighbouring Coral Sea, and previous observational and modelling efforts to study flow through the GBR are summarised. Sources of variability to flow in the GBR are also briefly discussed. The second part of the chapter looks in more detail at different definitions of connectivity, and includes a summary of previous attempts to measure and model connectivity. This is followed by a discussion on how the output from numerical models could be used to improve marine management.

The integrated biophysical model is described in greater detail in **Chapter 3**. The

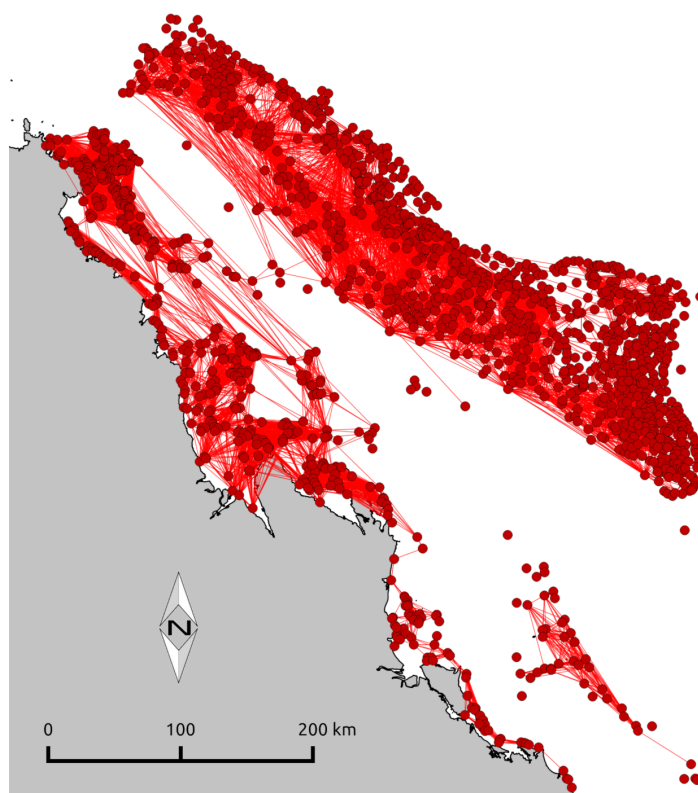


Figure 1.4: Illustration of an inter-reef connectivity network for *A. millepora* coral in the southern GBR, as simulated using SLIM. Nodes (circles) represent reefs, and arcs (lines) represent larval exchange between reefs, so an arc is shown linking two nodes if larvae from either node are found to settle on the other node. The complexity of the connectivity network is immediately apparent, but equally apparent is the clustering of the network into a number of communities, whose members are highly inter-connected with each other. This issue will be explored in Chapter 4. Note that in reality, arcs are weighted and directed, a property not shown here.

hydrodynamic model is presented along with its forcings, parameterisations and mesh. The Lagrangian particle-tracking module is also presented, and their respective advantages and limitations are discussed.

As discussed above, the connectivity networks generated by biophysical models can contain an enormous amount of data (see Figure 1.4). A set of tools is needed to extract useful information from them. In Chapter 4, a graph theoretical approach is explored to identify spatial patterns in large-scale connectivity of coral larvae. Specifically, a novel community detection method is used to identify clusters of highly-connected reefs (known as “reef communities”) over multiple spatial scales. This is one of the first attempts to transfer clustering tools from graph theory into the domain of marine connectivity, and the first known application of this particular community detection approach, so the precise physical meaning of the results produced are explored. Some possible uses of this method to inform marine planning are discussed at the end of the chapter.

The two following chapters present practical applications of the biophysical model. In Chapter 5, it is used to model connectivity between reefs of different morphologies (near-sea-surface [NSS] and submerged reefs) and depths. Recent undersea mapping ef-

forts have revealed the widespread presence of reefs deeper than about 10 metres which were not previously mapped. As a result, previous studies of larval dispersal ignored a huge number of potential habitats. In this chapter, the biophysical model is used to estimate their connectivity potential for the first time. The characteristics of the connectivity networks for each of the two reef types is compared. The shallow reef habitats most vulnerable to depth-dependent disturbances (such as bleaching or tropical cyclones) are identified, and a qualitative comparison with observed coral cover data shows that the areas predicted to be most vulnerable have seen the highest rates of coral cover decline.

The past few decades have seen a significant deterioration in the health of many coral reef ecosystems worldwide, including the GBR (De'ath et al. 2012; Pandolfi et al. 2003; Sweatman et al. 2011). This has been ascribed both to localised anthropogenic impacts such as marine pollution, increased nutrient runoff from land and overfishing, and to global changes resulting from man-made climate change (Furnas et al. 2013; Hughes et al. 2003; Loya et al. 2001; Pandolfi et al. 2011; Wakeford et al. 2007). In the GBR, climate change is likely to have a significant effect on the health of the ecosystem (Hoegh-Guldberg et al. 2007; Kirtman et al. 2013). Its potential impacts on larval dispersal are poorly known, yet there is reason to believe they could be significant.

Chapter 6 deals with the possible effects of climate change on connectivity in the GBR. Analysis of data from CMIP5³ global climate models reveals that most models predict a strengthening of the South Equatorial Current (SEC) reaching the GBR shelf by the years 2081-2100. Additionally, water temperatures in the GBR are expected to increase, leading to a change in larval development rates. By modelling larval dispersal in future scenarios incorporating these changes, the biophysical model is used to estimate the possible effect of climate change on connectivity in the GBR. A simple coral metapopulation model is also used to evaluate whether these changes could affect the recovery times of coral populations following different types of disturbances. This study is the first known attempt to downscale projected regional-scale circulation changes to the GBR, and to model the effects of these changes, and of a temperature increase, on connectivity.

Finally, **Chapter 7** summarises the main conclusions obtained from the work presented in this thesis, and presents some ideas for future developments.

The main original contributions of this thesis are contained in Chapters 4-6, which are presented in the form of journal articles and can be taken to be self-contained.

³CMIP5: Coupled Model Intercomparison Project Phase 5 of the World Climate Research Programme (WCRP); see <http://cmip-pcmdi.llnl.gov/>

1.3 Supporting publications

The research carried out in the framework of this doctoral thesis has led to the following articles:

Wolanski, E., Lambrechts, J., **Thomas, C.**, Deleersnijder, E. (2013) The net water circulation through Torres Strait. *Continental Shelf Research*, 64: 66–74.

Thomas, C. J. (2014) Reefs form friendship groups in the Great Barrier Reef. *Reef Encounter*, 29: 36–40.

Thomas, C. J., Lambrechts, J., Wolanski, E., Traag, V. A., Blondel, V. D., Deleersnijder, E. and Hanert, E. (2014) Numerical modelling and graph theory tools to study ecological connectivity in the Great Barrier Reef. *Ecological Modelling*, 272: 160–174.

Thomas, C. J., Bridge, T. C. L., Figueiredo, J., Deleersnijder, E. and Hanert, E. (2015) Connectivity between submerged and near-sea-surface coral reefs: can submerged reef populations act as refuges? *Diversity and Distributions*, doi: 10.1111/ddi.12360.

Thomas, C. J., Figueiredo, J., Lambrechts, J., Deleersnijder, E. and Hanert, E. (2015) Changes to coral larval dispersal in the Great Barrier Reef in a future scenario. *In preparation*.

1.4 Glossary of ecological terms

Biophysical model: a model of larval dispersal which simulates the hydrodynamics in the region of dispersal and the physical transport of larvae through the region (the “physical” part), as well as the biological processes taking place on the larvae which most affect their dispersal potential, such as mortality and settling (the “bio” part).

Connectivity (potential): a measure of connectivity obtained only considering larval dispersal. Whether or not this connectivity is actually “realised” depends on pre- and post-dispersal processes.

Connectivity (realised): a measure of connectivity obtained considering the entire set of processes susceptible to influence the transfer of individuals from origin to destination populations, i.e. considering a) pre-dispersal processes such as egg production, b) larval dispersal, and c) post-dispersal processes such as recruitment.

Connectivity (demographic): the exchange of individuals between the different subpopulations of a metapopulation, in numbers large enough to affect the size and persistence of the subpopulations⁴. Also known as ecological connectivity, or population connectivity.

Connectivity (genetic): the exchange of individuals between the different subpopulations of a metapopulation, in numbers large enough to genetically homogenise the populations (the threshold for genetically significant connectivity is typically several orders of magnitude smaller than that required for demographic connectivity, see discussion in §2.2.3). This is a measure of realised connectivity. Also known as evolutionary connectivity.

Connectivity matrix: a matrix representing the connectivity network between a number of origin and destination habitats. Each matrix element represents the strength of connectivity from the origin habitat identified by the row (/column) to the destination habitat represented by the column (/row). Various different normalisations of this matrix can be applied to define what exactly is meant by “strength” of connectivity. For instance this could simply refer to the number of larvae which dispersed from the origin to the destination (no normalisation applied), or to the probability of a larva from the source arriving at the destination (this would be obtained by normalising each matrix element by the sum of its rows) (Largier 2003).

Connectivity network: a network representation of the connectivity matrix in which nodes represent habitats and arcs represent the exchange of individuals between habitats. Connectivity networks are directed and weighted.

Coral bleaching: the process of coral losing their zooxanthellae, triggered by prolonged thermal stress, leading to a decline in coral health.

⁴The exact point at which connectivity may be considered to be great enough to have a “significant impact” on demographic rates of a subpopulation is a threshold for which there is no single precise definition, and as such it can either be arbitrarily chosen (by stipulating that the recruitment subsidy provided by larval imports is greater than a given proportion of total recruits, e.g. 10%), or chosen more systematically by finding the point at which removing a given subsidy has little to no effect on population size and persistence (Cowen and Sponaugle 2009).

Coral reef: a type of marine ecosystem which is fundamentally dependent on the presence of so-called reef-building, or *hermatypic* corals. The calcium carbonate structure secreted by these corals creates a very rough, intricate surface which provides ideal living conditions for a whole host of marine organisms.

Hermatypic coral: a type of coral which secretes a calcium carbonate structure for their skeleton.

Larval dispersal: the process of larvae being transported from the habitat they were spawned at (their origin, or source) to the habitat they settle onto (their destination, or sink).

Local retention: the proportion of larvae spawned at a given habitat which settle onto the same habitat (i.e. which are locally retained).

Marine Protected Area (MPA): a marine reserve within which anthropogenic influences damaging to marine life (e.g. fishing, mining, tourism) are limited to a greater or lesser extent.

Metapopulation: a set of physically separate subpopulations of a given species with some level of connectivity between them.

Persistence: the persistence of a population is its ability to maintain its existence over time.

Population: a discrete set of individuals which inhabit the same habitat patch and which interact with each other.

Self recruitment: the proportion of larvae settling onto a given habitat which were also spawned there.

Spillover: the effect of living organisms being exported to areas surrounding their habitat, leading to conservation benefits to these populations.

Recruitment: the process of a larva which has settled onto a habitat successfully joining the host population by growing into an individual which contributes to the size and persistence of that population.

Resilience: the capacity of a population to resist the influence of external stressors.

Some definitions were modified from: Botsford et al. (2009b), Cowen and Sponaugle (2009), Green et al. (2014), and Lowe and Allendorf (2010).

1.5 Glossary of hydrodynamical terms

Baroclinic fluid: a fluid whose density does not only depend on pressure. In baroclinic oceanographic flows, the fluid density can depend on pressure, temperature and salinity. In a baroclinic fluid, isobars are not parallel with isopycnals.

Barotropic fluid: a fluid whose density is a function of pressure only, and vice-versa. In barotropic flows, isobars and isopycnals are always parallel.

Diurnal tide: a tidal component with a near-daily period.

Downwelling: the phenomenon of surface water sinking downwards in response to the surface convergence of water in a given area. The opposite effect is termed *upwelling*.

Eddy: a fluid current with a circular or swirling motion whose direction differs from the the general flow direction. Eddies are unstable and break down into a number of smaller eddies over time. In oceanographic flows, they generally form downstream of obstacles such as islands or in areas with large current shear.

Eulerian frame of reference: a frame of reference which is fixed in space. See also *Lagrangian* frame of reference.

Isobar: a surface passing through points with equal fluid pressure.

Isopycnal: a surface passing through points with equal fluid density.

Lagrangian frame of reference: a frame of reference which follows a fluid parcel, moving through time and (potentially) space. See also *Eulerian* frame of reference.

River plume: the mass of riverine water extending out of the estuary into the coastal ocean.

Semi-diurnal tide: a tidal component with a period of around half a day.

Sverdrup: a standard measure of flow volume transport used in geophysical fluid dynamics. $1 \text{ Sverdrup} = 1 \times 10^6 \text{ m}^3 \text{ s}^{-1}$.

Thermocline: the thin, vertical layer of water separating the uppermost mixed layer, within which the temperature is relatively uniform, and the deeper water layer, within which the temperature is typically much colder. In the thermocline itself the temperature therefore decreases rapidly.

Upwelling: the phenomenon of sub-surface water rising upwards towards the surface in response to divergence of water at the surface. The opposite effect is termed *downwelling*.

1.6 List of acronyms and abbreviations

CMIP5: Coupled Model Intercomparison Phase 5; see <http://cmip-pcmdi.llnl.gov/>

CPM: Constant Potts Model; see §4.2.3.2

ENSO: El Niño-Southern Oscillation; see §2.1.7.1

GBR: Great Barrier Reef

GBROOS: Great Barrier Reef Ocean Observing System; see <https://imos.aodn.org.au/imos123/>

IBM: Individual Based Model; see §4.2.2

LEP : Lifetime Egg Production; see §2.2.3

mtc: mean time to competence; see §5.2.3

MPA: Marine Protected Area; see §2.2.6

NSS reef: Near-Sea-Surface reef; see Chapter 5

PLD: Pelagic Larval Duration; see §2.2

SEC: Southern Oscillation Index; see §2.1.7.1

SLP: Sea Level Pressure

SLIM: Second-generation Louvain-la-neuve Ice-ocean Model; see www.climate.be/slim

Sv: Sverdrup; see Glossary of Hydrodynamical Terms

WCL: Weighted Connectivity Length; see §4.2.3.1

CHAPTER 2

WHAT IS KNOWN ABOUT WATER CIRCULATION AND CONNECTIVITY IN THE GREAT BARRIER REEF?

Summary

In this chapter I will present an overview of what we know about a) larval dispersal and connectivity, and b) the physical mechanisms driving this process on the GBR continental shelf. I will start by dealing with this latter topic in §2.1, which reviews what we know about the water circulation through the GBR, as it is the fundamental physical basis driving larval dispersal, before moving on, in §2.2, to discuss how the water currents and larval biology influence dispersal and connectivity. I will briefly review the different methods we can use to characterise connectivity in the GBR and other coral reef ecosystems, and how the information obtained can be used in practice to support management of marine areas. This overview provides the context needed to motivate the model choices presented in Chapter 3, and serves to explain the larval dispersal patterns seen in the results presented in Chapters 4-6.

2.1 Water circulation in and around the Great Barrier Reef

In order to understand which physical phenomena a numerical oceanographic model of the GBR should account for, it is important to understand which are the most significant in actually driving the circulation on the GBR shelf. The nature of these phenomena, and in particular the time- and space-scales over which they occur, should dictate the choice of model to use. Furthermore, having an understanding of the general flow patterns we can expect to see on the shelf is important in allowing us to explain the larval dispersal patterns, and the connectivity networks, that we will see in later chapters. What follows is an overview of the state of our knowledge about the main physical oceanographic processes driving circulation on the GBR shelf.

The water circulation on the GBR's continental shelf is strongly influenced by three main factors: a) **the tides**, b) **the wind** and c) **water exchanges with the neighbouring Coral Sea** (Brinkman et al. 2001; Wolanski 1994; Wolanski et al. 2003; Wolanski and Pickard 1985). The relative importance of these three factors can vary significantly in time and space; for instance winds can drive shelf-scale circulation when they are strong but have little effect when they are weak, whilst tidal currents tend to dominate flow in the North and South of the GBR but not in the centre, as well as varying in time. Likewise, different factors dominate transport over different timescales: tidal currents generally dominate over timescales of hours, whereas wind-driven currents and Coral Sea exchanges dominate over longer timescales.

Since larval dispersal occurs over timescales of hours to weeks, all three influences are liable to affect it, and must therefore be accounted for in our model. We shall now consider each one in turn, discuss what is known about it and weigh up how and to what extent it is likely to shape connectivity patterns.

2.1.1 Tides

The tides on the GBR shelf have been extensively studied, and are documented in a number of research articles dating back to the 1970s and 80s (see Hamon 1984; Pickard et al. 1977; Wolanski 1983); as such they can nowadays be considered to be amongst the most well-understood oceanographic phenomena in the GBR. Tides are an important driver of circulation on the shelf, and particularly dominate cross-shelf processes (Andrews and Bode 1988). They also contribute significantly to local mixing in and around reefs, as well as exerting an important retarding influence on low-frequency¹ currents (Burrage et al. 1997).

The dominant tides controlling sea level elevation are *diurnal* and *semi-diurnal* in most of the GBR, except around the Broad Sound estuary where semi-diurnal tidal components alone dominate. Tidal elevation amplitudes and phases are far from uniform throughout the GBR shelf however, with some changes in the contribution of each tidal component with latitude, and a significant increase in tidal range close to the coast, particularly in the southern GBR (Wolanski 1994).

Most of the outer GBR is permeable to tides, particularly the more reef-sparse central section. Tidal ellipses constructed from current-meter data and from numerical simulations both show that tidal currents are mainly oriented in the cross-shelf direction in the central GBR (Andrews and Bode 1988; Wolanski 1994), although these currents can locally be steered by reefs and islands. Andrews and Bode (1988) found that current speeds

¹Low frequency currents are currents varying periodically on timescales of weeks to months

along the longshore axis were typically only 10-25% of cross-shelf speeds. In the more reef-dense southern GBR however, Middleton et al. (1984) showed that the reef density is high enough to block the tidal wave impinging from the Coral Sea, so that the semi-diurnal flood tide propagates onto the mid-shelf in two separate waves: one from the north and one from the south. The convergence of these two waves acts to amplify the semi-diurnal tidal elevation by a factor of 4 compared to the shelf-break, confirming the intuition of the English navigator Matthew Flinders in 1814². There is therefore a significant periodic longshore tidal current in this area. This type of phenomenon has also been observed in the far north of the GBR, between 9°S and 11°S, an area with a particularly dense outer reef matrix (Wolanski 1983).

The magnitude of the tidal currents varies significantly with latitude, and depends mainly on the width of the shelf. Tidal currents are strongest in the southern GBR, where the shelf is at its widest, weakest in the central GBR, where the shelf is narrowest, and stronger in the northern GBR where the shelf widens again. Andrews and Bode (1988), who studied the tides in the central section of the GBR, observed that from 20°S there was a marked fall in current amplitudes towards the north, “essentially to a null point” at 17.5°S near the shelf break, with similar but less marked behaviour observed closer to the coast. The authors conclude that tidal currents have increasing dominance towards the south, where the shelf widens, but a greatly diminished relevance in the centre and north of the central GBR, where the shelf is narrowest. Wolanski and Pickard (1985) also observed weak tidal currents in the central GBR in their long-term current data at different mooring sites. In the northern GBR, Wolanski (1983) observed a similar phenomenon, finding that “the amplitude of the longshore tidal currents near-shore closely follows the width of the shelf, i.e., increases (decreases) with increasing (decreasing) shelf width”, and notably observing that tidal currents increase in strength as the shelf widens between 11°S and 13°S. Since the shelf in the northern section of the GBR is widest in the north and narrowest in the south (where it meets the central section studied by Andrews and Bode (1988) and Wolanski and Pickard (1985)), this results of the two studies dovetail with each other.

These findings are in line with the equations describing tidal wave propagation across continental shelves given by Clarke and Battisti (1981), in which tidal amplitude is a function of shelf width, so wider shelves cause a greater amplification of the tidal amplitude. Tidal amplitude is also a (squared) function of frequency, so the higher frequency tidal components (i.e. semi-diurnal) experience the greatest amplification.

Modelling and observational studies have shown that there is very significant small-scale variability in tidal current flows between reefs in reef-dense parts of the GBR. For instance, Wolanski and King (1990) found that currents through inter-reef passages can exhibit phase lags of up to 2 hours in their M2 tidal components at positions of only a

²In his account of his travels through the seas of Australia, *Voyage to Terra Australis* (Flinders 1814), Flinders states:

“At the distance of about thirty leagues to the N. N. W. from Break-sea Spit, commences a vast mass of reefs, which lie from twenty to thirty leagues from the coast, and extend past Broad Sound. These reefs, being mostly dry at low water, will impede the free access of the tide; and the greater proportion of it will come in between Break-sea Spit and the reefs, and be late in reaching the remoter parts; and if we suppose the reefs to terminate to the north, or north-west of the Sound, or that a large opening in them there exist, another flood tide will come from the northward, and meet the former; and the accumulation of water from this meeting, will cause an extraordinary rise in Broad Sound and the neighbouring bays, in the same manner as the meeting of the tides in the English and Irish Channels causes a great rise upon the north coast of France and the west coast of England.”

few kilometres apart. Subsequent modelling by King and Wolanski (1996) showed that tidal flows around topographically complex reef areas can induce a significant localised residual circulation, with speeds in the range of 5-15 cm/s. This residual current was not found in the nearby reef-free lagoonal shelf area, where there are no impediments to tidal transport.

Further work by Wolanski and Spagnol (2000), based on observations and modelling, described an occurrence referred to as the “Sticky Water” effect, whereby tidal currents are steered around regions of high reef density during spring tides, but not during neap tides³. This occurs because in very shallow waters, when the water speed is high, a higher proportion of the flow’s energy is dissipated through friction with the sea bed (which is non-linear) than when the speed is low. In reef-dense parts of the GBR, this effect is compounded by the widespread presence of secondary flows in the wakes of reefs, where a lot of energy is dissipated through bottom friction. During stronger flow events therefore, the presence of these secondary flows leads to a very significant increase in energy dissipation through bottom friction, such that during spring tides, when tidal currents are strongest, the reef matrix is effectively rendered impermeable to low-frequency currents, whilst during neap tides, with less energy being dissipated in the reef matrix, low-frequency currents can once more be felt through the area. Conversely to what might be intuitively expected therefore, water residence times inside the reef can actually be greater during spring tides than during neap tides, due to the decrease in low-frequency current strength. This phenomenon also explains the observation that low frequency currents near Bowden Reef are modulated by the spring-neap tidal cycle, being stronger during neap tides and weaker during spring tides (Wolanski 1994).

These localised effects demonstrate the importance of being able to resolve the topography and bathymetry down to the reef scale in any oceanic model of the GBR; failure to do so would lead to missing significant flow features such as the Sticky Water effect, or the residual circulation caused by tidal flows around certain reefs.

2.1.2 Winds

The wind around the GBR – both on and off the shelf – is a very significant driver of currents through the GBR shelf (Wolanski 1994). Many studies have shown that the wind is one of the two main drivers of on-shelf low frequency currents, at least as important as water exchanges with the Coral Sea (e.g. see Pickard et al. 1977; Wolanski and Pickard 1985; Wolanski and Thomson 1984; Wolanski 1982).

The wind over the GBR is mainly driven by an area of high mean Sea Level Pressure (SLP) at around 30°S, and a low pressure area over the equatorial region, as shown in Figure 2.1. This results in a strong SLP gradient over the intervening area, which includes the entire GBR, and leads to strong south-easterly trade winds blowing towards the north-west⁴ over the GBR (Redondo-Rodriguez et al. 2012). These SE trade winds have a significant seasonal variation, with the area of low SLP migrating northwards during the

³Spring and neap tides refer to the 28-day tidal cycle: at spring tides the Moon and the Sun are aligned with the Earth (new Moon and full Moon), and tidal effects are amplified; the tidal range is therefore greatest at this time, whilst at neap tides the Sun and the Moon are at right angles to each other and their respective tidal effects partially cancel each other out; the tidal range is therefore smallest during this period.

⁴In meteorological parlance, the direction denotes the origin rather than the destination, so south-easterly trade winds blow from the South-East towards the North-West. This is in contrast to oceanographic convention, in which the direction gives the destination, so that a westward flow denotes a flow from East to West.

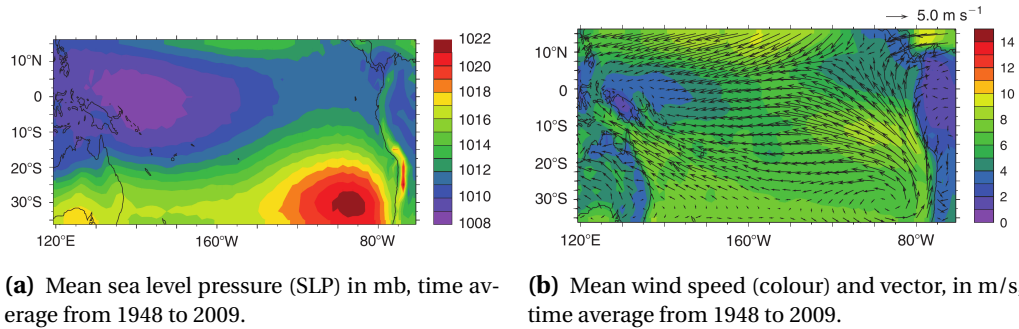


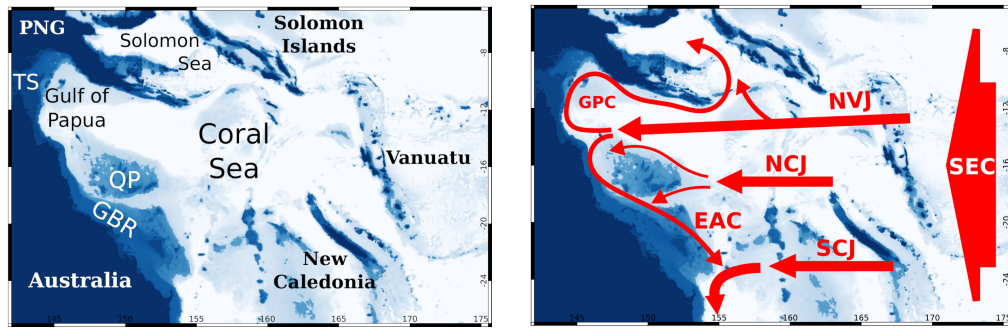
Figure 2.1: Mean SLP and wind field over the Southern Pacific Ocean. The zonal and meridional SLP gradient clearly visible in Figure 2.1(a) drives the SE trade winds over the Coral Sea and the GBR visible in Figure 2.1(b). Image reproduced from Redondo-Rodriguez et al. (2012).

austral winter, resulting in more intense SE trade winds over the GBR, particularly in the northern-central section (north of 18°S). Inversely, during the austral summer (during which most corals spawn) the low pressure area moves south, resulting in slightly weaker SE trade winds over the GBR, most notably in the north, which becomes dominated by north-westerly monsoonal winds from November to April. The effects of these summer monsoonal winds can sometimes be felt as far south as 18°S. Despite this weakening in summer, SE trade winds tend to prevail throughout the year south of 20°S, and thus affect circulation in the central and southern GBR all year round.

The SE trade winds have been shown to have a large impact on circulation through the GBR. The experimental study of Andrews and Furnas (1986) found a clear correlation between wind and current vectors, with periods of relaxation or reversal of SE trade winds coinciding with a southward acceleration of water currents⁵. Wolanski and Bennett (1983) also showed that during a period of strong SE trade winds, the observed currents were proportional with the longshore component of the observed wind, which was highly coherent over large distances, with a factor of proportionality of roughly 4% and a lag of 15h to 22h, nearshore and offshore respectively. In the central-northern GBR section, the low-frequency wind-driven current was found to dominate the much smaller tidal currents, whilst further south, towards Mackay, tidal currents were larger, though a strong low-frequency signal was still present. The authors also found that variations in SE trade winds can cause *barotropic* continental shelf waves which remain trapped on the shelf and propagate northwards, potentially displacing large amounts of water. These findings were not applicable to the northern GBR (north of Cape Melville at 14.2°S), where the high density of reefs causes a different set of dynamics. Wolanski and Pickard (1985) further showed that a simple model for wind-driven circulation was able to account for most of the variance in the currents over periods smaller than 20 days.

As they are directed northwestward roughly parallel to the coast, the SE trade winds drive a net northward longshore flow through the GBR, with only a much smaller, more variable cross-shelf component (Wolanski and Bennett 1983). During sustained periods of strong SE trade winds, this flow is strong enough to overcome the southward longshore flow caused by Coral Sea intrusions and the Coral Sea Lagoonal Current (described in the next section) in the central and southern GBR, effectively stopping it and deflecting it seawards (Andrews and Furnas 1986; Wolanski et al. 2013). Thus, the direction of the

⁵This net southward tendency was put down to Coral Sea inflow - see next section



(a) Map of the Coral Sea, with countries and features labelled. PNG: Papua New Guinea; QP: Queensland Plateau; TS: Torres Strait.

(b) Map of the Coral Sea showing the major surface currents, as discussed in the text. Note that when the NCJ reaches the GBR shelf it mainly drives the sub-surface (therefore not shown) northward-flowing North Queensland Current which sits underneath the southward-flowing, nascent EAC.

Figure 2.2: Reference maps of the Coral Sea. EAC: East Australian Current, GPC: Gulf of Papua Current, SEC: South Equatorial Current, NVJ: North Vanuatu Jet, NCJ: North Caledonian Jet, SCJ: South Caledonian Jet.

net circulation through the GBR over a given period is heavily dependent on the strength of the SE trade winds during this time.

2.1.3 Exchanges with the Coral Sea

In order to understand the water exchanges between the GBR shelf and the neighbouring Coral Sea, it is necessary to have an understanding of the basin-scale circulation of the Coral Sea and more in general the south-western Pacific Ocean. I will now outline the main characteristics of the circulation in this region.

Large-scale flow in the south-western Pacific Ocean is dominated by the South Pacific sub-tropical gyre: an anti-cyclonic (anti-clockwise) water circulation extending roughly from 150°W up to the coast of Australia at roughly 150°E, and from New Zealand in the south to Papua New Guinea in the north (Gasparin 2012). It is predominantly driven by the south-easterly trade winds forming a westward flow of water at low latitudes, known as the South Equatorial Current (SEC), and strong westerly winds at higher latitudes forming the eastward-flowing, highly energetic circumpolar current in the Southern Ocean (Steinberg 2007).

2.1.3.1 The South Equatorial Current (SEC)

The northward branch of the gyre – the westward-flowing SEC – is the one which most affects the GBR shelf. As it enters the Coral Sea from the east, at around 160-170°E it hits the islands of Vanuatu and New Caledonia, at which point it splits into three distinct jets, as illustrated in Figure 2.2(b): the North Vanuatu Jet (NVJ), the North Caledonian Jet (NCJ) and the South Caledonian Jet (SCJ). These jets traverse the Coral Sea, from east to west, in three distinct bands, each one impinging on the GBR shelf at a different latitude (Kessler and Cravatte 2013a; Kessler and Cravatte 2013b). The characteristics of these jets are as follows:

- The **NVJ**, the northernmost jet, enters the Coral Sea to the north of Vanuatu. It is a broad (400 km wide), shallow current, found between 11.5–15°S, occurring mostly above 300 m, and with a maximum speed of around 8.5 cm/s at a depth of 50–75 m. As the jet traverses the central part of the Coral Sea, roughly half breaks off northwards into the Solomon Sea, whilst the remaining half continues up to the shelf break. At this point it bifurcates: about half, or just over, turns northwards, forming the Gulf of Papua Current (GPC, also known as the Coral Sea Coastal Current, CSCC⁶), whilst the rest turns southwards, forming the shallow beginnings of the East Australian Current (EAC), which continues southwards along the entire Australian east coast.
- Further south, the narrower (100 km wide), deeper (up to 1500 m or more) **NCJ** has a maximum speed of about 11 cm/s at a depth of about 275 m, weakening at the surface and at higher depths. It is formed when the SEC hits the island of New Caledonia from the East and splits into 2 westward flowing jets: the NCJ to the North and the SCJ to the South. After crossing the Coral Sea, the NCJ arrives at the Queensland Plateau⁷ at around 18°S, whereby it splits around the relatively shallow plateau. At the shelf break, both branches turn mostly or entirely northwards, forming a deep northward western boundary current underneath the southward-flowing, shallow NVJ-driven EAC, which still dominates down to about 200 m. This deeper, northward current eventually feeds into the GPC.
- The **SCJ** forms the southernmost branch of the SEC. It is less clearly defined (more turbulent) and is mainly subsurface. It reaches the shelf at around 23°S and turns southwards, supplying the bulk of the EAC flow at this point, and extending the EAC to much greater depths.

These three jets together form the main source of water inflow into the Coral Sea, and have a total transport of around 30 Sv⁸, a value obtained following an analysis of drift velocities of Argo floats (Kessler and Cravatte 2013a; Ridgway and Dunn 2003). They serve to import warm, clean, nutrient-poor tropical surface waters into the outer GBR, and significantly affect the water circulation and nutrient levels on the GBR shelf (Burrage et al. 1997). They also give rise to the Gulf of Papua Current in the north and the East Australian Current in the south, the two main western boundary currents off the east coast of Queensland.

2.1.3.2 The Western Boundary Currents

The GPC, fed by NVJ and NCJ waters, flows northwards just to the east of the GBR shelf, passes by the eastern side of the Torres Strait⁹, and turns into the Solomon Sea in the

⁶There are a number of overlapping definitions in use for the coastal currents in the north-eastern Coral Sea. The northward current off the GBR shelf is sometimes called the Coral Sea Coastal Current, the Great Barrier Reef Undercurrent or the North Queensland Current (NQC), whilst east of Torres Strait and in the Gulf of Papua it is sometimes referred to as the Hiri Current. The most recent consensus however is that these different labels describe a single continuous current which, following historical practice in physical oceanography, should together be referred to as the Gulf of Papua Current, GPC (Community 2012).

⁷The Queensland Plateau is a raised plateau to the east of the GBR shelf and separated from it by a narrow but deep channel – see Figure 2.2(a).

⁸1 Sverdrup = 10×10^6 m³/s.

⁹The Torres Strait is the narrow, shallow stretch of sea, dotted with islands, which divides Cape York in Australia with Papua New Guinea.

CSCC:	Coral Sea Coastal Current
CSLC:	Coral Sea Lagoonal Current
EAC:	East Australian Current
GPC:	Gulf of Papua Current
NQC:	North Queensland Current
NCJ:	North Caledonian Jet
NVJ:	North Vanuatu Jet
SCJ:	South Caledonian Jet
SEC:	South Equatorial Current

Table 2.1: List of acronyms of the main currents in the Coral Sea and the Great Barrier Reef.

north. The dense outer reef in the northernmost part of the GBR shelf, coupled with the fact that the current itself is mainly subsurface, means it doesn't penetrate onto the shelf, with on-shelf circulation in this region mainly driven by wind and wave breaking effects (Wolanski et al. 2013).

To the south, the EAC begins as a shallow southward flow about 200 m deep fed by the NVJ at around 15°S, in the Queensland Passage, and it remains a relatively shallow current until the influx of the SCJ at around 23°S causes it to deepen and strengthen significantly. It is not considered fully developed until around 26°S (Steinberg 2007).

2.1.3.3 Intrusion of Coral Sea waters onto the GBR shelf

The main source of intrusion of Coral Sea waters onto the GBR shelf is the SEC, and in particular the NVJ and NCJ, which impinge on the shelf just off the central part of the GBR (which is also the least reef-dense GBR section, and thus the most permeable to intrusions of water). Using hydrographic data from cruises and satellite-tracked drifters, Church (1987) identified a strong westward flow impinging on the GBR at around 18°S, moving up to 14°S during the monsoon season (November-February), whilst Andrews and Clegg (1989) found a westward flow at the shelf break roughly between 16°S and 19°S, splitting into northward and southward components. Burrage et al. (1997) found this bifurcation point to be located at around 14°S (with significant shifts possible), and Brinkman et al. (2001) speculate that it may migrate between 14°S and 20°S, which seems like a plausible conclusion based on the aforementioned findings.

Observations using long-term current moorings on the continental shelf itself have shown that waters from the Coral Sea do intrude onto the shelf in the central section of the GBR, with Andrews and Furnas (1986) finding intrusive activity throughout the year, particularly during the austral summer, and throughout the full latitudinal extent of their array of moorings (17°S to 20°S), whilst Wolanski et al. (2003) report an observed oceanic inflow occurring between 14.7°S and 16.75°S. Brinkman et al. (2001) used modelling to estimate the size of this inflow in the central GBR to be 0.58 Sv, and found that the presence of reefs close to the shelf break impeded the inflow, so that whilst the area of inflow was spread along 500 km of the shelf break, more than half of the inflow occurred along a stretch 150 km long where the reef density was lower than elsewhere.

The effect of this shelfward intrusion of Coral Sea water, combined with the longshelf pressure gradient due to the nascent EAC present just off the shelf and on the shelf break, drives a southward current on the shelf itself, with studies finding a southward longshore current attributable to Coral Sea inflow present on the shelf everywhere south of 14°S

(Wolanski and Pickard 1985). This current, known as the Coral Sea Lagoonal Current (CSLC), was measured by Wolanski and Pickard (1985) to be in the order of 20 cm/s in the central GBR, and was found to exhibit significant variability on seasonal and annual time-scales¹⁰. Andrews and Furnas (1986) observed a similar effect, finding a seasonally varying poleward flow on the shelf modulated by wind-forced interior surges. During periods of sustained south-east trade winds, the wind-driven current on the shelf overpowers and reverses the CSLC, but during periods of low winds the net on-shelf flow is mainly driven by the CSLC. As such, the southward flow tends to peak in November to December¹¹ (when SE trade winds are weakest), and is at a minimum in April to May (Steinberg 2007).

The Coral Sea inflow causes no net longshore current in the northern section of the GBR, as the narrow, reef-dense shelf between Lizard Island and the coast does not allow Coral Sea waters to intrude (Wolanski et al. 2013).

In the far south of the GBR, on the wedge of continental shelf which extends southwards from 23°S, the circulation patterns are different to the rest of the GBR due to the presence of a stable, cyclonic, mesoscale eddy in the indentation of the continental shelf just in front of the mouth of the Capricorn Channel, known as the “Capricorn Eddy” (Weeks et al. 2010). The presence of this eddy is due to a combination of the particular topography of the shelf, with its marked indentation beneath the Swains Reefs, and the presence of the fast-flowing EAC just off the shelf. As it passes this indentation, where the shelf break turns abruptly landwards, the EAC continues southwards, separating from the shelf break, as illustrated in Figure 2.3 (Burrage et al. 1996). As a result, a zone of strong current shear is formed on the seaward edge of this indentation, and a cyclonic torque is exerted on the water inside indentation.

The cyclonic motion of the water in the Capricorn Eddy horizontally entrains the water on the shelf, and causes the currents on the narrow, southern wedge of the GBR to be directed northwards, even during periods of weak or no SE trade winds. We note in passing that a cyclonic eddy in the Southern Hemisphere experiences upwelling at its centre and outward transport of water at its periphery; this results in nutrient-rich, cooler waters entering the shelf on the Capricorn-Bunker reef group section, a result which is clearly visible in satellite imagery for mean surface sea temperatures (Weeks et al. 2010). The presence of the eddy is also a mechanism which facilitates continual mixing of shelf waters with EAC waters (Burrage et al. 1996).

2.1.4 Observations of the net water circulation on the GBR shelf

The net effect of tides, wind and Coral Sea inflow is to create a complex and changeable water circulation on the GBR shelf. Whilst numerous observational studies have focused on different sections of the GBR, very few have looked at the entire GBR at the same time, due to the logistical difficulties of monitoring water currents region measuring 2,500 km by 200 km, much of which is found in extremely remote locations.

From the numerous sources described above, it is apparent that residual currents on the shelf, due to the wind and to Coral Sea exchanges, are mainly oriented in the longshore direction, whilst the oscillating tidal currents are mainly oriented along the

¹⁰This reinforces the validity of our approach in Chapters 5 and 6 of running simulations for a number of successive spawning seasons, and calibrating the model separately using real data for each spawning season.

¹¹This period corresponds to the coral mass spawning period over much of the GBR.

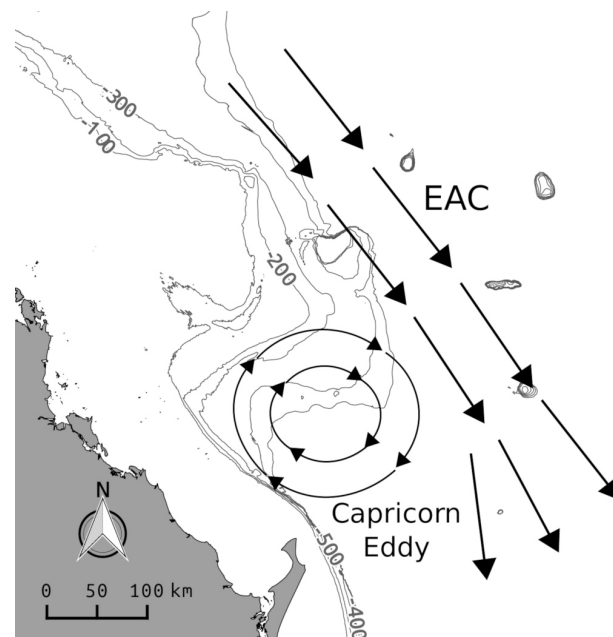


Figure 2.3: Top-down view illustrating the Capricorn Eddy. Bathymetry contours are shown; the thick arrows illustrate the general motion of the eddy. Image after Weeks et al. (2010).

cross-shelf direction (though close to shore and in the south they also have longshore components). At different times, and at different locations in the GBR, any of these three currents can dominate the flow. Mainly however, the wind dominates in the longshore direction during periods of moderate to strong SE trade winds, whilst the tides dominate in the cross-shelf direction, except where the shelf is narrow in the central GBR. When the wind is weak or blowing from the north west, the net longshore currents reverse and flow southwards, driven by the water inflow from the Coral Sea.

A study by Choukroun et al. (2010) used data from surface velocity drifters in the Coral Sea and the GBR to reconstruct an *Eulerian field* of the mean surface circulation, and to calculate water residence times. On the shelf, the authors found that mean surface velocities were fairly small south of 18°S (5 cm/s) and tended to be oriented north-westwards, implying that the northwestward wind-driven currents tend to overpower the southward longshore CSLC most of the time. North of 18°S, the surface velocities were stronger to the northwest (18 cm/s), and there was found to be very little transport between the northern and southern parts of the GBR (ie. north and south of 18°S). The authors concluded that passive waterborne larvae can potentially move hundreds of kilometres along the shelf over periods of a week to months.

Putting together data from long-term mooring arrays, radar altimeters, statistical models and 4 ocean models of the GBR and Coral Sea, Burrage et al. (1997) attempted to describe the long-term circulation patterns in the GBR. They found that dispersal of drifters occurs mainly in the alongshelf direction, though limited cross-shelf transport can occur through a combination of random fluctuations and periodic excursions of the tides. They also found that the western boundary currents had a significant impact on on-shelf flow, particularly on the outer shelf, and identified the SEC bifurcation point at approximately 14°S. Based on data from long-term moorings, the authors identify a 7–15 year fluctuation in low frequency currents through the GBR, though they do not specu-

late on the cause of this fluctuation.

2.1.5 Previous efforts to model the water circulation on the GBR shelf

Modelling the circulation in the entire GBR is problematic due to the topographical complexity of the region, and the resulting need for a high resolution ocean model. A number of mainly small-scale studies on water circulation have been carried out however, and have helped to explain various properties of the on-shelf flow. One of the first attempts was that of Andrews and Bode (1988), who used a numerical tidal model to study energy propagation in the central GBR, and found it agreed relatively well with observations, despite the coarseness of their 9.3 km resolution grid, a model feature reflecting the technological constraints at the time.

A 3D ocean model was developed and used by Black et al. (1991) to study the small-scale flow around a specific reef in the central GBR (Davis Reef) at a resolution of 400 m. This resolution was found to be sufficient to accurately resolve all the major features of the reef, to simulate the eddies in its lee and to effectively model particle retention. They found that the depth-averaged currents were very similar to those obtained with an equivalent 2D model, indicating waters were well-mixed. On a larger scale, Bode et al. (1997) attempted to develop a 2D model capable of accounting for the presence of reefs on a coarse grid using parameterisation schemes, and used this to model tidal flow in the reef-dense southern GBR on grid with a 1.8 km resolution. More recently, Saint-Cast (2008) used the 3D SHOC model to study water circulation in the northern GBR and Torres Strait using a grid with a 4 km horizontal resolution, thus ignoring virtually all of the reefs on the GBR shelf, and leaving its accuracy open to doubt (Wolanski et al. 2013).

The first effort to model the entire GBR was made by Luick et al. (2007), who used a 2D model with a grid size of 1.8 km to compute circulation over a year, and compared it with a coarser 3D model (with 9 km horizontal grid size) run over the same period. They found that tracer distributions predicted by the two models were very similar, and that the 2D model could be used in place of the 3D one for most applications. The model validation showed a good agreement between observed and predicted depth-averaged currents from the 2D model. However, the fact that these were only compared at a single site for the entire GBR leaves questions unanswered as to the model's ability to simulate accurate circulation patterns on the rest of the shelf. This question appears especially pertinent considering that the boundary conditions imposed came from a larger-scale, coarse (9 km resolution) unvalidated model of circulation in the Coral Sea, with an artificially flat bottom of 300 m, and forced only by wind stress and average annual sea level signals from tide gauges at the boundary. Furthermore, the accuracy of both models was limited by the coarse grid size which, even in the 2D model, led to them missing most reefs on the shelf.

These previous attempts to simulate the water circulation in the GBR have employed models which resolve flow on a structured grid. Such models have the advantage of being simple, efficient and very widespread, but have the disadvantage of having a fixed resolution which cannot be readily varied in space or time. In an area as large and intricate as the GBR this is an important hindrance, because it means that in order to resolve flow at the reef-scale – say, in the order of 100 m – all grid cells must be 100 m in length, which is very computationally demanding over such a vast area. Whilst it is possible to vary the resolution in space to some extent by using grid nesting, whereby grid cells in certain areas are subdivided into smaller grid cells (e.g. see Debreu and Blayo 2008; Zavatarelli

and Pinardi 2003), this approach introduces new problems, as the mesh resolution can exhibit large jumps at the interface between large and small cells. Furthermore, two-way grid nesting can introduce numerical artefacts, requiring the use of advanced techniques to reduce artificially introduced wave reflections (see Debreu and Blayo 2008), so its use is best limited to as few locations as possible. Given the complex nature of the GBR, the number of locations requiring increased resolution is so great as to render grid nesting impractical. This explains why most existing models of water circulation in the GBR either have a resolution much coarser than the reef scale or restrict themselves to small sections of the GBR.

Many of the drawbacks of using structured-grid ocean models in the GBR can be avoided by using unstructured mesh models, specifically the constraint of using a fixed resolution, and the “staircase”-like representation of coastlines which results from having cell boundaries all aligned along the same set of axes. The SLIM ocean model was the first unstructured mesh model used to simulate flow in the GBR. Building on the work of Legrand et al. (2006), who generated meshes for use in a hydrodynamic model of the GBR, Lambrechts et al. (2008) showed that SLIM was capable of modelling the circulation on the entire GBR shelf down to the scale of individual reefs (150 m) close to islands and coastlines, thus simultaneously simulating most major scales of motion. The model was able to reproduce predicted sea surface elevation time series at various points on the GBR shelf, and accurately reproduced the flow around an island as predicted by a very high resolution 3D finite element model, notably the formation of shallow water island wake eddies. It was not calibrated or validated with data from real measurements however. The 2D SLIM model has subsequently been used to study many aspects of the water circulation in the GBR, from sediment dynamics in Cleveland Bay (Lambrechts et al. 2010), to the Sticky Water phenomenon¹² in the southern GBR (Andutta et al. 2012), to the dynamics of hypersaline coastal waters in the central GBR (Andutta et al. 2011), to modelling the fate of marine turtle hatchlings (Hamann et al. 2011), to studying the net water circulation through Torres Strait (Wolanski et al. 2013). The 3D, *baroclinic* version of SLIM has recently been used to study the transport of sediment from the Burdekin River through a 250 x 50 km region in the central GBR (Delandmeter et al. 2015), though its use over larger regions remains prohibitively computationally expensive for the moment. The present thesis is a continuation of this effort to use SLIM to reveal properties and effects of the water circulation through the GBR.

Efforts have recently been made by Australian government institutions to model the entire GBR at high resolution, notably as part of the eReefs project, which plans to operate a near real-time circulation model of the GBR coastal ocean at 1 km resolution¹³. Whilst slightly too coarse in resolution to be able to study flow at the reef-scale, the ocean model, which is based on the SHOC code of Herzfeld (2006), nonetheless has the potential to offer insights into water flow through the GBR. Limited use has been made of the eReefs high-resolution coastal ocean model to study the GBR’s circulation in the published literature however.

2.1.6 How well mixed is the water column?

Various observational and modelling studies have tried to measure the importance of stratification and 3D effects in the GBR waters. The observational study of Wolanski

¹²See §2.1.1 for a description of the Sticky Water phenomenon.

¹³See <http://www.emg.cmar.csiro.au/www/en/emg/projects/eReefs/Overview.html>

(1983) analysed data from a large number of hydrological casts in the northern GBR shelf and concluded that “*it is clear that the shelf waters are everywhere vertically well mixed over the shelf, so that the current data over the shelf should not be aliased by baroclinic effects.*”. The *thermocline* was found to be typically located offshore from the shelf break. Middleton and Cunningham (1984) further found the water column to be well mixed throughout the year at 3 sites on the GBR shelf where they maintained current moorings; they therefore assumed that flow on the shelf was *barotropic*.

Upwelling and stratification effects on the GBR shelf can become important in certain situations however. For instance Andrews and Furnas (1986) found that intrusions of Coral Sea water onto the GBR shelf can lead to upwelling events close to the shelf break. Wolanski and Van Senden (1983) found that *river plumes* extending into the shelf during flood events can also lead to localised upwelling. Both of these occurrences are localised events which occur at specific points in time and space and do not have a significant impact on overall water circulation at other times. It is additionally known that reef-scale *eddies* in the wakes of islands in the GBR can have a three-dimensional structure with localised upwelling and downwelling (see, for example, Deleersnijder et al. 1992; White and Deleersnijder 2007). This feature is more common than the two aforementioned phenomena, but which can nonetheless be adequately captured using depth-integrated hydrodynamic models, at least if we are only interested in the depth-integrated horizontal currents, as shown by Wolanski et al. (2003) and Lambrechts et al. (2008).

Two modelling studies, Black et al. (1991) and Luick et al. (2007), compared the results from 2D and 3D models of the GBR. Both studies found that the 2 models they compared gave very similar results, and that tracer distributions simulated by the 2D models were very similar to the distributions from the 3D models. The latter study showed that this was mainly because the 3D model predicted rapid vertical mixing of the water column, in agreement with empirical observations. The former study additionally found that particle retention rates around reefs predicted by 2D and 3D models were very similar for vertically well-mixed particles, although this result did not always hold for particles which preferentially resided at certain depth levels due to vertical variation in horizontal currents.

2.1.7 Sources of variability in water circulation

The currents on the continental slope of the GBR have been found to undergo seasonal, annual and decadal changes in strength and position (Burrage et al. 1997). Whilst much of the seasonal variation in currents can be ascribed to seasonal variability in the wind field, another notable driver of variations on annual and multi-annual time scales is the El Niño-Southern Oscillation (ENSO) phenomenon, which is outlined in this section. I will then proceed to look at what we know about projected changes to water circulation in the GBR in the future.

2.1.7.1 El Niño-Southern Oscillation (ENSO)

One of the major drivers of variability on the multi-annual scale is El Niño-Southern Oscillation (ENSO) events (Burrage et al. 1997; Steinberg 2007), which generally oscillates between its two phases – El Niño and La Niña – over a 3 to 7 year period, with each phase typically evolving over 12 to 18 months (Lough 2007). The two different phases have long been associated with certain distinct atmospheric and oceanic conditions, in-

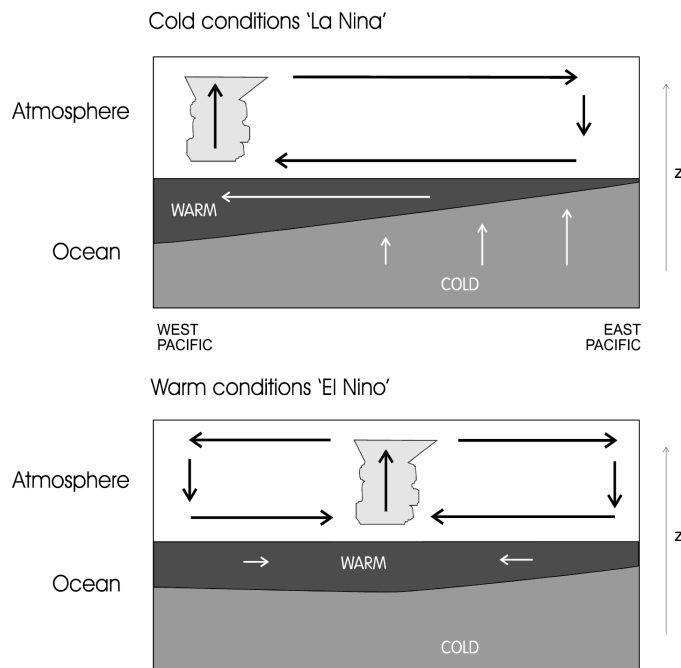


Figure 2.4: Illustration of the conditions in the Pacific Ocean and atmosphere during La Niña (top) and El Niño (bottom). During La Niña events, stronger SE trade winds lead to a build up of warm water in the West, a steepening of the thermocline, and greater precipitation in the West. During El Niño events the SE trade winds weaken, the thermocline is flatter, and precipitation occurs further to the East. Image reproduced from Marshall and Plumb (2008).

cluding rainfall anomalies, changes in sea surface temperature and variability in cyclone activity (Lough 2007; Redondo-Rodriguez et al. 2012).

The physical mechanism can be explained by considering that under normal, or “neutral” conditions, the trade winds blow from east to west across the tropical Southern Pacific, transporting warm, equatorial waters westward whilst causing the formation of cooler waters through upwelling off the coast of South America. This causes the thermocline to deepen in the west and rise in the east. El Niño events are associated with a weakening of the trade winds, causing weaker westward transport of warm water, and meaning that warm, equatorial water can extend further eastward towards South America, as shown in the diagram in Figure 2.4. The unusually warm waters in the central and eastern Pacific cause increased cloud formation and heavy rain in these areas, whilst areas in the western Pacific and Australia can suffer from severe drought. The other ENSO phase, La Niña, is essentially the opposite of El Niño. La Niña events are associated with strengthened trade winds, which push warm equatorial waters further west, causing waters in the eastern Pacific to be cooler than normal, and increasing the slope of the thermocline. This results in increased cloud formation and rainfall to the west, above the warmer waters, decreased rainfall to the east, and an increase in coastal upwelling off the coast of South America (Gasparin 2012; Steinberg 2007), as illustrated in Figure 2.4.

An important signature of an ENSO event is measured by the so-called Southern Oscillation Index (SOI), which is based on the difference in atmospheric pressure at sea level between Darwin (Australia) and Tahiti. As discussed in §2.1.2, this difference in atmospheric pressure drives the trade winds, so a sustained positive SOI index, which

represents above-normal air pressure at Tahiti and low pressure at Darwin, corresponds to a La Niña event, whilst a sustained negative index, which represents low air pressure at Tahiti and high pressure at Darwin, corresponds to an El Niño event (Sarachik and Cane 2010).

The influence of ENSO on the water circulation in the GBR is not very well known (Redondo-Rodriguez et al. 2012). On the large scale, it is known that ENSO dominates the inter-annual transport variability of the SEC: westward transport entering the Coral Sea increases a few months after El Niño events and decreases a few months after La Niña events, a time length consistent with the propagation time of Rossby waves from the centre of the area of ENSO wind variability (Kessler and Cravatte 2013a). Gasparin (2012) found that ENSO can affect mass transport into the Coral Sea by 15-20%, with these effects lagging their associated ENSO events by about 3 months. More specifically, Kessler and Cravatte (2013a) reported a 50% increase in NVJ current speeds following the 2009-10 El Niño, and a corresponding decrease of the same amount following the 2007-8 La Niña, with changes associated with the NCJ being much smaller.

Since the NVJ is a major cause of intrusion of Coral Sea waters onto the GBR shelf, ENSO events could plausibly have an effect on water flow onto the shelf. This subject has received very little attention in the literature however. Burrage et al. (1997) found a link between ENSO events and alongshelf currents, with strong northward flows appearing to occur prior to ENSO events followed by a rapid transition to strong southward flows in the later stages of the event. The authors claim to have identified such “signatures” of ENSO events for 5 ENSO events over 20 years, however they do not uniquely ascribe these current variations to ENSO, as they were sometimes also seen in non-ENSO years. Furthermore, the authors do not differentiate between El Niño and La Niña events, making it hard to use these results in any subsequent modelling study.

The strength of ENSO extremes is modulated by the so-called Pacific Decadal Oscillation (PDO), an oscillatory process with a very roughly decadal period. The PDO leads to prolonged warm or cold periods lasting in the region of 20-30 years (Lough 2007). However, other than affecting river flow into the GBR, the PDO has so far not been found to have a strong influence on the on-shelf circulation. Studies on links between both ENSO/PDO and circulation on the shelf are rather few and far between however, and more information would be needed to explicitly model the effects of these phenomena on flow in the GBR, in particular on how the PDO affects circulation in the Coral Sea adjacent to the GBR.

2.1.7.2 Future water circulation in the Coral Sea and GBR continental shelf

Global climate change is likely to have a significant impact on oceanographic conditions in the Coral Sea and on the GBR shelf over the next 50-100 years, causing rising temperatures, modified river flow, increased acidification, increased frequency of extreme tropical cyclones and a possible shift in water circulation (Lough 2007; Steinberg 2007).

On the large scale, most climate models consistently project a strengthening of the SE trade winds (Ganachaud et al. 2011), caused by changes in radiative forcing which are then amplified by a wind-evaporation-SST feedback mechanism (Xie et al. 2010). This change in the SE trade winds in turn contributes to a strengthening and southward shift of the wind stress curl in the South Pacific (Sun et al. 2012), with a possible resulting spin up of the South Pacific sub-tropical gyre. There is some debate as to whether the gyre will

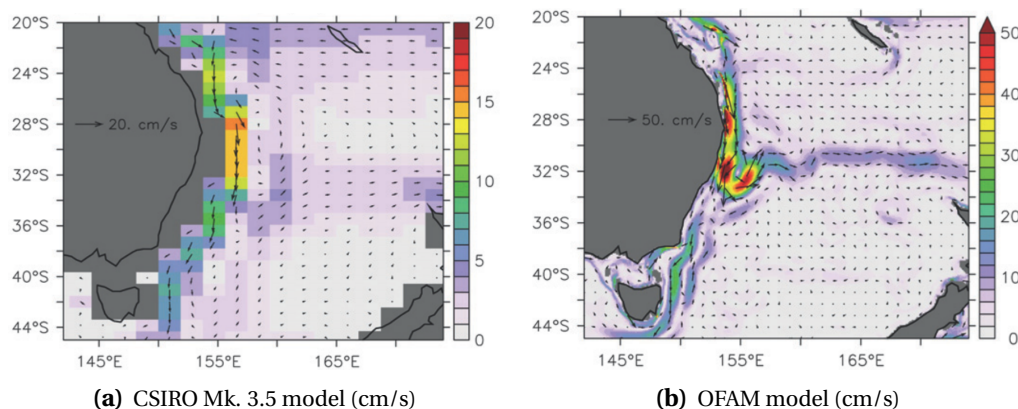


Figure 2.5: Mean circulation off the south-east coast of Australia predicted for a future climate scenario around 2060 by a) the coarse CSIRO Mk. 3.5 climate model, and b) the higher-resolution, mesoscale-resolving, Ocean Forecasting Australia Model (OFAM) obtained by downscaling the CSIRO Mk. 3.5 model. The level of detail of the coarser model is typical of global climate models, and these figures show the extent of the fine-scale structures missing from such models. Images reproduced from Sun et al. (2012).

simply spin up, and if so by how much, and/or shift southwards, with different models predicting different trends in this regard (Sen Gupta et al. 2012).

For the core section of the EAC¹⁴, most models predict a small increase in poleward transport (Oliver and Holbrook 2014; Sen Gupta et al. 2012). Some models also predict a small southward shift of the EAC, with a resulting increase of flow at higher latitudes and decrease at lower latitudes (e.g. Cai et al. 2005), though other models do not predict such a shift (e.g. Wu et al. 2012) so there is a reduced consensus on this feature. Climate models are almost unanimous in predicting an increase in the strength of the EAC extension (the residual southward component of the EAC from about 32°S reaching Tasmania) (Ganachaud et al. 2014; Oliver and Holbrook 2014), and observations show it has already extended southwards by about 350 km in the past 60 years (Ridgway and Hill 2012).

It is important to bear in mind that all of these results were obtained from global climate models with a relatively very coarse resolution, and whilst they may be able resolve the large-scale wind field driving the SEC and EAC, they are not able to capture the fine scale structure of the EAC system, let alone the impact of changes to these currents on the GBR shelf itself (Ridgway and Hill 2012; Sun et al. 2012). As a result there are no clear predictions of the impact of any such changes on the GBR shelf, and until either the resolution of these models is significantly increased, or adequate downscaling simulations are carried out, projections for on-shelf circulation changes are therefore based on inference. The study of Sun et al. (2012) is, to my knowledge, the only one which has downscaled a global climate model to the region around Australia to make future projections; however this study focuses mainly on the coastal ocean around south-east Australia and western Australia. It nonetheless shows the importance of downscaling to capture fine-scale features, as can be seen in Figure 2.5.

Considerable uncertainty surrounds the evolution of ENSO strength and frequency in the future, both because of a lack of clear patterns in historical records, and also due to the uncertainty on how climate change will affect ENSO, with projections diverging

¹⁴Defined as the EAC northward of the Tasman front-EAC extension separation point, at roughly 32 °S

significantly across different models (Sen Gupta et al. [2012](#)). Whilst some models have predicted an increase in extreme ENSO events (Cai et al. [2014](#)), there currently appears to be no clear consensus on this issue amongst modellers (Ganachaud et al. [2014](#)).

2.2 Studying dispersal and connectivity of coral larvae

The process of coral larvae dispersing from their spawning site to their settlement site is fundamentally controlled by two factors: biology and physical oceanography. The first defines when larvae are released into the water, how they behave once they are in the water column, when they are ready to settle at a suitable habitat site and how likely they are to die beforehand. The second dictates where the larvae could potentially spread to during the time they are in the water column, a duration known as their Pelagic Larval Duration (PLD).

Larval dispersal is a key factor leading to population connectivity – i.e. different populations of a species being connected with each other – but it is not the only one. A given proportion of larvae arriving at a suitable settlement habitat may instead die before they can become a part of its population, for instance if the local environmental conditions are inhospitable, or if there is no space available. The process of a larva successfully joining a given host population is known as *recruitment*. As such, numerical models of larval dispersal – which ignore recruitment – provide estimates of *potential* connectivity, insofar as populations which exchange larvae with each other have the potential to be demographically connected, though whether or not this connectivity is *realised* depends on recruitment success of larvae (Burgess et al. 2014). Since various empirical methods also exist to estimate connectivity, it is important to be aware of which factors driving connectivity a given method is measuring, whether only larval dispersal or also pre- and/or post-dispersal processes such as recruitment.

In the rest of this section, I will begin by briefly outlining some basic facts about coral biology and the types of coral present in the GBR and will then describe what we know about the biology of coral larvae during dispersal. I will subsequently move on to look at present-day patterns of larval dispersal and connectivity, both in the GBR and more in general. I will discuss what different measures of connectivity exist, what they mean, and whether they can be compared to the output of a biophysical model such as the one presented in this thesis. Finally, I will touch upon the possible ways in which estimates of population connectivity can be used to improve reef management, and what role biophysical modelling can play in this process.

2.2.1 Coral in the Great Barrier Reef

The term *coral reef* is commonly used to refer to a type of marine ecosystem which is fundamentally dependent on the presence of so-called reef-building, or *hermatypic* corals, as mentioned in Chapter 1. The calcium carbonate structure secreted by these corals creates a very rough, intricate surface which provides ideal living conditions for a whole host of marine organisms. As such, the corals inhabiting coral reefs are in reality a component of a much larger ecosystem, albeit a vitally important component.

Corals themselves are formed of many smaller organisms called polyps, which can vary in size from less than a millimetre to around 30 cm in diameter, depending on the species. The shape of a coral is characteristic of the species of the polyp from which it is composed. Polyps belong to the family of *cnidaria*, in common with jellyfish and sea anemone, and can feed on a variety of organisms, from zooplankton to some types of very small fish, using their tentacles to grab the prey and bring it to their stomach (US Environmental Protection Agency 2007). For most corals however, their largest source of energy comes from their symbiotic relationship with *zooxanthellae*, a class of algae of the

appropriately named genus *Symbiodinium*. Zooxanthellae often live within the tissues of polyps, and supply their polyp hosts with nutrients; they in turn obtain energy through photosynthesis (Barnes 1987). This explains why most corals live inside the photic zone - the upper layer of water penetrated by the Sun's rays, generally extending no more than 50 m down from the surface. Unfortunately this is also the water layer most prone to temperature anomalies, and the effect of prolonged, exceptionally high water temperatures on coral can be devastating, as this can lead to a break down in the symbiotic relationship between polyp and zooxanthellae ultimately resulting in the zooxanthellae abandoning their hosts, and facilitating the death of the coral by starvation or disease, a process known as *coral bleaching* (Marshall and Schuttenberg 2006).

The Great Barrier reef hosts about 600 species of coral, which can be broadly divided into the categories of hard coral, also known as hexacorals as their number of tentacles is always a multiple of six, and which hermatypic corals are a sub-category of, and soft coral, also known as octacorals as they have eight tentacles, and which do not have a solid outer skeleton (Fabricius 2009). Both types of coral are well-represented in the GBR. On a global level, six families of hard coral dominate modern world reef composition – Acroporidae, Faviidae and Mussidae (both also known as “brain coral”), Poritidae, Fungiidae (also known as “mushroom coral”), and Pocilloporidae (Hopley et al. 2007; Peach and Hoegh-Guldberg 1999), and all are present in large numbers in the GBR (Harriott and Fisk 1987). Of these families, Acroporidae dominate the diversity and coral cover of most reefs in the Indo-Pacific region through the two most species-rich genera *Acropora* and *Montipora* (Hopley et al. 2007).

2.2.2 Biology of coral larval dispersal

Knowing the fate of marine larvae is an issue which has long troubled scientists and fishermen¹⁵. Yet despite the plethora of technological tools at our disposal, efforts to empirically measure larval dispersal have still yielded at best preliminary results (Green et al. 2014).

An aspect of larval dispersal which is relatively well understood is the basic biology behind their dispersal process (Baird et al. 2009). Corals either release fully formed planulae¹⁶, in the case of so-called *brooding* species, or they release gametes¹⁷ which fertilise each other in the water, in the case of broadcast spawning species¹⁸). These gametes are generally found to be neutrally or positively buoyant initially, depending on the species, and tend to lose buoyancy as they age. Brooders release planulae following internal fertilization, resulting in fewer, larger, better-developed larvae (Veron 2000) compared to broadcast spawners. Larvae from brooding corals generally disperse much shorter distances and exhibit stronger population structures than broadcast spawning species as they are negatively buoyant, and therefore have a lower dispersal potential (Ayre and Hughes 2000; Hughes et al. 2000).

¹⁵In his key study into what caused fluctuations in cod populations in the great northern European fisheries, Johann Hjort already effectively identified the importance of larval dispersal in connecting populations, finding that *the very earliest larval and young fry stages [are] most important* in the development of fishes (Hjort 1914).

¹⁶Coral planulae are the larval form of coral.

¹⁷Gametes are eggs and sperm.

¹⁸Broadcast spawners account for around three quarters of all reef building coral species and 85% of coral in the Indo-Pacific (Baird et al. 2009; Hughes et al. 1999)

Spawning of gametes can occur in large, synchronised spawning events whose timing depends on the species, the phase of the moon, the water temperature, and quite possibly the amount of solar insolation (van Woesik 2010; van Woesik et al. 2006); this is the case of the Great Barrier Reef, where large-scale mass spawning events were first studied by Harrison et al. (1984). Coral spawning events are not always large-scale, synchronised affairs however, and in other parts of the world coral spawning can be a much more long-drawn out process, for instance in Kenya, where corals spawn over seven months of the year (van Woesik 2010). Spawning generally, but not always, occurs at night, depending on the species (van Woesik 2010).

It is known that larvae develop the ability to sense when they are over a reef, using environmental and mechanical cues such as light, noise or vibrations (Gleason and Hofmann 2011), or biotic cues such as those produced by crustose coralline algae which inhabit reefs, to select settlement sites (Price 2010). This ability to sense the presence of a nearby reef – known as “competence” – is typically obtained a few days after spawning, though the time taken to become competent can vary significantly between species. Competence can also be lost as the larva ages (Connolly and Baird 2010). A larva can therefore potentially go through a pre-competent period, followed by a competent period, followed by a post-competent period.

During the pre-competent period, larvae are technically not yet fully-formed larvae but embryos that are developing to become larvae, and cannot swim. As mentioned above, newly released eggs tend to be positively buoyant, however their mass is so small that coral embryos are often found to be well mixed throughout the water column. Once they are competent, coral larvae have a small swimming ability, though this is negligible compared with crustacean and fish larvae (Kingsford et al. 2002). Whilst there is currently some debate about the exact ability of coral larvae to swim horizontally (see Dixon et al. (2014), and response of Baird et al. (2014)), the consensus is that their potential maximum swimming speeds of larvae are well below the typical speeds of inter-reef currents – around two orders of magnitude smaller – with the highest observed speeds being in the order of 3.45 mm/s, whilst inter-reef currents are typically in the order of 100 mm/s (Baird et al. 2014). As such, horizontal swimming capabilities are practically negligible. Larvae of most broadcasting species are also thought to be positively buoyant initially, with buoyancy decreasing as they age; however accurate measurements of larval buoyancy in the ocean (i.e. outside of idealised laboratory conditions) are lacking, and in well-mixed waters it appears likely they would be well-distributed over an extended vertical range.

Once a competent larva senses it is near a reef, it will typically swim downwards and attempt to attach itself to the reef’s surface, a process known as settlement. The larvae which manage to successfully complete the process of settlement and survive to become a part of the host population are known as recruits. The proportion of larvae attempting settlement which manage to successfully recruit is hard to measure and not well known (Botsford et al. 2009b).

Recent laboratory experiments have been able to accurately characterise the natural mortality of various common coral species over their lifespan using exponential, Weibull and generalised Weibull distributions, reflecting a trend for either a constant mortality rate, a high initial and monotonically decreasing mortality rate, or a bathtub-shaped mortality rate, with high initial mortality, low subsequent mortality, and high mortality again as the larva reaches “old age” (Connolly and Baird 2010; Figueiredo et al. 2013; Figueiredo et al. 2014), depending on the species. The mortality of larvae due to preda-

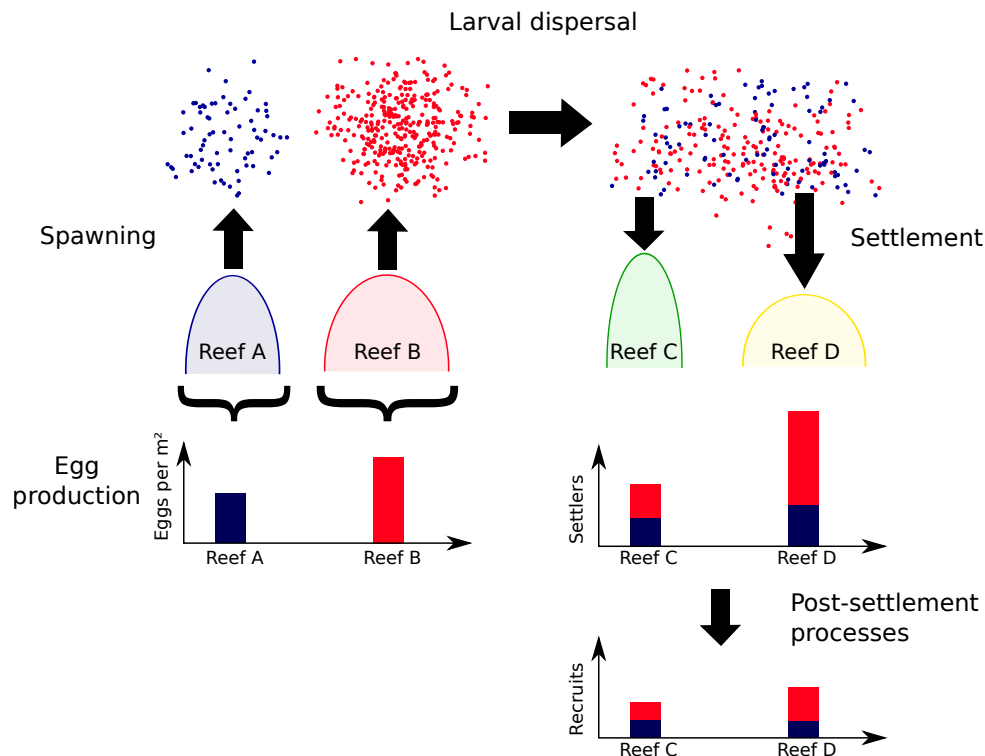


Figure 2.6: Illustration of the process of population connectivity through larval dispersal. In the first stage (left) reefs A and B spawn gametes according to a given egg production rate. These gametes fertilise each other and become larvae, whereupon the process of larval dispersal carries them over to reefs C and D. Settlement onto these reefs can then occur. However, post-settlement mortality reduces the number of settlers which can successfully recruit onto the reef. This mortality can be both habitat-dependent (some reefs offer a more supportive habitat) and density-dependent (reefs with high existing coral cover have less space for new arrivals). See also Botsford et al. (2009b).

tion, for instance by fish and jellyfish, is unknown, though it is likely to be significant, and to vary in space and time as predators would position themselves in areas likely to contain high densities of coral larvae, for instance around reefs during the coral spawning period.

2.2.3 What is connectivity and how does it differ from larval dispersal?

At the most basic level two separate reefs, say reefs A and B, may be considered to be connected if an organism from reef A travels to reef B and becomes a part of its population. This process not only serves to increase the population of reef B, but also introduces genetic information from reef A onto reef B. Clearly, for corals, which are physically attached to their reef, the process of larval dispersal is essential to ensure population connectivity, since adult coral are unable to physically migrate between reefs. Larval dispersal is therefore a prerequisite for connectivity between coral populations, but it is not the only prerequisite.

What else is needed for two populations to be connected? Firstly, corals need to produce gametes or planulae in the first place, otherwise larval dispersal cannot take place. The net egg production ability of an organism, known as the Lifetime Egg Production

(LEP), can vary in space and time (Botsford et al. 2009b). Secondly, larvae which have dispersed from one reef to another must be able to settle onto the destination reef, and once settled, successfully survive to become a part of the host population; this whole process is illustrated in Figure 2.6. How successful corals are at producing gametes or planulae, and subsequently how successful larvae are at carrying out these post-dispersal operations can have an important impact on the connectivity between reefs (Kinlan and Gaines 2003). For instance if lots of larvae from a given reef arrive at another reef, but are then unable to settle onto it, connectivity between these reefs will be zero, despite the large larval dispersal from one to the other.

Given the importance of pre- and post-settlement processes in defining population connectivity, we might expect that the term “connectivity”, when used in marine ecology, would have a precise meaning. In fact it still is a surprisingly vague concept, often used in different studies to refer to different things. The definition of “connectivity” used in a given study generally depends on: a) what processes are included, and b) how sensitive the measurement method is. I will deal with each of these points in turn:

a) In studies using larval dispersal as a proxy for connectivity, the authors assume that connectivity between any two reefs is high if larval dispersal between these reefs is high. This definition ignores both pre- and post-dispersal processes and therefore implicitly assumes that LEP, and recruitment success rates, will be the same everywhere in time and space. Typically this is the case for biophysical modelling studies, where numerical models are capable of accurately predicting larval dispersal patterns, but are unable to include pre- and post-dispersal processes because parameters are unknown and very hard to measure. As such, these models provide estimates of *potential connectivity*, whilst empirical methods such as parentage analysis or natural tags (discussed below) measure *realised connectivity* (Burgess et al. 2014).

b) Some studies are more sensitive to small-scale larval exchange, whilst others can only detect large-scale larval exchange. Studies using genetic methods to characterise connectivity are much more sensitive to very small scale exchange than either empirical methods or biophysical modelling. The reason for this lies in the difference between so-called *genetic connectivity* and *demographic connectivity*: as mentioned above, populations are demographically connected if there is movement of individuals (in our case larvae) between them, leading to a change in population size and exchange of genetic information. In order to have a significant impact on its population, reef A must send large numbers of larvae to reef B. However, the exchange of even just a few larvae between two reefs may well be enough to homogenise their genetics over the course of a generation, despite having an insignificant impact on population size (Slatkin 1993; Spieth 1974). In fact the threshold for genetically significant connectivity is several orders of magnitude below that required for connectivity to have an impact on population size (Cowen and Sponaugle 2009). Therein lies the difficulty in comparing measures of genetic connectivity (also known as evolutionary connectivity), which is defined by how genetically similar different populations are, with measures of demographic connectivity, which is concerned with the exchange of larvae in large enough numbers to affect population size and persistence (Leis et al. 2011; Lowe and Allendorf 2010). Studies which employ genetic tools to quantify the genetic similarity between different populations will yield measurements of genetic connectivity, whilst biophysical models and empirical methods, lacking the resolution (in time and space) to look at connectivity on the scale of individual larvae, will instead measure demographic connectivity.

These different types of “connectivity” can lead to confusion and complicate the task

of comparing estimates of connectivity between different studies. As such, it is essential to know what method was used to measure connectivity in any given study. I will now provide a brief overview of the different methods which currently exist to do so, and what kind of connectivity they can be used to measure. All of these methods may produce a *connectivity matrix* measuring a different set of processes.

2.2.4 Different techniques to measure connectivity

2.2.4.1 Population genetics

The method of population genetics consists of comparing the frequency of alleles¹⁹ occurring in individuals taken from separate populations. This allows us to characterise how genetically similar the two populations are, and therefore infer how much gene flow there is between them, since having very similar allele frequencies implies that gene flow between them has occurred at some point in the past (Botsford et al. 2009b).

The individuals sampled from different populations are adults, and their genetic make-up is therefore the result of the accumulation of genetic signals from different sources of larvae over an extended time period. Natural selection and genetic drift can act to affect their genetic make-up over this period (Botsford et al. 2009b). This makes it hard to know if the gene flow between two “similar” populations occurred recently or a long time ago (e.g. tens or hundreds of spawning seasons ago) (Bossart and Pashley Prowell 1998). Since coral colonies can survive through asexual reproduction for decades to centuries, genetic similarity between populations could potentially be due to gene flow which occurred decades to centuries ago (Botsford et al. 2009b), so this method has an extremely poor temporal resolution for measuring connectivity between coral populations.

Furthermore, as mentioned above, it is potentially sufficient for a single larva to disperse between two populations in order for them to become genetically homogenised²⁰, so even accounting for the poor temporal resolution, genetic methods will only find significant differences between populations with extremely low levels of larval exchange. They cannot therefore resolve differences in the strength of connectivity between populations (Whitlock and McCauley 1999), all they can do is tell us whether, at some point over the past adult life expectancy, at least very low levels of larval exchange have occurred.

I note in passing that for species with relatively short life spans, such as many reef fish, population genetics would have a more reasonable temporal resolution and could therefore be employed to produce estimates of contemporary connectivity.

2.2.4.2 Parentage analysis

This technique aims to identify the parents of sampled individuals from a given population. By taking many samples of both adults and juveniles (in the case of fish), it may be possible to link a given juvenile to a given adult. Doing so obviously requires that a large fraction of the adult population be sampled, in order that, for a given juvenile, there is a non-negligible chance that their parent(s) has/have been sampled. If a parent is located in a different population to the juvenile, then clearly connectivity has occurred between

¹⁹Alleles are alternative forms of the same gene, and an isolated population with no genetic inflow will typically exhibit a certain allele frequency inherent to that population.

²⁰To quote Spieth (1974), “*In terms of gene flow, the distinction between absolutely none and almost none is enormous*”.

the two populations within the lifespan of the juvenile (and for reef fish this would typically occur during the larval stage, as most species are very sedentary). Assuming the above condition can be met (and this generally requires extensive resources), parentage analysis can be a very powerful tool to analyse connectivity patterns in reef fishes. For instance this technique was recently used to quantify overspill from an MPA in the southern GBR (Harrison et al. 2012).

For corals on the other hand, this technique is much more challenging to apply, and to date no studies that I know of have published results on coral connectivity using this method, though attempts are in progress to do so²¹. An important difficulty is that it is much harder to sample a significant proportion of the potential adult population which could have spawned a given set of recruits at a given location. Indeed, an important limitation of the parentage analysis method (for fish as well as corals) is that failure to sample a significant enough proportion of the potential adult population will lead to an underestimation of the extent of connectivity. For example if a researcher samples all adults within a 1 km radius of a set of recruits and finds a significant number of parents in this area, he/she may conclude that there is connectivity over a scale of, say, 5-600 m; however there is no way of him/her knowing if a small number of the recruits actually come from much further away (say, 20 km), so it is necessary to sample a large number of adults over a very wide area. This would clearly become prohibitively resource-intensive in many areas and for many species, so this limitation poses a restriction on which types of taxa can be investigated using parentage analysis, and where (Botsford et al. 2009b; Green et al. 2014).

2.2.4.3 Natural and artificial tags

An instinctive reaction to the question “how can we measure larval dispersal?” can be to suggest simply tracking the position of larvae using aerial or satellite photography, or even underwater robots or divers, to see “where they go” during the PLD. These approaches are based on the implicit assumption that larvae have one or more features which allow us to easily recognise them from the marine “background”. Unfortunately the reality is not so simple, due to the small size of the larvae, the relative vastness of the ocean, and the fact that they would need to be tracked for days to weeks.

These difficulties notwithstanding, attempts instead have been made to use geochemical tags inherent in certain species to indirectly track larval dispersal. This method relies on the fact that some species have inbuilt geochemical signatures which are a function of their natural environment, so organisms living a certain distance apart, in areas with different natural environments, may have differences in their geochemical composition of certain features, for instance their otolith²² or their shell. Since their offspring would share their geochemical composition, it should be possible, by sampling a large number of individuals in different environments, to see if there has been transport between the two environments (Botsford et al. 2009b).

In addition to naturally-occurring tags, it is also possible to artificially mark a set of larvae with tags. For instance Jones et al. (1999) marked the otoliths of over 10 million developing embryos of damselfish, a common reef fish, at Lizard Island (GBR), and subsequently took thousands of samples of juvenile fish at the same location a certain time later; this allowed them to estimate the *self-recruitment* rate at the reef, which was found

²¹V. Lukoschek, Research Seminar, Sept 2013, James Cook University

²²An otolith is an ear bone.

to be in the region of 15-60%. Subsequent work focused on different species of reef fishes (see Jones et al. 2005).

In general, artificial tagging methods are only applied for reef fish, as invertebrates tend to be harder to tag (Burgess et al. 2014). Both methods are very resource-intensive however, and become increasingly so as the size and complexity of the study region increases. As such they have been mainly used to estimate self-recruitment rates (s.g. see Jones et al. (1999) and Jones et al. (2005) for reef fish larvae, or Becker et al. (2007) for invertebrate larvae) rather than to quantify connectivity between different locations. This latter approach has only been rarely attempted, and over a limited geographic range (e.g. Carson et al. (2010) looked at connectivity in mussel populations off a section of the Californian coastline).

2.2.4.4 Numerical modelling

Numerical biophysical modelling has been increasingly used to estimate marine larval dispersal in different parts of the world (Miller 2007; Werner et al. 2007). In contrast to empirical methods, most models focus only on the larval dispersal process, which is driven by oceanographic conditions and larval biology, two factors which can be effectively modelled and to some extent independently validated using observed oceanographic data or laboratory experiments. These models rarely account for pre- and post-dispersal processes, as the parameters needed to incorporate these into models are poorly known. As a result, it is very challenging to accurately validate the dispersal patterns predicted by such models using the empirical methods described above (Botsford et al. 2009b; Burgess et al. 2014), though see Sponaugle et al. (2012) for an example of such a comparison for damselfish.

This limitation notwithstanding, biophysical models of larval dispersal have gained considerably in importance and number over the past decade. Some examples of the most commonly used dispersal models include the Connectivity Modelling System (CMS) of Paris et al. (2013), which reads hydrodynamic data in standard gridded format (NetCDF) and simulates larval transport using an Individual Based Model (IBM) approach, with an extensive list of optional biological behaviours which can be activated such as active horizontal and/or vertical swimming based on various possible cues (e.g. tidal, age-related, diel), time-varying buoyancy, and mortality. Another similar model is Ichthyop (Lett et al. 2008), which reads hydrodynamic data from a choice of 4 standard structured-grid community ocean models, and uses a similar IBM approach to model larval dispersal, with buoyancy, growth and swimming all potentially incorporated. The LTRANS model of North et al. (2013) adopts a similar approach, reading hydrodynamic data from a widely used community ocean model to drive an IBM which includes larval mortality, swimming and settlement behaviour.

These models were originally developed to simulate larval transport for different species (CMS: fish larvae, Ichthyop: anchovy eggs/larvae, LTRANS: oyster larvae) in different parts of the world (CMS: Caribbean Sea, Ichthyop: Southern Benguela upwelling system (South Africa), LTRANS: Chesapeake Bay (USA)), though they have all since been generalised and used to model different species in various parts of the world. Models are generally either driven by publicly available current fields from global or regional reanalysis products (e.g. Kool and Nichol 2015; Kool et al. 2011) or, more often, coupled to a specific hydrodynamic model, typically when a higher spatial or temporal resolution is required (e.g. Andrello et al. 2014; Golbuu et al. 2012; Paris et al. 2007; Radford et al. 2014).

Since most publicly available reanalysis products have a relatively coarse temporal resolution (e.g. 24 hours for HYCOM current fields), the latter solution is generally necessary in areas with significant circulation processes with a period of less than 24 hours, e.g. tides. Very few of these models have been applied in an area as topographically complex as the GBR, and their coupling to structured grid models prohibits the use of the intrinsically multi-scale modelling approach allowed by unstructured mesh models²³.

Despite the sometimes complex larval behaviour traits included in certain models, the resolution of the hydrodynamic models used can vary considerably. The impact of using a hydrodynamic model with very coarse spatial or temporal resolution has not received much attention, even though it has been shown that excluding small scale features can lead to missing ecologically important flow features (Crowder and Diplas 2000), and significantly mis-representing dispersal of larvae (Nickols et al. 2012). The sensitivity of predictions to model resolution should be the focus of future study, given how many studies make use of such models, and how little attention many marine biologists and ecologists give to it. Indeed, some articles do not even explicitly mention the resolution of the model used (e.g. Andreello et al. 2014; Kool et al. 2011), much less the sensitivity of their results to model resolution. Typically the resolution employed is in the range of 1-2 km for regional studies, but this can vary considerably based on the size of the study area. Table 2.2 reports the spatial resolutions of a selection of recent studies using biophysical modelling to simulate larval dispersal; resolution varies from around 10 km for large-scale studies to 200 m for small-scale simulations (40 x 45 km) using structured grids. Likewise, a small-scale study using an unstructured grid achieved a maximal resolution of a only 40 m, however the use of unstructured grid models remains very rare in this field, and no known studies have used unstructured grid models to simulate larval dispersal in the GBR, other than SLIM. Generally speaking, the model resolution employed was also a function of the study area, since areas with a simpler bathymetry may not require as high a resolution as more topographically complex areas.

Using hydrodynamic models with coarse spatial resolutions has led some studies to make very gross ad hoc approximations in the particle-tracking module to attempt to compensate for the shortcomings of the hydrodynamic forcings. For instance Hock et al. (2014) arbitrarily reduced the pre-competence time of the *Acanthaster planci* modelled from 9 days to 1 day to compensate for the fact that the model was thought to over-predict the strength of currents, as well as increasing the size of the reefs in the domain by 1 km (buffering) to account for the trapping effects of eddies in the wakes of reefs, seemingly without any calibration. The coarseness of the model grid (4 x 4 km resolution) would nonetheless have led to most reefs being entirely missed from the bathymetry even with this 1 km buffer.

Likewise, a significant number of modelling studies have used hydrodynamic forcings with daily temporal resolution (i.e. one output per day), for instance the study of Andreello et al. (2014) on connectivity in the Mediterranean Sea and the studies of Kool et al. (2011) and Kool and Nichol (2015) on larval dispersal in the Indo-West Pacific Ocean and around Australia, respectively. By not explicitly resolving any hydrodynamic process

²³Of the most well-known open source larval dispersal models, only the CMS model of Paris et al. (2013) appears to allow for the possibility a coupling with an unstructured mesh hydrodynamic model, but it also necessitates the projection of hydrodynamic data onto a structured grid, leading either to a loss in model resolution (if the grid resolution is greater than the smallest element), or to huge file sizes and significant increases in run time from reading the hydrodynamic data, (if the structured grid resolution is made equal to the size of the smallest unstructured element). Such a coupling therefore appears highly inefficient.

Study	Spatial resolution	Temporal resolution	Hydrodynamic model (2D/3D)	Study region
Andreello et al. (2014)	9–12 km	24 hrs	NEMOMED (3D)	Mediterranean Sea
Kool et al. (2011)	9.5 km	24 hrs	HYCOM Reanalysis (N/A)	Indo-West Pacific Ocean
Lacroix et al. (2013)	5.6x4.6 km	10 mins	COHERENS (3D)	Central & southern North Sea
Nilsson Jacobi et al. (2012)	3.7 km	1 hr	RCO (3D)	Baltic Sea (1000x250 km)
Paris et al. (2007)	2–6 km	24 hrs	ROMS (3D)	Western Caribbean
Pujolar et al. (2013)	2.2 km	N/A	AFS (3D)	Adriatic Sea
Radford et al. (2014)	0.5–1 km	N/A	GCOM3D (3D)	NW Australian Shelf
Tay et al. (2012)	*40–675 m	N/A	MIKE21 (2D)	Singapore Southern Islands (ca. 120x200km)
Watson et al. (2010)	1–20 km (nested)	N/A	ROMS (2D)	Southern California Bight (ca. 385x220 km)
Burgess et al. (2007)	300–750 m	N/A	3DD (3D)	Capricorn-Bunker GBR (40x45 km)
Hock et al. (2014)	4 km	1 hr	SHOC/Connie2 (3D)	Entire GBR (2000x200 km)
James et al. (2002)	1.8 km	30 mins	Bode and Mason (1994), (2D)	Central GBR (ca. 550x150 km)
Kool and Nichol (2015)	9.5 km	24 hrs	HYCOM Reanalysis (N/A)	Entire Australian coastal ocean
Thomas et al. (2015)	0.2–5 km	25 mins	SLIM (2D)	Central GBR (ca. 550x150 km)
Wolanski and Kingsford (2014)	200–750 m	N/A	3DD (3D)	Capricorn-Bunker GBR (40x45 km)

Table 2.2: Non-exhaustive round-up of some recent studies on larval dispersal using biophysical modelling around the world (top) and in the Great Barrier Reef (bottom). Temporal resolution refers to the resolution of the hydrodynamic data used for larval dispersal simulations. N/A indicates information was not reported. Asterisk (*) indicates the use of an unstructured mesh model.

with a period of under 24 hrs, such studies may provide an inaccurate representation of larval dispersal, particularly in the GBR where tidal currents often dominate, as discussed in §2.1.1.

Some studies do not explicitly include a model validation for the study region (e.g. comparison of predicted currents, elevation or concentration field with observed data), and as such are unable to quantify either the uncertainty inherent in the models due to factors such as resolution limits, quality of forcing data, parameterisations or physical processes missing from the models (e.g. waves), or the skill of their model in being able to recreate realistic current fields.

Whilst numerical modelling studies of larval dispersal are potentially very powerful in the level of detail they can provide, there are therefore a certain number of limitations to this method. The first is that they do not account for pre- and post-settlement processes, and by consequence cannot be easily validated using empirical data. The second is that the quality of the predictions of the process they *do* simulate, larval dispersal, is heavily dependent on the accuracy of the hydrodynamic and biological models, both of which are sometimes overlooked in such studies. Indeed, managers using such predictions may first need to consider whether the model resolution (temporal and spatial) is sufficient to capture the major circulation features susceptible to affect larval dispersal

(which, for the GBR, are discussed in §2.1), as well as whether the model has been validated with observed oceanographic data from the study region.

2.2.5 Using connectivity estimates to measure population persistence

The ultimate aim of most marine conservation efforts is to maintain or increase the persistence of a given population or network of populations (Blowes and Connolly 2012; Botsford et al. 2009a; Burgess et al. 2014). As such, most research into marine population connectivity is ultimately concerned with quantifying the persistence of the populations studied. Many studies only focus on one or more aspects which affect population persistence (e.g. larval dispersal) due to the difficulty of studying the entire set of factors affecting it. Nonetheless, it is crucial to understand which factors make a population persistent in order to be able to produce the most useful results possible for reef managers and conservationists.

A population is persistent if, on average, each adult replaces itself during its lifetime. For a closed population, with no connectivity, this is a simple concept: each adult must produce at least one offspring which lives long enough to reproduce. For an open population with incoming and outgoing connectivity, a population can persist either through “self persistence”, whereby each adult replaces itself as in a closed population, or through “network persistence”, whereby closed loops in its connectivity network bring enough net imports to maintain the population. Often, persistence occurs through a combination of these two modes (Burgess et al. 2014).

Self persistence for coral depends fundamentally on the ability of the population to produce enough larvae, and for these larvae to be locally retained on their natal reef. Correspondingly, two key metrics are needed to estimate a population’s self persistence: its Lifetime Egg Production (i.e. LEP), which measures the fecundity of the population, and its *local retention*, which measures the proportion of larvae produced which are locally retained, i.e. which settle on their natal reef. As such, local retention is a key indicator of self-persistence, and is of high interest to reef managers (Botsford et al. 2009b; Burgess et al. 2014); it is also very hard to measure empirically, yet straightforward to estimate using numerical biophysical models. Most empirical studies (and many biophysical studies) have instead focused on *self recruitment* as an indicator of the tendency of larvae to disperse²⁴: this measures the proportion of recruits to a population which were spawned by that population, and is much easier to measure. Unfortunately however it tells us nothing about the persistence of the population, and is thus of limited ecological interest (Burgess et al. 2014).

Estimating the persistence of coral sub-populations in a network additionally requires knowledge of the connectivity network, as well as the spatial variability of the LEP, since some reefs may have more productive coral populations than others (for instance reefs in MPAs may be expected to be healthier and thus have a higher fecundity). Whilst this latter quantity is hard to empirically measure, attempts have been made to estimate the LEP needed for a given fish population to persist (the so-called Critical Replacement Threshold, CRT), and therefore to infer a range of possible actual values of the LEP in a persistent population (see Botsford et al. 2009a)

²⁴Burgess et al. (2014) found that out of 21 studies reviewed which used empirical methods to estimate marine population connectivity, 19 reported self-recruitment, 4 reported a connectivity matrix, and only 2 reported local retention.

Estimates of LEP for a given population could be hypothetically used in conjunction with a biophysical dispersal model to estimate the self-persistence of a given population. Doing so for an entire network of connected populations is more challenging however, as it requires knowledge of the spatial variation of LEP. However, this would be extremely useful as, used in conjunction with a biophysical model, it would allow an estimate to be made of the network persistence of a connected coral reef system. This could be of great usefulness for reef managers, as it would allow them to understand how resilient the entire system, and each reef in it, would be to any kind of perturbation.

2.2.6 Implications for marine management

As mentioned previously, the general aim of marine conservation planning is to maintain the persistence of populations, and if possible to increase the resilience of the ecosystem (McLeod et al. 2012). The scientific consensus in recent years is converging towards promoting greater use of Marine Protected Areas (MPAs) as tools to protect population persistence and increase resilience in vulnerable ecosystems (Botsford et al. 2009a; Gaines et al. 2010; Lester et al. 2009). MPAs are marine areas which are protected from destructive anthropogenic activities, such as resource extraction or fishing. MPAs have been found to increase the diversity, density, biomass, body size and reproductive potential of coral reef fishes within their boundaries (Green et al. 2014; Lester et al. 2009), as well as in the surrounding areas through a greater export of larvae, juveniles and adults to nearby unprotected areas (i.e. *overspill*) (Green et al. 2014; Harrison et al. 2012). As such, the potential effectiveness of MPAs depends critically on connectivity (Almany et al. 2009); information from biophysical models of larval dispersal can therefore be useful in optimising their placement to maximise their positive impact on the ecosystem.

Whilst MPAs do not provide a physical refuge for coral, insofar as they cannot protect against water temperature increases, acidification, bleaching or pollution (Jones et al. 2007), they can significantly reduce some sources of biological stress, for instance damage from tourism or from overfishing, which has been found to lead to decline in coral populations, and to increased macroalgae growth to the detriment of coral (Hughes et al. 2010; Mumby and Harborne 2010). As such, populations inside MPAs are likely to have higher reproduction and lower mortality (and therefore higher LEP) than those outside (Burgess et al. 2014), and therefore contain larger, healthier populations producing more larvae. Due to their small size, larvae leaving an MPA can generally disperse away through unprotected areas without any increased risk (Gaines et al. 2010).

Placing a network of inter-connected MPAs is thought to produce greater ecosystem benefits than placing a single large MPA, partly through increased *spillover*, and partly due to increased resilience of the MPAs themselves (Almany et al. 2009; Drew and Barber 2012; Gaines et al. 2010). This is because inter-connected MPAs can re-populate each other through larval dispersal following major disturbances such as bleaching or cyclones. It is therefore optimal to have MPA networks with multiple, strong connections between each other (Christie et al. 2010). A further benefit of placing multiple MPAs is that it may reduce the impact of placement errors of individual MPAs (Drew and Barber 2012).

Numerical biophysical models can potentially provide information which could be used to optimise MPA placement. In particular, models can estimate the capacity of every reef to export larvae to other reefs (their “performance” as exporters), so that MPAs can be used to protect the reefs which export the most larvae (the major “source” habi-

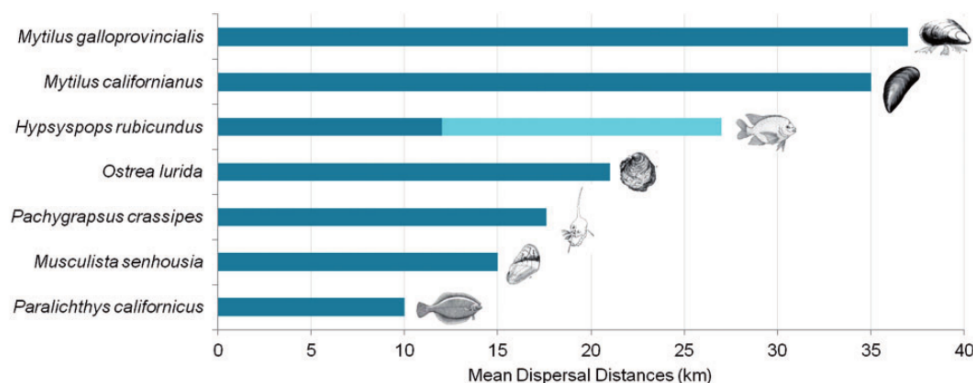


Figure 2.7: Graph showing mean dispersal distances for 7 marine species inhabiting a 100km stretch of coastal ocean off the coastline of California. Light blue indicates the average extra distance travelled by *Hypsypops rubicundus* in 2009 as opposed to 2008. This figure shows the large differences in average dispersal distance between common species inhabiting the same ecosystem. This highlights the issues with using estimates of dispersal distance to inform MPA placement: which species' dispersal distance should be used as a guideline? Image reproduced from López-Duarte et al. (2012).

tats), thus maximising spillover benefits, whilst opening up certain “sink” habitats (i.e. areas importing large numbers of larvae, and therefore more persistent) for fishing (López-Duarte et al. 2012). Models can also estimate the typical dispersal distances of larvae from every reef, so that MPAs can be placed close enough together that connectivity can occur between them. The use of numerical models to inform MPA placement has been trialled by White et al. (2013), who used a biophysical model to estimate the relative effectiveness of a number of different MPA network proposals in California. Whilst not yet commonplace, such studies may increase in number in the coming years as numerical models become more accurate and more rigorously validated, and gain widespread acceptance amongst ecologists and marine planners.

A significant challenge is posed by how to deal with multiple species. Whilst integrating connectivity estimates into MPA placement sounds simple for a single species, most marine ecosystems in the real world are composed of many species with vastly different dispersal potentials inhabiting the same habitats (see Figure 2.7): indeed one species' major source habitat may be another species' major sink habitat. Only by knowing the connectivity patterns of all of the major species we wish to protect, can we then identify all the source and sink populations in common amongst all the species, and protect them as appropriate (López-Duarte et al. 2012). Achieving such a detailed knowledge is impossible using the empirical methods available to us, and is still extremely challenging to estimate using numerical biophysical models, as they would need to simulate the behavioural traits of all of the major functional groups, which is no mean feat. This is a challenge which has so far gone untackled.

CHAPTER 3

BUILDING A BIOPHYSICAL MODEL OF LARVAL DISPERSAL IN THE GBR

Summary

In this chapter I will present a biophysical model capable of simulating larval dispersal in the GBR, and generating a connectivity matrix encapsulating reef-to-reef connectivity information. As discussed in previous chapters, there are a number of requirements which such a model should fulfil: it should be able to simulate realistic large-scale circulation in the region, it should be able to realistically resolve small-scale flow (and larval dispersal) down to the scale of reefs and it must be able to simulate the transport of coral larvae whilst accounting for life-history traits such as mortality and competence acquisition and loss. The chapter which follows will describe a model capable of fulfilling these requirements to a greater extent than any previous model of larval dispersal in the GBR. This chapter lays the basis for the three following chapters, which will present different applications of this biophysical model.

3.1 Overview of the biophysical model

The numerical model used to simulate larval dispersal is composed of two parts: at its core is the hydrodynamic model, which calculates the depth-averaged water velocity and elevation in the GBR, and coupled to this there is the Lagrangian model, which takes these fields as input to calculate the trajectories of “virtual larvae” released in domain, whilst also accounting for life-history traits of these larvae. Taken together, these two parts form a biophysical model of larval dispersal.

The biophysical model presented in this chapter builds on the work of previous research efforts by various members of the SLIM team to develop the capabilities of the underlying hydrodynamic model (e.g. Lambrechts et al. 2008; Legrand et al. 2006; Seny et al. 2012). In many aspects, the hydrodynamic part of the model presented in this study follows the approach of Lambrechts et al. (2008), who used an earlier version of SLIM to simulate the hydrodynamics on the GBR shelf using an unstructured mesh for the first time. The model presented in this chapter builds on this one, refining the forcings where needed, extensively calibrating and validating the model to ensure the predicted currents are realistic during the periods of coral spawning, and adding a Lagrangian particle-tracking module capable of simulating the main life-history traits of coral and fish larvae: mortality, competence loss/acquisition, directed horizontal swimming and settlement onto a reef, in as realistic a way as possible.

The Lagrangian model is run offline from the hydrodynamic model. This means that the hydrodynamic model is first run on its own, and the outputs it generates (water elevation and velocity) are saved to disk with a temporal resolution of 25 minutes. Subsequently, once the hydrodynamic simulation is finished, the Lagrangian model is run, reading these hydrodynamic outputs as inputs in order to calculate the trajectories of virtual larvae through the domain.

What follows is a description of how the model was set up and what motivated these choices, including how the meshes were generated, which parameters and forcings were used and why they were chosen, and how the hydrodynamic and Lagrangian models were both tested. I will first describe the hydrodynamic model, and then move on to describe the Lagrangian model.

3.2 Hydrodynamic model

3.2.1 Model equations and parameterisations

The hydrodynamic model employed was the Second-generation Louvain-la-neuve Ice-ocean Model (**SLIM**¹), a discontinuous Galerkin finite element model which resolves the water elevation and depth-integrated velocity by solving the shallow water equations:

$$\frac{\partial \eta}{\partial t} + \nabla \cdot (H\mathbf{u}) = 0 \quad (3.1)$$

$$\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} = -f\mathbf{e}_z \times \mathbf{u} - g\nabla \eta - C_{BD}|\mathbf{u}|\mathbf{u} + \frac{\boldsymbol{\tau}}{\rho H} + \frac{1}{H}\nabla \cdot [H\nu(\nabla \mathbf{u})] \quad (3.2)$$

where H is the water column depth in m (defined as $H = h + \eta$ where h is a reference depth level and η is the variation from this depth), f is the Coriolis factor, $\mathbf{e}_z$ is a unit

¹More information and publications on SLIM can be found at the project website: www.climate.be/slim

vector pointing vertically upwards, C_{BD} is the bottom stress coefficient, $\boldsymbol{\tau}$ is the surface wind stress, g is the gravitational acceleration, ρ is the water density and ν is the horizontal eddy viscosity. The depth-integrated water velocity is $\mathbf{u}$.

The bottom stress coefficient is calculated as $C_{BD} = \frac{g}{C^2 H}$, where $C = \frac{H^{1/6}}{n}$ is known as the Chezy coefficient, and n is the Manning coefficient. The Manning coefficient was taken to be $n = 2.5 \times 10^{-2} \text{ m}^{1/3} \text{ s}^{-1}$, a value which is typical for sandy or muddy sea beds (e.g. see de Brye et al. 2010), and was found to be applicable in the GBR by King and Wolanski (1996). A number of calibration simulations were run using a range of values of the Manning coefficient from $n = 1.6 \times 10^{-2} \text{ m}^{1/3} \text{ s}^{-1}$ (which was the lowest value allowed by the model without parts of the domain emerging from the water) to $n = 5 \times 10^{-2} \text{ m}^{1/3} \text{ s}^{-1}$, and the value chosen was found to result in the best agreement of tidal current phase and amplitude with observation at various points on the shelf. Furthermore, as reefs are known to have a particularly rough surface, this value was multiplied by 10 over reefs, following the approach of Andutta et al. (2011). Empirical measurements of reef roughness also report an increase in the bottom stress corresponding to an increase in the Manning coefficient of roughly an order of magnitude compared to an open shelf (Lugo-Fernández et al. 1998).

The positions of shallow reefs in the GBR were obtained using a shapefile layer provided by the Great Barrier Reef Marine Park Authority (GBRMPA 2007). The bathymetry data for the entire GBR shelf were extracted from the Project 3DGBR dataset (Beaman 2010), which collates data from a number of different sources (LiDaR, ship-based single-beam and multi-beam echosounders, satellites) to give the most accurately known bathymetry at each point in the GBR, interpolated onto a grid of 100 m resolution. Due to the fact that some parts of the GBR are more difficult to access than others, the actual precision of the data is not the same everywhere, with greater accuracy achieved in areas which are easier to access. When the bathymetry data were read into the hydrodynamic model, the minimum depth was set to $h = 5 \text{ m}$ in order to ensure that the entire domain was underwater at all times, as wetting/drying was not enabled in the hydrodynamic model.

The surface wind stress exerted by the atmosphere on the sea is calculated as follows:

$$\boldsymbol{\tau} = \rho_{\text{air}} C_D |\mathbf{u}_{10}| \mathbf{u}_{10}, \quad (3.3)$$

where ρ_{air} is the air density, C_D is the drag coefficient and $\mathbf{u}_{10}$ is the wind speed at 10 metres above the sea surface, given in m s^{-1} (Cushman-Roisin and Beckers 2011). In order account for the fact that stronger winds cause a rougher sea surface and therefore increase the value of C_D , the drag coefficient is often parameterised using a formula which includes the wind speed term. The parameterisation used in the model is the one of Smith and Banke (1975):

$$C_D = 0.001(\alpha + \beta |\mathbf{u}_{10}|), \quad (3.4)$$

with the two coefficients $\alpha = 0.63$ and $\beta = 0.066 \text{ s m}^{-1}$. This parameterisation is applicable for wind speeds in the range commonly found over the GBR (3–21 m s^{-1} - see Geenaert (1987)).

Smagorinsky's parameterisation was used to account for the effect of unresolved turbulent features, with horizontal eddy viscosity, ν , dependent on the local mesh element size, Δ , and the flow structure (Smagorinsky 1963):

$$v = (C_S \Delta)^2 \sqrt{2 \left(\frac{\partial u}{\partial x} \right)^2 + 2 \left(\frac{\partial v}{\partial y} \right)^2 + \left(\frac{\partial u}{\partial y} + \frac{\partial v}{\partial x} \right)^2}, \quad (3.5)$$

where (x, y) are perpendicular horizontal axes, (u, v) represent the corresponding depth-integrated water velocities, and C_S is a constant, taken as $C_S = 0.1$ following Lambrechts et al. (2008).

The time-stepping method used was an explicit second order Runge-Kutta scheme with multi-rate time steps, so that large elements had larger time steps than the smaller ones. The use of multi-rate time-stepping decreased the run time of simulations roughly by a factor of two to three, and as the method also parallelises effectively, the simulations could be run on many CPUs to further decrease the runtime. Details about the time-stepping scheme used can be found in Seny et al. (2012). For the spatial discretisation, a discontinuous Galerkin finite element scheme was used with first order basis functions, following the approach of (de Brye et al. 2010).

3.2.2 Unstructured mesh

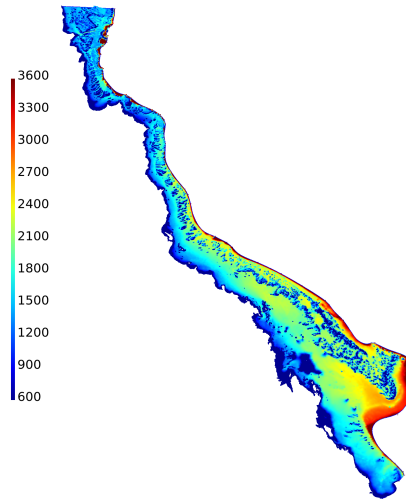
SLIM resolves flow on an unstructured mesh, an approach which allows the model resolution to be varied in space. The aim was therefore to increase the resolution in areas where small-scale flow features are thought to be important, whilst keeping it coarser in areas where flow is expected to be more uniform, effectively allowing computational resources to be directed to where they are most needed.

The meshes used in this study were generated using the open source meshing software Gmsh (Geuzaine and Remacle 2009), and the local element size was made to depend on:

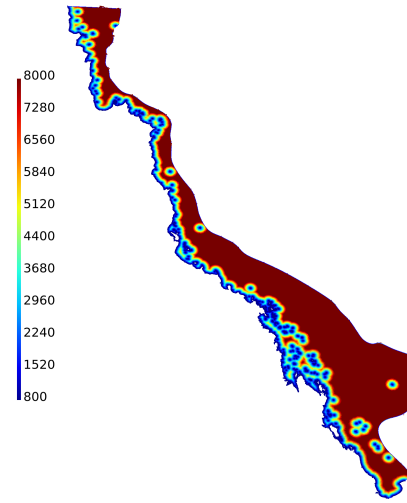
- a) the square root of the water depth
- b) the distance to the nearest coastline
- c) the distance to the nearest reef
- d) the distance to an arbitrarily defined point

This was done by defining four continuous fields corresponding to each of these factors (as shown in Figure 3.1), and then instructing Gmsh to make the local element size depend on the value of the field which was smallest at every given point in the domain - see Figures 3.1 and 3.2 for an example.

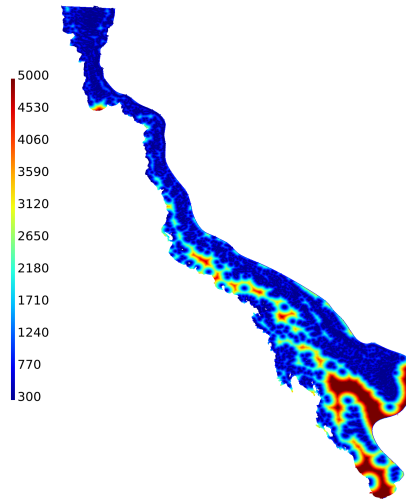
Factor a) was imposed to make the size of each element proportional to the speed of surface gravity waves propagating through it (i.e. the most rapidly propagating waves in the simulation), meaning that gravity waves would traverse the same fraction of any element in a given time Δt . This results in an optimal mesh for the Courant-Friedrichs-Lewy (CFL) condition, as the minimum time-step needed for every element should be similar. Factors b) and c) result in the mesh being more refined in areas where small-scale circulation features are known to be important, i.e. close to reefs and islands. Reef topography also needs to be resolved particularly well since larval dispersal predominantly occurs on and around them. Finally, factor d) was imposed so that the mesh could be further refined in the region being studied, whilst being kept coarse in areas outside the region of interest.



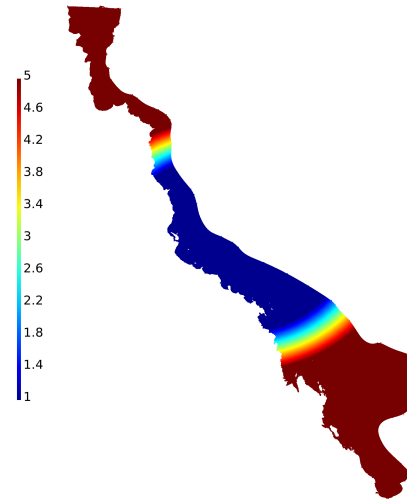
(a) Field value proportional to square root of the bathymetry



(b) Field value proportional to distance from coastlines.



(c) Field value proportional to distance from reefs



(d) Field value proportional to distance from a specified point, in this case in the central GBR.

Figure 3.1: Examples of fields used to generate the model mesh. The meshing software takes the smallest value of the three fields 3.1(a) to 3.1(c) at every point, and multiplies this by field 3.1(d) to get the local element size. In this example, the mesh would be more refined in the central part of the GBR due to the shape of field d). The resulting mesh, shown in Figure 3.2, was used in the study presented in Chapter 5.

The meshes used spanned the entire shelf, despite the fact that the regions under study were generally limited to areas covering only one third to half of the GBR. This is because the forcings applied at the boundaries, and in particular the tidal forcing, are less accurate on the shelf than at the shelf break.

In order to assess the impact of mesh resolution on model accuracy, a number of simulations were carried with exactly the same parameters, but where the mesh reso-

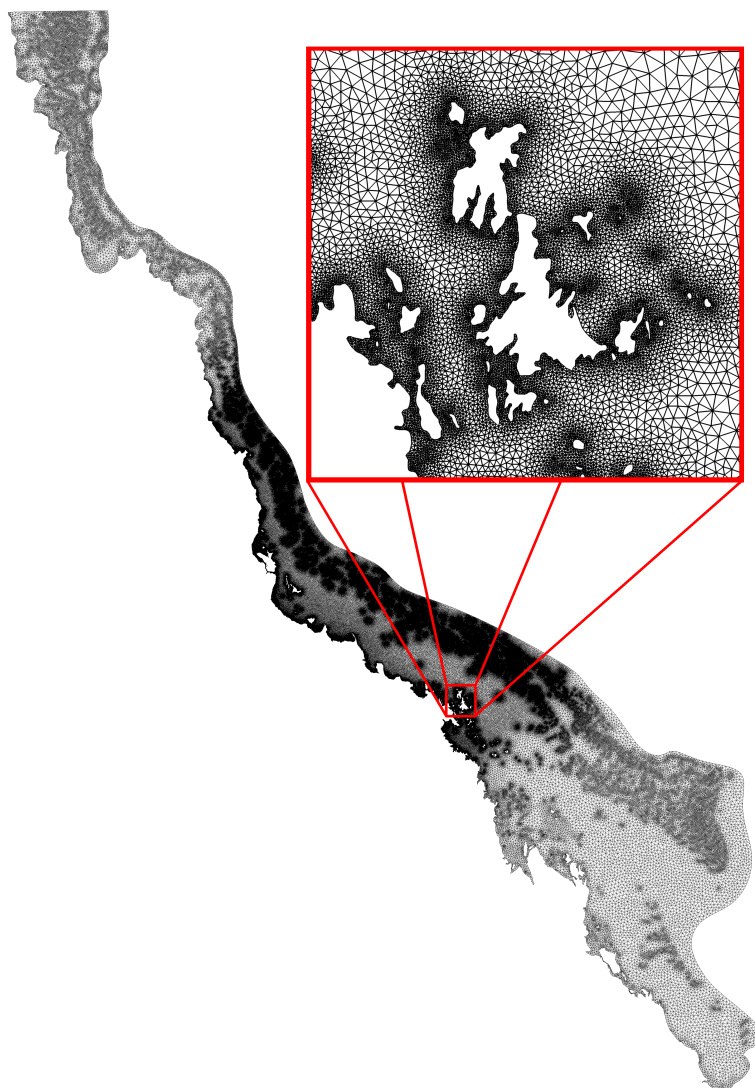


Figure 3.2: Example of a mesh of the central GBR containing about 650,000 elements, with a minimum element size of 200 m and a maximum of around 5 km. This mesh was generated using the fields shown in Figure 3.1.

lution was varied, such that the minimum element size was 2 km, 1 km, 640 m, 400 m and 200 m, respectively. The only forcings applied were a constant residual circulation due to water exchange with the Coral Sea, and the M2 tidal component, which was subsequently filtered out in the results, so the residual circulation in the model eventually reached a stable state. The currents predicted by each of these simulations at 9 given sites in the GBR (most of them in open-sea areas) were then compared to each other. Figure 3.3 reports the mean current speeds at these sites for the 4 finest meshes. The size of the currents varied with mesh resolution, although these differences were not major between 640 m and 400 m, and became much smaller between 400 m and 200 m resolutions. This result tallies with the finding of Black et al. (1991), who found that a 400 m resolution was sufficient to model the important flow features around a reef (discussed in §2.1.5). As a result, a minimum resolution of 2-300 m was used for all of the simulations presented in this thesis.

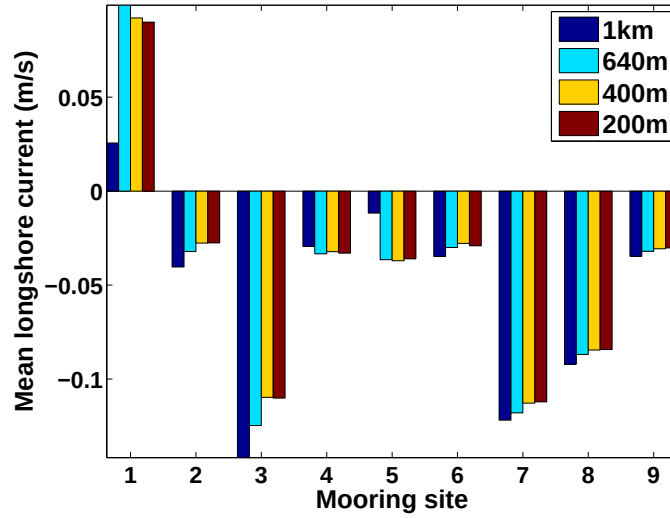


Figure 3.3: Bar chart showing the mean longshore currents at the end of the simulation at 9 sites throughout the GBR, as predicted by simulations using 4 different mesh sizes. Positive values correspond to the northward longshore axis, and negative to southward longshore. The maximum resolution of the mesh used in each simulation is shown in the legend. All parameters were the same in every simulation, the only difference was the maximum resolution of the mesh used. The simulations were forced only with residual circulation at the boundaries due to Coral Sea water exchange, and the M2 component of the tidal current, which was filtered out in post-processing; as such the currents shown are the steady residual currents.

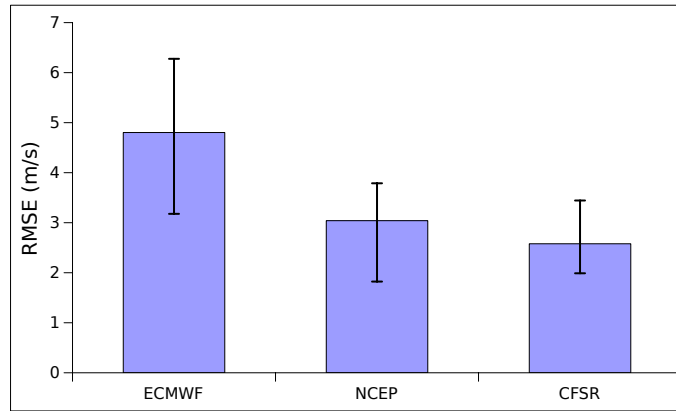


Figure 3.4: Root Mean Square Error (RMSE) of the wind velocity at 10m predicted by 3 different wind reanalysis datasets (ECMWF, NCEP, CFSR), compared with observation. The RMSE was calculated at 8 sites by first averaging RMSEs of daily wind velocities over 1 year (from 1 Dec. 2008 to 1 Dec. 2009) at each site, and then averaging these year-averaged RMSEs across all 8 sites. The bars show the mean of the RMSEs over all the sites, whilst the error bars show the RMSE at the site with the greatest and smallest RMSE, respectively.

3.2.3 Model forcings

The aim of the hydrodynamic model was to simulate realistic circulation conditions on the GBR shelf. To this end, three separate external forcings were applied to account for the effects of tides, wind and water exchanges with the Coral Sea, corresponding to the three main drivers of circulation in the GBR, as discussed in §2.1.

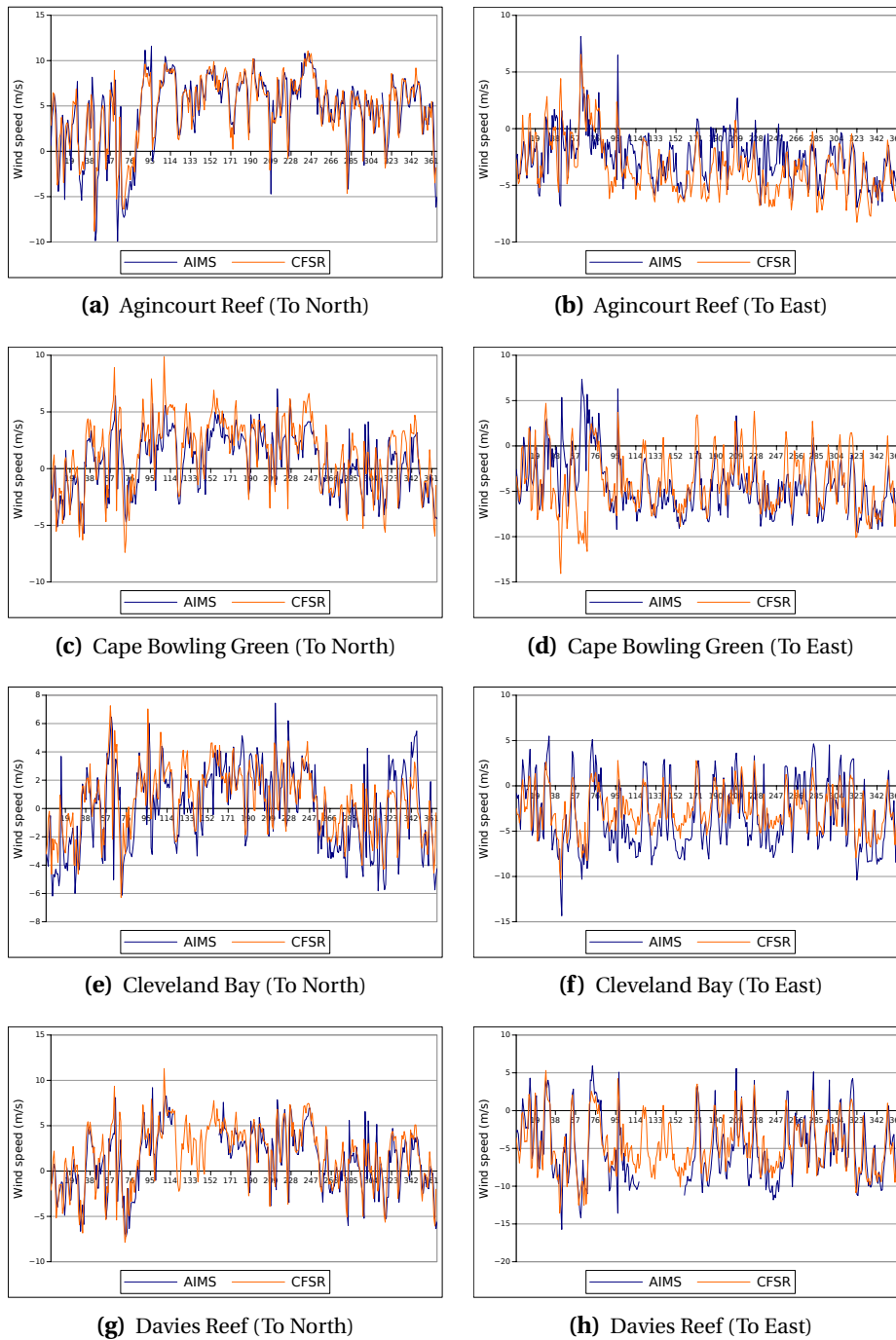


Figure 3.5: Wind speeds at different points in the GBR region from observed data (AIMS) and from the CFSR dataset, part 1/2.

The **tidal** forcing was imposed using the OSU TOPEX/Poseidon Global Inverse Solution dataset (Egbert and Erofeeva 2002), which gives the amplitude and phase of the main tidal components on a $1/4^\circ$ resolution global grid. These were used to reconstruct tidal elevation and velocity, which were imposed at the model boundaries.

In order to impose the **wind stress**, time-series data of the wind speed at 10 m above

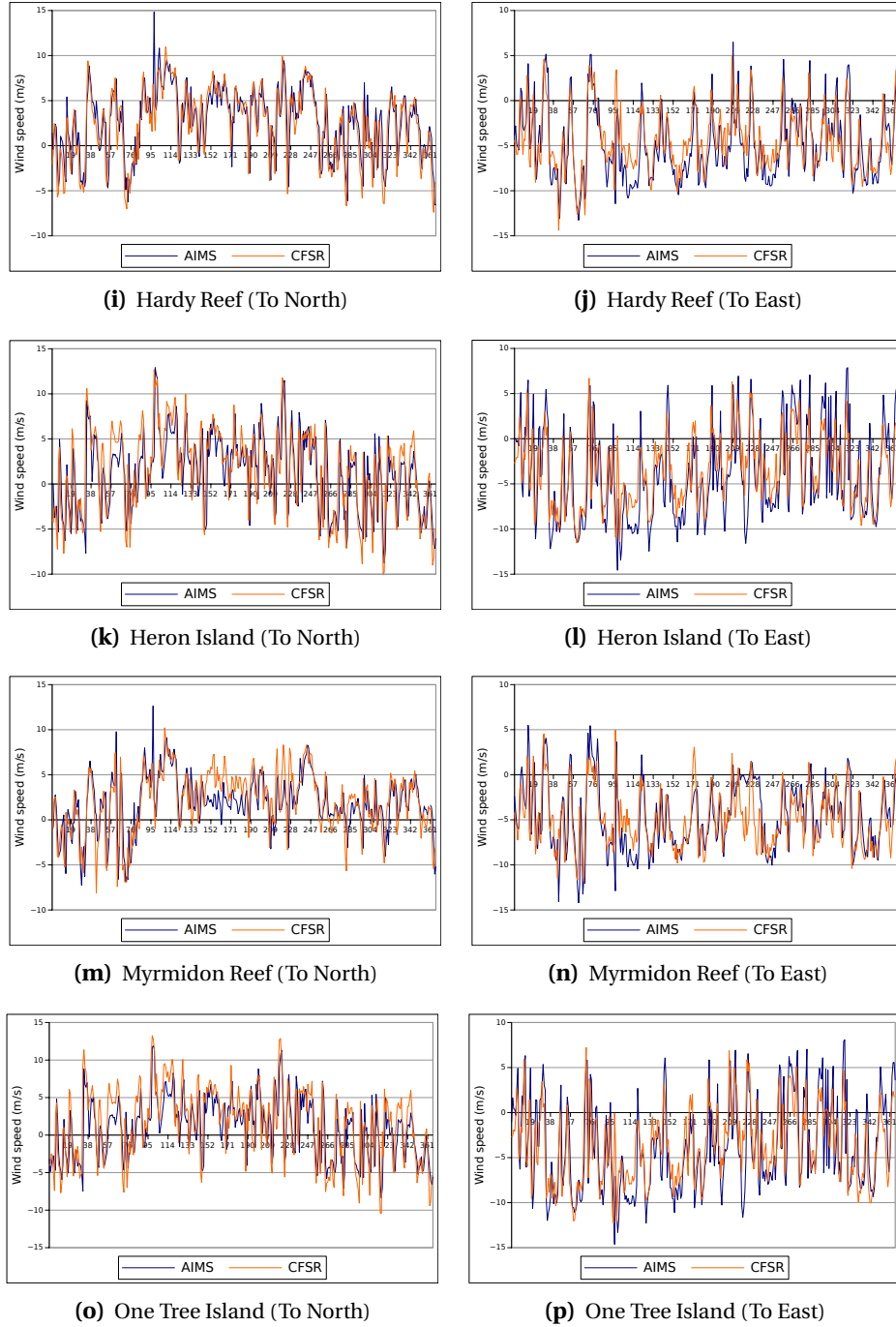


Figure 3.5: Wind speeds at different points in the GBR region from observed data (AIMS) and from the CFSR dataset, part 2/2. The x-axes show time, in days, from 1 Dec 2008.

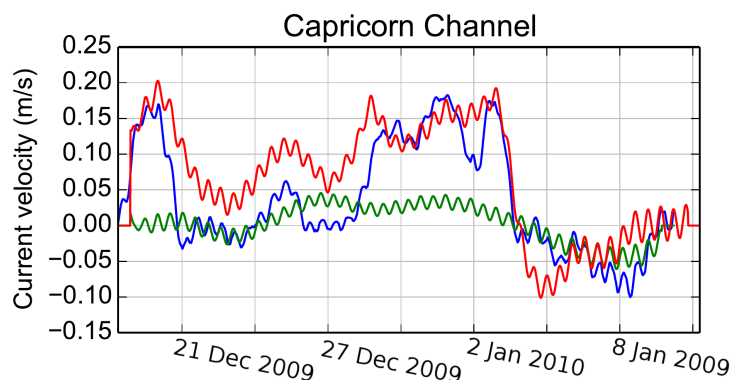


Figure 3.6: Graph showing depth-integrated current at Capricorn Channel mooring site from observed GBROOS data (blue), and as predicted by SLIM simulation without (green) and with (red) the addition of a current at the boundaries corresponding to 2% of local wind speed. This figure shows that not including this additional forcing leads the model to significantly underestimate variability caused by wind-driven currents. A 24-hr running average was applied to filter out most tidal effects. Currents shown are along the East-West axis.

sea surface is needed. Given the importance of the wind in driving the circulation on the GBR shelf (see §2.1.2), the quality of the wind data used is critical in determining the accuracy of the predicted circulation in the region. Initially, the dataset employed was the NCEP/NCAR reanalysis provided by NOAA/OAR/ESRL PSD (Kalnay et al. 1996), which was used to force the model for the study presented in Chapter 4. In order to improve the model accuracy however, I then proceeded to compare the wind speeds reported by this dataset to measured wind speeds at a number of locations in the GBR over a year (1 Dec 2008 to 1 Dec 2009). I additionally considered two other widely used, higher-resolution global reanalysis datasets, and compared them to the NCEP/NCAR dataset and to the observed wind data in order to find which model performed best. The other datasets were the ECMWF ERA-Interim reanalysis product (Dee et al. 2011) and the NCEP Climate Forecast System Reanalysis (CFSR) product (Saha et al. 2014). The observed wind data came from 8 weather stations located at various sites in the GBR for which data was publicly available from the AIMS website (AIMS 2010). Figure 3.4 reports the average Root Mean Square Error (RMSE) of each dataset compared with the observed data. This was obtained by first averaging the RMSE at each site over a whole year, and then obtaining the average of this year-averaged RMSE across all 8 sites. The CFSR dataset was found to give the best fit with the observed data, having both the lowest mean RMSE and the lowest maximum RMSE, followed by the NCEP dataset. The ECMWF dataset was found to perform worst out of the three. The best-performing dataset – the CFSR reanalysis – was found to give a wind field which was either accurate or at least realistic (i.e. within the same range of values as the observed data) at all the sites, as shown in Figure 3.5. This dataset was used to provide the model’s wind forcing in the studies presented in Chapters 5 and 6.

In addition to applying the wind stress over the water surface, it was found necessary to add a current at the boundaries which was a function of the local wind speed. Failure to do so resulted in a significant underestimation of wind-driven current variability in the model (see Figure 3.6). By comparing wind speeds from the CFSR dataset with observed currents from the Great Barrier Reef Ocean Observing System (GBROOS) mooring array (IMOS 2013), it was found that currents were correlated with the wind, with a constant of

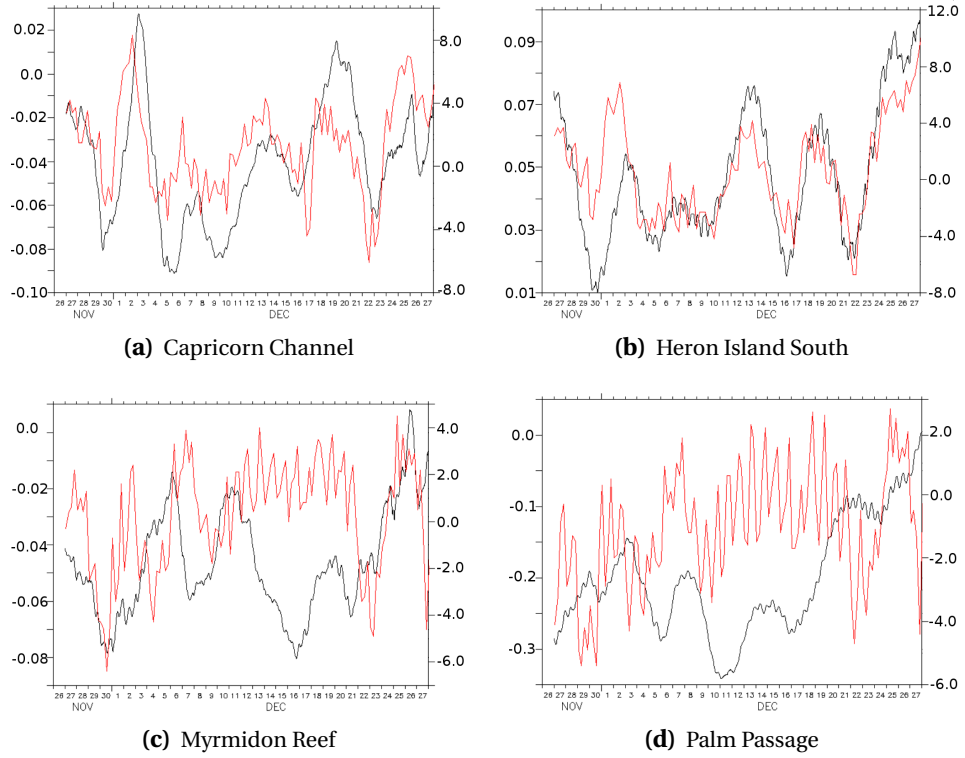


Figure 3.7: Northward velocities of observed depth-averaged currents (black) and CFSR wind (red) at 4 mooring sites at different points on the GBR shelf. The left axis corresponds to water current velocity and the right axis to wind velocity. Units are m/s; negative numbers indicate southward flow. Whilst wind is clearly not the only driver of currents, there is a significant correlation between wind and current velocity, particularly at sites 3.7(a) and 3.7(b). Sites 3.7(c) and 3.7(d), which are both situated close to the zone of strong inflow from the Coral Sea, are more susceptible to also be influenced by other factors, presumably relating to variability in inflow from the Coral Sea.

proportionality of about 2%, meaning that currents were roughly found to be 2% the size of the local wind, as illustrated in Figure 3.7. This value is similar to the slightly larger value of 4% found by Wolanski and Bennett (1983) (see §2.1.2). A range of coefficients of proportionality were applied using the SLIM model, and it was found that the best fit of simulated currents with observed currents from the GBROOS dataset was indeed achieved when wind-driven currents corresponding to 2% of the local wind speed were applied along the open sea boundary. This additional wind-driven current forcing at the boundary was applied for all the simulations presented in Chapters 5 and 6.

The **water exchange with the Coral Sea** was simulated by dividing the domain boundaries into 3 sectors corresponding to the northern, central and southern sections of the boundary (Figure 3.8(a)), and imposing a net water flux entering the domain through the central segment, with corresponding water fluxes leaving the domain through the northern and southern segments. The water velocity at the boundary, $\mathbf{u}_b$, was calculated by dividing the net water flux, Φ (defined by the user), by the integral, along the entire boundary sector, of the water depth, H , multiplied by the scalar product between the unit vector normal to the boundary, $\hat{\mathbf{n}}$, and a user-specified unit vector, $\hat{\mathbf{v}}$, so that:

$$\mathbf{u}_b = \left(\frac{\Phi}{\int_{boundary} H(\hat{\mathbf{v}} \cdot \hat{\mathbf{n}}) dl} \right) \hat{\mathbf{v}}. \quad (3.6)$$

The two variables set by the user are therefore the net flux through the boundary, Φ , which was found by calibrating the model using observed current data, and the direction of this flux, $\hat{\mathbf{v}}$, which was pre-defined for each sector as shown in Figure 3.8. The flow through the boundary is oriented along the axis of $\hat{\mathbf{v}}$, and is greatest along the sections of the boundary which are perpendicular to this axis, whilst it falls to zero along sections where the boundary is parallel to it. As such, when there are boundaries which turn back on themselves, such as the southern open sea boundary in Figure 3.8(a), there can be sections of those boundaries where the water flow is opposite to the direction of the net flux $\hat{\mathbf{v}}$. In the specific case of this southern boundary, the vector $\hat{\mathbf{v}}$ was specified as pointing south-eastwards, so that the net water flux was out of the domain through the Capricorn Channel. However, a small inflow therefore occurred through the upper section of the boundary which runs along the east-south-east axis. The above setup approximates the known patterns of on-shelf circulation discussed in §2.1, and broadly follows the approach of Lambrechts (2011).

The size of the net water flux, Φ , to impose along each segment was found through extensive calibration of the model using observed data from the GBROOS mooring array. Predicted currents were compared to observed currents at the Myrmidon, Capricorn Channel, Lizard Island Shelf and One Tree Island moorings (when available), all three of which are located close to the domain's open sea boundary, as shown in Figure 3.9. This calibration was carried out separately for each spawning season modelled, since the observed Coral Sea inflow could be different from year to year; a very time- and resource-intensive – but necessary – process.

Dividing the boundary into three segments was found to yield acceptable agreement with observed currents in the central GBR. For the southern GBR however the situation was more problematic, particularly for years when there was strong observed outflow through the Capricorn Channel. This was for two main reasons: firstly, imposing a correspondingly strong outflow through the southern domain boundary along the south-eastern axis resulted in the creation of a significant water flux entering the domain through the upper part of the southern boundary, where it is oriented along the east-south-east axis. To counteract this, the southern boundary was split into two, as shown in Figure 3.8(b), and a smaller incoming flux was imposed along the east-south-eastern part of this boundary. Secondly, the strong outflow through the Capricorn Channel boundary generated an unrealistically strong northward current on the Capricorn-Bunker shelf peninsula, as water was effectively “sucked” out of this area from the open boundary. As a result, predicted water speeds at the Heron Island and One Tree Island sites in the Capricorn-Bunker reef group were significantly greater than the observed northward flow in the area. To counteract this, the model's open boundary was further split into 5 segments (shown in Figure 3.8(c)), and an additional east-south-eastward outflow was applied along the open sea boundary with the Capricorn-Bunker peninsula for years in which the simulated flow through the southern boundary was great enough to necessitate it.

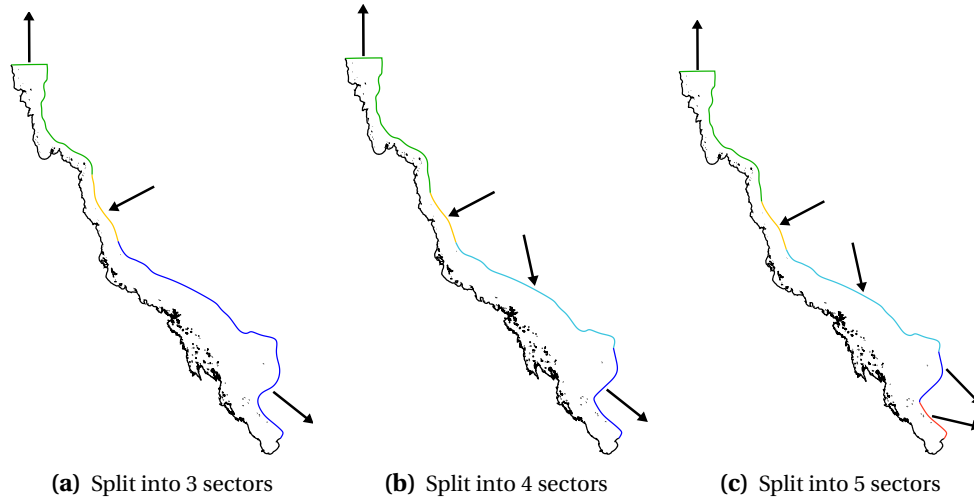


Figure 3.8: Boundaries of the model domain, split into 3, 4 and 5 sectors in Figures 3.8(a)-3.8(c) respectively, with different colours denoting different sectors, and black lines denoting coastlines. The black arrows show the direction of the unit vector $\hat{v}$ in Equation 3.6, which denotes the axis of the imposed water flux. Different values of the water flux were applied along each sector, and these values were re-calibrated for every simulation using observed current data. Note that tidal and wind-driven currents were also imposed in addition to this constant water exchange, so in practice water flow through the boundaries could change direction during the course of the simulation, depending on the strength and direction of these additional currents at every moment in time.

3.2.4 Validation of the hydrodynamics

Time-series data of observed water elevation and currents from the GBROOS dataset were used to validate the hydrodynamics simulated by the model. The positions of the mooring sites is shown in Figure 3.9. Data from the moorings at Elusive Reef and Lizard Island Slope were unusable as these moorings are situated off the continental shelf and thus outside the model domain. For the remaining moorings, data from certain sites were not available for all the periods modelled as some gaps were present in the time-series. As such, the number of usable mooring sites varied from one simulation to the next.

As the model was calibrated and validated separately for each spawning season modelled, the model validations are presented individually in each chapter of this thesis.

3.2.5 Limitations

Model forcing setup

To obtain a realistic water circulation, three different datasets have been used, together, to force the model. This approach was chosen primarily as it gave the best agreement with observed data, and also because it allowed us to see the impact of each forcing (tides, wind, Coral Sea inflow) in shaping circulation patterns. This made it possible to simulate projected circulation in a future scenario, by changing only one of these forcings (Coral Sea inflow) whilst leaving the others unchanged. However, this approach does have its drawbacks. On a practical level, it is very time-consuming, as it requires the user

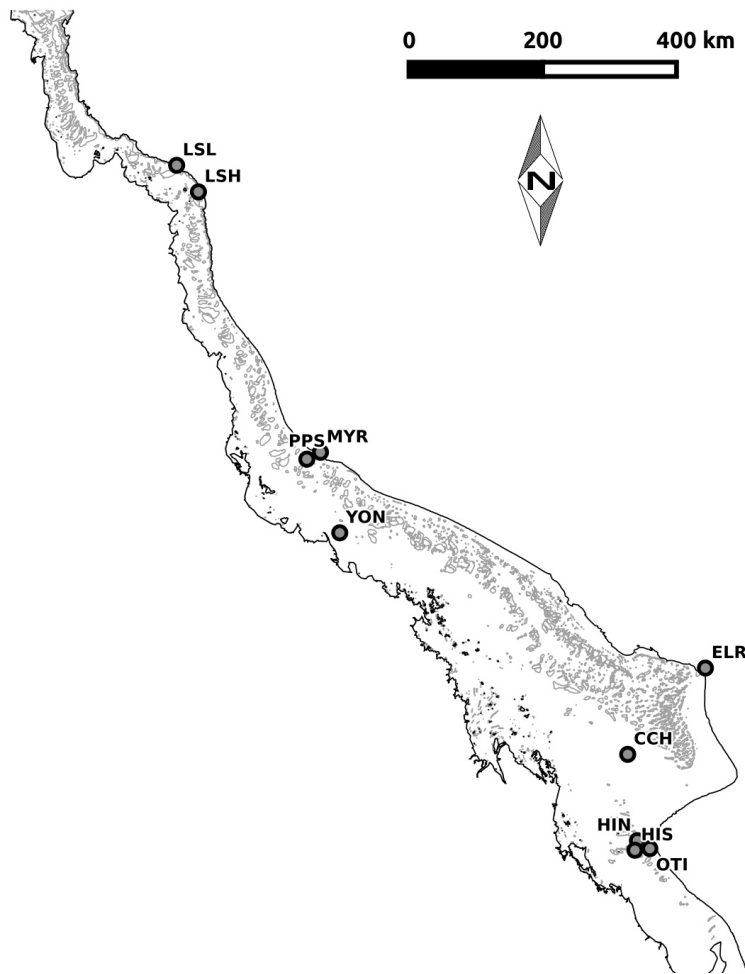


Figure 3.9: Map of the GBR shelf with reefs and islands shown in grey. The thick black line on the left represents the coastline, and the thinner line on the right is the 200 m isobath. The dots indicate the positions of GBROOS mooring sites. LSL: Lizard Island Slope; LSH: Lizard Island Shelf; MYR: Myrmidon Reef; PPS: Palm Passage; YON: Yongala; ELR: Elusive Reef; CCH: Capricorn Channel; HIN: Heron Island North; OTI: One Tree Island; HIS: Heron Island South.

to recalibrate the Coral Sea inflow for every simulation, which means it is necessary to run a number of calibration simulations in order to obtain the best forcing parameters². On a physical level, it also simplifies the dynamics of Coral Sea inflow by assuming that a) the flow rate into/out of the shelf is constant throughout the simulation, and b) the sections of the boundary through which water flows in/out, which are manually chosen during the mesh generation process (based on published observations from the literature), are fixed in time. Whilst making these approximations still allows us to obtain a reasonably good agreement with observed current speeds at most mooring sites over periods of 1-2 months, it is reasonable to assume that if longer simulations are required, this approach will probably be too rudimentary, as the size and location of Coral Sea in/outflow will likely change significantly over seasonal timescales (as discussed in §2.1.3.3). Even

²Given that each simulation takes between 3 and 5 days to run in parallel on 144 CPUs, and that each period simulated typically required 5 or 6 different calibration runs, the time needed to calibrate the model for, say, 5 different years' runs is very significant.

for simulations lasting 1-2 months, it has proved to be practically impossible to successfully calibrate the model for more than approximately one third of the GBR at the same time: when the model is well calibrated in the central region it is not well calibrated in the south, and vice-versa. As a result, this setup cannot be used to realistically model flow on the entire GBR shelf at the same time.

An improved approach may be to force the water currents and elevation at the boundaries with the output of a larger-scale model. I attempted to follow such an approach by running a one-way coupling of SLIM with two different large-scale models: a) a recent version of the HYCOM global reanalysis dataset³ and b) an early version of the Bluelink ReAnalysis (BRAN) dataset from a model of circulation around Australia⁴. Both runs gave a significantly worse agreement with observed data on the shelf than the approach presented in the previous section however, and as such the one-way coupling approach was dropped. A significant limitation of the HYCOM global reanalysis dataset was that the temporal resolution of the data was once daily, and as such most tidal effects were missed, which, as discussed in §2.1.1, is an unacceptable approximation to make for the GBR. Even when the tidal forcing presented in the previous section was combined with the HYCOM forcing however, the results were still poor. A better approach for the future may be to attempt a one-way coupling of SLIM with the latest version of the SHOC model, which forms part of the eReefs project to model the GBR's circulation at a resolution of 1km (see §2.1.5).

Waves

A further limitation of the model described in this chapter is that it does not take into account the effects of waves. In particular, the phenomenon of waves breaking over reefs can potentially drive significant currents over fringing reefs exposed to the Coral Sea (Monismith 2007; Wolanski 1994). Empirical studies in Caribbean reef systems have shown that breaking waves can drive periodic current bursts of $50\text{--}80\text{ cm s}^{-1}$ over reef crests, and that water crossing the reef crest in this way can dominate the flow in a back-reef lagoon, if it is present (Roberts 1981). On reefs with strong wave breaking effects, these can potentially equal if not dominate the tidal currents over the reef, so wave breaking is clearly not negligible in such areas. However, since this effect is only thought to dominate on ocean-facing fringing reefs, it is not thought to have a significant impact on GBR-wide flow, or on larval dispersal averaged over a large number of reefs (Monismith 2007). Further modelling work would however be useful to quantify the impact of wave breaking effects on larval dispersal in the GBR, and, if it is shown to be significant, to incorporate this into future models of larval dispersal. A simple approach used by Wolanski (1994) involves imposing an artificial wind stress over reef crests to mimic the effects of waves breaking, however calibration and validation data were insufficient to quantitatively test the validity of this approach.

Model resolution

The sensitivity analysis carried out during the model setup showed that differences in predicted currents were apparent if the model's maximal resolution was increased, up to a limit of about 200-400m. This sensitivity analysis consisted of comparing currents at

³Data accessed on 17th March 2014.

⁴BRAN 2.2, from 2008.

9 separate sites however, which only provides a limited picture given the complexity of the model domain. Furthermore, most of the sites were not in the immediate vicinity of reefs, since they were chosen in order to allow comparison with observed data from moorings located at these points, and as such they may well not be the places which would benefit the most from increasing the resolution.

An analysis focusing specifically on the effect of resolution size in the immediate vicinity of reefs would be particularly useful, and appears to be lacking in the literature⁵. Despite this level of uncertainty however, the model presented here is likely to be considerably less limited in accuracy by its resolution than other models of circulation in the GBR, as its horizontal resolution is significantly higher than other models used to study the whole region.

Use of a depth-integrated model

Another legitimate question is whether it is appropriate to use a depth-integrated model to simulate water circulation over a large, topographically complex area such as the GBR. Various experimental and modelling studies have found that the waters on the GBR shelf are vertically well mixed throughout the shelf at most times of year, with important upwelling events being temporally and spatially localised, as discussed (with various references) in §2.1.6, so the conditions are broadly appropriate for using a depth-integrated model of flow on the shelf. Whilst having a 3D model would allow us to better represent these upwelling events, it would also necessitate sacrificing horizontal resolution to keep computational costs acceptable. Given the importance of small-scale circulation close to reefs in determining large scale circulation, partly through non-linear effects such as the Sticky Water effect which are hard to parameterise (see §2.1.1), achieving reef-scale resolution is essential in being able to resolve flow patterns correctly. This is more strongly the case in the GBR than in many other, topographically simpler, coastal seas. Furthermore, since the main aim of this study is to model the dispersal of larvae, which mainly occurs close to reefs, it is imperative for the model to explicitly resolve flow close to reefs, which requires a very high horizontal resolution (in the order of 100m), to avoid significantly overestimating larval dispersal (Burgess et al. 2007).

If we are to model an area the size of the GBR, or even a substantial part of it, then running a full 3D model at a high enough horizontal resolution becomes very computationally demanding. The validity of using a 2D model appears to be borne out by the good performance of 2D models in simulating circulation patterns compared with full 3D models (again, the reader is referred to the discussion in §2.1.6), as well as with observations (e.g. see Andutta et al. 2011; Andutta et al. 2013; King and Wolanski 1996; Wolanski et al. 2013, and the model validations in Chapters 4-6), which justifies their continued use in the GBR.

Using a 2D model necessitates the assumption that larvae are well-mixed in the water column. We make this assumption on the basis that coral larvae cannot swim against currents (their swimming speeds are about 2 orders of magnitude below current speeds; see Baird et al. (2014)), and, crucially, that vertical mixing of the water will act to rapidly mix the larvae throughout the water column. In addition to the aforementioned empirical studies showing that GBR waters are well mixed, a simple tracer transport test case

⁵A study not too dissimilar from the one proposed has been carried out to measure the impact of increased model resolution on modelling the hydrology of a river channel however (Crowder and Diplas 2000), and has proved to be highly useful, with 178 citations according to ScienceDirect, as of 27 March 2015.

can be used to estimate the order of magnitude of the time- and length-scales of vertical mixing processes, and suggests that these should occur rapidly over reefs, supporting the empirical observations⁶.

I will consider a domain which is unbounded in the horizontal plane, and which varies between depths of $-h$ and 0 in the vertical, so the extent of the domain is

$$-\infty < x < \infty, -\infty < y < \infty, -h < z < 0. \quad (3.7)$$

A uniform horizontal current U acts parallel to the x -axis throughout the domain. A certain tracer, undergoing a first-order decay process characterised by a decay rate γ , is abruptly injected into the domain at a given time and location. The characteristic mixing time- and length-scales of this tracer will be calculated. The reactive-transport equation describing the tracer concentration⁷, C , in the domain is:

$$\frac{\partial C}{\partial t} + U \frac{\partial C}{\partial x} = q - \gamma C + K_h \frac{\partial^2 C}{\partial x^2} + K_h \frac{\partial^2 C}{\partial y^2} + \frac{\bar{K}_v}{h^2} \frac{\partial}{\partial \sigma} \left(\kappa \frac{\partial C}{\partial \sigma} \right), \quad (3.8)$$

where $\sigma = (z + h)/h$ is a normalised vertical coordinate, q is the tracer injection rate, K_h is the horizontal diffusivity, $\bar{K}_v$ is the depth-averaged vertical diffusivity and $\kappa(\sigma)$ represents the vertical profile of diffusivity, such that $K_v(\sigma) = \bar{K}_v \kappa(\sigma)$.

In order to keep the solution relatively simple, we will consider that there is no tracer in our domain initially, such that

$$C(0, x, y, \sigma) = 0, \quad (3.9)$$

and that a mass M of the tracer is abruptly injected into the domain at time $t = 0$ and point (x_i, y_i, σ_i) , so that

$$q(t, x, y, \sigma) = \frac{M}{\rho h} \delta(t - 0) \delta(x - x_i) \delta(y - y_i) \delta(\sigma - \sigma_i) \quad (3.10)$$

where ρ is the water density (assumed to be constant), and δ is the Dirac delta function. The bottom and surface impermeability conditions to apply are

$$\left[\kappa \frac{\partial C}{\partial \sigma} \right]_{\sigma=0} = \left[\kappa \frac{\partial C}{\partial \sigma} \right]_{\sigma=1} = 0. \quad (3.11)$$

The derivation of the analytical solution of the tracer concentration for this problem is detailed in the document cited in the aforementioned footnote and will not be reproduced here for reasons of space, but I will directly reproduce the expression for the tracer concentration:

$$C(t, x, y, \sigma) = \frac{M}{\rho h} \frac{e^{-\gamma t}}{4\pi K_h t} \exp \left[-\frac{(x - x_i - Ut)^2 + (y - y_i)^2}{4K_h t} \right] \sum_{n=0}^{\infty} \exp \left(-\frac{\bar{K}_v \lambda_n t}{h^2} \right) \psi_n(\sigma_i) \psi_n(\sigma), \quad (3.12)$$

where λ_n and $\psi_n(\sigma)$ are the n -th eigenvalues and eigenfunctions, respectively, of the vertical diffusivity operator, detailed in Deleersnijder (2014).

⁶The test case used, described herein, is detailed in: Deleersnijder (2014) *Solutions of a tracer transport problem with a variable vertical eddy diffusivity*; <http://hdl.handle.net/2078.1/155333>

⁷The tracer concentration is expressed as a mass fraction and is therefore dimensionless.

As can be seen from Equation 3.12, the vertical mixing time scale of the n -th mode is given by $t_c = h^2 / (\bar{K}_v \lambda_n)$. The mixing time scale of the system is limited by the mode with the smallest vertical variability. We will assume the vertical diffusivity profile has the parabolic form $K_v(\sigma) \sim 6\sigma(1 - \sigma)$, so that diffusivity is highest in the middle of the water column and falls to zero at the top and bottom, decreasing roughly as a linear function close to the boundaries, consistent with the existence of a logarithmic layer (see Deleersnijder (2014) Figure 2 for a schematic representation of this profile). The eigenvalues and eigenfunctions of the vertical diffusivity operator are then:

$$\begin{aligned} \lambda_n &= \frac{3}{2} n(n+1) \\ \psi_0 &= 1 \\ \psi_n &= \sqrt{2n+1} P_n(-1+2\sigma) \quad (\text{for } n \geq 1) \end{aligned} \quad (3.13)$$

where the integer subscript $n = 0, 1, 2, \dots$ gives the order of the mode, and P_n represents the n -th order Legendre polynomial. The mode with the smallest vertical variability (ignoring the depth-mean case $n = 0$) is $n = 1$, yielding $\lambda_1 = 3$. The depth-averaged diffusivity can be calculated as $\bar{K}_v = kh u_*$, where k is the von Karman constant and u_* is the friction velocity (cf. Deleersnijder et al. 1992, Equation 12).

If we take realistic values to describe flow over a reef of 10 m depth ($U = 10 \text{ cm s}^{-1}$, $h = 10 \text{ m}$, $C_{BD} = 0.028$; where C_{BD} is obtained using the same formula as in the SLIM model (cf. §3.2.1), with a Manning coefficient of $0.25 \text{ m}^{1/3} \text{ s}^{-1}$ to account for the high roughness of the reef surface (Lugo-Fernández et al. 1998)), we get a characteristic time scale for vertical mixing of 49 mins, and a horizontal length scale of 119 m (obtained as $(49 * 60) \text{ s} * 0.1 \text{ m s}^{-1}$). This mixing time scale is well below the period of the semi-diurnal tidal currents – the process which drives flushing of water over most reefs in the GBR – and also well below the mean time to competence of most coral larvae (which is measured in days for broadcast spawning coral). Consequently, larvae would rapidly become well mixed over reefs before a) becoming competent, and b) being flushed from the reef.

Similarly, the mixing length scale is well below the typical length of most reefs. Even on a relatively deep reef (e.g. 20 m), the characteristic mixing time and length scales are 157 mins and 376 m, respectively. These values are obviously higher than on shallow reefs, but still smaller than the time-scale of flushing from reefs and reef length scales respectively. Vertical mixing is significantly enhanced by the high surface roughness of reefs (Lugo-Fernández et al. 1998), which leads to faster mixing.

Taking the above values as order-of-magnitude estimates, they support the empirical observations that GBR waters are vertically well mixed, and specifically indicate that vertical mixing over reefs should be particularly rapid. It should also be noted that the simple idealised test case considered does not account for wave- and wind-induced mixing, which would be expected to increase vertical mixing in shallow waters, thus further reducing mixing time- and length-scales.

3.3 Lagrangian model

3.3.1 Model equations, paramaterisations

Transport of particles through the domain was modelled using a random walk formulation of the advection-diffusion equation, following the approach described in Dimou and Adams (1993) and discussed in Spagnol et al. (2002), reproduced below. To arrive at

this formulation, we first consider that the position, $\mathbf{x}(t)$ of each particle in the domain can be described by the non-linear Langevin equation:

$$\frac{d\mathbf{x}}{dt} = \mathbf{A}(\mathbf{x}, t) + \mathbf{B}(\mathbf{x}, t) \cdot \zeta(t), \quad (3.14)$$

where $\mathbf{A}(\mathbf{x}, t)$ is a vector representing deterministic forces, $\mathbf{B}(\mathbf{x}, t)$ is a tensor characterising random forces, and $\zeta(t)$ is a vector of random numbers representing the random and/or chaotic nature of sub-grid scale turbulent mixing. By defining $\mathbf{W}(t) = \int_0^t \zeta(s) ds$, and using the Itô assumption (Tompson and Gelhar 1990), we arrive at the Itô stochastic differential equation

$$d\mathbf{x} = \mathbf{x}(t + dt) - \mathbf{x}(t) = \mathbf{A}(\mathbf{x}(t), t)dt + \mathbf{B}(\mathbf{x}(t), t) \cdot d\mathbf{W}(t), \quad (3.15)$$

where $d\mathbf{W}(t)$ is a Wiener process with a mean of zero (i.e. $\langle d\mathbf{W} \rangle = 0$) and a mean square proportional to dt (i.e. $\langle d\mathbf{W}^2 \rangle = dt$). The discretised form of this equation becomes

$$\Delta \mathbf{x}_n = \mathbf{x}_n - \mathbf{x}_{n-1} = \mathbf{A}(\mathbf{x}_{n-1}, t_{n-1})\Delta t + \mathbf{B}(\mathbf{x}_{n-1}, t_{n-1}) \cdot \frac{\mathbf{R}_n}{\sqrt{r}}\sqrt{\Delta t}, \quad (3.16)$$

where $\mathbf{R}_n$ is a two-dimensional vector of random numbers with a mean of zero and a variance of $r \equiv \langle R^2 \rangle$ (so the term $\frac{\mathbf{R}_n}{\sqrt{r}}$ is a vector of random numbers with unit variance). If we take the limit of the number of particles $N \rightarrow \infty$ and $\Delta t \rightarrow 0$, this equation becomes equivalent to the Fokker-Planck equation

$$\frac{\partial f}{\partial t} + \frac{\partial}{\partial x_i} (A_i f) = \frac{\partial^2}{\partial x_i \partial x_j} \left(\frac{1}{2} B_{ik} B_{jk} f \right), \quad (3.17)$$

where $f = f(\mathbf{x}, t | \mathbf{x}_0, t_0)$ is the conditional probability density function for $\mathbf{x}(t)$.

We can describe the depth-averaged tracer concentration, C , for a non-reactive substance in a 2D domain without sources or sinks using the following transport equation:

$$\frac{\partial(CH)}{\partial t} + \frac{\partial(uCH)}{\partial x} + \frac{\partial(vCH)}{\partial y} = \frac{\partial}{\partial x} \left[HK_{xx} \frac{\partial C}{\partial x} + HK_{xy} \frac{\partial C}{\partial y} \right] + \frac{\partial}{\partial y} \left[HK_{yx} \frac{\partial C}{\partial x} + HK_{yy} \frac{\partial C}{\partial y} \right] \quad (3.18)$$

where $K_{xx}(t, x, y)$, $K_{xy}(t, x, y)$, $K_{yx}(t, x, y)$, $K_{yy}(t, x, y)$ are diffusion coefficients, H is water depth and (u, v) are horizontal water velocities. This equation can be rewritten as

$$\begin{aligned} \frac{\partial CH}{\partial t} + \frac{\partial}{\partial x} \left[\left(\frac{K_{xx}}{H} \frac{\partial H}{\partial x} + \frac{\partial K_{xx}}{\partial x} + \frac{K_{xy}}{H} \frac{\partial H}{\partial y} + \frac{\partial K_{xy}}{\partial y} + u \right) CH \right] \\ + \frac{\partial}{\partial y} \left[\left(\frac{K_{yy}}{H} \frac{\partial H}{\partial y} + \frac{\partial K_{yy}}{\partial y} + \frac{K_{yx}}{H} \frac{\partial H}{\partial x} + \frac{\partial K_{yx}}{\partial x} + v \right) CH \right] \\ = \frac{\partial^2}{\partial x^2} (K_{xx} CH) + \frac{\partial^2}{\partial y^2} (K_{yy} CH) + \frac{\partial^2}{\partial x \partial y} (K_{xy} CH) + \frac{\partial^2}{\partial x \partial y} (K_{yx} CH). \end{aligned} \quad (3.19)$$

Comparing this advection-diffusion equation (Equation 3.19) with the Fokker-Planck equation above (Equation 3.17), we can see they are equivalent as long as:

$$\mathbf{A} = \begin{bmatrix} \frac{K_{xx}}{H} \frac{\partial H}{\partial x} + \frac{\partial K_{xx}}{\partial x} + \frac{K_{xy}}{H} \frac{\partial H}{\partial y} + \frac{\partial K_{xy}}{\partial y} + u \\ \frac{K_{yy}}{H} \frac{\partial H}{\partial y} + \frac{\partial K_{yy}}{\partial y} + \frac{K_{yx}}{H} \frac{\partial H}{\partial x} + \frac{\partial K_{yx}}{\partial x} + v \end{bmatrix} \quad (3.20)$$

$$\frac{1}{2}\mathbf{B}\mathbf{B}^T = \begin{bmatrix} K_{xx} & K_{xy} \\ K_{yx} & K_{yy} \end{bmatrix} \quad (3.21)$$

$$f = CH \quad (3.22)$$

If we consider that dispersion is isotropic, so that $K_{xy} = K_{yx} = 0$ and $K_{xx} = K_{yy}$, then, using Equation 3.16, we arrive at the following formulation for a random-walk particle-tracking scheme, which was implemented in the Lagrangian model to simulate transport of larvae:

$$\mathbf{x}_{n+1} = \mathbf{x}_n + \mathbf{v}_n \Delta t + \frac{\mathbf{R}_n}{\sqrt{r}} \sqrt{2K\Delta t} \quad (3.23)$$

$$\mathbf{v}_n = \left(\mathbf{u} + \frac{K}{H} \nabla H + \nabla K \right) \Big|_{\mathbf{x}_n} \quad (3.24)$$

where $\mathbf{x}_n$ and $\mathbf{x}_{n+1}$ are the particle positions at time iterations n and $n + 1$ respectively, Δt is the time difference between iterations, K is the horizontal diffusivity coefficient and $\mathbf{u} = \mathbf{u}(t, x, y)$ is the instantaneous depth-averaged horizontal water velocity. The time step used for the simulations was kept at $\Delta t = 90$ s, so that the distance travelled by a particle in a single time step would be smaller than the size of the smallest mesh elements.

The Lagrangian model was implemented as an additional module for the SLIM ocean model. This module is run offline from the core hydrodynamic model, meaning that it reads the water elevation and velocity fields previously generated, and saved to disk, by the hydrodynamic model as inputs (H and $\mathbf{u}$ in Equation 3.24), and these are subsequently used to calculate the advection velocity of every particle. H and $\mathbf{u}$ were recorded to disk with a temporal resolution of 25 mins, to allow semi-diurnal tidal constituents to be accurately captured. The horizontal diffusivity coefficient, K , was calculated using the paramaterisation presented in de Brye et al. (2010), which makes use of the formula of Okubo (1971) to introduce a dependence on the local element size of the hydrodynamic model mesh as:

$$K = \alpha \Delta^{1.15}, \quad (3.25)$$

where Δ is again taken to be the local element size, and the coefficient $\alpha = 0.041 \text{ m}^{0.85} \text{ s}^{-1}$ was calibrated for coastal waters in the Great Barrier Reef by Andutta et al. (2011). Whilst this paramaterisation of diffusivity is by no means the only one available, it was used as it was considered to be one of the simplest which accounts for the most important feature that such a paramaterisation should have – a dependence on the local mesh resolution (since larger elements have a greater range of unresolved water motion than smaller elements). This approach has also been used in numerous studies of coastal seas and estuaries using multi-scale models (e.g. see Andutta et al. 2011; de Brauwere et al. 2011; Lambrechts et al. 2008; Pham Van et al. 2015).

3.3.2 Life history traits

In addition to modelling the transport of particles, a certain number of life history traits were implemented in the module to account for the life histories of the virtual larvae. These were included as additional options which can be individually activated or deactivated by the user whenever necessary. Whilst the exact behaviour and life histories of

larvae in the ocean is not known for certain owing to the difficulty of observing them over prolonged periods in their natural environment, recent empirical laboratory-based observations have shed new light on their life history traits (see Connolly and Baird 2010; Figueiredo et al. 2013; Figueiredo et al. 2014) – the model presented in this thesis is the first known biophysical model of larval dispersal to model larval life history traits using this empirically derived data. The following optional life history traits were implemented in the Lagrangian module:

Mortality: Each larva has a certain probability of dying during every time step. The model can calculate this probability either by assuming a constant mortality rate, or by assuming a mortality rate following a Weibull distribution (high initial mortality rate, decreasing with time) or a generalised Weibull distribution (high initial mortality rate, decreasing with time, then increasing again as particles get older, like a bathtub shape), depending on the species, according to the findings of Connolly and Baird (2010), Figueiredo et al. (2013), and Figueiredo et al. (2014). These studies have fitted observed mortality data for various common species of coral larvae to these three types of mortality distributions. Predation mortality was not accounted for due to the difficulty inherent in measuring and parameterising it.

Competence: Competence represents the ability of a larva to settle onto a reef. In the Lagrangian module, larvae have a certain probability of acquiring competence following a constant competence acquisition rate, and once they are competent, a certain probability of losing competence following a constant competence loss rate. This description approximates observations of coral larvae in laboratory experiments described by Connolly and Baird (2010).

Settlement: Once a larva in the Lagrangian module becomes competent, it will then settle onto the first reef it travels over. When this happens, the element in the connectivity matrix corresponding to the row given by the larva's origin reef and the column given by the destination reef is incremented by one, and the larva is removed from the remainder of the simulation. This behavioural trait reflects the fact that once they are competent, coral larvae are known to be able to change their buoyancy to sink down to the reef surface and attempt to attach onto it (settle), using environmental or biotic cues (Price 2010).

Whilst assuming that a larva will settle onto the first reef it comes across is a simplification of reality (e.g. it is plausible that a larva may not have time to settle if it only brushes past the edge of a reef rapidly, or if turbulent mixing keeps it away from the reef surface), our present lack of understanding of a) the exact settlement cues used by larvae and b) the extent of their ability to settle rapidly to the bottom means that it is not possible to formulate a more elaborate description for a lack of empirical data.

Swimming: Whilst swimming speeds of coral larvae are known to be negligible compared with typical inter-reef current speeds (Baird et al. 2014), larvae of reef fish are known to have swimming abilities which can be very significant in shaping dispersal patterns, potentially using olfactory and auditory cues to swim towards reefs (Wolanski and Kingsford 2014), and as such an optional swimming module was incorporated in order to allow the model to be used to model reef fish larvae in the future. Enabling swimming behaviour causes larvae to swim towards reefs

when they are within a user-defined distance from them. This behavioural trait was deactivated to simulate the dispersal of coral larvae presented in this thesis.

3.3.3 Validation of the Lagrangian module

3.3.3.1 Particle transport

In addition to verifying that the Lagrangian module was correctly simulating the advection of particles (not shown), the ability of the module to simulate diffusion of particles in a domain with a non-flat bathymetry was also verified. This was done by numerically simulating particle transport for a test case with a known analytical solution⁸, and comparing the results obtained numerically with this exact solution. The test case is now described.

We will consider a passive, inert tracer in a two-dimensional domain with a non-uniform bathymetry and null water velocity (so advection is ignored). A mass M of the tracer is considered to be released into the domain at time $t = 0$ and position $(x, y) = (0, 0)$, with no tracer previously present in the domain. The diffusion equation describing the tracer concentration in the domain is:

$$\frac{\partial(HC)}{\partial t} = \nabla \cdot (HK \nabla C), \quad (3.26)$$

where $C(t, \mathbf{x})$ is the depth-averaged tracer concentration, $H(\mathbf{x})$ is the water depth and K is the diffusivity. The initial condition, as described above, is:

$$C(0, \mathbf{x}) = \frac{M}{\rho H_0} \delta(\mathbf{x}), \quad (3.27)$$

where H_0 is the water depth at $(0, 0)$, ρ is the fluid density and δ is the Dirac delta function.

Equation 3.26 can be rewritten as:

$$C \frac{\partial H}{\partial t} + H \frac{\partial C}{\partial t} = \nabla(HK) \cdot \nabla C + HK \nabla^2 C. \quad (3.28)$$

In order to find an analytical solution to this equation, we will need to make two assumptions: firstly that the diffusivity, K , is constant, so that $\nabla(HK) \cdot \nabla C = K \nabla H \cdot \nabla C$, and secondly that the water depth does not depend on time and has the following form:

$$H(\mathbf{x}) = H_0 e^{x/L}, \quad (3.29)$$

where L is a characteristic length scale (taken to be $L = 5$ km). The space derivative of the bathymetry is therefore:

$$\nabla H = \frac{H(\mathbf{x})}{L} \mathbf{e}_x. \quad (3.30)$$

In this particular case, Equation 3.28 then becomes:

$$\frac{\partial C}{\partial t} = \frac{K}{L} \frac{\partial C}{\partial x} + K \nabla^2 C. \quad (3.31)$$

⁸The test case used, described herein, is detailed in: Deleersnijder (2015) *A depth-integrated diffusion problem in a depth-varying, unbounded domain for assessing Lagrangian schemes*; <http://hdl.handle.net/2078.1/160980>

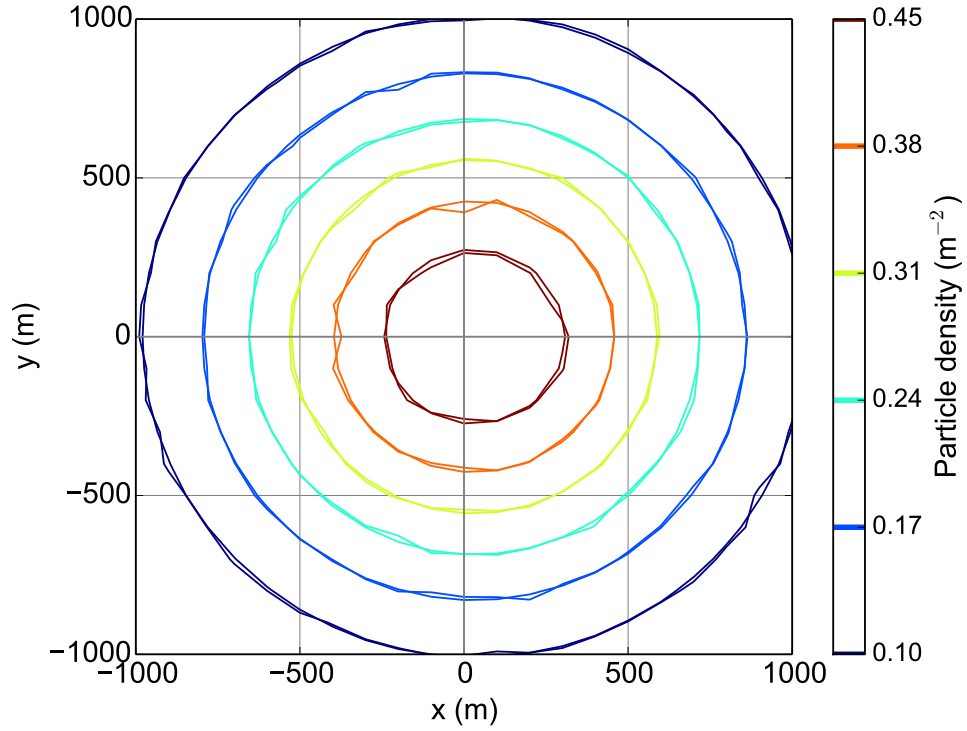


Figure 3.10: Particle density contours for the numerical and analytical solutions overlaid onto each other. The numerical solution was obtained using 1,000,000 particles. These contours show the particle densities at the end of the simulation (i.e. after 7 days). Compared to the initial release point, the centre of mass of the tracer has moved along the positive x -axis by a distance of about 30 m, as also shown in Figure 3.11.

The analytical solution to this problem is:

$$C(t, \mathbf{x}) = \frac{M}{4\pi\rho H_0 K t} \exp\left(-\frac{|\mathbf{x} + \frac{K t \mathbf{e}_x}{L}|^2}{4K t}\right). \quad (3.32)$$

The centre of mass, $\mathbf{r}_c(t)$, can be found to move towards the deeper part of the domain at a known velocity:

$$\begin{aligned} \mathbf{r}_c(t) &\equiv \frac{1}{M} \int \rho H(\mathbf{x}) C(t, \mathbf{x}) \mathbf{x} d\mathbf{x} \\ &= \frac{1}{4\pi K t} \int \exp\left(-\frac{|\mathbf{x} - \frac{K t \mathbf{e}_x}{L}|^2}{4K t}\right) \mathbf{x} d\mathbf{x} \\ &= \frac{K t}{L} \mathbf{e}_x. \end{aligned} \quad (3.33)$$

The position variance of the tracer distribution is a linear function of time:

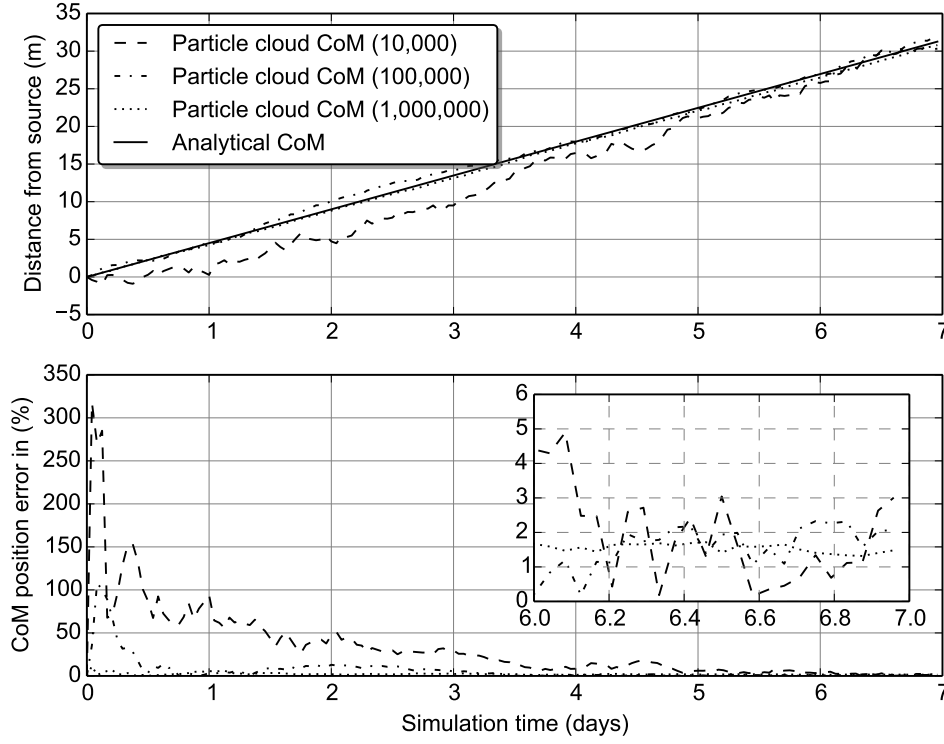


Figure 3.11: Graph showing the evolution in time of the positions (along the x -axis) of the centres of mass (CoM) of the analytical tracer concentration, and the equivalent particle cloud simulated numerically. 3 numerical simulations were run, featuring 10,000, 100,000 and 1,000,000 particles.

$$\begin{aligned}
 \sigma^2(t) &\equiv \frac{1}{M} \int \rho H(\mathbf{x}) C(t, \mathbf{x}) |\mathbf{x} - \mathbf{r}_c(t)|^2 d\mathbf{x} \\
 &= \frac{1}{4\pi K t} \int \exp\left(-\frac{|\mathbf{x} - \frac{Kt\mathbf{e}_x}{L}|^2}{4Kt}\right) |\mathbf{x} - \mathbf{r}_c(t)|^2 d\mathbf{x} \\
 &= 4Kt.
 \end{aligned} \tag{3.34}$$

We note in passing that Equation 3.32 also shows that the point where the concentration reaches its maximum value is located at $\mathbf{x}_m(t) = -\frac{Kt}{L}\mathbf{e}_x$, i.e. it moves towards the shallower part of the domain. Perhaps somewhat counter-intuitively, the point of maximum concentration therefore moves in the opposite direction to the centre of mass of the tracer field (Equation 3.33), and at the same speed, meaning that a greater tracer mass moving towards the deeper part of the domain, but as the water here is deeper, the concentration is nonetheless lower than in the shallower part of the domain.

In order to compare the output of the Lagrangian model with this analytical solution, we can calculate the centre of mass and variance of the particles in our computational domain as:

$$\tilde{\mathbf{r}}_c(t) = \frac{1}{N} \sum_{n=1}^N \mathbf{r}_n(t), \tag{3.35}$$

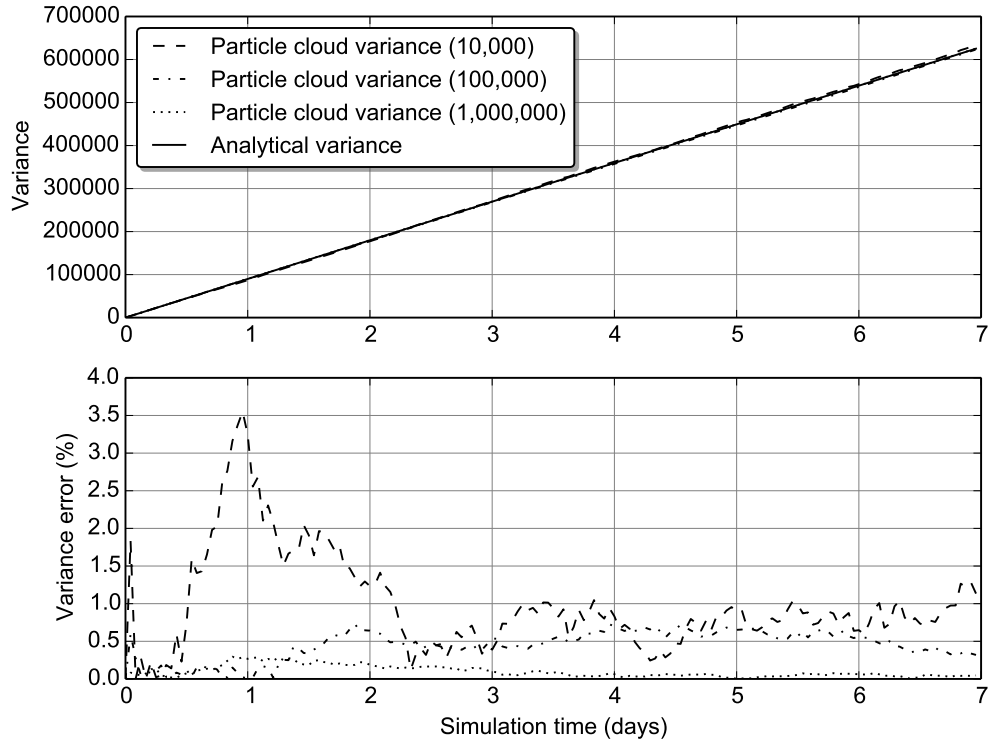


Figure 3.12: Graph showing the evolution of the variance of the analytical tracer concentration and of the particle cloud. 3 numerical simulations were run, featuring 10,000, 100,000 and 1,000,000 particles.

and

$$\bar{\sigma}_c^2(t) = \frac{1}{N} \sum_{n=1}^N |\mathbf{r}_n(t) - \mathbf{r}_c(t)|^2, \quad (3.36)$$

where N gives the number of particles and $\mathbf{r}_n(t)$ is the position vector of the n -th particle. Each particle is therefore considered to have a mass of M/N .

To verify that the model could correctly reproduce the above properties of the tracer transport problem, a simulation was set up to model the transport of particles in the idealised domain with the bathymetry given by Equation 3.29. The domain boundaries were wide enough apart that no particle approached them during the course of the simulation. Particles were released at the point $(0, 0)$ at the start of the simulation, and their positions were tracked over 1 week. All particle behaviour was deactivated, and water velocity was set to zero everywhere. A square-shaped mesh was used with triangular elements of a constant resolution of 500 m, and a constant diffusivity coefficient of $K = 0.26 \text{ m}^2 \text{ s}^{-1}$ was used, a value obtained using Equation 3.25.

The particle densities predicted by the analytical and numerical solutions after 7 days are shown overlaid on each other in Figure 3.10; there is a good match between the two. Figures 3.11 and 3.12 additionally show the evolution of the position of the centres of mass of the two solutions and their variances, respectively. Numerical solutions are shown for simulations with $N=10,000$, $N=100,000$ and $N=1,000,000$ particles. Both the analytical and the numerical solutions show the particle cloud moving along the posi-

tive y -axis by a total distance of just over 30 m by the end of the simulation (note this is relatively small compared to the characteristic length scale $L = 5$ km. The numerical solution can be seen to converge to the analytical solution, and does so more quickly as the number of particles is increased. The graphs indicate that the numerical solution shows no sign of diverging from the analytical solution as the simulation progresses. It should be noted that the simulation was run on a mesh with a (constant) element size of 500 m, typical of the meshes used for simulating particle transport in the GBR in the following chapters of this thesis, but which is an order of magnitude greater than the mean distance travelled by the particle cloud over a week (as can be seen in the graph); as such there may be some numerical errors introduced by the fact that the bathymetry is linearly interpolated between 3 points about 500 m from each other. Even so, these results suggest that any such numerical errors are not great enough to have a very significant untoward effect on the simulation of particle transport (centre of mass error $< 2\%$ and variance error $< 0.01\%$ for $N = 1,000,000$), and that the model is correctly diffusing particles through the domain.

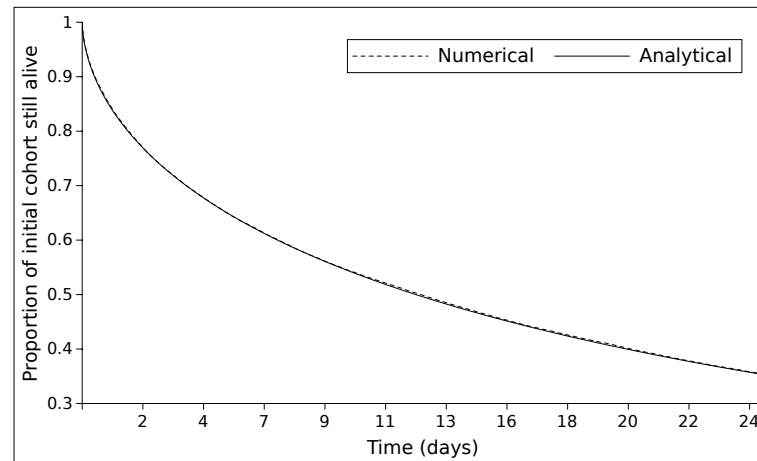
3.3.3.2 Larval behaviour

The implementation of the mortality and competence acquisition traits was validated by running simulations where only these features were enabled (in turn). The number of particles alive, and the number of particles competent, were then compared with the expected number of particles alive, and particles competent, using the analytical formulae given in Connolly and Baird (2010). The graphs, shown in Figures 3.13, show that the model correctly reproduces the expected particle behaviour.

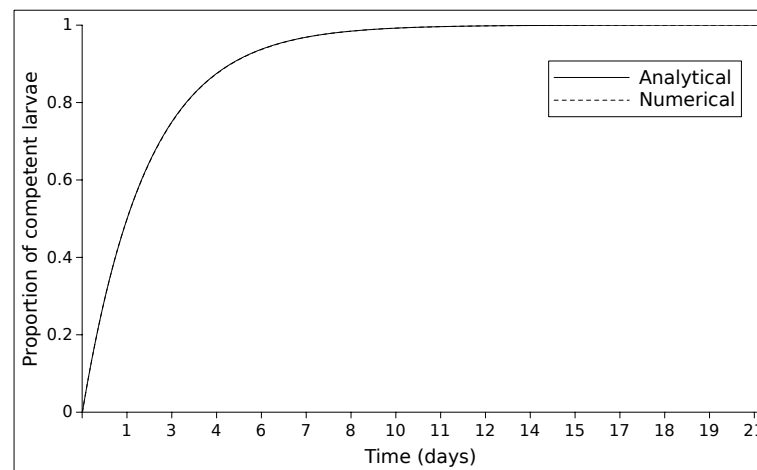
3.3.4 Limitations

The use of a depth-integrated hydrodynamical model to drive the Lagrangian model necessitates the approximation that larvae are neutrally buoyant and are equally spread out along the vertical axis of the water column. It is therefore assumed that a larva released over a reef at a depth of, say, 30 m subsequently has the same likelihood of settling onto a reef at 5 m depth as another larva released at 5 m depth. Whilst this may appear counter-intuitive, empirical studies of coral colonies in the Caribbean using DNA microsatellites found a significant level of connectivity occurring between coral colonies at different depth levels from < 10 m to > 25 m, implying that larvae released at a given depth level do indeed have a realistic chance of settling at a different depth level. This process would be facilitated by rapid vertical mixing of the water column. As such, given the lack of more detailed knowledge about the vertical distribution of larvae in the water column, and given the rapid vertical mixing thought to occur, the most robust assumption appears to be to consider that they are equally distributed throughout the water column.

Lagrangian models considering discrete particles only agree with their Eulerian counterparts if the number of particles in the model is high enough. In a spatial domain as large as the GBR, it is necessary to release many particles during the simulations, which in turn requires a certain amount of computational resources. Whilst much smaller than those needed for the hydrodynamic simulations, they are nonetheless far from negligible. For instance a typical 30-day simulation of larval dispersal with 5 million larvae released over 1,000 reefs (covering roughly a third of the GBR's surface area) can take up



(a) Mortality



(b) Competence acquisition

Figure 3.13: Graphs showing the validation of the implementation of a) mortality and b) competence acquisition traits in the particle-tracking module. The curve labelled Numerical shows the results from a numerical simulation for *A. millepora*, using the parameters reported in Connolly and Baird (2010), and with all life history traits disabled except the one being observed (i.e. either mortality or competence, respectively), whilst the curve labelled Analytical shows the solution calculated analytically using the formulae given in Connolly and Baird (2010). Note that the delay prior to the start of competence acquisition was disabled in this simulation.

to 3 days on 5 CPUs. The number of particles used in the simulations was chosen following a sensitivity analysis on global connectivity indicators (such as self-recruitment and dispersal distances), by finding the number of particles at which multiplying this number by 2 had no discernible effect on the indicators. However, given the detailed spatial analyses which can potentially be carried out on the resulting connectivity matrices, a safer approach in the future may be to carry out sensitivity analyses individually for each reef, by calculating connectivity indicators such as self-recruitment per reef, and identifying the point at which adding particles has no discernible effect on every reef in the domain.

CHAPTER 4

TOOLS TO STUDY CONNECTIVITY IN THE GBR

Summary

In order to be able to study the process of connectivity in the GBR, we need to first assemble a set of tools we can use to model it, and then make sense of the huge quantity of data produced by the model. This chapter introduces and describes the set of tools assembled to undertake this task. First, the coupled SLIM-particle tracker setup is described along with the output it produces, and then a graph theoretical method known as community detection is employed to find spatial patterns in the results. Applying this method allows useful information to be extracted over multiple spatial scales by partitioning the GBR's network of reefs into clusters, known as reef communities, and then studying connectivity on the community scale. Reef communities isolated from the rest of the network to a greater or lesser extent can be identified by varying a user-defined resolution parameter. The results can be used to infer where the major “boundaries to dispersal” of coral larvae are found in the GBR. They also illustrate the large differences in dispersal potential between different species. A comparison of the community detection method employed with another equivalent method is also included at the end of the chapter.

This chapter reproduces the following article (with minor corrections and improvements):

Thomas, C. J., Lambrechts, J., Wolanski, E., Traag, V. A., Blondel, V. D., Deleersnijder, E. and Hanert, E. (2014). Numerical modelling and graph theory tools to study ecological connectivity in the Great Barrier Reef. *Ecological Modelling*, 272: 160-174.

4.1 Introduction

For most types of coastal marine species, the process of larvae dispersing through the ocean prior to reaching adulthood – known as the pelagic larval phase – is vital in enabling population exchange between geographically separated sub-populations (Cowen et al. 2006; Cowen and Sponaugle 2009). In coral reef ecosystems the pelagic larval phase takes on an added importance as marine life is predominantly concentrated onto reefs of varying size separated by open sea. Many species of reef fish never leave their home reef as adults (Jones et al. 2009a), whilst coral is physically fixed to the reef surface and is thus unable to travel between reefs. It is therefore only during the pelagic larval phase that these species can spread to new reefs, repopulate damaged reef populations and maintain a healthy gene pool by exchanging larvae between separate sub-populations (Buston et al. 2012).

Understanding how larvae disperse, where they can disperse to, and how resilient this process is to environmental change is essential to understanding the dynamics – and resilience – of coral reef ecosystems. Conservation strategies for coral reefs often involve the designation of Marine Protected Areas (MPAs) in which local anthropogenic interference is limited. In order for reefs in MPA networks to be effective in replenishing coral and reef fish populations in neighbouring reefs, the size and spacing of MPAs should account for the dispersal potential of marine species present in the region (Largier 2003; Munday et al. 2009; Olds et al. 2012), which is not currently the case for most major coral reef ecosystems (Almany et al. 2009; Jones et al. 2009a). Whilst some recent studies have proposed MPA designs which incorporate connectivity estimates to improve conservation performance (e.g. Guizien et al. 2012; Mumby et al. 2011), a major stumbling block so far has been a lack of location-specific knowledge of larval dispersal and connectivity patterns (Drew and Barber 2012). Spatially explicit modelling studies such as the one presented in this article aim to fill this knowledge gap.

Larval dispersal remains very difficult to directly observe or measure, due to the small size of the larvae, the vastness of the ocean, and the fact that dispersal can occur over time-scales of days to weeks (Drew and Barber 2012). Genetic tools can be used to measure the level of genetic connectivity between two given sub-populations, however these tools, whilst useful in quantifying present-day and historical connectivity, are by their nature unable to explain the processes driving the dispersal of larvae or to predict future trends (Palumbi 2003), and are unable to provide spatially continuous detailed information over large regions. Numerical modelling tools can be used to fill this knowledge gap, both by providing large-scale estimates of present-day larval dispersal and connectivity patterns, and by showing how a change in physical or biological factors driving the dispersal process could alter inter-reef connectivity patterns (Werner et al. 2007).

The transport of larvae between separate reefs can be described in terms of “ecological” (or demographic) connectivity, which concerns the movement of individual larvae, or in terms of “genetic” connectivity, which concerns the exchange of genetic information. Ecological connectivity occurs over the time- and space-scales over which most larvae disperse (typically days to weeks and 0.1 km to 100 km for coral) and is of primary interest for fisheries, reef management and MPA planning. Genetic connectivity on the other hand is a more complex process which plays out over many generations, with time- and space-scales spanning a greater range than ecological connectivity. For instance, the migration of just a few individuals per generation between two sub-populations can be enough to prevent genetic differences from developing, and can therefore represent a

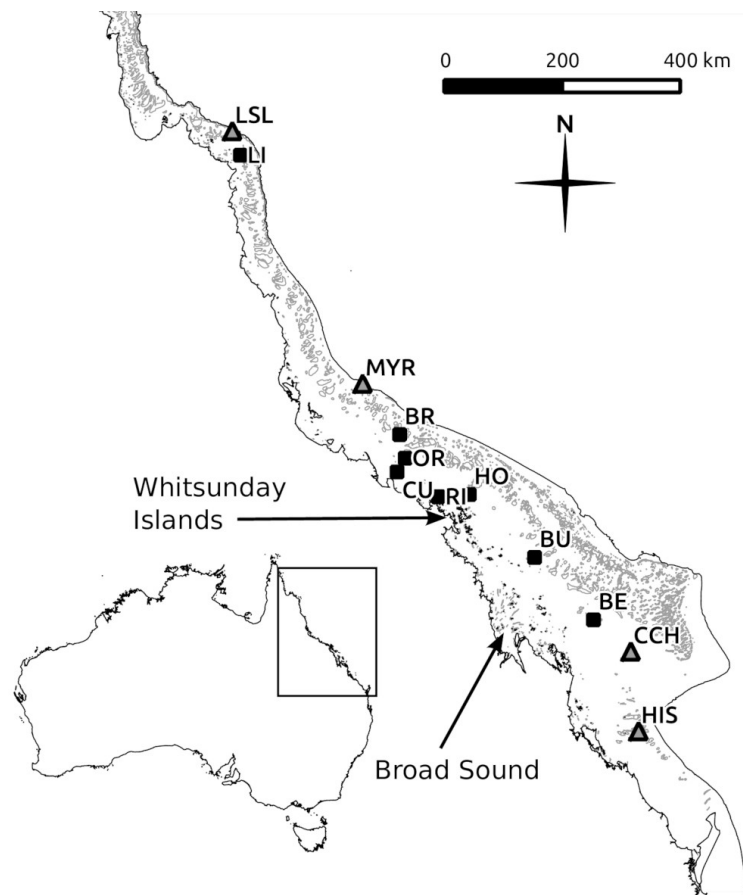


Figure 4.1: Map of the GBR topography. The coastline is shown to the left, the 200m-isobath to the right, and reefs are shaded in grey. Triangles show positions of moorings used to validate elevation, squares represent moorings used to validate currents. Legend: LSL: Lizard Island Slope, MYR: Myrmidon Reef, CCH: Capricorn Channel, HIS: Heron Island South, LI: Lizard Island, BR: Bowden Reef, OR: Old Reef, CU: Cape Upstart, RI: Rattray Island, HO: Hook, BU: Bushy, BE: Bell.

genetically significant level of connectivity (Cowen and Sponaugle 2009; Leis et al. 2011), despite being ecologically insignificant. It is not a straightforward exercise to compare observed genetic connectivity with ecological connectivity predicted using large-scale numerical models as these models typically do not have enough precision to estimate transport down to ecologically insignificant (but still genetically significant) numbers of larvae, over time periods in the order of years.

In this paper we present a modelling approach to simulate larval dispersal down to reef-scale spatial resolution, and use this to study ecological connectivity in the region covering the central section of the Great Barrier Reef (GBR) in Australia, which includes roughly 1,000 reefs. The GBR is a region with a particularly complex bathymetry and a correspondingly complex water circulation (Wolanski 1994). Small-scale circulation at the reef-scale has been shown to interact significantly with large-scale circulation, for instance through the ‘sticky water’ effect (Andutta et al. 2012; Wolanski et al. 2003; Wolanski and Spagnol 2000). In order to capture all major scales of motion, it is therefore necessary to resolve currents down to the reef scale: 100 m to 1 km. Present-day models of circulation in the GBR and other reef areas tend to have a horizontal resolution of 1-2 km

however (e.g. Luick et al. (2007) and Paris et al. (2007)), too large to explicitly resolve flow at the lower range of larval dispersal length-scales, or even to capture many significant flow features in the reef-dense GBR. The use of nested structured grids is unfeasible in the GBR as the areas requiring enhanced resolution would be too numerous. In this study we instead use a finite element ocean model, SLIM¹, to model water circulation in the GBR using an unstructured grid. This allows us to achieve reef-scale resolution around reefs at an acceptable computational cost (Lambrechts et al. 2008). We then employ an Individual Based Model (IBM) to simulate the dispersal and settling of coral larvae through the domain.

Large-scale spatially-explicit simulations such as this can produce a huge amount of data, so a set of tools is needed to interpret this output if we are to draw useful conclusions. A number of mathematical tools have been developed to study properties of networks, including biological and ecological networks of geographically separate, connected populations (Proulx et al. 2005). The use of these tools in studies of coral connectivity has so far been limited however. Trembl et al. (2008) showed how graph theory can be used to investigate dispersal pathways and identify ‘stepping-stone’ islands linking distant populations and, more recently, Kininmonth et al. used a graph theoretical approach to explore the robustness and scale (Kininmonth et al. 2010a) of a reef network, as well as spatial clustering of connections (Kininmonth et al. 2010b). Nilsson Jacobi et al. (2012) used community detection tools to identify sub-populations in a network of marine habitats for generic sessile invertebrates in the Baltic Sea, and to infer the presence of dispersal barriers. They also investigated how many clusters contained MPAs, and concluded that MPAs were poorly distributed amongst the clusters.

In the present study we explore the use of a graph theoretical approach to identify spatial patterns in large-scale connectivity of coral larvae. We use a community detection method to identify clusters of reefs which are ecologically isolated from each other, and we partition the central section of the GBR into such clusters, known as “reef communities”. Each reef community can be seen as a self-contained ecological sub-region, with little or no larvae exchanged with reefs in other communities. We establish maps delimiting separate reef communities in the GBR for 4 different species of coral commonly found in the region, and find that significant inter-species differences exist in the size and shapes of the communities. These differences can be explained by variations in the biological characteristics of each species, and in particular their pre-competence periods. We also explore the differences in connectivity length scales across the different communities, and compare these to average MPA spacing. Such findings can potentially be used to inform the placement and spacing of MPAs to better take into account the different connectivity potential of larvae in each ecological sub-region.

This study has some parallels with Nilsson Jacobi et al. (2012), in which a similar graph theoretical approach to identify communities of generic sessile invertebrates in the Baltic Sea. Some differences of implementation between the two approaches are discussed in Section 4.2.3.2. No study that we are aware of has used these tools to compare the connectivity patterns of different marine species however, or to investigate whether dispersal patterns vary significantly in different sub-populations and how community-specific dispersal distances compare with MPA spacing.

¹Second-generation Louvain-la-Neuve Ice-ocean Model; see www.climate.be/slim for more information.

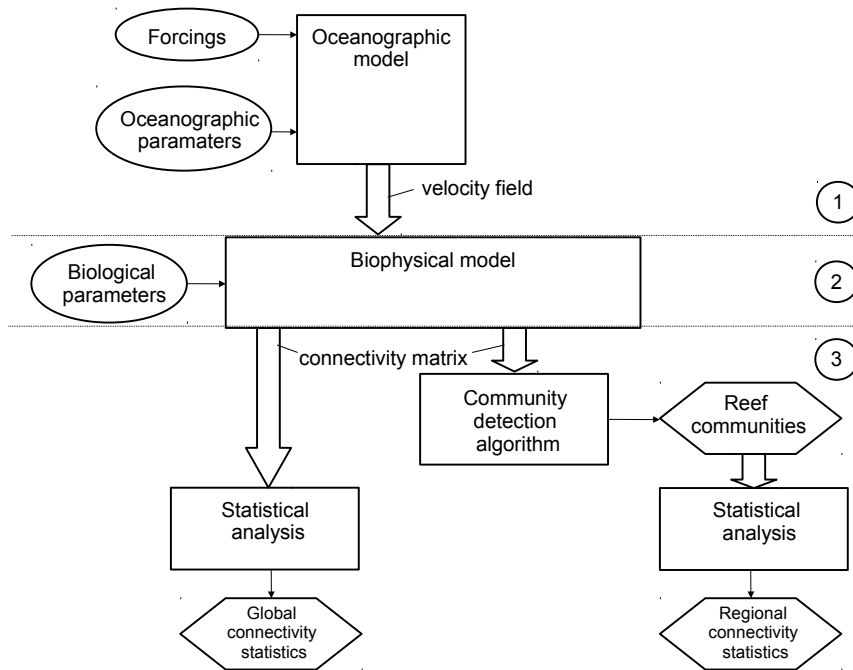


Figure 4.2: Flow chart summarising the connectivity modelling process. Input parameters obtained from observations are shown in ovals, modelling stages are shown in rectangles and outputs are shown in hexagons. Thick arrows represent model outputs subsequently used as inputs for the next modelling stage. Circled numbers indicate the modelling stages: 1: simulating the hydrodynamics, 2: simulating larval dispersal, 3: extracting useful information.

4.2 Numerical modelling and graph theory tools to study connectivity

The numerical modelling approach presented in this paper can be broadly divided into three stages: 1) modelling the hydrodynamics of the region, 2) simulating the transport of larvae, and 3) interpreting the model output. Each stage is now discussed, and a flow-chart summarising this process is presented in Figure 4.2.

4.2.1 Resolving the hydrodynamics

4.2.1.1 Oceanographic model

Given the highly multi-scale nature of the water circulation in the GBR (as discussed in Section 4.1), it is important to use an ocean model able to cope with a large range of length scales. We used the finite element, unstructured-grid ocean model SLIM, in its depth-integrated, barotropic version. SLIM is ideally suited to modelling water circulation in coastal and multi-scale regions due to its use of an unstructured grid, which allows the model resolution to be varied in space (Legrand et al. 2006). The grid used in this study is shown in Figure 4.3. The element size varies from 400 m close to reefs and coastlines to 10 km in deeper ‘open-sea’ areas. This allows the model to explicitly capture small-scale circulation features through reef passages and around islands, which are known to have a significant impact on large-scale circulation (Wolanski and Spagnol 2000), whilst using a coarser resolution in ‘open-sea’ areas where flow is known to be

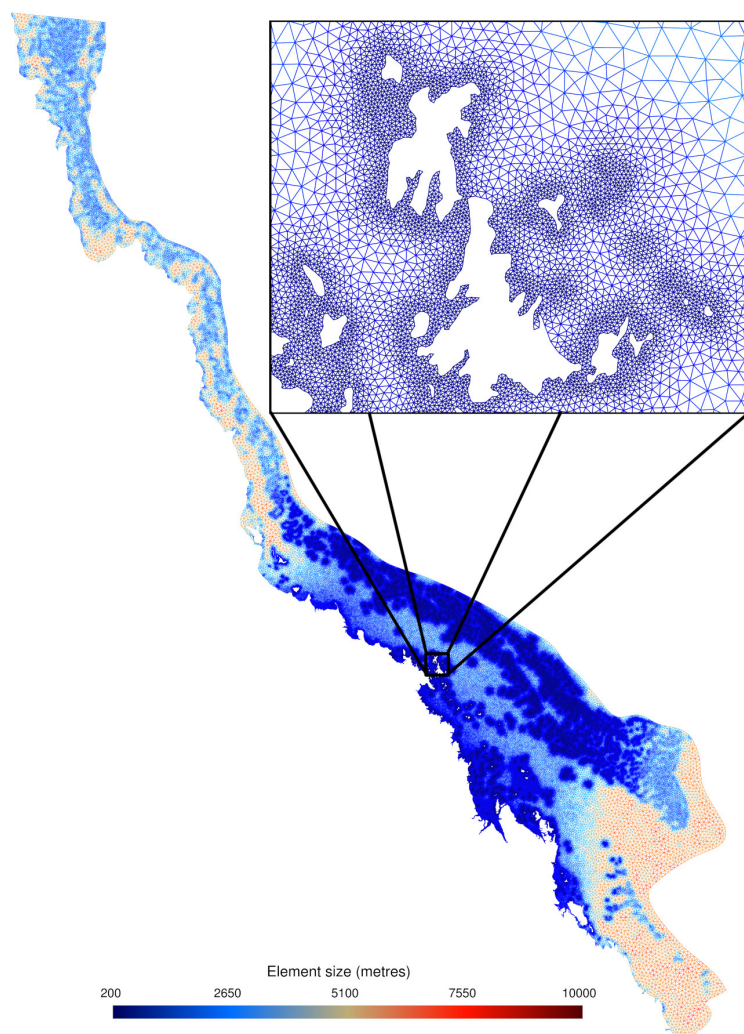


Figure 4.3: The oceanographic grid used for simulations. The grid is colour-coded by the local characteristic element size – smaller elements are shown in blue and larger elements are shown in red. The element size is a function of water depth and distance to the nearest reef. In addition, the element size is further reduced in the central GBR region. The grid contains roughly 500,000 triangular elements. The western boundary is the North Queensland coastline whilst the northern, eastern and southern boundaries are with the open sea. The box shows grid detail around the Whitsunday Islands.

more uniform. This modelling approach allows computational resources to be focused to where they are needed most.

The SLIM model has already been shown to be capable of reproducing important small- and large-scale circulation features in the GBR by Lambrechts et al. (2008), and has been used and validated in various studies of the hydrodynamics and ecology of the GBR (e.g. Andutta et al. (2012), Andutta et al. (2011), Hamann et al. (2011), and Wolanski et al. (2013)) and other coastal oceans and estuaries around the world (e.g. de Brye et al. (2010) and Sassi et al. (2011)).

Whilst this study focuses on larval dispersal in the central third of the GBR, from just north of Townsville (18.7°S) down to just south of Broad Sound (22.5°S), the grid covers

the entire coastal ocean of the GBR from 11°S down to 25.5°S, but with a lower resolution in the northern and southern thirds, where larval dispersal is not simulated. This is to allow the boundary conditions to be imposed at the shelf break where the data are more reliable, and has very little effect on the computational cost of simulation due to the low resolution outside of the central third of the GBR.

4.2.1.2 Governing equations, forcings and paramaterisations

SLIM was used to solve the depth-integrated shallow water equations to calculate the water elevation η and the current velocity $\mathbf{u}$:

$$\frac{\partial \eta}{\partial t} + \nabla \cdot (H\mathbf{u}) = 0 \quad (4.1)$$

$$\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla) \mathbf{u} = -f \mathbf{e}_z \times \mathbf{u} - g \nabla \eta - C_{BD} |\mathbf{u}| \mathbf{u} + \frac{\boldsymbol{\tau}}{\rho H} + \frac{1}{H} \nabla \cdot [H\nu(\nabla \mathbf{u})] \quad (4.2)$$

where H is the water column depth, f is the Coriolis factor, $\mathbf{e}_z$ is a unit vector pointing vertically upwards, C_{BD} is the bottom stress coefficient, $\boldsymbol{\tau}$ is the surface wind stress, g is the gravitational acceleration, ρ is the water density and ν is the horizontal eddy viscosity.

The model was set up in a similar way to that described by Lambrechts et al. (2008) and Andutta et al. (2011). The bathymetry data used were from the 100m resolution dataset produced by Project 3DGBR (Beaman 2010). The bottom stress coefficient is given as $C_{BD} = \frac{g}{C^2 H}$, with the Chezy coefficient $C = H^{1/6}/n$, and where the Manning coefficient used was $n = 2.5 \times 10^{-2} m^{1/3} s^{-1}$. This value was multiplied by 10 over shallow reefs to account for the increased roughness of reef surfaces. The positions of shallow reefs in the GBR were taken from the global distribution of coral reefs provided by the Great Barrier Reef Marine Park Authority (GBRMPA 2007). The reefs are not considered emergent and have water over them at all times. Smagorinsky's paramaterisation was used to account for unresolved turbulent features and boundary layer effects around coastlines and islands, with horizontal kinematic eddy viscosity dependent on the local grid element size.

The external forcings applied to the model consisted of tides and residual currents at the open-sea boundaries and wind over the entire domain. Tidal forcing was applied at the boundaries using the OSU TOPEX/Poseidon Global Inverse Solution dataset (Egbert and Erofeeva 2002), whilst wind data extracted from NCEP reanalysis was provided by NOAA/OAR/ESRL PSD (Kalnay et al. 1996). The wind stress acting on the sea surface was modelled using the paramaterisation proposed by Smith and Banke (1975). The effect of the East Australian Current was accounted for by imposing a constant residual flow into the domain at the boundary with the Coral Sea between 15.0°S and 17.6°S, and allowing this water to flow out through the southern and northern open-sea boundaries, following the same approach as Brinkman et al. (2001). The hydrodynamics were validated using observed oceanographic elevation and current data. This validation is presented and discussed in 4.A.

4.2.2 Biophysical particle transport

The dispersal and settlement of larvae was modelled by considering millions of “virtual larvae” released into the domain as autonomous, buoyant, individual organisms, pas-

sively transported by the ocean currents and subject to some very simple biological processes. This is a type of Individual Based Model (see Grimm et al. (2006) for an introduction to IBMs).

Transport of larvae was modelled using a random walk formulation of the 2D advection-diffusion equation² as outlined in Spagnol et al. (2002) and Hunter et al. (1993). The equations used were:

$$\mathbf{x}_{n+1} = \mathbf{x}_n + \mathbf{v}_n \Delta t + \frac{\mathbf{R}_n}{\sqrt{r}} \sqrt{2K\Delta t} \quad (4.3)$$

$$\mathbf{v}_n = \left(\mathbf{u} + \frac{K}{H} \nabla H + \nabla K \right) \Big|_{\mathbf{x}_n} \quad (4.4)$$

where $\mathbf{x}_n$ and $\mathbf{x}_{n+1}$ are the particle positions at time iterations n and $n+1$ respectively, Δt is the time difference between iterations, $\mathbf{R}_n$ is a horizontal vector of zero-mean random numbers with variance r , K is the horizontal diffusivity coefficient, H denotes water depth and $\mathbf{u}$ is the depth-averaged horizontal water velocity supplied by the ocean model. The time step used for the simulations in this study was set to $\Delta t = 90s$. The horizontal diffusivity coefficient, K , was calculated using the parameterisation presented in de Brye et al. (2010), which makes use of the formula of Okubo (1971) to introduce a dependence on the local hydrodynamic grid element size. This approach has been used in numerous studies of coastal seas and estuaries using multi-scale models (e.g. see Andutta et al. (2011), de Brauwere et al. (2011), Hamann et al. (2011), and Lambrechts et al. (2008)).

The advantages of modelling larval transport with an IBM are: 1) that we can know the start and end points of each larva released into the domain, and therefore directly measure the relative strength of larval exchange between every pair of reefs, and 2) that we can directly simulate age- and location-specific processes taking place on larvae (e.g. mortality, acquisition/loss of competence).

The particle-tracker used in this study also modelled two simple age-related biological processes taking place on the virtual larvae: mortality and acquisition/loss of competence, and these were modelled as described by Connolly and Baird (2010), with the mortality rate being either constant or taken from a Weibull distribution, depending on the species, and the onset and loss of competence modelled as a gradual process governed by fixed competence acquisition and loss rates. A larva was only considered capable of settling onto a reef whilst it was competent. The values of the parameters used, and the type of mortality model used for each species (constant rate or taken from a Weibull distribution) were based on the experimental observations of Connolly and Baird (2010).

The virtual larvae were released over all of the shallow-water reefs in the domain of interest. The number of larvae released over each reef was a proportional function of the reef's surface area, with greater numbers of larvae released over larger reefs. In the absence of widespread reef-specific coral cover data, this assumption was necessary, despite the fact that coral density may vary from one reef to another, for a variety of reasons (e.g. pollution, perturbation frequency, reef topography). Larvae were then tracked for the duration of the simulation. Once a larva had acquired competency, it was considered to settle onto the first reef it travelled over. As soon as a larva settled onto a reef it was immediately removed from the remainder of the simulation.

² $\frac{\partial}{\partial t}(Hc) + \nabla \cdot (\mathbf{u}Hc) = \nabla \cdot (HK\nabla c)$ where t is time, c is depth-integrated tracer concentration, H is water depth, $\mathbf{u}$ is the depth-averaged horizontal water velocity and K is the horizontal diffusivity coefficient.

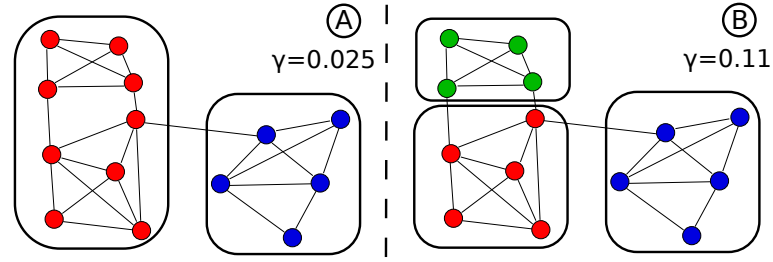


Figure 4.4: Example illustrating the role of the resolution parameter γ in the community detection method. Diagrams A (left) and B (right) show two identical graphs, with the circles representing nodes and the lines between them representing connections. These connections all have equal weight. Both graphs have been partitioned using the community detection algorithm described in Section 4.2.3.2, and the thick lines and colour-coding demarcate the communities. The graph in diagram A was partitioned with the resolution parameter, $\gamma = 0.025$, whilst the graph in diagram B was partitioned using $\gamma = 0.11$. Using a lower value of gamma imposes a stronger constraint on the maximum connectivity allowed between any two communities, and so results in fewer communities being detected.

4.2.3 Extracting useful information

The output of the biophysical model is a large connectivity matrix whose elements give the strength of the connectivity between every pair of reefs in the domain, where the connectivity strength is at this point defined as the number of larvae released over the source reef which settled onto the sink reef. Thus the connectivity matrix encapsulates all of the relevant output from the particle tracking simulation.

Given the large number of reefs in the domain (over 1,000), finding useful information from this matrix is a challenge in itself. The strategies employed can be broadly divided into two categories: statistical analysis and identifying spatial patterns. These will now be outlined in turn.

4.2.3.1 Statistical analysis

We can define some appropriate statistical quantities to characterise connectivity patterns within a given region. These can be used both to describe connectivity in the whole domain, and to compare the connectivity patterns seen in various well-chosen sub-regions.

- **Weighted connectivity length:** the characteristic length scale of connectivity between reefs. It is calculated as:

$$\frac{\sum_{\text{all connections}} \text{connection strength} \times \text{connection length}}{\sum_{\text{all connections}} \text{connection strength}} \quad (4.5)$$

where the connection strength is given by the number of larvae released over the source reef that settled onto the sink reef, whilst the connection length is the radial distance between source and sink reefs.

- **Proportion of self-recruitment:** the proportion of connections for which the source and sink reefs are the same.

- **Average plume length:** the furthest distance from the source reef at which connections occur, averaged over all connections. This is an indication of how far away a typical reef's influence extends. This may be a useful indicator of the furthest distance at which genetic connectivity can occur.

4.2.3.2 Identifying spatial patterns

Another way of characterising the connectivity of the reef network is to look for spatial patterns. It would be useful to identify clusters of reefs which are strongly connected to each other, but weakly connected to reefs outside of their cluster. By partitioning the GBR reef network into such clusters we can identify ecologically separate groups of reefs, and therefore infer the presence of barriers to larval dispersal between these groups.

We propose a graph theoretical approach to partition the GBR into reef clusters. The GBR can be cast as a directional, weighted graph by considering its reefs as nodes in the graph, and the transport of larvae between reefs as connections, or “edges”, linking the nodes. The strength of each edge, known as its “weight”, is given by the connection strength between the two nodes it connects (i.e. the number of larvae travelling from one node to the other), denoted by w_{ij} for an edge linking source reef i to sink reef j .

One particularity of this graph is that an edge linking two small reefs will have a much smaller weight than an edge linking two large reefs, as fewer larvae are released over the small reefs during the simulation. Connections between larger reefs then play a larger role than connections between smaller reefs, even where they only account for a small fraction of the total larvae released over the source reef. We mitigate this problem by normalising the edge weight by an appropriate quantity to make it “non-dimensional”; we chose to normalise the edge weight w_{ij} by the total number of larvae released at reef i (that have settled somewhere), denoted by s_i . We thus arrive at the normalised edge weight $A_{ij} = w_{ij}/s_i$. The net effect is to increase the importance of edges between small reefs, which would otherwise be dwarfed by the edges between the larger reefs.

The aim is then to partition this graph into a number of coherent clusters, known as communities, whose members are strongly connected with each other and weakly connected to the other nodes in the network. Many methods have been developed in recent years to partition a graph into communities (see Fortunato (2010) for an extensive review). One of the most popular methods has been to optimise a quantity called “modularity”, which is a measure of how strongly a graph is divided into clusters compared to a random graph (Newman and Girvan 2004). A significant drawback of this method is that it suffers from a resolution limit (Fortunato 2007), meaning that communities smaller than a certain scale (relative to the size of the graph) cannot be identified. In addition, the ecological significance of communities identified using modularity is not entirely clear, due to the comparison to a random graph.

We therefore chose to use a variant of modularity which does not suffer from these problems. Specifically, we employed the Constant Potts Model (CPM) developed by Traag et al. (2011) and Ronhovde and Nussinov (2010), which is based on the principle of comparing the density of edges within the communities to a constant resolution parameter, rather than to a random graph. More specifically, if we denote by S_c the set of nodes that belong to a community c , we can define by $e_{cd} = \sum_{i \in S_c, j \in S_d} A_{ij}$ the total weight between community c and d , and denote by n_c the total number of nodes in community c . CPM is then defined as

$$\mathcal{H} = - \sum_c e_{cc} - \gamma n_c^2, \quad (4.6)$$

where e_{cc} is simply the total weight inside community c , and γ is the user-defined resolution parameter. The minus sign is simply a matter of convention. The goal is to find a partition into communities for which $\mathcal{H}$ is minimal. The optimisation of $\mathcal{H}$ was carried out using a modified Louvain Method algorithm (Blondel et al. 2008), following the approach described in Traag et al. (2011). The CPM approach has also been used to study the community structure of a marine network by Nilsson Jacobi et al. (2012), who instead used a spectral based algorithm to optimise the objective function. A comparison of the performance of this algorithm with the Louvain Method algorithm is included in 4.B. Both methods returned partitions of similar quality on benchmark networks, and returned similar partitions for a set of central GBR connectivity networks.

CPM has two principal advantages (Traag et al. 2011). Firstly, it doesn't suffer from a resolution limit. Hence, there is no theoretical smallest or largest scale beyond which it is unable to identify communities. Secondly, the communities have a natural interpretation, which is twofold. First, in an optimal partition, each community has an internal connectivity of at least γ , i.e. $\frac{e_{cc}}{n_c^2} \geq \gamma$. Second, two communities in an optimal partition are separated by a connectivity of at most γ , i.e. $\frac{e_{cd}}{n_c n_d} \leq \gamma$. In other words, the communities identified by the algorithm should have the two following properties:

Inner connectivity The average connection strength between members of the same community is greater than γ

External connectivity The average connection strength between any two reefs in different communities is less than γ

This approach allows us to detect reef communities at different spatial scales. If we use a low value of γ , the connectivity between any two communities will be small (i.e. we have nearly impermeable community boundaries), but the internal connectivity may also be low and the size of the communities will tend to be large. If instead we use a higher value of γ , the connectivity between any two communities may be higher, but the internal connectivity will also be higher and communities will tend to be smaller and boundaries more permeable. The γ value is therefore an indication of how much inter- and intra-community connectivity there is. This concept is illustrated in Figure 4.4.

This naturally leads to the question of how to find the “optimal” value of the resolution parameter, γ . In reality there is no “optimal” value: the size of the value used clearly depends on what question we want to answer. Imposing a small value of γ will partition the GBR into a small number of large, weakly connected communities. This will allow us to identify the most ecologically isolated reef communities, and will therefore allow us to find the strongest boundaries to larval dispersal in the GBR. Imposing a higher value of γ will allow us to identify smaller communities which may exist within the boundaries of the larger communities, and thus identify more localised or weaker barriers to dispersal.

A sensitivity analysis is carried out to identify how 1) the number of communities and 2) the percentage of inter-community connectivity vary over a range of γ values. An example of such a sensitivity analysis, showing the variation of the proportion of inter-community connectivity with γ , is shown in Figure 4.5. This figure illustrates how the inter-community connectivity increases in distinct steps as γ is increased. Each jump in the curve generally corresponds to a significant change in the community partitions identified by the algorithm. Between two jumps there are plateaux of relatively stable connectivity over some interval $[\gamma_1, \gamma_2]$. Larger plateaux then correspond to especially

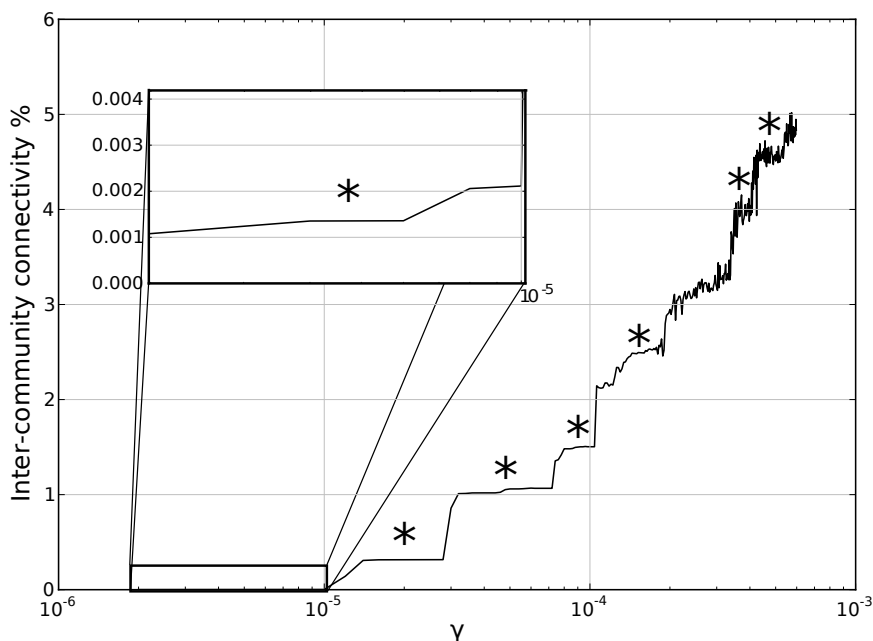


Figure 4.5: The percentage of connectivity crossing community boundaries as a function of the resolution parameter, γ for *G. retiformis* coral larvae. The jumps correspond to significant changes in the partitioning configuration. The asterisks identify ‘stable’ partitioning configurations. The scale is logarithmic in x , as a given interval of γ at the lower end of the scale will be more significant, proportional to the local value of γ , than at the higher end of the scale.

pertinent partitions, since the external connectivity will in general be lower than γ_1 while the internal connectivity will be higher than γ_2 . We then choose a selection of values of γ for which these variables are relatively stable, indicated by the asterisks in Figure 4.5, and compare the community configurations obtained using each of these values.

Since boundaries to larval dispersal generally arise due to topographic features or between areas with distinct water circulation patterns, we can reasonably expect that the characteristics of larval dispersal in each community may be distinct from each other. We therefore calculate the statistical quantities defined in Section 4.2.3.1 for each reef community and compare them, to see if there is a significant variation in connectivity length-scales in the different communities. If, for a given value of γ , all of the communities identified have similar connectivity length-scales then we will generally choose to ignore that particular configuration, as it does not identify communities with significantly different connectivity patterns. Ultimately the goal is to identify the configurations which partition reefs into communities with physically distinct dispersal patterns.

4.3 Results and Discussion

Virtual larvae were released over all reefs in an area encompassing the central GBR - roughly one third of the GBR’s total area. Larval dispersal was simulated for 4 different species of broadcast spawning larvae for which mortality and settling data were readily available: *Goniastrea retiformis*, *Acropora gemmifera*, *Platygyra daedalea* and *Acropora millepora*. All four species are known to be present in the GBR. The oceanographic forc-

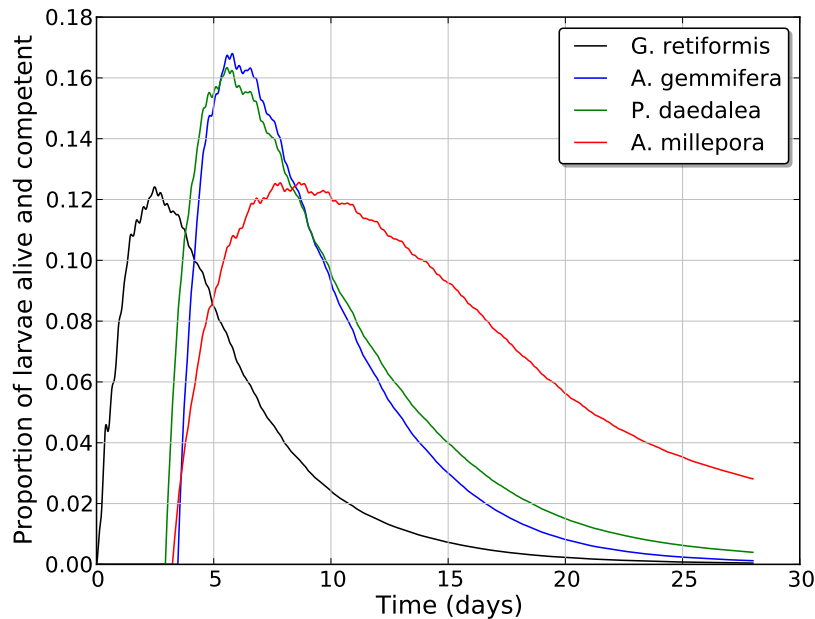


Figure 4.6: Graph showing the proportion of larvae that are alive and competent to settle, as a proportion of the total number of particles released, for each species during the simulation (lasting 4 weeks after particle release). A greater proportion of *G. retiformis* larvae are alive and competent in the days immediately after release than any of the other species, which explains their higher self-recruitment rate and lower weighted connectivity length.

ings used were for the period of December 2007, corresponding to a typical coral mass spawning period, and the positions of the larvae were tracked for 4 weeks. After this period the proportion of larvae still alive was very small (<4% for all species). Whilst variations in oceanographic conditions between successive annual spawning seasons may modify larval dispersal patterns year-on-year, we chose to focus on one single season, as the scope of this paper is not to provide yearly estimates of dispersal patterns but rather to develop tools which can be used to study connectivity patterns for any given spawning season.

4.3.1 Dispersal statistics

The graph showing connection strength against distance for the different species studied is shown in Figure 4.7. Inter-species differences in dispersal potential are clearly visible. Table 4.1, showing the global connectivity statistics, provides some additional detail. The proportion of larvae self-recruiting varies significantly between species, from 55% for *G. retiformis* to 18-19% for *A. gemmifera* and *P. daedalea* and down to only 13% for *A. millepora*. This difference is explained by the fact that the latter three species have much longer average pre-competency periods than *G. retiformis*: their larvae typically start to acquire competence after 3-4 days, whereas larvae of *G. retiformis* start to become competent immediately, and so are more likely to settle close to their release site. This is shown in Figure 4.6, which shows the proportion of larvae alive and competent during the simulations. The later this curve peaks, the longer the average pre-competence peri-

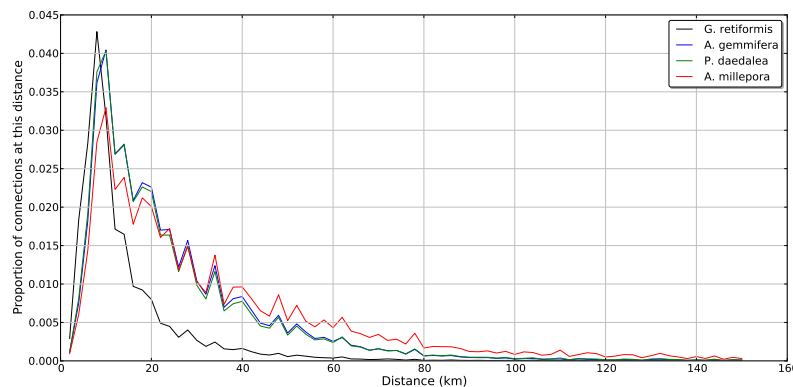


Figure 4.7: Graph showing the connection strength against distance for larvae of 4 different species of coral, after a 4-week simulation. The distance is measured as radial distance between source and sink reefs. The x-axis (distance) is cut at 150 km. Self-recruitment is not shown in this graph, however it is used to calculate all other connectivity length-scale statistics.

Coral species	Self-recruitment	Weighted connectivity length	Long-distance connectivity	Average plume length
<i>G. retiformis</i>	55%	6 km	0.3%	80 ± 60 km
<i>P. daedalea</i>	19%	20 km	1.6%	117 ± 69 km
<i>A. gemmifera</i>	18%	20 km	1.2%	112 ± 68 km
<i>A. millepora</i>	13%	31 km	5.0%	131 ± 73 km

Table 4.1: Summary of global connectivity characteristics for each species of coral after a 4-week simulation of larval dispersal. For an explanation of each quantity see Section 4.2.3.1. Average plume length is shown with its standard deviation.

ods, and so the longer the period during which the larvae can be advected and diffused away from their natal reef prior to settlement.

The typical length-scales over which most connectivity occurs tell a similar story to the self-recruitment statistics: *G. retiformis* larvae settle closer to their natal reef than the other species, with an average connectivity length of 6 km, whilst *A. millepora* tend to settle furthest from their natal reef, with an average connectivity length of 31 km. Long-distance connectivity (where long-distance is here defined as >100 km) is marginal in ecological terms for all 3 coral species, though not entirely insignificant for *A. gemmifera*, *P. daedalea* and *A. millepora*. Finally, the average plume lengths indicate that we would expect to see some minimal larval exchange at distances of over 80-130 km from the source reef, depending on the species.

4.3.2 Spatial patterns for *G. retiformis*

The community detection method described in Section 4.2.3.2 was used to partition the reefs into reef communities. For each species a set of different possible partitioning arrangements was generated by varying the value of the resolution parameter, γ , through a given range. A selection of different partitioning arrangements for the species *G. retiformis* is given in Figure 4.8, showing different partitioning arrangements obtained using a low, a medium and a high value of γ . These correspond to arrangements with low,

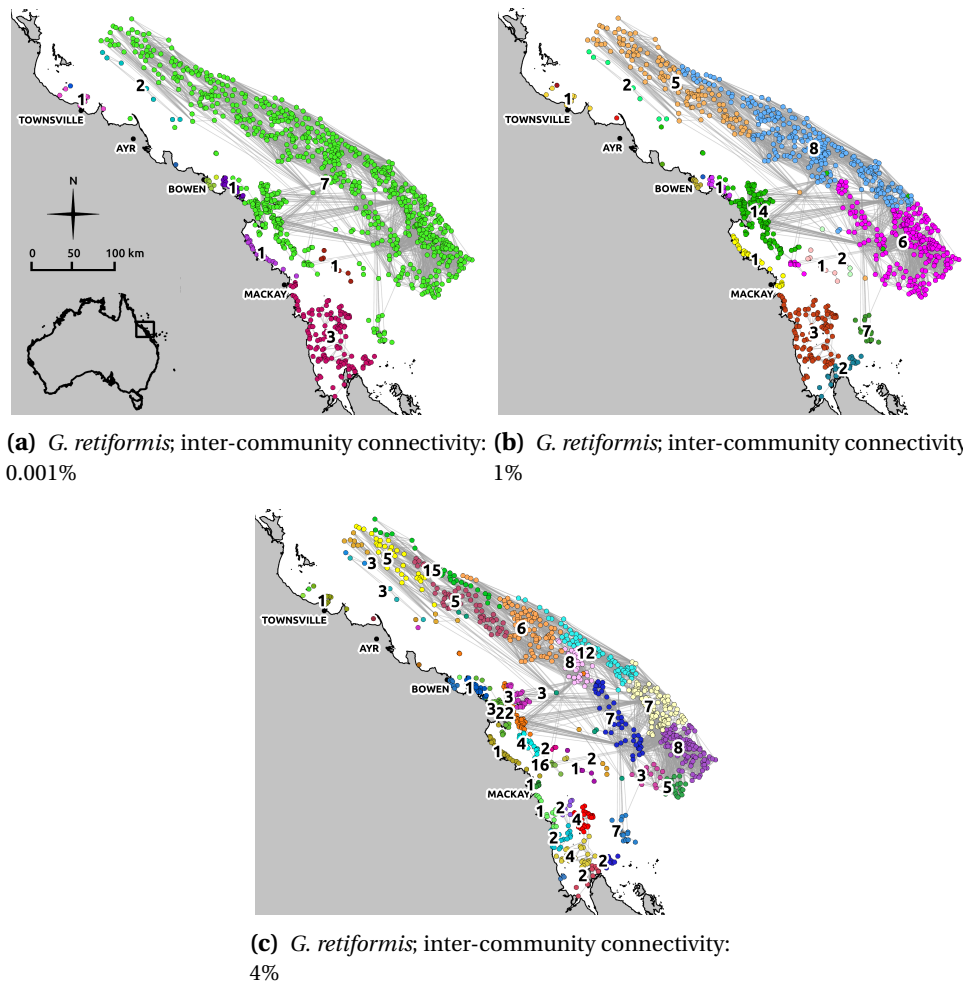


Figure 4.8: Different sets of reef communities obtained using different values of the resolution parameter, γ , for *G. retiformis* larvae, with reefs in the same community shown in the same colour. These partitions were obtained by increasing the value of the resolution parameter in the community detection method from a low value (4.8(a)) to a high value (4.8(c)). The numbers in the white circles show the average weighted connectivity length in each community, in kilometres. Connections between reefs are shown in light grey for illustrative purposes, with the weaker connections filtered out.

medium and high levels of inter-community connectivity respectively. We will focus our description on *G. retiformis* for now, as the effect of varying γ has a similar effect for the other species. We will subsequently compare equivalent community configurations obtained for different species.

The partitioning arrangement obtained with the lower value of γ , shown in Figure 4.8(a), exhibits a very low level of inter-community connectivity – just 0.001%. In other words only 1 in every 100,000 settled larvae settled outside of their reef community, so broadly speaking the number of larvae crossing community boundaries is ecologically insignificant. We can see that the reefs around the Whitsunday Islands have been grouped together in the same community as the offshore reefs, as the level of transport between the two areas is not entirely insignificant. Perhaps surprisingly, the group of coastal reefs just south of the Whitsunday Islands is in a separate reef community, imply-

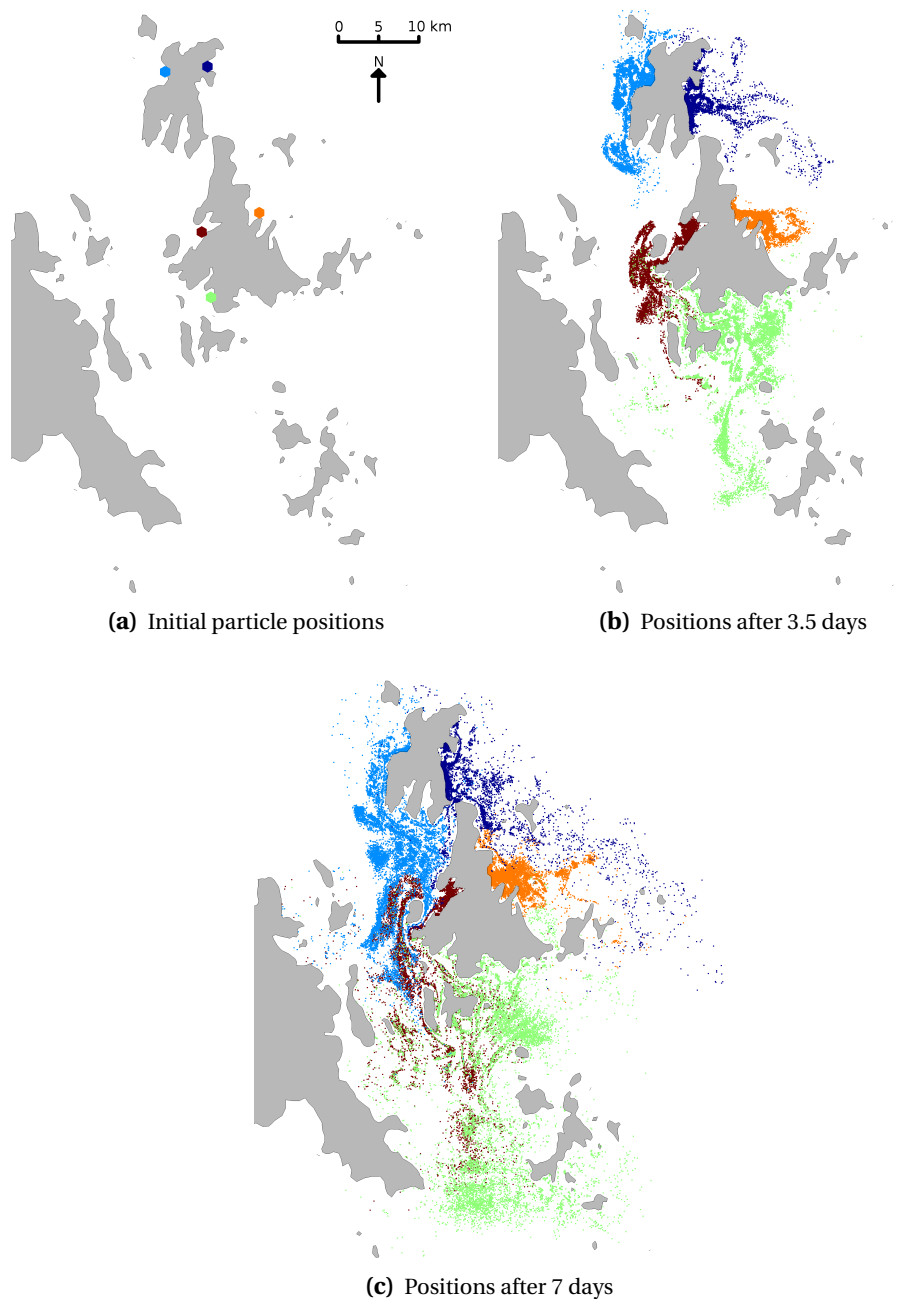


Figure 4.9: Images showing the dispersal of particles released at five chosen sites around the Whitsunday Islands over a week. Particles are colour-coded by release site. Mortality and settling were ignored.

ing that the model predicted negligible levels of transport between the two communities, despite their geographic proximity. This is an indication that the “isolation-by-distance” method for estimating inter-reef connectivity is not always accurate in areas with complex topography and flow patterns, at least at small scales. We can also see that the average length of the connections within each community, also shown on the diagram, can vary from one community to the next, suggesting that larval dispersal dynamics are dif-

ferent in each community.

Figure 4.8(b) shows a partitioning arrangement if we increase the value of the resolution parameter such that inter-community connectivity now accounts for 1% of all connections. The reef communities are therefore still ecologically isolated units, as only 1 in every 100 settled larvae crosses a community boundary, but these boundaries can now be considered to be slightly less rigid. Looking at this partitioning arrangement, we can see that many smaller-scale community structures exist within the large-scale community structure shown in Figure 4.8(a). In particular, the large block of offshore reefs has been separated from the Whitsunday Islands community, meaning that the “barrier” to dispersal between the Whitsunday Islands group and the offshore reefs (which physically corresponds to a channel of southward-flowing open water), whilst not as significant as the “barrier” between the Whitsunday Islands and the coastal reefs south of them seen in Figure 4.8(a), is still more significant than any “barrier” within the Whitsunday Islands themselves, since these are still a whole community. It is also revealing that the difference in the weighted connectivity lengths in the offshore reef communities and in the Whitsunday Islands community is much more significant than any difference seen in Figure 4.8(a). This suggests that the different reef communities identified with this “medium” value of γ , and shown in Figure 4.8(b), have much more distinctive dispersal dynamics.

A partitioning arrangement obtained using a higher value of γ , in which 4% of connectivity crosses community boundaries, is shown in Figure 4.8(c). This figure reveals a more complex structure of communities in both the offshore group of reefs and in the Whitsunday Islands group. Most offshore reef communities are inclined along the long-shore axis suggesting that reefs are better connected along this axis rather than along the cross-shelf axis. This is because the net currents act in the south-eastward longshore direction. With a couple of exceptions, most of the offshore reef communities have very similar average connectivity lengths. This suggests that there are no major differences in the dispersal dynamics amongst the offshore reefs.

It is more interesting however to look at the reefs around the Whitsunday Islands. At the higher γ , they have been split into three separate communities: one “coastal” community of nearshore reefs, with a very small weighted connectivity length (3 km), another “middle” community of reefs with a much greater weighted connectivity length of 22 km, suggesting that some larvae from this community settle far away from their natal reef, and finally another “external” community of reefs on the outer, eastward-facing side of the Whitsunday Islands. Somewhat surprisingly, these reefs also have a small weighted connectivity length - only 3 km - suggesting that either these reefs are more sheltered than those in the “middle” community, or else simply that most of the larvae released here are lost to sea and don’t find any reefs to settle onto far away.

We can gain an insight into the physical processes causing this difference by looking at the effects of the water circulation on transport around the Whitsunday Islands. Figure 4.9 shows the simulated dispersal of particles released at 5 different carefully chosen sites around the Whitsunday Islands after 3.5 days and after 1 week. In the simulation used to create these figures, the particles underwent no mortality or settling processes, so we can use these images purely as a guide to potential dispersal rather than as a prediction of real dispersal for a given species. We should note that in the species-specific simulations, after 3.5 days 93% of *G. retiformis* had settled onto a reef, whilst after 7 days this number was 97%. This means that very few *G. retiformis* larvae would have dispersed further from their release point than shown in both figures. It is clear from these images that particles

released on the eastward-facing external side of the Islands tend to stay closer to their release point and are advected to the open sea where there are no reefs, whilst particles released in middle section tend to disperse further away and pass through other reef-dense areas. Furthermore, there is little mixing between particles released on either side. This explains why the two sides are placed in different communities for *G. retiformis*, and why the connectivity length scales are so different in these communities.

In summary, Figures 4.8(a)-4.8(c) show different possible partitioning arrangements for *G. retiformis*, each of which gives us a different set of information. The question is which is the most useful? We suggest that all three are useful in that they complement each other, and provide us with information about the network over different length scales. Figure 4.8(a) suggests that as a first large-scale approximation we should at least treat the coastal reefs south of the Whitsunday Islands, and the reefs in Broad Sound, separately from the other reefs in the domain. Figure 4.8(b) shows that, in addition to this clear separation, there are also very significant differences on a smaller scale between the dispersal patterns of larvae released around the Whitsunday Islands and those released on the offshore reefs, and finally Figure 4.8(c) shows that the Whitsunday Island reefs can themselves be subdivided into three different areas with distinct patterns of larval dispersal. Depending on the scale at which we want to look at the system, we should select a value of gamma which highlights the information relevant for that scale. We note that the most meaningful community partitioning configurations are those obtained using ranges of the resolution parameter which are not sensitive to small changes in its value (cf. Figure 4.5): it is these sets of communities which are most clearly defined. As such there are only a certain number of values of Inter-Community Connectivity for which it is possible to find a meaningful set of communities (for instance for *G. retiformis*, shown in Figure 4.5, we can count 7 different stable partitioning configurations).

4.3.3 Spatial patterns for all species

Figure 4.10 shows partitioning arrangements for all four species studied, where the percentage of inter-reef connectivity is fixed at around 4% – high enough to see the smaller reef communities but low enough to be ecologically marginal or insignificant. This figure shows that the species with the highest dispersal potentials – primarily *A. millepora* – form the largest communities, whilst *G. retiformis* form the smallest communities. This is because *A. millepora* larvae take longer to acquire competence and thus tend to travel further from their natal reef before settling (as reported in Table 4.1); they are therefore more capable of overcoming physical barriers to dispersal than other species.

Despite these differences in community size however, we can still see some patterns recurring for all of the species in the central GBR. For instance, the dispersal boundary between the Whitsunday Islands and the offshore reefs is always present (see Figure 4.1 for a map of the area). The boundary between the Whitsunday Islands and the coastal reefs just south of them is also present for all species, despite their geographical proximity. The typical connectivity length scales also vary significantly from one community to another, and tend to be smaller for nearshore reef communities and larger for offshore communities. This suggests that community boundaries often coincide with boundaries between areas with different larval dispersal dynamics.

Figure 4.10 also reports the average distance between the nearest neighbouring MPAs (GBRMPA-designated “green zones”, or no-take areas) in every community containing 2 or more MPAs. These figures show that MPA spacing does to some extent follow the same

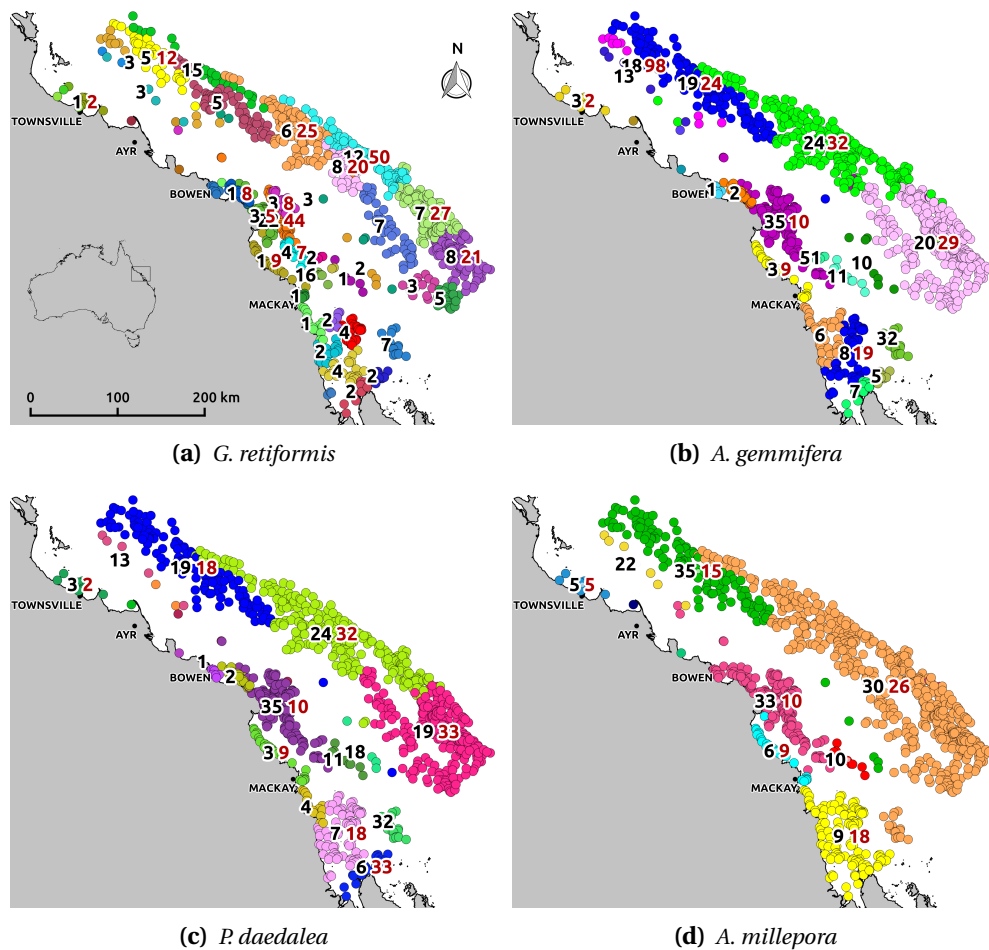


Figure 4.10: Equivalent reef community configurations for 4 species of coral larvae. Reefs of the same colour belong to the same community. Black numbers show the weighted connectivity length (km) for reefs in each community. Red numbers show the average MPA spacing (km) in communities containing more than one MPA. The proportion of connectivity crossing community boundaries is approximately 4% for all configurations, so they are directly comparable with each other.

trends as larval dispersal distances; in nearshore areas MPAs tend to be closer together, whilst they tend to be further apart in offshore reef areas. This is positive for promoting connectivity between separate MPAs, as larvae tend to settle closer to their natal reef in nearshore areas. One notable exception is in Broad Sound, where MPA spacing is larger than in other nearshore areas, yet larval dispersal distances remain small.

For the three species which disperse the furthest (*A. millepora*, *P. daedalea* and *A. gemmifera*), the dispersal distances are not too dissimilar to the MPA spacing³, suggesting that many MPAs may be ecologically connected to their neighbours. It is notable that some reef communities do not even contain 2 MPAs however, particularly the smaller communities. For *G. retiformis*, whose larvae disperse over smaller distances, typical

³It is important to bear in mind that the weighted connectivity length reported is only showing the average distance travelled by larvae; thus some larvae will be travelling further than this, as shown in Figure 4.7.

dispersal distances tend to be much smaller than average MPA spacing, and most communities do not contain 2 MPAs. This suggests that the level of connectivity between MPAs is likely to be very species-dependent.

4.4 Conclusions: identifying spatial patterns in connectivity

The process of larvae dispersing through the Great Barrier Reef is controlled by a multitude of factors, both physical (relating to marine transport) and biological (relating to the behaviour and development rate of the larvae). By using an unstructured-grid ocean model as a tool to simulate the ocean circulation in the GBR, we have been able to resolve flow from the large-scale down to the reef-scale, an essential pre-requisite for modelling larval dispersal in the GBR, as this can occur on length-scales ranging from hundreds of metres to hundreds of kilometres.

Using a relatively simple biological model, we have made large-scale predictions of larval dispersal using a small number of biological parameters, following the best available present knowledge of larval mortality and development rates as found by Connolly and Baird (2010). Whilst this simple model of larvae as passive massless objects is deemed sufficient to model the transport of coral larvae, an increase in model complexity would be essential for modelling fish larvae instead, in particular to account for their ability to directionally swim (see Fisher and Bellwood (2003), Gerlach et al. (2007), and Vermeij et al. (2010)). This is an area we plan to study in the future.

We have used a novel strategy to extract useful information from the connectivity matrix by employing a graph theoretical approach to identify ecologically separate reef communities. We have calculated connectivity characteristics separately for each reef community, and we have shown that the dispersal potential of larvae in different communities can vary significantly. We have provided estimates of dispersal potential in each community for 4 different coral species for a given spawning season, and we have shown that there are significant differences in the dispersal patterns and potentials between these 4 species. We have also compared these community-specific dispersal distances to the average spacing between neighbouring no-take MPAs in each community, and found that connectivity between MPAs is species-specific, and that MPA spacing does not always reflect the spatial patterns seen in larval dispersal distances.

In order to translate this approach into practical advice on MPA placement, the next step should be to quantify the effects of annual variation of larval dispersal patterns on the shape and positions of communities, and on the connectivity characteristics of each community for a given species. Results obtained by Kininmonth et al. (2010a) suggest that the dispersal network structure of the GBR may undergo significant annual changes, but that stronger connections are highly likely to remain in place, at least for the stretch of the GBR considered in their study. It would also be useful to consider a much larger number of different coral species, as it is known that significant inter-species variations in connectivity can exist (Drew and Barber 2012), though this may be hampered to some extent by a lack of biological data. Finally more work is needed to find a way to achieve an “optimal” MPA spacing which accounts for the different connectivity characteristics of many different species, for instance by identifying “source” and “sink” habitats common to multiple species.

Acknowledgements

This work was carried out under the auspices of ARC grant 10/15-028 of the *Communauté française de Belgique*, “Taking up the challenges of multi-scale marine modelling”. Computational resources were provided by the *Centre de Calcul Intensif et Stockage de Masse* (CISM) at the Université catholique de Louvain and the *Consortium des Équipements de Calcul Intensif en Fédération Wallonie Bruxelles* (CÉCI). J. Lambrechts is a post-doctoral researcher with the Belgian Fund for Scientific Research (FNRS). C.J. Thomas thanks Benjamin de Brye, Bruno Seny and Tuomas Kärnä for constructive discussions.

APPENDIX

4.A Validation of hydrodynamics

It is known that reef-scale eddies in the wakes of islands in the GBR have a 3D structure with localised upwelling and downwelling (see e.g. Deleersnijder et al. (1992) and White and Deleersnijder (2007)), which raises the question of whether a depth-integrated model is sufficient to model circulation in the region. The relatively shallow coastal waters of the GBR have, however, been shown to be generally well-mixed throughout the year, and flow on the continental shelf is known to be primarily horizontal (Middleton and Cunningham 1984; Wolanski 1994). Several studies have shown that two-dimensional models can predict physically accurate horizontal currents, even for tidal circulation around islands and headland eddies (e.g. Falconer et al. (1986)), as well as for large-scale flow in parts of the GBR (Luick et al. 2007). More specifically Lambrechts et al. (2008) found that the horizontal flow around islands in the GBR simulated using the depth-integrated SLIM model compared favourably to a high-resolution full three-

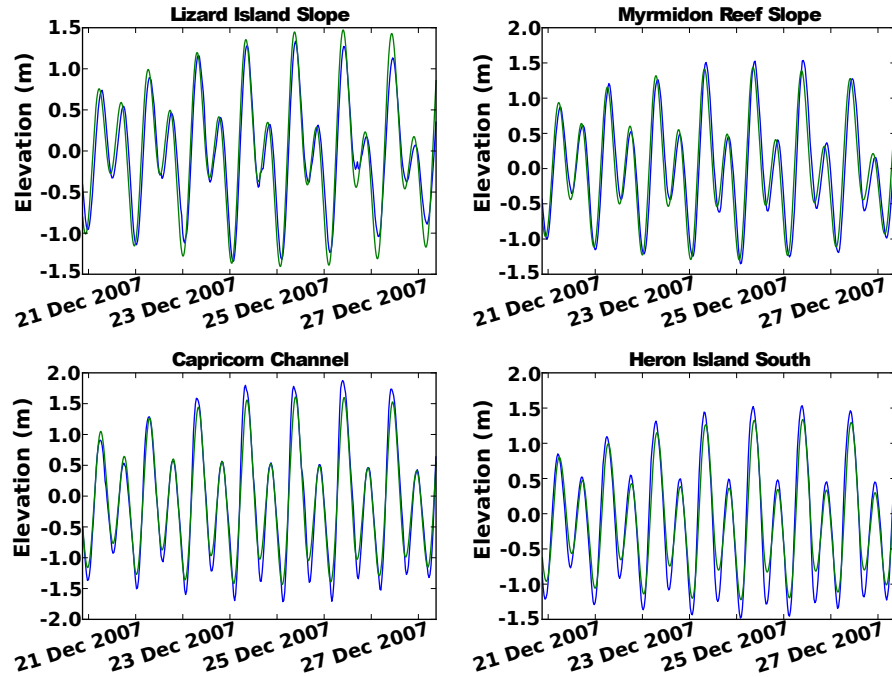


Figure 4.A.1: Graphs showing time-series of elevations at 4 different sites in the model domain. The blue curve shows observed data from the GBROOS mooring network and the green curve shows the model's predictions. The locations of the GBROOS moorings are shown in Figure 4.1.

dimensional model validated with observed data. Given the shallow depth and complex topography of the GBR shelf, as well as the well-mixed nature of GBR shelf waters, we therefore argue that it is more useful to achieve reef-scale resolution in the horizontal plane than it is to resolve vertical variations which, in most cases, are relatively small.

The work carried out by Lambrechts et al. (2008) shows that the hydrodynamic model used is able to reproduce small-scale circulation features well, however it is also necessary to validate the model's ability to realistically reproduce large-scale circulation through the region. This was done by comparing predictions of sea surface elevation (SSE) and water currents with observed data at various mooring sites. Data from long-term moorings obtained from the Integrated Marine Observing System's (IMOS) Great Barrier Reef Ocean Observing System (GBROOS) program run by AIMS/CSIRO were used to validate SSE, whilst current meter data from a variety of sources were used to validate water currents. The locations of the mooring points used are shown in Figure 4.1. The SSE observed at different GBROOS mooring sites is shown alongside model predictions for a typical weekly period in Figure 4.A.1. There is a good agreement between the two datasets both in terms of amplitude and phase.

Table 4.A.1 shows average longshore current velocities for the different mooring sites compared with model predictions. It should be considered that comparing currents at a given point is very delicate, as any discrepancy in spatial position and water depth can lead to a relatively large change in the observed current, especially close to reefs and islands – which is where most observing stations are situated – as the horizontal shear is often significant in these areas. In this context, Table 4.A.1 shows that there is a relatively good agreement between the model predictions and the observed dataset. We can therefore be relatively confident in the ability of the ocean model to realistically reproduce currents and SSE in the domain.

4.B Comparison of two CPM community detection algorithms

We compared the performance of the community detection algorithm employed in this study (described in Traag et al. (2011)) with the one used by Nilsson Jacobi et al. (2012), in order to test the validity of using either approach. We used two methods: first we com-

Site	Latitude (°S)	Longitude (°E)	U_{SLIM}	U_O	Source
Lizard Island	14.7406	145.4253	0.05	0.05	A
Cape Upstart	19.6253	147.9142	-0.04	-0.11	A
Old Reef	19.4071	148.0197	-0.14	-0.10	B
Bowden Reef	19.0600	147.9597	0.00	-0.02	C
Rattray Island	19.9826	148.5833	-0.03	-0.08	B
Hook	19.9400	149.1100	-0.14	-0.15	D
Bushy	20.8900	150.1600	-0.11	-0.13	D
Bell	21.8200	151.1400	-0.04	-0.06	D

Table 4.A.1: Observed longshore residual currents (U_O) and simulated longshore residual currents (U_{SLIM}), in ms^{-1} at various sites in the GBR. Positive indicates a northerly longshore direction, whereas negative indicates a southerly longshore direction. The Source column gives the source of U_O . Locations of moorings shown in Figure 4.1. Sources: A: Brinkman et al. (2001), B: Andutta et al. (2012), C: Wolanski et al. (1989), D: Middleton and Cunningham (1984)

pared the performance of each algorithm in partitioning a standard benchmark network with a known solution, and then we compared the partitions generated by each method for an actual GBR connectivity network.

4.B.1 Benchmark networks

The standard benchmark networks used were those described in Lancichinetti et al. (2008) and Lancichinetti and Fortunato (2009). We generated directed, weighted benchmark networks and measured the performance of both algorithms in identifying the correct partitions for a range of values of weight and topology mixing parameters (μ_w and μ_t respectively). The resolution parameter used to partition each network (labelled as γ in Traag et al. (2011) and $1/\beta$ in Nilsson Jacobi et al. (2012)) was calculated as the geometric mean of p_{in} and p_{out} , i.e. $\sqrt{p_{in}p_{out}}$, using the notation and definitions from Lancichinetti and Fortunato (2009), and following the same approach as Traag et al. (2011). Ten different networks were generated for each combination of μ_w and μ_t , and the two algorithms were in turn applied to partition each network. The quality of these partitions was measured by calculating the normalised mutual information (NMI) between these partitions and the true partitions for the network. NMI provides a measure of how similar two sets of partitions are. An average value of NMI was calculated for each combination of μ_w and μ_t , along with its standard deviation.

The results of the comparison are shown in Figure 4.B.1, where the x -axis spans a range of values of μ_w , and the y -axis shows NMI. The higher the NMI, the better the quality of the partitions found by the algorithm. These results show that both methods performed well, though the method of Nilsson Jacobi et al. (2012) worked better for networks with lower values of μ_t , whilst the method of Traag et al. (2011) worked marginally better for networks with higher values of μ_t .

4.B.2 GBR network

Both community detection methods were then used to partition the set of GBR connectivity networks discussed in Section 4.3.2. Table 4.B.1 shows the number of communities identified by each method for each network, as well as the NMI between the two partitions. These indicate that the high- and low- γ networks match well, whilst the middle- γ network has a slightly lower NMI. The differences between the partitions created by the two algorithms are generally limited to reefs close to the boundaries of communities being placed in one or the other neighbouring community. Figure 4.B.2 compares typical partitioning configurations generated by each algorithm for the low- γ case. Overall, the communities identified were not very sensitive to the community detection method used.

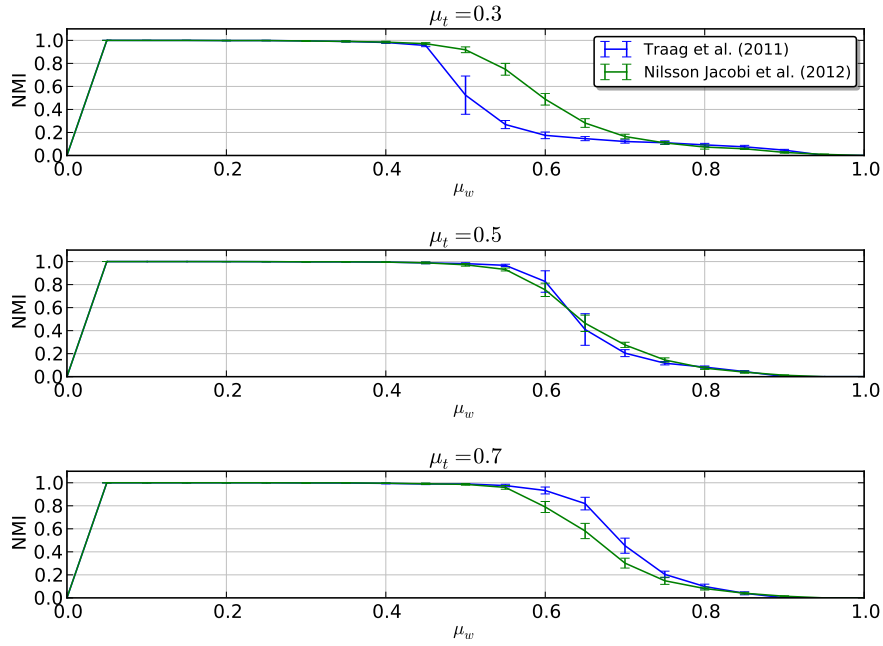


Figure 4.B.1: Results of the tests of the algorithm benchmark tests. Higher values of NMI indicate better performance. Error bars show standard deviation of NMI across repeated runs at the same value of μ_w .

γ	NMI	Number of communities	
		Traag et al. (2011)	Nilsson Jacobi et al. (2012)
0.0004	0.90	44	42
0.00003	0.79	17	15
0.000006	0.87	11	9

Table 4.B.1: Comparison of Traag et al. (2011) and Nilsson Jacobi et al. (2012) community detection methods for *G. retiformis* connectivity networks at low, medium and high values of γ . Each algorithm was run 10 times and average values are shown.

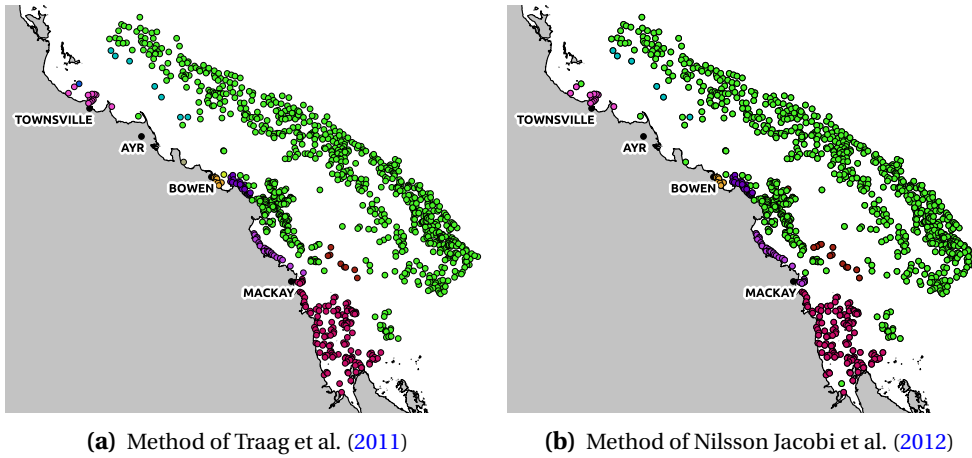


Figure 4.B.2: Typical partitioning configurations generated for low- γ *G. retiformis* network using both community detection algorithms. Reefs are colour-coded by community.

CHAPTER 5

CONNECTIVITY BETWEEN SUBMERGED AND NEAR-SEA-SURFACE CORAL REEFS

Summary

Recent technological advances in undersea mapping have revealed the presence of many reefs in the GBR at depths greater than 10 metres which were previously unmapped. As such, past studies on larval dispersal in the region have ignored a huge number of potential coral habitats. In this chapter, the potential contribution of these “submerged” reefs on coral connectivity is evaluated. The biophysical model of larval dispersal is used to model connectivity between near-sea-surface (NSS) reefs, whose upper reaches approach the sea surface, and submerged reefs, whose shallowest parts lie at greater depths. Connectivity patterns for the two reef types are compared, and the potential for submerged reefs to contribute larvae to NSS reefs is evaluated, and vice-versa. Connectivity between deeper and shallower parts of reefs is also evaluated, and we identify the shallow habitats most dependent on other shallow habitats for their larvae (and thus potentially most vulnerable to shallow-water disturbances). The most vulnerable areas are found to have undergone the greatest declines in observed coral cover over 19 years. The presence of submerged reefs is suggested as an important, stable source of larvae to other reefs, and potential implications for marine management are discussed.

This chapter reproduces the following article (with minor corrections and improvements):

Thomas, C. J., Bridge, T. C. L., Figueiredo, J., Deleersnijder, E. and Hanert, E. (2015) Connectivity between submerged and near-sea-surface coral reefs: can submerged reef populations act as refuges? *Diversity and Distributions*, doi: 10.1111/ddi.12360.

5.1 Introduction

Reef-building corals are the key ecosystem engineers of tropical coral reefs, the most diverse marine ecosystems on Earth. Increasing disturbance frequency is causing declines in the abundance and shifts in the composition of coral assemblages (Hughes et al. 2003; Loya et al. 2001; Wakeford et al. 2007). Altered coral assemblages can affect many other taxa dependent on structurally complex reefs (e.g. reef-associated fishes), leading to altered ecosystem processes and impacting the provision of ecosystem services (Graham and Nash 2013; Hughes et al. 2010; Pratchett et al. 2014). Consequently, the ability of reefs to recover from disturbance and maintain a coral-dominated state (termed 'resilience') is a key objective of coral reef management (Hughes et al. 2010; Mumby and Hastings 2008; Mumby and Steneck 2008).

Like many marine invertebrates, adult corals are sessile and rely on larval transport for dispersal and population persistence (Burgess et al. 2014; Shanks et al. 2003). Consequently, the recovery of coral populations following disturbance is often dependent on recruitment of larvae from elsewhere (Connell et al. 1997; Hughes and Tanner 2000). Understanding the potential for larval dispersal between reefs is important for predicting reef resilience. Well-connected reefs will receive a greater number of larvae from many sources, and may be more resilient to disturbances (Cowen et al. 2006; Hughes et al. 2005), but may also be more vulnerable to biological invasions (Hock et al. 2014; Johnston and Purkis 2011). Identifying reefs that export larvae to many other reefs is therefore a key consideration when designing marine protected areas (MPAs) (Almany et al. 2009; Palumbi 2003; Roberts 1997). In addition, MPA networks can be made more resilient by ensuring that protected reefs are also well connected with each other (Christie et al. 2010; Kininmonth et al. 2011).

Despite the implied importance of pelagic larval dispersal, a growing body of research on marine benthic organisms suggests that a large proportion of larvae are retained locally, even in species with the potential for long distance dispersal (Cowen and Sponaugle 2009; Shanks 2009; Swearer et al. 2002). For example, mark-recapture and parentage analysis of reef fishes indicate remarkably high levels (5–72%) of recruitment back to the natal population (Jones et al. 2009a). Corals also tend to exhibit high levels of local retention (fraction of offspring produced by a population that recruits back into that population), and therefore rely heavily on local sources of larvae for population replenishment (Figueiredo et al. 2013; Gilmour et al. 2009). Rising sea temperatures result in higher mortality and more rapid development of coral larvae, therefore climate change is predicted to further reduce dispersal capacity and reef connectivity (Figueiredo et al. 2014), though the additional impact of potential changes to water circulation patterns may also affect dispersal in as-yet unknown ways in different parts of the world. Consequently, accurate knowledge of connectivity patterns are essential for effective implementation of marine reserve networks (Almany et al. 2009).

Despite widespread acknowledgement of its importance (Harrison et al. 2012; McCook et al. 2010), connectivity patterns remain poorly understood at regional scales relevant to management (Drew and Barber 2012). For most marine species it is practically impossible to empirically track a significant number of larvae during the dispersal stage. Measures of genetic similarity are often used to infer connectivity between different populations (Burton 2009; Hedgecock et al. 2007; Palumbi 2003). However, these tools can only infer genetic connectivity (the flow of genes between populations), and not demographic connectivity, which concerns the flow of individuals in sufficient numbers to

influence population growth and persistence (Leis et al. 2011; Lowe and Allendorf 2010).

In light of these limitations, numerical modelling has become an important tool for estimating patterns of larval dispersal and connectivity (Werner et al. 2007). For example, Individual-Based Models (IBMs) coupled with hydrodynamic models have successfully been used to explicitly model larval dispersal (North et al. 2009). However, accurately modelling water circulation at the spatial scales that affect larval dispersal remains a key challenge. For example, small-scale circulation features close to reefs and islands increases local retention of larvae on their natal reef (Burgess et al. 2007; Figueiredo et al. 2013), and can also influence large-scale circulation patterns in reef-dense regions (Andutta et al. 2012; Wolanski and Spagnol 2000). Consequently, hydrodynamic models must resolve circulation down to the scale of reefs and reef passages, typically in the order of 100 – 1000 m in regions with complex topography. To date, very few regional-scale models exist at this resolution, due to both the paucity of data at this level of detail and the large computational resources required. Recent advances in hydrodynamic models using unstructured meshes offer a potential solution to the latter problem by allowing for spatially variable model resolution (Bernard et al. 2007; Hanert et al. 2009; Pietrzak et al. 2005). Unstructured meshes allow the model resolution to be increased close to reefs and coastlines whilst keeping computational costs manageable, making them particularly useful in areas of complex topography such as Australia's Great Barrier Reef (GBR), where grid nesting is impractical (Lambrechts et al. 2008). A further challenge lies in obtaining accurate, high-resolution data to force such models, such as high-resolution bathymetry of topographically complex reef ecosystems, or sufficient hydrodynamic time-series data to calibrate model parameterisations. Even relatively small inaccuracies in forcings or parameters can lead to considerable inaccuracies in model predictions, potentially nullifying the gains in precision, for both the hydrodynamic model (e.g. see Camacho et al. 2014) and the coupled IBM (e.g. see Hrycik et al. 2013).

Technological advances in recent years (e.g. multibeam sonar, autonomous imaging systems and mixed-gas diving) have facilitated research in remote and/or deeper habitats that were previously inaccessible or prohibitively expensive (Kahng et al. 2014). Submerged banks, defined as isolated elevations of the sea floor over which the depth of water is relatively shallow but sufficient for safe surface navigation (IHO 2008), are common features of continental shelves, oceanic islands and seamounts worldwide (Abbey and Webster 2011). Many submerged banks provide habitat for reef-building corals, but their location and spatial extent is poorly known in many parts of the world (Harris et al. 2013; Heyward et al. 1997). Submerged banks composed of reef carbonates (hereafter 'submerged reefs') are common on the continental shelf of the GBR (Harris et al. 2013), and are known to support diverse coral assemblages (Bridge et al. 2011; Roberts et al. 2015). Despite many submerged reefs rising to within 10 m of the surface at their shallowest points, the location of most submerged reefs in the GBR has been delineated only recently with the use of new remote sensing technology (Bridge et al. 2012; Harris et al. 2013). In this study, we define reefs as being either 'submerged' if they are at least 10 m deep at their shallowest point, or 'near-sea-surface' (NSS) if they are shallower than 10 m at their shallowest point (and potentially subaerially exposed at low tide). It is important to note that NSS reefs may also support substantial areas of coral habitat in deeper waters on their lower slopes.

Deeper reefs have been proposed as potential refuges for coral reef taxa from environmental stress (Bongaerts et al. 2010a; Bridge et al. 2013; Riegl and Piller 2003) because disturbance impacts are often most severe in shallow waters (Bridge et al. 2014; Sheppard

and Obura 2005; Smith et al. 2014). Recent observations have confirmed that deep populations can mitigate against local extinction following severe disturbance (Sinniger et al. 2013; Smith et al. 2014). Many corals can occur over a depth range of at least 30 m (Bridge et al. 2013), indicating potential for movement of propagules between deep and shallow coral populations (defined here as occurring deeper or shallower than 10 m). However, connectivity among deep and shallow populations appears variable both geographically and among species (Serrano et al. 2014; van Oppen et al. 2011), and the true extent of demographic connectivity between deep- and shallow-water coral populations remains unclear.

Here, we use a newly-developed high-resolution model to estimate larval dispersal and potential connectivity patterns among deep and shallow coral populations on two reef types (submerged and near-sea-surface) in the central Great Barrier Reef, Australia. Our model identifies the relative contribution of submerged reefs to larval supply in the central GBR, allowing us to estimate their capacity to act as a source of larval recruits. Specifically, we will 1) compare patterns of connectivity between reefs of differing morphologies (submerged and NSS); 2) investigate the potential for connectivity between areas of reefs at different depths (shallower than 10 m and deeper than 10 m); and 3) identify regions in the central GBR most vulnerable to depth-dependent disturbances (e.g. storms or bleaching events) based on their potential connectivity to other deep reef habitats, and identify the morphology and depth of the source reefs that potentially contribute recruits to the most vulnerable areas.

5.2 Modelling connectivity between NSS and submerged reefs

5.2.1 Study Site

The Great Barrier Reef Marine Park (GBRMP) is located off north-eastern Australia, and covers an area of 344,000 km². Until recently, coral reefs were thought to occupy 20,000 km² within the GBRMP; however, recent studies have shown that submerged reefs may provide an additional 20,000 km² of coral habitat (Harris et al. 2013). Consequently, previous studies examining connectivity patterns and source-sink dynamics among reefs in the GBR (e.g. Bode et al. 2006; Caley et al. 1996; Thomas et al. 2014) have not accounted for submerged and deep reefs.

Over the 14° of latitudinal extent of the GBR, there are substantial changes in the geomorphic and environmental characteristics of the continental shelf which strongly affect the development and morphology of reefs (Hopley et al. 2007; Hopley 2006). To account for potential confounding effects of this variability, our study focused on a subset of the GBRMP (central GBR, 16.3 – 20.4° S, Fig S1) where the shelf morphology is relatively uniform, reefs are well-mapped and water circulation patterns are relatively well-known. NSS reefs are well-spaced and set back from the shelf-edge, while submerged reefs occur on the shelf-edge approximately 70 km from the coast (Hopley 2006). Additional submerged reefs occur on the mid-shelf throughout the lagoon (Harris et al. 2013). Few reefs occur within 30 km of the coast, primarily because of turbidity from several large rivers in the region. The study area contained a total of 1,023 reefs, 607 of which were NSS reefs. A map of the study region is shown in Figure 5.1.

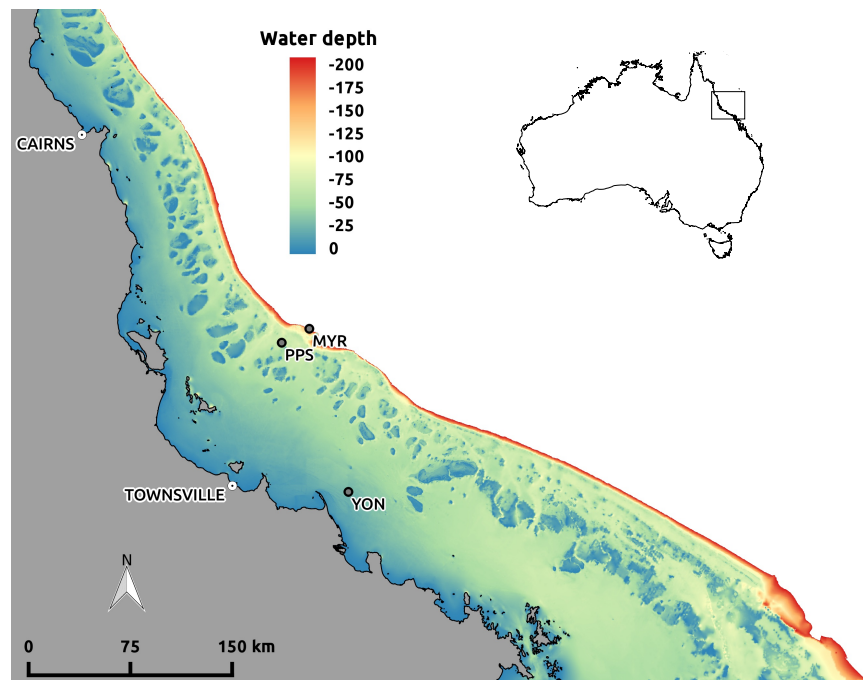


Figure 5.1: Map showing the bathymetry of the study area in the central GBR, down to the 200 m isobath. The grey dots show the positions of the GBROOS mooring sites in the domain; PPS: Palm Passage, YON: Yongala, MYR: Myrmidon Reef. Data from the first two sites were used for model validation, whilst data from the latter site were used for model calibration.

5.2.2 Distribution of reefs

The locations of submerged and NSS reefs in the central GBR were delineated using a newly-developed feature layer for the Great Barrier Reef, which represents an updated version of the GBR Reef Features GIS Database (GBRMPA 2013). The incorporation of satellite-derived bathymetry allowed delineation of many submerged reefs shallower than depths of 20-30 m that had not been identified in previous versions of GBR features, which missed many reefs greater than 5-10 m in depth at their shallowest points. Although extensive reef habitat also occurs in mesophotic depths >30 m (Bridge et al. 2012; Bridge et al. 2011), this study considered only habitat shallower than 30 m likely to support the common shallow-water coral species used in our model. Field surveys of coral assemblages occupying submerged reef in the central GBR (Beaman et al. 2011; Roberts et al. 2015) confirmed the accuracy of the new feature layer for delineating previously unidentified submerged coral reef habitat.

5.2.3 Larval dispersal model

Larval dispersal patterns were simulated for five coral species: *Platygyra daedalea*, *Acropora humilis*, *Acropora valida*, *Seriatopora hystrix* and *Stylophora pistillata*. These species were chosen because 1) they are common in the study region (DeVantier et al. 2006; Done 1982); 2) they exhibit relatively broad depth distributions (at least 20 m; Bridge et al. (2013) and Roberts et al. (2015); and 3) they represent different reproductive modes (Baird et al. 2009). Most importantly, empirical larval competence and mortality data are available for these species (see below), enabling greater accuracy in predictions of demo-

graphic connectivity, since even small differences in competence and/or mortality rates can have large effects on estimates of larval dispersal (Connolly and Baird 2010).

Larval dispersal was modelled using the biophysical model of Thomas et al. (2014), which couples the unstructured-mesh, depth-integrated hydrodynamic model SLIM¹ with an Individual-Based Model to simulate particle transport and behaviour. SLIM's multi-scale capabilities make it ideally suited to modelling water circulation in complex environments such as the GBR (e.g. see Andutta et al. 2011; Lambrechts et al. 2008; Wolanski et al. 2013). The model mesh covered the entire GBR shelf and the size of the mesh elements was kept proportional to their distance from the nearest reef or coastline and inversely proportional to water depth (see Legrand et al. 2006). The model resolution ranged from 200 m close to reefs to 5 km in open-sea areas, and therefore captured small-scale features such as reef wake eddies which can strongly affect particle dispersal. Additional details and validation of the hydrodynamic model are provided in Appendix 5.A.

We simulated water circulation in the GBR for the 35 days following coral spawning in four years for which hydrodynamic data were available to calibrate and validate the model (2007, 2008, 2010 and 2012). Analysis of wind and tide data over several years indicated that these years exhibited typical flow patterns in the central GBR during the Nov-Dec spawning season. Dispersal and settlement of larvae through the region was then modelled with the IBM presented in Thomas et al. (2014). "Virtual larvae" were gradually released over all reefs in the domain over 48 hours following the observed initiation of spawning². We assumed corals to be equally abundant throughout the reefs in the domain, therefore the number of larvae released over each reef was proportional to the reef's surface area, a necessary assumption given the lack of widespread species-specific coral density data across the region.

Larval mortality and competence acquisition was modelled using the parameters reported in Figueiredo et al. (2013), which quantifies natural mortality of larvae in a laboratory environment (i.e. excluding predation). Larvae were considered to acquire competence at a fixed rate following an initial delay after spawning (tc), and to die off at a constant mortality rate. Mortality rates and competence acquisition delay times were different for each species, meaning that the mean time-to-competence (mtc) was species-specific (the observed values of mtc for the species studied are given in Table 5.B.1 in the Appendix to this chapter). Larvae that died or strayed outside the model domain were removed from the remainder of the simulation. Larvae were assumed to settle on the first reef they travelled over after acquiring competence and were subsequently removed from the simulation. At the end of each simulation a connectivity matrix was produced, with each element recording the number of larvae released over the source reef identified by the row index which had settled onto the destination reef identified by the column index, over the course of the simulation. All larvae settling on reefs which were inside a 30 km "buffer zone" from the northern and southern domain boundaries were disregarded from the connectivity analysis, to account for the fact that upstream sources north or south of the domain can contribute larvae inside the domain. Larval dispersal statistics such as self-recruitment and mean dispersal distance were calculated separately for each year's simulation and then averaged over the 4 years, to obtain a single value for

¹SLIM is the Second-generation Louvain-la-neuve Ice-ocean Model; see www.climate.be/SLIM for more information.

²Spawning dates for each year were obtained from Prof. A. Baird, James Cook University (pers. comm.).

each species. Appendix 5.C additionally presents year-by-year dispersal statistics and discusses their inter-annual variation.

5.2.4 Connectivity among reef morphologies and depths

Connectivity matrices were used to examine the extent of the connectivity between reefs of different morphologies (submerged versus NSS) and depths ('shallow': <10 m; and 'deep': >10 m). Ten metres was considered as a suitable cut-off between 'deep' and 'shallow' reefs, since reefs deeper than 10 m are often less affected by depth-dependent disturbances such as warm-water coral bleaching (Bridge et al. 2014; Smith et al. 2014). Although disturbances can clearly extend into deeper waters, reefs on the GBR deeper than 10 m likely experience less frequent disturbances than those in shallower waters (e.g. Marshall and Baird 2000; Roberts et al. 2015). Using this cut-off value meant that all submerged reefs in the domain were entirely classed as 'deep' areas (since, by their definition, their shallowest points were deeper than 10 m), whereas NSS reefs could have both deep and shallow areas. We identified the proportion of larvae settling at <10 m depth on each reef originating from i) < 10 m depth on the same reef; ii) > 10 m depth on the same reef; iii) < 10 m depth on another reef; and iv) > 10 m depth on another reef. This allowed examination of both the potential for deep to shallow connectivity, and also the importance of self-recruitment in the recovery of shallow and deep habitats.

5.2.5 Identification of vulnerable shallow-water reef habitats

Larval dispersal models can provide insight into the vulnerability or resilience of reefs to disturbance based on the extent of connectivity to potential larval sources. Reefs that can potentially receive many larvae from other reefs, and therefore do not rely only on locally retained larvae for persistence, are likely to recover more rapidly from localised disturbances by having a more stable supply of recruits (Burgess et al. 2014; Jones et al. 2009b; Mumby and Hastings 2008). Furthermore, reefs which rely heavily only on other shallow reef habitats for larval recruits would be expected to be more vulnerable to coral decline associated with depth-dependent disturbances, whereas reefs receiving a demographically significant quantity of larvae from deeper populations (where demographically significant means enough to contribute significantly to the size and persistence of the population) could be expected to show greater resilience.

We assessed the predicted vulnerability of shallow-water reef habitats in 16 subregions in the central GBR by qualitatively categorizing the subregions as either 'low', 'medium' or 'high' vulnerability, depending on the proportion of shallow water reefs dependent on other shallow reef habitats for larval replenishment. Vulnerability was estimated by qualitatively assessing the number of reefs within a subregion that rely heavily on recruitment from habitats shallower than 10 m. Subregions were derived from the Australian Institute of Marine Science's Long-term Monitoring Program (LTMP) (Sweatman et al. 2011), which assesses coral cover trends on 200 shallow reefs (6-9 m depth) in 29 subregions of the GBR. Each subregion was defined by its position across and along the GBR shelf (11 sectors comprising approximately equal bands of latitude, and three cross-shelf zones: inner-, mid- and outer-shelf). Sixteen of the 29 subregions examined by the LTMP occur within the domain covered by our model. We compared vulnerability within each subregion predicted by our model to the observed linear trend (in % coral cover yr⁻¹) for the period 1986-2004 (Sweatman et al. 2011).

5.3 Results

The model revealed clear cross-shelf differences in connectivity, with inshore reefs consistently having higher rates of self-recruitment (Figure 5.2) and exporting fewer larvae (Figure 5.3a) than mid- and outer-shelf reefs. Mid- and outer-shelf reefs in the southern part of the domain also exported greater numbers of larvae than reefs in the north.

Connectivity variables, such as self-recruitment and dispersal distances, also varied considerably between species due to differences in mean time-to-competence and mortality rates. As expected, the three broadcast-spawning species (*P. daedalea*, *A. humilis* and *A. valida*) dispersed further and were less reliant on self-recruitment than the two brooding species (*S. hystrix* and *S. pistillata*) (Table 5.1), due to their much lower mtc (Table 5.B.1). Among the three broadcasters, the species with lower mtc showed higher rates of self-recruitment and smaller mean dispersal distances. Despite these differences, all three broadcast spawners had similar geographical dispersal patterns. Therefore, below we present data for *A. humilis* only (except where explicitly indicated), which has an intermediate mtc and is considered representative of broadcast spawning species. Both brooding species also exhibited almost identical dispersal patterns.

5.3.1 Connectivity between submerged and near-sea surface reefs

Significant differences in connectivity patterns were found between larvae released from NSS and submerged reefs (Table 5.1). For broadcast spawners, self-recruitment rates were three to five times higher for NSS reefs than for submerged reefs, and larvae released over submerged reefs dispersed 40% to 83% further.

The number of larvae produced by a reef was assumed to be proportional to its size, therefore larger reefs exported greater numbers of larvae to other reefs, in absolute terms, than smaller reefs (Figure 5.3b). The largest reefs were all NSS reefs, so NSS reefs contributed most to the total larval production. However, submerged reefs exported a greater number of larvae per unit area than NSS reefs (Figure 5.3b). The majority of connections

Coral Species	Reef type	Self-Rec.	Av. Dispersal Distance
<i>Platygyra daedalea</i> (Broadcast)	NSS	21.8%	26.2 ± 5.8 km
	Submerged	3.9%	36.7 ± 11.8 km
<i>Acropora humilis</i> (Broadcast)	NSS	30.9%	16.2 ± 2.9 km
	Submerged	5.8%	28.1 ± 7.8 km
<i>Acropora valida</i> (Broadcast)	NSS	42.8%	11.0 ± 1.1 km
	Submerged	11.6%	20.7 ± 3.8 km
<i>Seriatopora hystrix</i> (Brooder)	NSS	70.2%	3.3 ± 0.3 km
	Submerged	34.7%	8.9 ± 1.3 km
<i>Stylophora pistillata</i> (Brooder)	NSS	71.9%	3.1 ± 0.3 km
	Submerged	34.5%	9.2 ± 1.3 km

Table 5.1: Table showing larval dispersal statistics averaged over 4 spawning seasons as predicted by the SLIM model. The statistics describe all larvae released over the reef type specified in the first column and settling on any reef. Self-Rec. is the proportion of larvae which self-recruited and Av. Dispersal Distance is the average distance from their natal reef at which larvae settled, given with its standard deviation. The parentheses identify the reproductive mode of each species (broadcast spawning or brooding).

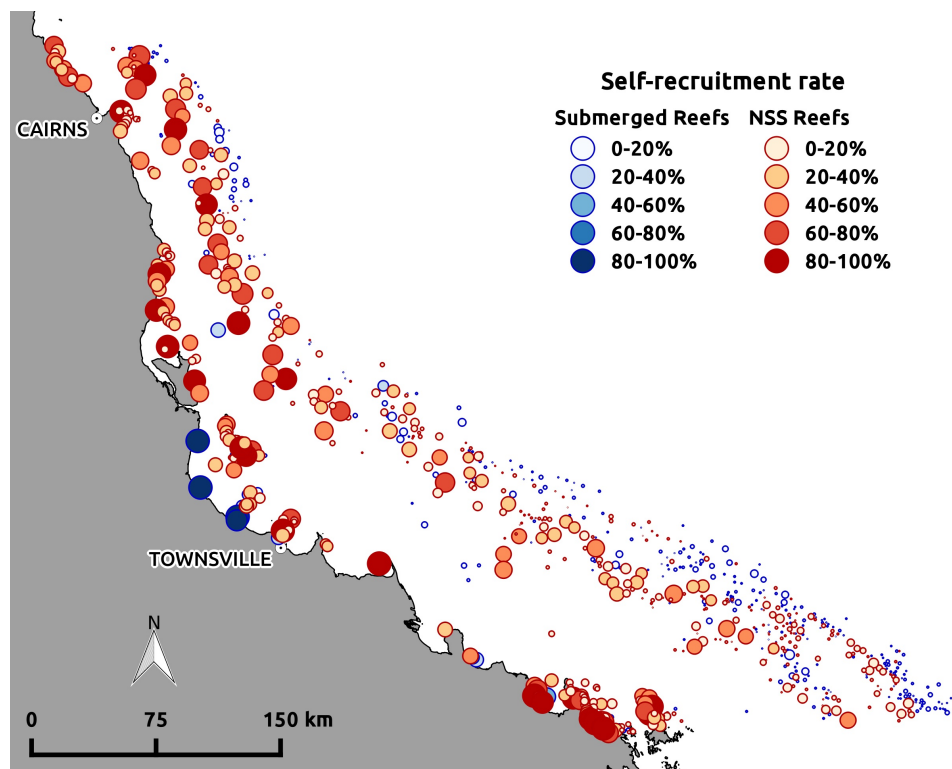


Figure 5.2: Map of self-recruitment in the central GBR predicted by the SLIM model. Coloured dots represent NSS (red scale) and submerged (blue scale) reefs, with the colour scale showing the self-recruitment rate on each reef, from white (0%) to dark red or blue (100%), for *Acropora humilis*. Reef size is also scaled by self-recruitment rate, so larger reefs have the highest self-recruitment.

within the domain occurred exclusively between NSS reefs, and the strength of connections between NSS reefs was greater than between other reef morphologies (Figure 5.4). However, NSS reefs also exported a significant quantity of larvae to submerged reefs, and vice-versa. For the broadcast spawning *A. humilis*, 79% of larvae released from NSS reefs settled on NSS reefs, while only 52% of larvae released from submerged reefs settled on submerged reefs. NSS reefs also provided 90% and 70% of settlers to NSS and submerged reefs, respectively. Brooding *S. hystrix* showed lower connectivity between submerged and NSS reefs: 91% of larvae released from NSS reefs settled on NSS reefs, and 73% from submerged reefs also settled on submerged reefs.

5.3.2 Connectivity among deep and shallow reef habitats

Horizontal connectivity (dispersal of larvae among habitats of the same depth) was more common than vertical connectivity (dispersal from deep to shallow, or vice-versa; note that vertical connectivity requires horizontal movement of larvae between habitats of different depths) (Figure 5.5). Only 24% of reef habitat in the domain was shallower than 10 m, but 52% of larvae recruiting to shallow habitats originated from other shallow habitats. Of this 52%, the majority (75%) originated from the same reef. However, deeper reef habitats still provided 48% of all recruits to shallow-water habitats, suggesting potential for demographically-significant connectivity from deep to shallow habitats. A higher

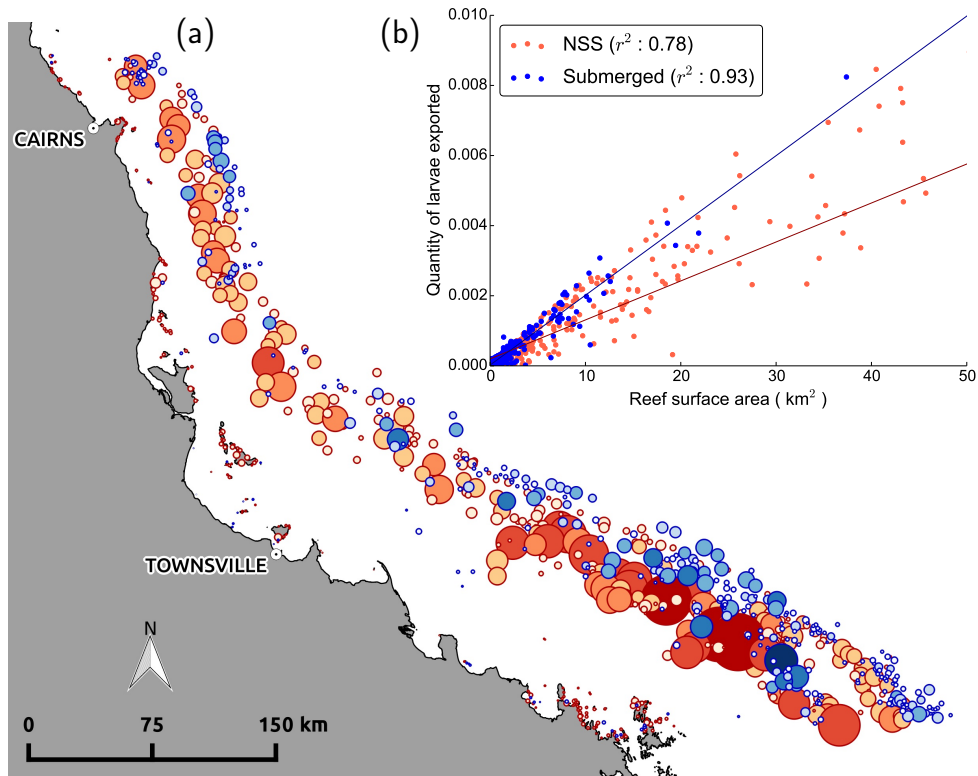


Figure 5.3: (a) Map showing the number of larvae exported by each reef in the central GBR as predicted by the SLIM model. Dots represent NSS (red scale) and submerged (blue scale) reefs, with size and colour scale indicating the number of larvae exported, from white (0) to red or blue (highest), for *Acropora humilis*. (b) Inset scatter graph shows the relationship between the number of larvae exported (normalised by the total number of recruited larvae) and reef surface area.

proportion of recruits to deep reef habitats originated from deep water, regardless of whether these habitats are on NSS (82%) or submerged (86%) reefs. Deep habitats on NSS reefs had higher self-recruitment than those on submerged reefs (28% against 2%), a reflection of the greater spatial extent of NSS reefs, and the different current regimes present around them, as described in the Discussion.

5.3.3 Predicted versus observed vulnerability of shallow-water reef habitats

Our model indicated that the most vulnerable subregions occur inshore and in the north of the domain (Figure 5.6). In contrast, shallow reef habitats on the mid- and outer-shelf in the southern half of the domain can receive larvae from a large number of sources, including a substantial proportion of larvae from adjacent deep habitats. Comparing our predicted vulnerability for shallow-water coral habitats to observed trends in coral cover from 1986-2004, we found that subregions with high predicted vulnerability corresponded to those that exhibited the steepest rate of coral cover decline (Figure 5.7). In contrast, subregions with low predicted vulnerability showed no negative trend in coral cover trajectories. In total, 43% of subregions predicted to have high vulnerability based on their reliance on shallow-water habitats for recruits showed substantial linear changes in coral cover over 19 years (Sweatman et al. 2011), compared to no subregions

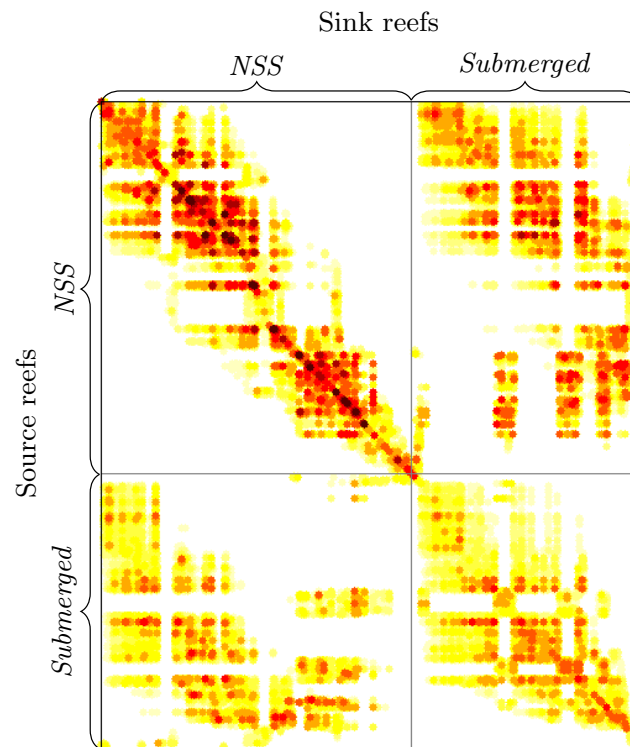


Figure 5.4: Connectivity matrix for *Acropora humilis*, averaged over 4 spawning seasons, as predicted by the SLIM model. Each matrix element represents an exchange of larvae from the source reef (row) to the sink reef (column). The strength of the larval exchange ranges from white (no larvae exchanged) to dark red (highest number of larvae). The matrix is rectangular as there are more sources than sinks, since reefs located in the 30 km buffer zones at the northern and southern domain boundaries are not included as sinks, as described in the main text.

where vulnerability was predicted to be low.

5.4 Discussion

5.4.1 Variability among submerged and NSS reefs

NSS reefs were the largest sources of larvae due to their greater spatial extent; however, larvae from submerged reefs dispersed further and were more likely to settle onto NSS reefs than vice-versa. Our results confirm that reef size is a key indicator of the importance of a reef as a larval source (James et al. 2002). However, our model also indicated that submerged reefs also represent important larval source reefs, exporting a greater number of larvae per unit area due to differences in water circulation patterns over submerged and NSS reefs. A submerged reef presents less of an obstacle to water flow compared with an NSS reef, so the turbulent features formed in the reef's wake will tend to be less pronounced than for an NSS reef. Reef wake eddies can be responsible for trapping significant numbers of larvae close to the reef, resulting in high self-recruitment rates on NSS reefs (Burgess et al. 2007; Figueiredo et al. 2013; Wolanski et al. 1989). Submerged reefs also tend to be found in slightly deeper water, where net water flow is stronger due to the smaller overall influence of friction with the sea bed, increasing the likelihood that larvae will be rapidly flushed from the reef. In addition to exporting a greater proportion

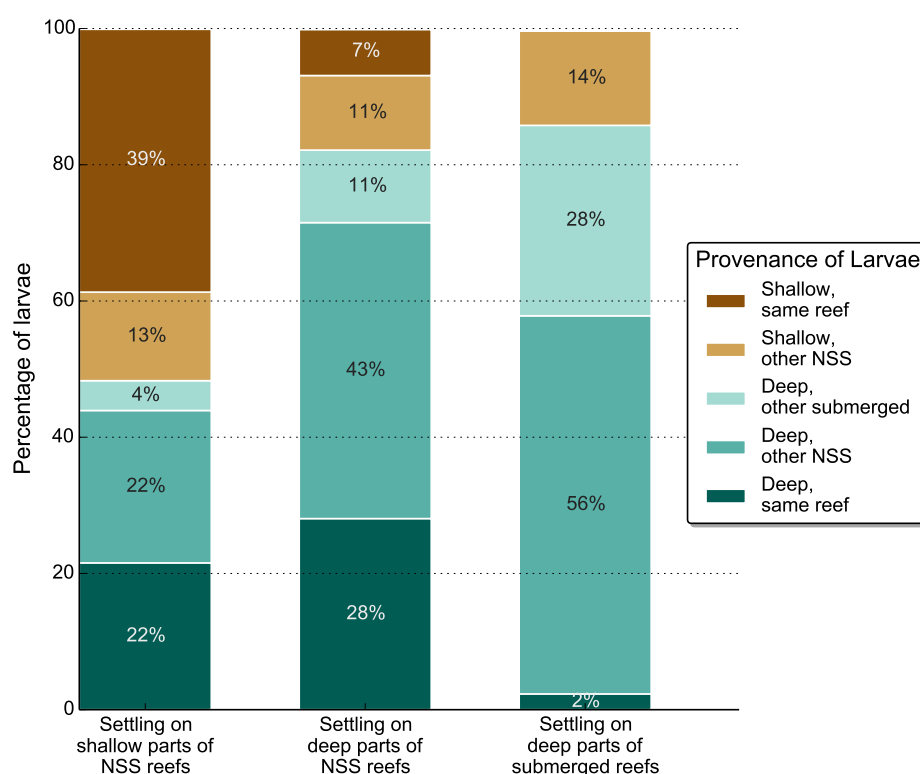


Figure 5.5: Bar charts showing the provenance of larvae settling on the shallowest parts (where depth < 10m) and deeper parts (where depth > 10 m) of NSS and submerged reefs as predicted by the SLIM model. The labels ‘shallow’ and ‘deep’ in the figure refer to larvae seeded in areas shallower and deeper than 10 m, respectively. ‘Same reef’ refers to larvae that settle on the same reef they are seeded over; ‘other’ refers to larvae that settle outside their natal reef. Note that most NSS reefs in the domain straddle the shallow/deep threshold, with their upper reaches in ‘shallow’ water and their lower banks in ‘deep’ water, whilst submerged reefs, by their definition, are all entirely located in ‘deep’ water.

of their larvae, our model indicated that submerged reefs are less reliant on other submerged reefs for their recruits, with most recruits on submerged reefs originating from NSS reefs, albeit from the deeper banks (depth > 10 m) of these reefs rather than from the shallower areas.

5.4.2 Influence of coral reproductive mode

As expected, larvae of broadcast spawning species dispersed greater distances than larvae of brooding species due to the significantly shorter mtc in brooders. Nonetheless, this finding highlights the importance of considering reproductive biology in connectivity models, and emphasizes the challenges posed by incorporating larval connectivity in planning MPA networks. Our results demonstrate the influence of life history traits on potential connectivity, a finding broadly applicable to any species with a pelagic larval dispersal stage. Managers must account for corals (and other taxa) with vastly different reproductive biology inhabiting the same reef. Accounting for additional factors that may influence dispersal potential (e.g. larval buoyancy and behaviour) could further accentuate the estimated differences in dispersal potential between broadcast spawners

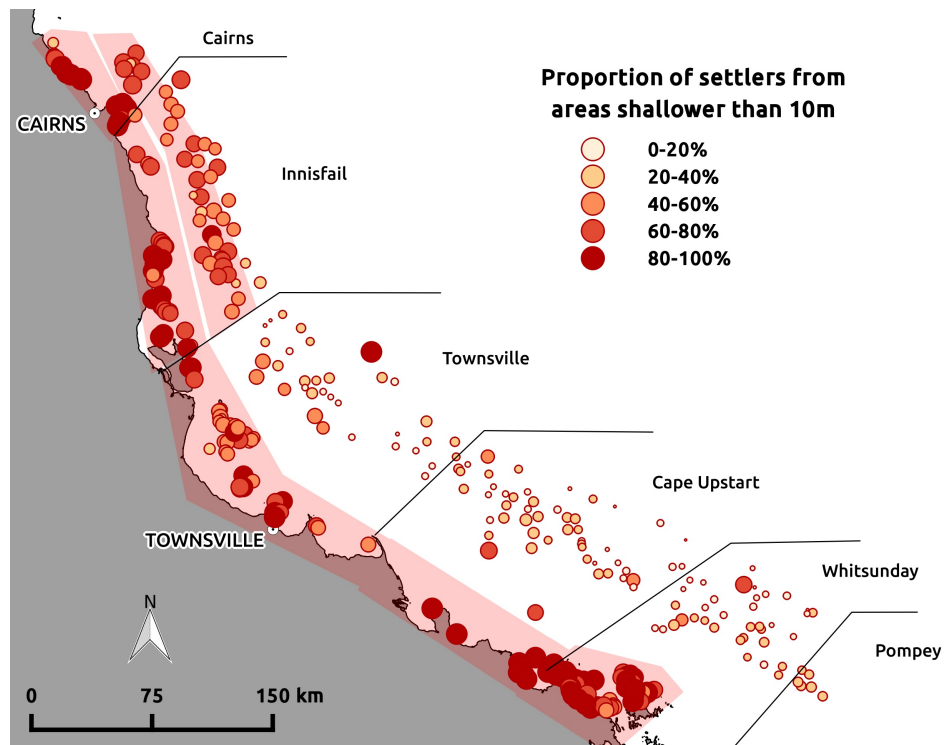


Figure 5.6: Map showing shallow reef areas in the domain (where depth < 10 m), with reef size and colour showing the proportion of recruits which come from other shallow reef areas, as predicted by the model for *A. humilis* larvae. Only reefs with at least part of their surface area in water shallower than 10m are shown. Black lines delineate sector boundaries used by Sweatman et al. (2011), and red boxes identify the subregions classed as most vulnerable by our numerical model.

and brooders, and would provide additional information on intraspecific differences in dispersal potential.

5.4.3 Connectivity between deep and shallow habitats

Our results indicate that vertical connectivity is less common than horizontal connectivity. The majority (52%) of recruits on shallow reef habitats originate from other shallow habitats, despite deeper habitats accounting for 76% of the total available coral reef habitat. This finding supports empirical studies of genetic connectivity in corals (Bongaerts et al. 2010b; Serrano et al. 2014), and suggests that dispersal limitation may play a role in population partitioning among reef habitats. However, the model also indicated that demographically significant two-way connectivity between deep and shallow habitats could constitute an important source of larvae to shallow habitats. The extent of connectivity between deep and shallow habitats was geographically variable (Figure 5.6): inner-shelf reefs were highly dependent on recruits from shallow water, and reefs in the north of the domain were also more reliant on larvae from shallow water than those further south. This is primarily due to spatial differences in current strength: inner-shelf reefs are mainly found in shallow water and experience weaker currents than offshore reefs, reducing larval dispersal. Meanwhile in the southern half of the domain, the wider continental shelf amplifies the tidal currents (Andrews and Bode 1988) leading to greater dispersal distances and more connections between reefs, enhancing deep-to-shallow

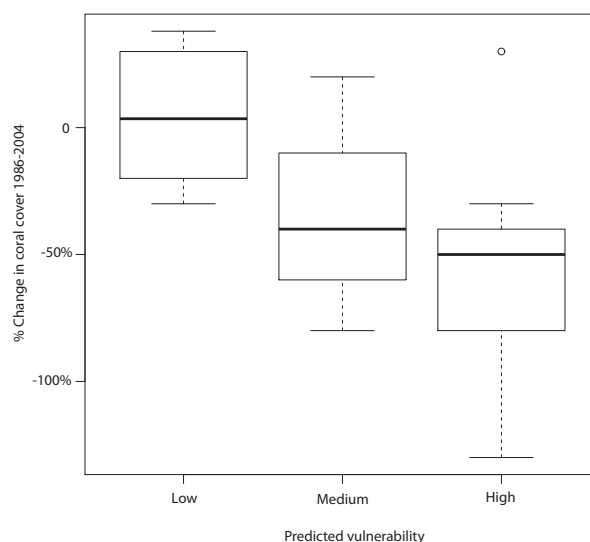


Figure 5.7: Vulnerability of shallow-water reefs predicted by our model versus the 19-year linear trend (in % coral cover yr^{-1}). Each point used in the analysis represents a value for one of 16 subregions reported in the Australian Institute of Marine Science Long-Term Monitoring Program (Sweatman et al. 2011). Seven subregions were classified as high predicted vulnerability, three 'medium' and six 'low'.

connectivity.

Ascertaining the true extent of vertical connectivity requires empirical testing, but our model suggests that the horizontal currents present no obvious barrier to connectivity between deep and shallow reef habitats in the region, assuming the water column is well mixed. Spatial variability in the extent of vertical connectivity has been previously reported using genetic techniques (Serrano et al. 2014; van Oppen et al. 2011), and our results support the hypothesis that oceanography may provide a mechanism to explain this variation. If connectivity between deep and shallow habitats promotes resilience in shallow-water reef habitats, then determining the spatial location, extent, and biodiversity of deep reefs should be afforded greater importance by marine resource managers.

Reef habitats in deeper waters are not immune from disturbance, but many disturbances are less frequent and/or severe at greater depths (Marshall and Baird 2000; Riegl and Piller 2003; Woodley et al. 1981). Consequently, deeper reefs often exhibit greater long-term stability than adjacent shallow habitats (Bak and Nieuwland 1995; Lesser et al. 2009). Our results indicate that most recruits on deep reef habitats originate from other deep habitats, therefore depth-dependent disturbances would have little influence on larval supply to deep habitats. Lower self-recruitment rates also suggest that deeper habitat may have greater capacity to recover than shallows if they are affected by a reef-scale disturbance. However, these factors may also result in slower recovery of deeper reefs if coral declines in deeper waters were widespread.

5.4.4 Assessing vulnerability of shallow-water habitats

Subregions where shallow-water reef habitats are predicted to source a greater proportion of recruits from deeper habitats showed no significant trends in coral cover from 1986-2004 (Figure 5.7). In contrast, subregions heavily reliant on shallow-water reef habitats for larval recruitment have shown much steeper declines in coral cover. However,

the response of vulnerable subregions was also highly variable. We propose two potential causes of variability, which are not mutually exclusive. Firstly, coral decline requires a cause, and it is possible that some highly vulnerable habitats may have escaped disturbance over the study period. However, the frequency and spatial scale of disturbance events in the central GBR over the study period (De'ath et al. 2012; Sweatman et al. 2011) would indicate that this pattern cannot be attributed entirely to differences in exposure to disturbance. Alternatively, it is possible that some reefs with low connectivity are actually relatively resilient to disturbances if: 1) the disturbance is not too severe and some breeding adults survive; and 2) local retention of larvae is high (e.g. Botsford et al. 2009b). Whatever the cause of variability in coral cover trajectories on vulnerable reefs, it is clear that shallow habitats with high predicted vulnerability have, on average, showed much steeper declines in coral cover than the shallow habitats with low predicted vulnerability. This finding supports the hypothesis that reefs receiving larvae from deeper sources may be more resilient than those reliant entirely on shallow sources.

It should be borne in mind that we have only considered one source of vulnerability to coral reefs. Generalising a concept commonly used in groundwater modelling (Pinte et al. 2004), we can consider that being located in shallow water is a *general* vulnerability factor for a reef, as shallow water depth is likely to increase the reef's vulnerability to a host of depth-dependent disturbances, irrespective of other reef-specific factors. It is important to note that in addition to this general vulnerability, a given reef may also have additional *specific* vulnerability factors unique to that reef or to a subgroup of reefs to which it belongs, which could further increase its vulnerability. In this study we have only considered general vulnerability, and the issue of whether specific vulnerability factors could additionally play an important role in reducing reef resilience is one which merits further study (e.g. abnormal water temperature or levels of pollution specific to a given reef or group of reefs). We have also not explicitly focused on inter-annual variability in connectivity patterns, which could act to increase or decrease a given reef's vulnerability from one year to the next. Whilst the conclusions presented here are based on results which were averaged over multiple simulations representing multiple spawning periods, and therefore are not specific any given year, the year-by-year connectivity results presented in Appendix 5.C suggest that inter-annual fluctuations in larval dispersal distances may be significant, and this is an issue which merits further study.

The capacity for reefs to maintain coral-dominated states or return to coral-dominated states following disturbances is influenced by the types of stressors to which the reef is exposed. Chronic 'press' type stressors (e.g. pollution, overfishing) reduce overall capacity to recover, whereas reefs can recover from acute 'pulse' disturbances (e.g. storms and bleaching events) if reef resilience is maintained (Anthony et al. 2015). For corals, connectivity is most beneficial against 'pulse' disturbances, where deeper areas that have avoided significant coral loss can provide propagules to repopulate shallower areas. It is important to consider that our model shows only potential connections between reefs based on hydrodynamics, larval survival and competence dynamics, and does not account for important factors such as adaptive divergence among habitat types or post-settlement processes affecting recruitment success (Bongaerts et al. 2011; Mundy and Babcock 2000). Some coral species are habitat specialists, restricted to either very shallow or very deep habitats, and such species will not colonise new habitats even if physically connected by larval dispersal. Nevertheless, our model suggests that deep habitats may constitute a source of larvae for depth-generalist species. Our predictions support empirical findings that whilst genetic connectivity between deep and shallow popula-

tions is not as common as horizontal connectivity (Serrano et al. 2014), demographically significant connectivity can occur between deep and shallow habitats. The concordance between our predicted vulnerability and observed trends in coral cover suggests that deep-to-shallow connectivity may be important for post-disturbance recovery in coral communities. This reinforces the need to consider deeper reef habitats when assessing the impacts of disturbances, trajectories of coral communities, and planning conservation measures.

Acknowledgements

The contributions of C.J.T., E.D. and E.H. were supported by ARC grant 10/15-028 of the Fédération Wallonie-Bruxelles, “Taking up the challenges of multi-scale marine modelling”. J.F. was supported by the Australian Research Council (DP110101168), and a Smart Futures Fellowship from the Queensland Government. E.D. is an honorary research associate with the Belgian Fund for Scientific Research (F.R.S.-FNRS). Computational resources were provided by the supercomputing facilities of the Université catholique de Louvain (UCLouvain/CISM) and the Consortium des Équipements de Calcul Intensif en Fédération Wallonie-Bruxelles (CÉCI). We thank R. Beaman and the Great Barrier Reef Marine Park Authority for providing feature layers on reef location.

APPENDIX

5.A Setup and validation of the hydrodynamic model

Tidal forcing was applied at the boundaries using the OSU TOPEX/Poseidon Global Inverse Solution dataset (Egbert and Erofeeva 2002), and 6-hourly wind data from the NCEP Climate Forecast System Reanalysis (CFSR) (Saha et al. 2014) dataset were used to force the model by applying a wind stress over the whole domain, and adding an additional current at the boundaries calculated as a fraction of the local wind to account for wind-driven currents entering or leaving the domain. The constant of proportionality used was 2%, which was found by comparing the CFSR wind field with currents from mooring sites close to the boundaries, which were found to be highly correlated. A constant residual circulation at the boundaries was also applied to account for exchanges with the neighbouring Coral Sea, using the method described in Thomas et al. (2014) following the approach of Brinkman et al. (2001). The size and position of this constant in/outflow was calibrated using publicly available current meter data from an IMOS GBR Ocean Observing System (GBROOS) (IMOS 2013) long-term mooring site located close to the domain boundary (Myrmidon Reef mooring). The bathymetry used was the GBR100 dataset (Beaman 2010). For further details of the model parameterisations and validation, the reader is referred to Section 2 of Thomas et al. (2014).

The relatively shallow and well-mixed nature of GBR waters (Middleton and Cunningham 1984; Wolanski 1983) means that depth-integrated models have often been successfully used to simulate water circulation on the shelf, and horizontal currents predicted by these models have been shown to agree well with both observations and other 3D models (e.g. Black et al. 1991; Luick et al. 2007), including eddies around islands and headlands (Falconer et al. 1986; Lambrechts et al. 2008). Our model calibration also indicated that the predicted currents were significantly affected by its resolution at low resolution, with this effect becoming marginal at resolutions at or above the reef scale (100 m – 1 km); we therefore argue that it is above all crucial to achieve reef scale resolution in the horizontal plane to capture as many scales of motion as possible.

Previous studies have demonstrated the ability of the SLIM model to accurately reproduce small-scale circulation features in the GBR (Lambrechts et al. 2008), tidal elevation (Lambrechts et al. 2008; Thomas et al. 2014), salinity concentration (Andutta et al. 2011), suspended sediment concentration (Lambrechts et al. 2010) and large scale flow through different regions of the GBR (Andutta et al. 2012; Andutta et al. 2011; Thomas et al. 2014; Wolanski et al. 2013). In this study the hydrodynamic model was additionally validated by comparing the currents at a number of points in or near the central GBR with the observed depth-averaged currents from the GBROOS moorings for the same time periods simulated. As the model was run for periods of 35 days in 4 separate years (2007, 2008, 2010 and 2012), the model was calibrated and the currents subsequently val-

idated for each of these years separately, to ensure that it was simulating accurate large scale flow in each spawning period. These years were chosen as the validation showed a good fit with observed data. The results of this validation are shown in Tables 5.A.1-5.A.4.

Of the 4 mooring sites used, 2 were located inside the region where particles were released (Palm Passage and Yongala), whilst the other 2 were located outside this region (Capricorn Channel and Lizard Island Shelf), where the hydrodynamic mesh was coarser. They were nonetheless included in the validation of the hydrodynamic model as both sites were located in areas of relatively uniform flow, where very high model resolution was not seen as imperative, and both were judged to be suitably placed to validate the accuracy of the large-scale circulation simulated by the model: the Capricorn Channel mooring is located in the main shipping channel crossing the central and southern GBR, through which the flow is highly correlated, whilst the Lizard Island Shelf mooring is located not far from the northern boundary of the area studied, and is also strongly affected by the same inflow boundary condition applied at the shelf break which affects flow through the study area. The results show that the model was able to reproduce realistic flow patterns through the region, with predicted mean speeds and standard deviations being close to the observed values. At the Palm Passage site, which is located in close proximity to mid-shelf reefs, the mean currents varied slightly more from the observed values than at the other sites, probably due to the influence of the more complex topography, however the standard deviation was always close to the observed values (the highest relative error out of the 4 years was 13%), indicating that the model was capable of reproducing the correct variability in currents in an inter-reef area. In less topographically complex areas such as at the Yongala and Capricorn Channel moorings, the mean predicted currents can be seen to give a better fit with the observed currents. The validation indicated that the model was able to realistically reproduce water circulation patterns through the region for the periods simulated.

Mooring site	Co-ordinates	$ u _{\text{obs}}$ (m/s)	std_{obs}	$ u _{\text{pred}}$ (m/s)	std_{pred}
Lizard Island Shelf	145.641°E, 14.702°S	n/a	n/a	0.23	0.11
Palm Passage	147.151°E, 18.131°S	0.28	0.11	0.21	0.10
Capricorn Channel	151.805°E, 23.383°S	0.25	0.12	0.26	0.15
Yongala	147.620°E, 19.306°S	n/a	n/a	0.24	0.11

Table 5.A.1: Validation data for the 2007 simulation (35 days following coral mass spawning on 28 Nov). Average observed depth-averaged current speed and standard deviation at different mooring sites from the GBROOS dataset are labelled $|u|_{\text{obs}}$ and std_{obs} respectively, and as predicted by the SLIM model labelled $|u|_{\text{pred}}$ and std_{pred} respectively. n/a indicates that GBROOS data were not available.

Mooring site	Co-ordinates	$ u _{\text{obs}}$ (m/s)	std_{obs}	$ u _{\text{pred}}$ (m/s)	std_{pred}
Lizard Island Shelf	145.641°E, 14.702°S	n/a	n/a	0.22	0.10
Palm Passage	147.151°E, 18.131°S	0.20	0.10	0.18	0.09
Capricorn Channel	151.805°E, 23.383°S	0.27	0.12	0.25	0.15
Yongala	147.620°E, 19.306°S	n/a	n/a	0.21	0.12

Table 5.A.2: Validation data for the 2008 simulation (35 days following coral mass spawning on 17 Nov).

Mooring site	Co-ordinates	$ \mathbf{u} _{\text{obs}}$ (m/s)	std_{obs}	$ \mathbf{u} _{\text{pred}}$ (m/s)	std_{pred}
Lizard Island Shelf	145.641°E, 14.702°S	0.20	0.14	0.22	0.11
Palm Passage	147.151°E, 18.131°S	0.21	0.08	0.20	0.09
Capricorn Channel	151.805°E, 23.383°S	0.25	0.10	0.24	0.14
Yongala	147.620°E, 19.306°S	n/a	n/a	0.22	0.11

Table 5.A.3: Validation data for the 2010 simulation (35 days following coral mass spawning on 26 Nov).

Mooring site	Co-ordinates	$ \mathbf{u} _{\text{obs}}$ (m/s)	std_{obs}	$ \mathbf{u} _{\text{pred}}$ (m/s)	std_{pred}
Lizard Island Shelf	145.641°E, 14.702°S	0.25	0.13	0.22	0.12
Palm Passage	147.151°E, 18.131°S	n/a	n/a	0.17	0.08
Capricorn Channel	151.805°E, 23.383°S	0.24	0.10	0.25	0.13
Yongala	147.620°E, 19.306°S	0.23	0.14	0.21	0.12

Table 5.A.4: Validation data for the 2012 simulation (35 days following coral mass spawning on 3 Dec).

5.B Mean times to competence of the 5 species modelled

Coral Species	mtc (days)
<i>Platygyra daedalea</i>	5.33
<i>Acropora humilis</i>	4.71
<i>Acropora valida</i>	3.07
<i>Seriatopora hystrix</i>	0.69
<i>Stylophora pistillata</i>	0.58

Table 5.B.1: Table of the mean times to competence (mtc) of the 5 species modelled in this study. Data reproduced from Figueiredo et al. (2013).

5.C Importance of inter-annual variability in larval dispersal

The quantitative connectivity indicators presented in this chapter, such as larval dispersal distances and self-recruitment, were all obtained by averaging these values over the results from 4 separate model runs corresponding to simulations of 4 separate coral spawning periods (in 2007, 2008, 2010 and 2012). This was done in order to account for possible changes in larval dispersal from one year to the next due to changes in water circulation patterns through the region. Water circulation through the GBR is driven by three main factors: the tides, the winds and water exchanges with the neighbouring Coral Sea. Whilst the tides can be expected to be reasonably constant over the same period from one year to the next, the same is not necessarily true of the latter two factors.

A full analysis of inter-annual variability in connectivity is out of the scope of this study and would require many more than 4 years' simulations. Nonetheless it is possible, using the data obtained from the simulations in this study, to at least ascertain whether or not there was significant inter-annual variability across the 4 years studied. To this end, Figure 5.C.1 shows year-by-year self-recruitment and dispersal distances estimated by the model, whilst Table 5.C.1 reports the inter-annual coefficients of variation for these data, to allow a numerical comparison to be made of the variation in these two indicators, and to allow a comparison in the variability of larval dispersal from NSS and submerged reefs.

Focusing initially on NSS reefs, two main trends appear to become apparent from the charts and data presented in Figure 5.C.1 and Table 5.C.1. Firstly, self-recruitment appears to be relatively stable from one year to the next (Figure 5.C.1(a)). This is to some

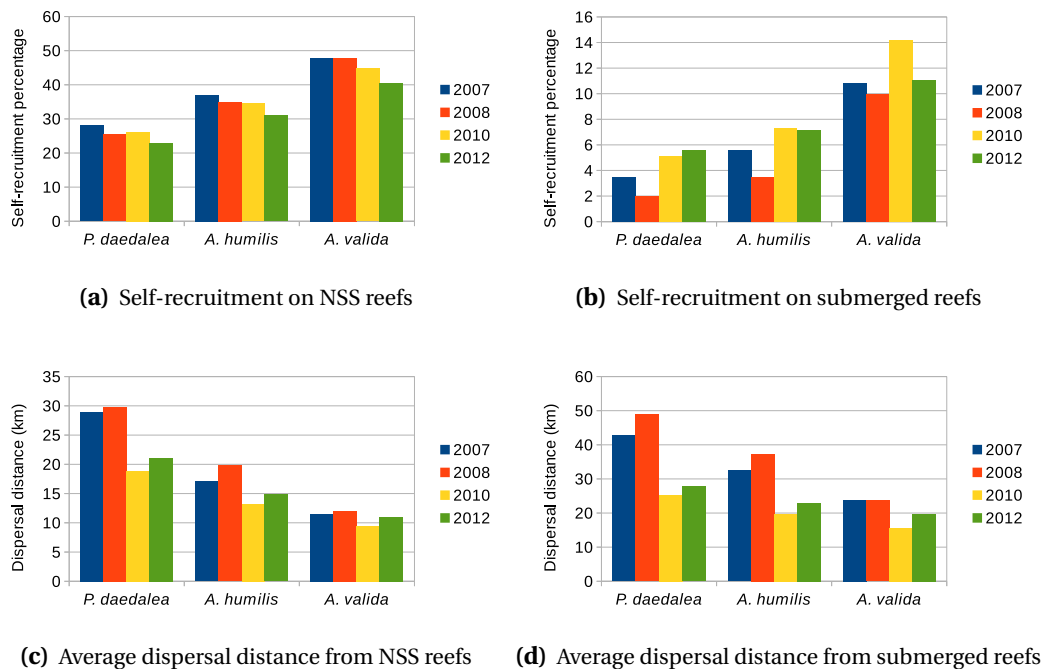


Figure 5.C.1: Bar charts showing self-recruitment by year for larvae from broadcast spawning coral on NSS (5.C.1(a)) and submerged (5.C.1(b)) reefs, and average dispersal distances from NSS (5.C.1(c)) and submerged (5.C.1(d)) reefs.

extent not a great surprise given that self-recruitment is mainly controlled by tidal currents over most of the GBR, as these strong, periodic currents act to flush larvae from their natal reefs more effectively than the weaker wind-driven currents or currents entering the shelf from the Coral Sea. Average larval dispersal distances, on the other hand, appear to fluctuate to a much greater extent from one year to the next (Figure 5.C.1(c)). This can again be ascribed to the nature of the currents controlling larval dispersal: once a larva has been flushed from its natal reef, its fate is then controlled by low-frequency currents such as wind-driven currents or currents from the Coral Sea, as these can act to transport larvae for long periods in the same direction, in contrast to tidal currents which, whilst being effective at flushing larvae from reefs, are less effective at transporting them long distances due to their oscillatory nature. As the wind over the GBR during the austral winter can vary considerably on timescales of days or weeks, and unlike the tides does not have any “phase” intrinsically linked to coral mass spawning, wind-driven currents flowing through the GBR can be very different from one year’s mass spawning period to the next. It therefore follows that the average distance travelled by larvae before settling can fluctuate between years.

For submerged reefs the picture is less clear cut. Overall, inter-annual variability is greater than for NSS reefs both in self-recruitment and average dispersal distances (Figures 5.C.1(b) and 5.C.1(d)). There appears to be no great difference in the variability of the two indicators. Both of these results are likely due to the fact that larvae released over submerged reefs, which on average are located in slightly deeper water, are flushed more rapidly than those released over NSS reefs, and as such are at the mercy of the wind-driven currents and Coral Sea-driven currents from an earlier stage of their dispersal process. As both of these currents are highly variable, the transport of larvae from these reefs is modulated by this variability to a greater extent than is the case for larvae from NSS reefs. Furthermore, since submerged reefs are less affected by the “Sticky water” effect, which acts to steer low-frequency currents away from dense clusters of NSS reefs (Wolanski and Spagnol 2000), submerged reefs may be expected to be generally more exposed to these high-variability, low-frequency currents.

Coral Species	Reef type	Self-recruitment coefficient of variation	Dispersal distance coefficient of variation
<i>Platygyra daedalea</i>	NSS	8.2%	22.4%
	Submerged	34.1%	31.7%
<i>Acropora humilis</i>	NSS	7.2%	11.7%
	Submerged	30.5%	29.1%
<i>Acropora valida</i>	NSS	7.6%	10.0%
	Submerged	15.9%	19.0%

Table 5.C.1: Coefficient of variation (defined as σ/μ where σ is the standard deviation and μ is the mean value, here reported as a percentage) for self-recruitment and dispersal distances, with σ and μ calculated across 4 years’ values.

CHAPTER 6

FUTURE SCENARIOS FOR CORAL CONNECTIVITY IN THE GREAT BARRIER REEF

Summary

Environmental changes in coral reef ecosystems are likely to have an impact on the connectivity patterns of many marine species over the next century. In this chapter, two major possible sources of environmental change to coral connectivity networks in the GBR are considered: an increase in water temperature and a change to the strength of water currents entering the continental shelf. The biophysical model of larval dispersal is used to estimate the impacts of these effects on connectivity patterns for a common species of reef-building coral in an 800 x 200 km region in the southern GBR. The expected rise in water temperature is found to have a greater impact on larval dispersal than the change to water transport entering the shelf, by about an order of magnitude. The possible implications of these changes for marine management are discussed. Finally, a metapopulation model is used to evaluate the impact of this temperature increase on the recovery times of coral populations following major disturbances; changes to recovery times are expected to be highly spatially variable, and depend strongly on the local hydrodynamics and the distribution of coral habitats.

This chapter reproduces the following article:

Thomas, C. J., Figueiredo, J., Lambrechts, J., Deleersnijder, E. and Hanert, E. (2015). Future scenarios for coral connectivity in the Great Barrier Reef. *In preparation*.

6.1 Introduction

The process of larvae dispersing from their natal habitat is a key driver of connectivity between physically separate marine populations for many species (Cowen and Sponaugle 2009; Largier 2003). This is especially true in coral reef ecosystems, which are generally composed of patchy and fragmented habitats, linked primarily by larval dispersal (Almany et al. 2009). Marine larvae can potentially disperse over a very wide range of scales, from a few metres to thousands of kilometres (Jones et al. 2005; Kinlan and Gaines 2003). Connectivity between separate habitats, driven by larval dispersal, serves to maintain genetic homogeneity amongst a metapopulation (Palumbi 2003; Trakhtenbrot et al. 2005), allows species to spread to new habitat patches (Gaylord and Gaines 2000; Trakhtenbrot et al. 2005), increases the persistence of isolated populations (James et al. 2002; Roughgarden et al. 1988), and increases the resilience of the metapopulation by enabling subpopulations to facilitate each other's recovery from disturbances (Cowen et al. 2006; Hughes and Tanner 2000). Understanding the extent of connectivity between habitats is therefore important in enabling optimal planning of marine management strategies (Gaines et al. 2010; Shanks et al. 2003).

Larval dispersal patterns are poorly known in many coral reef ecosystems (Drew and Barber 2012; Green et al. 2014). Given the difficulties inherent in directly tracking dispersing propagules, numerical modelling tools have been increasingly used to study potential connectivity patterns (Kool and Nichol 2015; North et al. 2009). In particular, biophysical models can be used to simulate the larval dispersal process by explicitly modelling the water circulation in a given area and predicting the trajectories of larvae released over suitable habitats (Werner et al. 2007). This results in the generation of connectivity matrices describing the potential connectivity between all the habitats in the domain, and these can then be analysed to look for spatial patterns and statistical trends in larval dispersal (Thomas et al. 2014).

Rapid climate change caused by human activities is widely expected to have a significant impact on the marine environments of many coral reef ecosystems (Pandolfi et al. 2011). The health of coral reefs is likely to be directly affected by increased water temperature and acidity leading to a higher frequency of bleaching events (Hoegh-Guldberg 1999), reduced coral growth rates and reef-building capacity (Hoegh-Guldberg et al. 2007; Kleypas et al. 1999), and increased occurrence of coral disease outbreaks (Hughes et al. 2003). These changes are likely to exacerbate local anthropogenic stresses such as pollution and overexploitation of marine resources, potentially causing a catastrophic decline in the health of coral reef ecosystems worldwide (Hoegh-Guldberg et al. 2007).

The effects of climate change are also likely to affect the larval dispersal process and resultant connectivity patterns for many coral reef species (Doney et al. 2012). In particular, warmer waters lead to higher mortality and faster development rates for coral larvae, which is likely to shorten the time they spend dispersing (their Pelagic Larval Duration, PLD) and therefore change their dispersal potential, as well as their probability of settling onto a suitable habitat (Figueiredo et al. 2014; Nozawa and Harrison 2007). Furthermore, changes in large-scale circulation patterns related to climate change could potentially alter the water circulation in various coral reef ecosystems, leading to changes to larval dispersal patterns (Munday et al. 2009). Changes to rainfall patterns and freshwater runoff may also affect larvae around nearshore reefs, though very little is known about this due to a lack of rainfall projections. The projected global rise in sea level is not

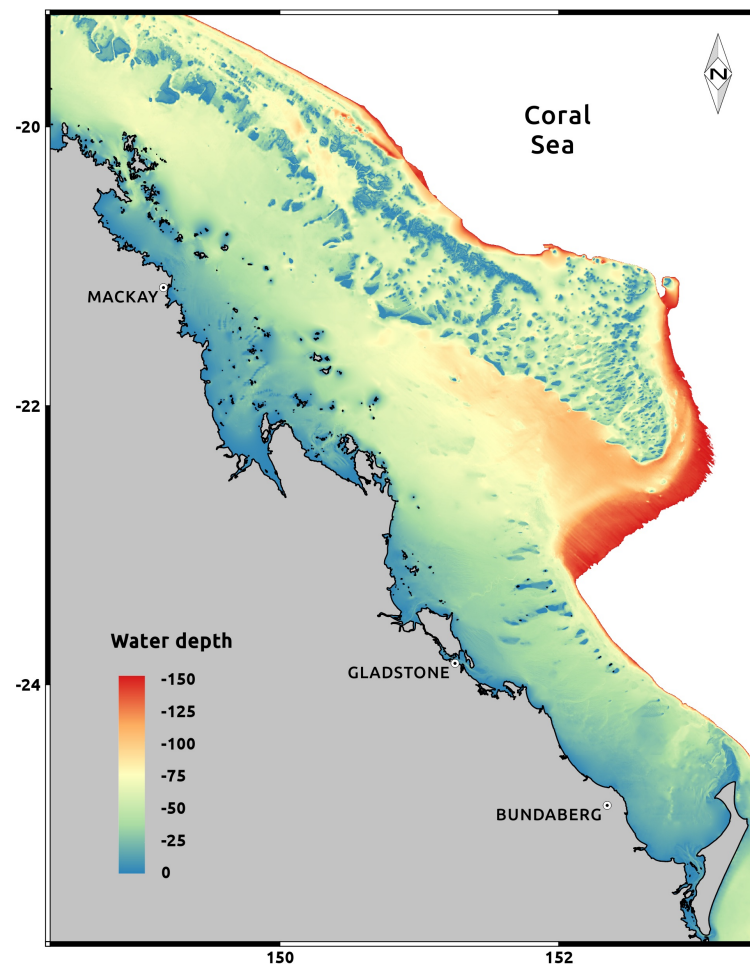


Figure 6.1: Reference map of the southern Great Barrier Reef. x-axis: longitude; y-axis: latitude.

thought likely to be a major source of stress to coral reefs on a local level (Munday et al. 2009), though on the much larger scale it could lead to changes in circulation patterns which may indirectly have some effect on the circulation in various coral reef systems.

The focus of this study is on quantifying the potential impact on larval dispersal and connectivity of two major possible climate change induced changes: increased water temperature and a change in water circulation patterns. The study focuses on the topographically intricate southernmost section of the Great Barrier Reef (GBR) in Australia, the world's largest and most complex coral reef ecosystem. This region, shown in Figure 6.1, is about 800 km in length by 200 km in width, encompasses over 1,200 reefs of greatly differing size and has a highly complex bathymetry, resulting in water currents with high spatial and temporal variability (Wolanski et al. 2003). The study will look at dispersal potential of *Acropora millepora*, a reef-building coral which is common and widespread in the region (DeVantier et al. 2006).

In common with most other, vitally important, reef-building corals, *A. millepora* coral are considered to be at high risk of future population decline due to the effects of global climate change, including higher frequency of coral bleaching events caused by warmer waters, in addition to a raft of other risks directly or indirectly related to anthropogenic activities (Hoegh-Guldberg et al. 2007; Hoegh-Guldberg 1999). The scope of the present

study however does not extend to consider the issue of how adult coral population sizes on different reefs may change due to climate change, but is limited to the effects of climate change on the dispersal of larvae assuming a uniform coral density. The aim is therefore to isolate the effects of climate change on the larval dispersal process, an issue which has so far received comparatively little attention.

Water temperatures in the GBR are expected to increase by 1°–3°C by 2080–2100 (Lough 2007). The effects of this increase on larval dispersal are difficult to predict *a priori*, owing to their contrasting effects on larval biology: on the one hand higher water temperature causes larvae to acquire competence more rapidly (competence is defined as the ability of larvae to sense when they are over a suitable habitat and settle onto it) (Heyward and Negri 2010; Nozawa and Harrison 2007), which would be expected to increase settlement success, whilst on the other hand it also induces increased mortality in larvae (Nozawa and Harrison 2007; Randall and Szmant 2009), which would instead be expected to decrease settlement success. Whether the probability of settlement increases or decreases therefore depends on the trade-off between the increase in mortality and the decrease in competence acquisition time. Additionally, a faster acquisition of competence may lead to an increase in the proportion of larvae settling close to their natal habitat, with a corresponding reduction in long-distance connectivity. The increase in mortality compounds this effect, leading to a net decrease in connectivity distances. Whether this leads to higher settlement success depends on whether there are many suitable reef habitats close to a larva's natal reef or not.

An important indicator used to evaluate the persistence of coral reef populations is the local retention rate, which is defined as the proportion of larvae released from a habitat which settle onto the same habitat (Burgess et al. 2014). The effect of the temperature increase on local retention depends on the hydrodynamic environment where the larvae are released: in habitats with rapid currents, where larvae are flushed rapidly from their natal habitat, then the reduction in the mean time to competence (mtc) of larvae causes local retention to increase, whilst in habitats with slower currents, where larvae are flushed more slowly, the increased mortality rate at higher temperature compensates for the shorter mtc, and local retention rates decrease (Figueiredo et al. 2014). The net effect of the temperature increase therefore depends strongly on the local hydrodynamic environment, and in a region with a water circulation as complex as the GBR, we can expect that different areas may respond in different ways to a temperature increase, with some habitats seeing an increase in local retention, and others a decrease.

In addition to the increase in water temperature, changes to large-scale water circulation in the neighbouring Coral Sea have been suggested as a potential source of change to population connectivity in the GBR (Munday et al. 2009). The westward-flowing South Equatorial Current (SEC) crosses the Coral Sea and approaches the GBR continental shelf roughly between 11° and 20°S (Kessler and Cravatte 2013b), causing a flow onto the shelf which has been observed between 14° and 20°S (Andrews and Clegg 1989; Brinkman et al. 2001; Church 1987). This in turn drives a southward residual flow on the shelf known as the Coastal Sea Lagoonal Current (CSLC; Wolanski et al. (2013)). Many large-scale climate models predict a strengthening of the South Pacific sub-tropical gyre, of which the SEC is the northern branch, with a corresponding increase in the strength of the poleward-flowing East Australian Current (EAC) parallel to the Australian coastline (Sen Gupta et al. 2012; Sun et al. 2012). Whilst the effects of the strengthening EAC along its central area and southern extension have been extensively studied (e.g. Oliver and Holbrook 2014), such studies rarely extend to include the nascent EAC off the GBR. Further-

more, the model resolution used in global climate models is generally much too coarse to be able to study coastal processes. As such, few if any studies currently exist into how projected changes in the Coral Sea water circulation could affect circulation on the GBR shelf.

An increase in the strength of Coral Sea inflow entering the GBR shelf may not necessarily lead to stronger currents over the whole shelf. Indeed, the water exchange with the Coral Sea is not the only driver of on-shelf circulation, and tides and wind also contribute at least as significantly (Wolanski et al. 2003). During prolonged periods of strong south-easterly trade winds, northward wind-driven currents can overpower the southward CSLC, causing a net northward residual flow instead, though south-east trade winds tend to be weaker during the coral spawning season in austral summer. Strong tidal currents are also present over most of the shelf, particularly in the southern GBR where the shelf is wider, and these currents can dominate cross-shelf processes (Andrews and Bode 1988). Whilst they generally act perpendicular to the southward-flowing CSLC, which acts parallel to the coast, they nonetheless play an important role in damping residual circulation through the mechanism of tidal friction. This arises because bottom friction is a non-linear function of water velocity, so as currents strengthen, a greater proportion of their energy is dissipated through friction with the sea bed. This effect can become significant in shallow coastal areas such as Torres Strait or the Gulf of Carpentaria (Wolanski et al. 1988; Wolanski 1993), though its effect is rapidly lessened in deeper areas. It has also been observed in the GBR, where the combination of the presence of many reefs in close proximity (which lead to increased secondary circulation features) and tidal friction effects act to steer low-frequency currents, such as the CSLC, away from areas dense with reefs; an occurrence coined the “Sticky Water” effect (Wolanski and Spagnol 2000). Any future increase in the strength of water currents entering the GBR shelf may therefore be mitigated to some extent by tidal friction, and potentially also by localised manifestations of the Sticky Water effect.

The aim of this study is to estimate to what extent population connectivity in the GBR may be affected by two major potential future changes to the marine environment: increased water temperatures and modified water circulation patterns. A biophysical model is first used to estimate connectivity in the present day, by simulating larval dispersal for a number of successive recent coral spawning periods. The effects of a temperature increase are then modelled by using data from laboratory experiments – measuring the effects of a 2°C temperature increase on larval mortality and competence acquisition and loss rates – to drive the biophysical model. Changes in connectivity are quantified by calculating the variation in a number of connectivity indicators. By analysing results from climate models in the Coupled Model Intercomparison Project phase 5 (CMIP5; Taylor et al. (2012)), we then calculate projected changes to the zonal water transport reaching the GBR shelf, and use these data to modify the boundary conditions of the on-shelf circulation model. Larval dispersal is then simulated for this modified circulation scenario. The effects of increased water temperature and modified circulation are compared and evaluated. Finally, a metapopulation model is used to evaluate the impact of these changes on the recovery times of coral populations following disturbances, to assess whether they are likely to increase or decrease the persistence of coral populations.

6.2 Methods

6.2.1 Numerically modelling larval dispersal

Larval dispersal was modelled using the SLIM ocean model¹ and particle-tracking module, following the same approach as Thomas et al. (2015). SLIM is a depth-integrated, finite element, unstructured mesh ocean model. SLIM's use of an unstructured mesh allows the model resolution to be varied in space (Legrand et al. 2006). The mesh was generated with the Gmsh software package (Geuzaine and Remacle 2009), and was made very fine close to reefs and coastlines, where small-scale flow features are known to be important, whilst being kept coarse in open-sea areas, where the flow is more uniform and high resolution is not essential. The model resolution ranged from 300 m to 5 km, and the model was able to explicitly resolve small-scale features such as tidal eddies formed in the wakes of reefs. Given the topographic complexity of the region, resolving these features is essential to accurately model larval dispersal, as they are known to have a significant impact on retaining larvae close to their natal reef (Burgess et al. 2007).

Details of the model equations and the parameterisations used can be found in Thomas et al. (2014). The depth-averaged version of the model has previously been shown to be able to realistically reproduce large-scale flow through different regions in the GBR (Andutta et al. 2012; Thomas et al. 2015; Thomas et al. 2014; Wolanski et al. 2013), as well as propagation of tides (Lambrechts et al. 2008; Thomas et al. 2014), salinity concentration (Andutta et al. 2011), suspended sediment concentration (Lambrechts et al. 2010) and small-scale features in the wakes of islands (Lambrechts et al. 2008). The use of a depth-integrated model is justified by the fact that waters in the GBR are generally vertically well-mixed throughout the year (Middleton and Cunningham 1984; Wolanski 1983), especially over reefs, where larval dispersal is concentrated, and where bottom roughness is at least an order of magnitude greater than elsewhere (this is accounted for in the model), further facilitating rapid vertical mixing. Depth-integrated models have been shown to compare favourably with full 3D models on the GBR shelf (Black et al. 1991; Luick et al. 2007).

External forcings were applied to the hydrodynamic model to account for the effects of the tides (OSU TOPEX/Poseidon Global Inverse Solution 7.2 dataset; Egbert and Erofeeva (2002)) and the wind (NCEP Climate Forecast System Reanalysis [CFSR] v2; Saha et al. (2014)) as described in Appendix S1 of Thomas et al. (2015). Water exchange with the neighbouring Coral Sea was accounted for by applying an additional water inflow along the central section of the open sea boundary (between 15°S and 17.6°S), with a corresponding outflow through the southern sections, resulting in the creation of a southward residual circulation (in the absence of other forcings). During periods of intense northward wind-driven currents, the direction of the net residual current was found to reverse and flow northward, in line with observations (Wolanski and Pickard 1985). The exact strength and position of the inflowing and outflowing currents was calibrated using current meter data from moorings of the Great Barrier Reef Ocean Observing System (GBROOS; IMOS (2013)) located close to the domain boundaries. Simulations were carried out for the 35 days following coral mass spawning in 4 successive years (2007, 2008, 2009, 2010), and calibration was carried out separately for each spawning season simulated, as the strength of the inflow from the Coral Sea is known to exhibit inter-annual

¹SLIM is the Second-generation Louvain-la-neuve Ice-ocean Model; see www.climate.be/SLIM for more information.

variability (Burrage et al. 1997). These three forcings are known to be the main drivers of water circulation on the GBR shelf (Wolanski and Pickard 1985). The model was validated for each spawning season simulated (shown in Appendix 6.A) and was found to realistically reproduce flow through the domain.

The dispersal of larvae through the region is modelled using a Lagrangian particle-tracking module integrated into SLIM. Details of the model equations and parameterisations can be found in (Thomas et al. 2014). Millions of “virtual larvae” are released over all reefs in the domain, and their transport is modelled using a random walk formulation of the 2D advection-diffusion equation. The positions of reefs are taken from the Great Barrier Reef Marine Park Authority Features shapefile layer (GBRMPA 2013). Only reef areas shallower than 10 m were considered in the present study, as reefs at greater depths in the domain are not yet consistently included in this map, and selective exclusion of deeper reefs can lead to a significant misrepresentation of connectivity patterns (Thomas et al. 2015). The number of reefs over which larvae were released was 1,223.

The output of the particle tracker is a large connectivity matrix. In order to characterise connectivity patterns, a number of standard “connectivity indicators” were calculated; these were:

Weighted Connectivity Length (WCL): a measure of the average dispersal distance from origin to destination reef, for all the larvae released over a given reef, defined as:

$$\frac{\sum_{\text{all connections}} \text{connection strength} \times \text{connection length}}{\sum_{\text{all connections}} \text{connection strength}}$$

where the connection strength is given by the number of larvae released over the origin reef that settled onto the destination reef, whilst the connection length is the radial distance between origin and destination reefs.

Local retention: the proportion of larvae released over a reef which settle on the same reef.

Self-recruitment: the proportion of larvae settling on a reef which were released over the same reef.

Proportion settled: the proportion of larvae released over a reef which settle on any other reef.

Number of incoming connections: the number of reefs a given reef receives larvae from.

Data on larval mortality and development rates at different water temperatures were acquired from J. Figueiredo (pers. comm.), who carried out laboratory experiments on *Acropora millepora* larvae at temperatures of 27°C and 29°C². Present-day water temperatures in the region focused on in this study (i.e. the southern GBR) are typically in the range of 26°– 28°C during the coral mass spawning period in Nov–Dec (McLeod et al. 2015); in the model the water temperature was considered to be uniform at 27°C in the present day, and at 29°C for the future scenario.

²Water temperatures in the GBR are expected to increase by about 2°C over the next century assuming a high-emissions future climate scenario (an A2 scenario in CSIRO (2011))

Larvae at 29°C developed faster and exhibited higher natural mortality, leading to a shorter mean time to competence (mtc) of 6.1 days compared to 7.1 days at 27°C. Mortality was modelled using a generalised Weibull distribution with parameters derived from the experimental data. Larvae obtained the ability to settle (competence) at a constant stochastic rate, and once competent they could lose competence at a rate given by a Weibull distribution, with parameters for both distributions taken from the observed data of J. Figueiredo following the same model and approach of Connolly and Baird (2010) and Figueiredo et al. (2013). Competent larvae were considered to settle onto the first reef they came across, whereupon +1 was added to the appropriate element in the connectivity matrix, and those larvae were then removed from the remainder of the simulation. A sensitivity analysis was carried out to gauge the uncertainty introduced into the model by the biological parameters, and is presented in Appendix 6.B.

6.2.2 Estimating projected changes in water flows into the GBR

Estimates for the change in water current strength entering the GBR shelf were obtained by analysing the output of 27 CMIP5 global climate models (Taylor et al. 2012). Zonal water currents were obtained for the top 200 m of the transect between 10° and 20°S (roughly corresponding to the known range of the SEC liable to impinge on the GBR shelf) at a longitude of 155°E for a) present-day simulated circulation, and b) projected circulation for 2080-2100 assuming a “business as usual” global climate scenario (corresponding to the Representative Concentration Pathway RCP8.5), in order to assess the greatest possible impact of climate change on water circulation on the shelf. Whilst the bulk of the impinging water does not enter the GBR shelf, we assume that the change in water transport onto the shelf is proportional to the change in transport impinging on the shelf.

The relative change in net westward zonal water velocity was calculated for each model, and a multi-model median of the relative change was calculated, as well as upper and lower quartiles of the distribution. Simulations were then run of the hydrodynamics on the GBR shelf using SLIM for future scenarios using the following approach: the residual currents entering the shelf at the open sea boundaries (described in the previous sections as representing water exchange with the neighbouring Coral Sea) were modulated by the multi-model median relative change, as well as the lower and upper quartiles, to obtain a set of 3 simulations which encompass the range of relative changes predicted by most models. All other model parameters were not modified compared with the present-day simulations. For each present-day simulation, a set of three future scenario simulations was run, for a total of 12 different hydrodynamic simulations. Larval dispersal simulations were then carried out using these “future scenario” hydrodynamic simulations, and connectivity matrices were obtained. Connectivity indicators were calculated separately for each of these future scenario simulations and were then averaged over the other simulations of the same type (i.e. a) the 4 forced by the multi-model-median change, b) the 4 forced by the upper quartile change and c) the 4 forced by the lower quartile change) to obtain a single set of 3 indicators representing median, upper and lower quartile predictions.

6.2.3 A simple metapopulation model

To gauge the effect of the altered connectivity patterns on the time taken for reefs to recover from disturbances, the following simple metapopulation model was employed to estimate the time evolution of the size of each coral colony:

$$\begin{aligned}
 S_{i,n+1} = & S_{i,n} \\
 & + S_{i,n} R_i \Delta t (1 - c_i) \\
 & + s_i \left(\sum_j C_{ij} \right) (1 - c_i [1 + R_i \Delta t (1 - c_i)])
 \end{aligned} \tag{6.1}$$

where $S_{i,n}$ is the size (counted as the number of coral polyps) of the coral colony on reef i at iteration n , R_i is the growth rate per coral polyp on reef i , c_i is the proportion of coral cover on reef i (i.e. the proportion of the reef's available surface area covered by coral polyps, with a polyp considered to measure 1 mm² based on Anthony 1999), s_i is proportion of coral larvae settling on reef i which survive to maturity, Δt is the time step, in years, from iteration n to iteration $n + 1$, and C is the connectivity matrix from the larval dispersal simulations, processed as described in the next paragraph, whose elements represent the number of larvae from origin reefs i settling on destination reef j . The term $\sum_j C_{ij}$ therefore sums the total number of incoming larvae at reef i from all other reefs (including reef i itself). The model accounts for the possibility of a coral colony growing asexually (via the term $R_i \Delta t (1 - c_i)$) and through settlement of larvae (via the term multiplied by the connectivity matrix). The factor of $(1 - c_i)$ accounts for the fact that space on a reef is limited, and as the free space on a reef diminishes, coral growth slows down and settlement success also decreases.

Parameters were estimated from the literature as $R_i = 0.1415$ (based on Gilmour et al. 2013, who saw an increase in coral cover from 9% to 44% within 12 years following a bleaching event) and $s_i = 0.5/\text{year}$ (Penin et al. 2010). Each row in the connectivity matrix was divided by the number of larvae released over that reef, so that its elements represented the probability of a larva released from reef p (row) settling on reef q (col), and then multiplied row-wise by the size of the coral population on that reef (estimated as the reef surface area multiplied by the surface area of a polyp, taken as before to be 1 mm² based on Anthony 1999) and by the number of eggs produced per polyp (estimated as 6/year, based on Hall and Hughes (1996)), so that its elements finally represented an estimate for the total number of larvae produced by reef p settling on reef q . The same connectivity matrix is used for every iteration. The model was run 4 times for each scenario, each time using a different year's connectivity matrix, and the 4 recovery times estimated for each reef were averaged.

Clearly these parameters represent gross estimates, but at present more detailed data is scarce. The model makes a number of simplifications, such as assuming that coral growth will be 2-dimensional, and that R_i and s_i are constant in space. However, since the goal was to calculate the relative change in recovery times between different scenarios (present day versus future scenario), rather than to accurately predict present-day recovery times, precise knowledge of these parameters was not considered essential. Furthermore, keeping the growth and survival rates constant allowed us to isolate the effect of the change in connectivity on recovery times.

Disturbances were simulated by reducing coral cover over certain reefs. Recovery times were obtained by seeing how many iterations it took for the disturbed reefs to re-

gain 99% of their initial coral cover. Two types of disturbances were simulated: single-reef disturbances, whereby coral cover was reduced by 85% over a single reef, and multiple-reef disturbances, whereby coral cover was reduced on groups of reefs at a time. These groups were composed of 3 neighbouring cross-shelf strips 30 km wide; all reefs in the outer strips had coral cover reduced by 40%, whilst reefs in the central strip had coral cover reduced by 70%, mimicking the effect of a cyclone passing through the GBR.

6.3 Results

The results will be presented in three parts: first the effect of the temperature increase is reported, then the effect of the modified circulation patterns are reported, and finally the results from the metapopulation model are considered in order to assess the potential impacts on the recovery times of reefs following disturbances.

6.3.1 Effect of temperature increase

The temperature increase from 27°C to 29°C caused a significant reduction in inter-reef connectivity, as is clear from Table 6.1, which reports the main connectivity indicators for both temperature scenarios. Local retention of larvae increased by 37%, and the average distance between larval origin and destination, i.e. the WCL, decreased by 11%. The mean number of incoming connections to each reef (i.e. the number of reefs from which each reef receives larvae) also decreased by 9%. All of these figures reflect a reduction in the potential for larvae to disperse away from their natal reef, driven by the decrease in mean time-to-competence (mtc) of *A. millepora* due to the 2°C increase in temperature. The proportion of larvae released which achieve settlement, meanwhile, remains practically unchanged (+2%).

We can get a clearer picture of the spatial structure of these changes by looking at Figure 6.2, which shows the relative change in connectivity indicators for each reef. The changes in larval dispersal distances (Figure 6.2(a)) were relatively uniform in space, with almost all reefs seeing a decrease in their outgoing WCL at 29°C, though some saw a greater decrease than others due to spatial differences in the distribution of reefs. This can be understood with a simple example: if we take two reefs, say reefs A and B, and imagine that reef A has a neighbour 10 km away and another 50 km away, whilst reef B has a neighbour 8 km away and another 10 km away, then if the mean distance travelled by larvae when they become competent decreases from 10 km to 8 km, reef B will see a change in WCL of -20%, whilst reef A will see a much smaller change, since its closest neighbour is 10 km away in any case.

The change in local retention was much more variable in space (Figure 6.2(b)). Despite the strong overall increase in local retention when averaged over the entire study domain, some reefs saw much larger increases than the average, whilst some reefs even

Temp.	WCL (km)	Local ret.	Self-rec.	Nb. incoming connections	Prop. settled
27°C	31.6	3.5%	7.0%	49.1	45.4%
29°C	28.1 (-11.3%)	4.9% (+37.1%)	7.7% (+10.3%)	44.6 (-9.2%)	46.4% (+2.1%)

Table 6.1: Connectivity measures for different temperature scenarios simulated, averaged over all reefs. All measures were averaged over the 4 different years simulated.

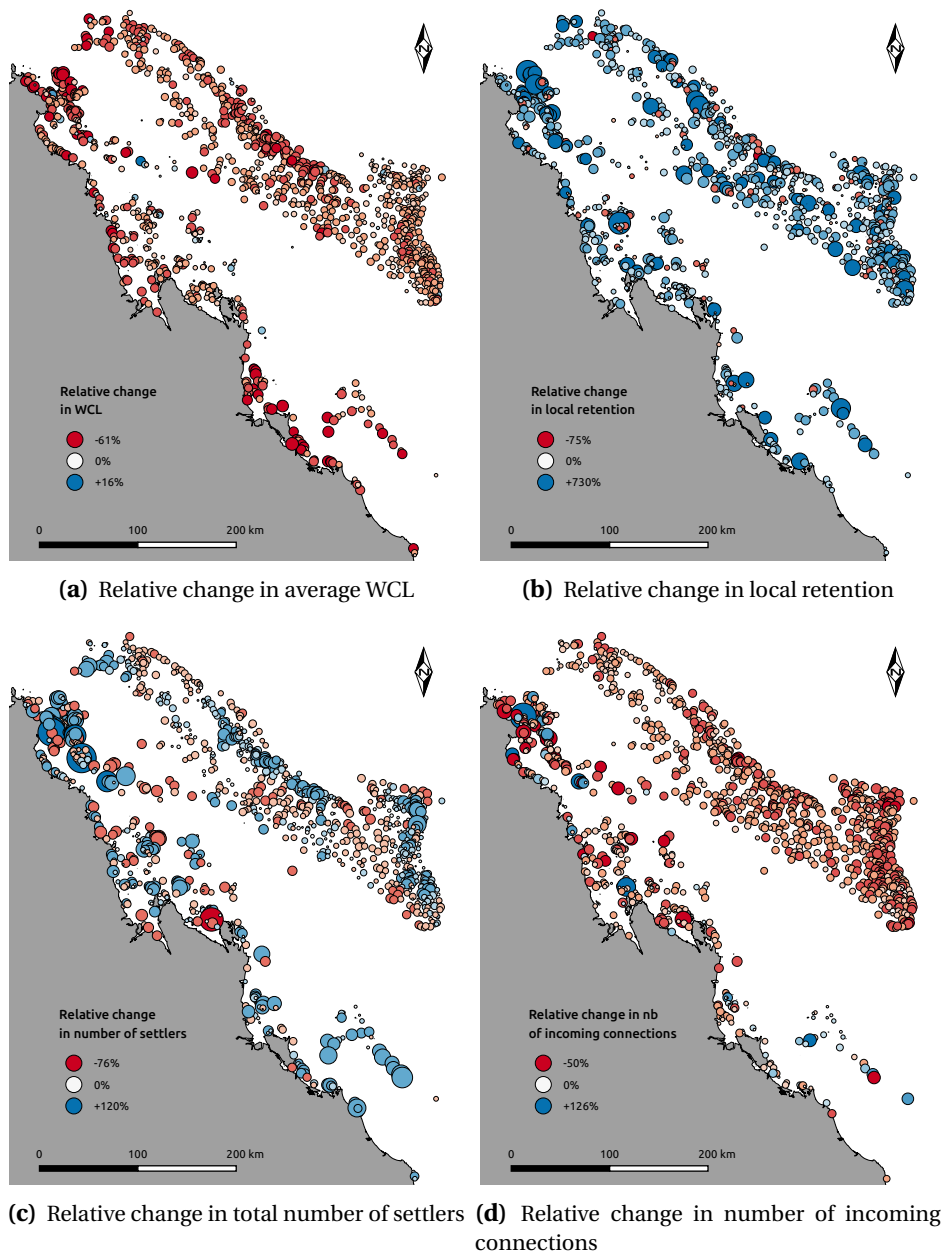


Figure 6.2: The effects of a 2°C temperature increase on different connectivity indicators on every reef in the southern GBR. The colour code (red: negative, blue: positive) and size of the reef (proportional to the absolute value) illustrate the change of each connectivity indicator on each reef. Max and min values are shown. Figure 6.2(a) shows the change in the average distance from source to sink for larvae released over each reef; Figure 6.2(b) shows change in local retention; Figure 6.2(c) shows the change in the total number of larvae settling on each reef (including those locally retained and those imported from other reefs); Figure 6.2(d) shows the change in the number of incoming connections to each reef (i.e. the number of other reefs it is receiving larvae from). Statistics are calculated per year and per reef, and averaged over 4 years.

saw decreases in local retention, a result of the complex water currents combined with the inhomogeneous spatial distribution of reefs. Some patterns do nonetheless appear

evident. The reefs with the largest increases in local retention tend to be clustered around the Whitsunday Islands in the north of the domain, with a smattering also found along the outer edge of the mid-shelf reefs. Excluding the Whitsunday Islands, most of the coastal reefs in the domain underwent very limited increases in local retention. It should be noted that most of these reefs had high rates of local retention to begin with, and that the absolute changes in local retention were actually greatest amongst these reefs.

The map showing the change in the number of larvae settling on each reef over the course of the simulation (Figure 6.2(c)) shows even greater spatial differences, despite the overall change in settlement of only +2%. In general, it appears that reefs in the most reef-dense areas see an increase in the number of settlers (for instance around the Whitsunday Islands, and in pockets of mid- and outer-shelf reefs where inter-reef distances are smallest), whilst reefs which are more spread out are more prone to undergoing a decrease in the number of settlers (for instance the few scattered reefs in the central “shipping channel”, and in the pockets of mid-shelf reefs where reef spacing is greatest). This may be explained to a large extent by the fact that decreased PLD leads to larvae travelling shorter distances (cf. Figure 6.2(a)), thus increasing short-distance connectivity and decreasing longer distance connectivity, so reefs close to many other reefs see an increase in the numbers of settlers, whilst reefs further from other reefs get fewer settlers. This general principle is muddled somewhat by the fact that the change in larval retention is not the same for all reefs, so the change in the number of settlers on a reef depends not only on the change in dispersal distances of larvae from neighbouring reefs, but also on the change in the local retention rate of that reef, which in turn is affected by the currents around the reef, which can vary considerably in space. Furthermore, increased larval mortality at 29°C acts to further limit long-distance connectivity, decreasing the number of larvae settling on the more isolated reefs.

Figure 6.2(d), showing the change in the number of incoming connections to each reef, highlights the extent of the net decline in connectivity due to the temperature increase. With the exception of a small number of primarily coastal reefs, almost all reefs in the domain undergo a reduction in the number of reefs they receive larvae from. This means that whilst the total number of larvae potentially settling on each reef may actually increase in certain areas, these settlers will almost always be coming from fewer sources.

6.3.2 Effect of altered circulation patterns

Analysis of the output of 27 CMIP5 climate models showed that the net zonal flow towards the GBR shelf was expected to exhibit strengthened westward transport, although variability in predictions between models was significant, as shown in Figure 6.3. The multi-model median was a westward increase in current strength of 10%, and the upper and lower quartiles were an increase of 28% and a decrease of 3%, respectively.

Simulations of the hydrodynamics on the GBR shelf were run with the residual currents at the boundaries modified by these values, and the output from these simulations were used to drive the larval dispersal model at a water temperature of 27°C. The change in the main connectivity indicators caused by the change in circulation patterns are shown in Table 6.2. The results show that changing the water in- and outflow at the boundaries had a minimal effect on connectivity patterns overall, with changes in most quantities being smaller than 1% relative to the present day scenario. The only indicators which saw changes bigger than 1% were self-recruitment for the +28% flow scenario

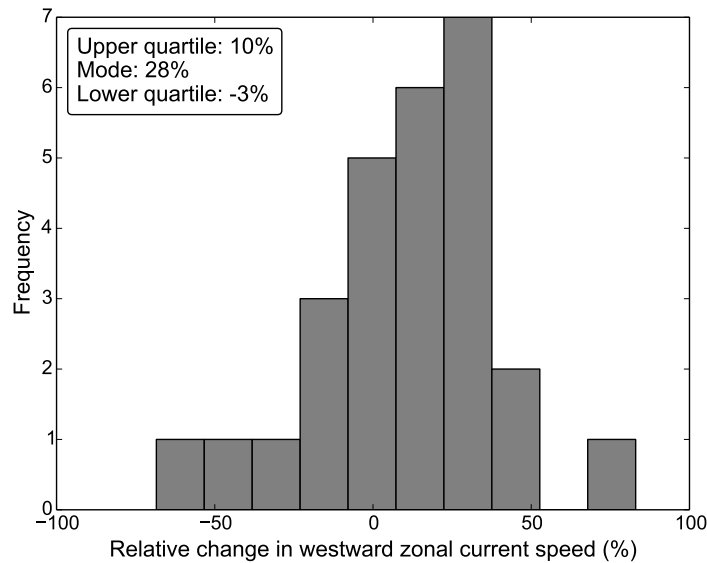


Figure 6.3: Histogram showing the distribution of the projected relative changes in westward zonal currents between 10° S and 20° S, averaged over the top 200 m of the water column.

(+1.2%) and the WCL for the +10% and +28% flow scenarios (+1.1% and +2.9% respectively). The changes in the self-recruitment and local retention indicators did not entirely follow expected patterns for the +28% flow scenario, as it showed an increase in both quantities rather than a decrease, which was the case for the +10% flow scenario. This could be due to the non-linear interaction between the currents and the topography, as imposing stronger currents at the boundaries does not necessarily lead to stronger currents over all the domain, and can even lead to a decrease in certain areas. For instance a large increase in the current strength can cause an increase in residence times in reef-dense areas due to increased steering of residual currents around reefs by the Sticky Water effect, as discussed in the Introduction.

For comparison, these changes are much smaller than typical inter-annual fluctuations in these indicators (for the 4 years simulated, the range in average self-recruitment was up to 14%, and in WCL up to 53%), and about an order of magnitude smaller than the impact of increasing the water temperature by 2°C (cf. results reported in the previous section). Thus, the effect of the altered circulation patterns was considered negligible

Scenario	$\Delta(\text{WCL})$	$\Delta(\text{local ret.})$	$\Delta(\text{self-rec.})$	$\Delta(\text{prop. settled})$
-3% inflow	-0.1%	-0.2%	+0.3%	+0.0%
+10% inflow	+1.1%	-0.6%	-0.6%	-0.0%
+28% inflow	+2.9%	+0.6%	+1.2%	-0.6%

Table 6.2: Change in connectivity measures for different circulation scenarios, compared with the present day scenario. The 3 scenarios listed correspond to a modulation of residual currents flowing through the domain of -3%, +10% and +28% relative to the present day scenario. Data shown are for a water temperature of 27°C. $\Delta(\text{self-rec.})$: change in self-recruitment; $\Delta(\text{WCL})$: change in WCL; $\Delta(\text{local ret.})$: change in local retention; $\Delta(\text{prop. settled})$: change in the proportion of larvae released which settled somewhere.

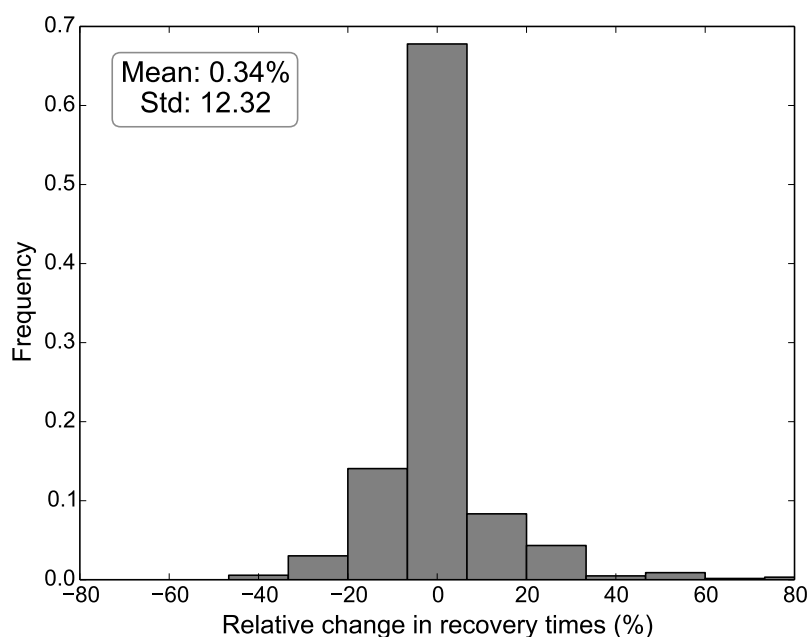


Figure 6.4: Histogram showing the relative changes in recovery times caused by the 2°C temperature increase for all the reefs in the domain. Mean and standard deviation are reported. Changes in recovery times were averaged over the 4 years simulated for each reef.

compared with the effect of the temperature increase. Given this finding, only the effects of the temperature increase were considered when assessing the impact of the projected changes on recovery times following a disturbance, presented in the next section.

6.3.3 Impact of modified connectivity patterns on recovery from disturbances

Single-reef disturbances

The results of the metapopulation model suggested that the average time taken by the reefs in the domain to recover from single-reef disturbances would not change significantly at 29°C compared with 27°C, with a net increase in recovery time of only 0.3%. There was, however, considerable variability between reefs, with some reefs recovering much more quickly at 29°C, whilst others recovered more slowly, as can be seen in the histogram in Figure 6.4, which has a standard deviation of 12.3%. Figure 6.5(b) shows the spatial structure in the change in recovery times; there is clearly a large spatial variability. This can be explained in part because recovery times are linked to local retention, with high local retention hastening recovery, and changes to local retention are predicted to be very spatially variable (see Figure 6.2(b)), and in part because the decrease in dispersal distances from most reefs slows down recovery on the reefs most reliant on larvae from relatively far-off reefs, whilst hastening recovery on reefs with lots of near neighbours.

To some extent, Figure 6.5(b) reflects Figure 6.2(c) which shows the change in the number of larvae settling on each reef, since an increase in this latter quantity will lead to a decrease in recovery times, and vice-versa. However, the size of the change in recovery times is not purely driven by the change in the number of settlers, since the reef surface area also plays a large role in the metapopulation model, with larger reefs requiring

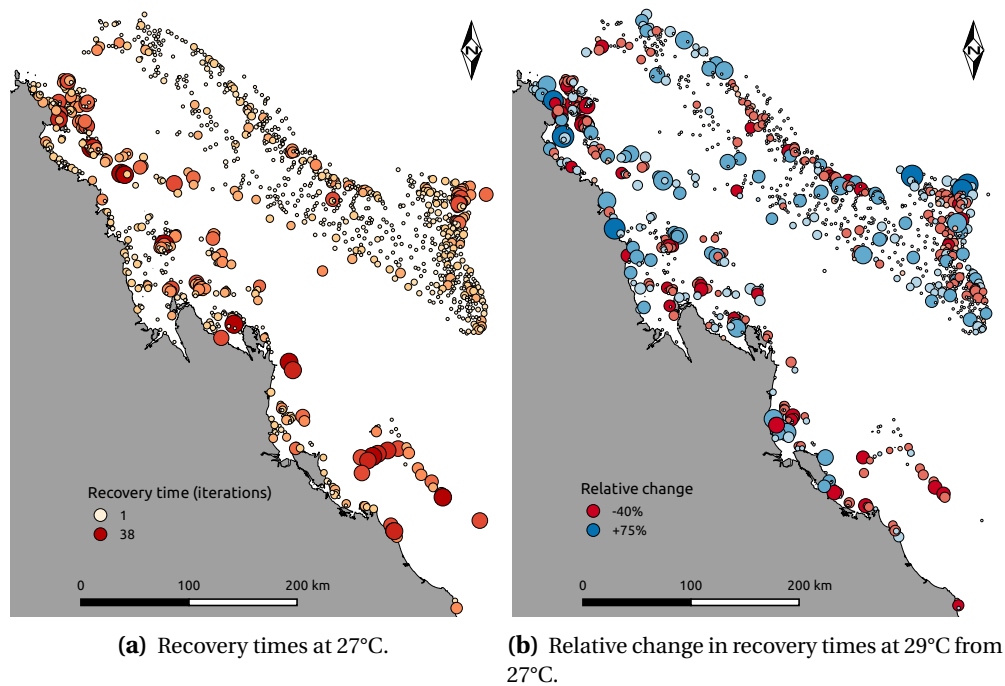


Figure 6.5: Effects of a 2°C temperature increase in recovery times following a single-reef disturbance. Each reef was disturbed in turn, with its initial coral cover reduced from 100% to 15%, and its time to recovery was calculated using a metapopulation model. Figure 6.5(a) shows the recovery times for each reef with a water temperature of 27°C; Figure 6.5(b) shows the relative change in recovery times when the temperature was increased to 29°C. The relative changes were averaged over the 4 years simulated.

more settlers to repopulate them, amplifying potential differences in recovery times. It is clear from Figure 6.5(b) that the biggest decreases in recovery times occur in areas with the highest reef densities, notably the Whitsunday Islands, the reef-dense easternmost pockets of mid-shelf reefs, and the strip of outer shelf reefs in the centre of the domain. Elsewhere, the general tendency is for recovery times to increase.

Multiple-reef disturbances

The overall change in recovery times for disturbances along “cyclone-track”-style bands due to the 2°C temperature increase was a 1.1% increase, slightly larger than for single-reef disturbances. This (small) difference is presumably due to the reduced connectivity associated with wider-area disturbances impeding recovery. The temperature increase had a bigger effect on the recovery times inside some bands than others, but inter-band variability was nonetheless small, with the largest positive and (only) negative changes averaged over all the reefs in each band being +2.4% and -1.1% respectively. The mean recovery times were also smaller than for the single-reef disturbances (multiple-reef: 3.2 iterations; single reef: 3.8), meaning that the multiple-reef disturbance had less overall impact than the more extreme single-reef disturbance.

There was slightly less variability in the change in recovery times from one reef to the next (standard deviation of 10.9, averaged over all bands), than when reefs were perturbed individually (where the standard deviation was 12.3). This can be ascribed to

there being a greater decrease in inter-reef connectivity when many neighbouring reefs are perturbed together, meaning that asexual growth therefore plays a bigger role in recovery, which acts to homogenise different reefs' recovery times.

6.4 Discussion

It is clear that larval dispersal patterns in the GBR will likely undergo some sort of shift over the next 100 years, if climate projections are proved to be correct. The considerable quantity of converging evidence on climate change and its effects in the region give a significant weight to these projections (Kirtman et al. 2013). We have investigated the possible effects of 2 of major projected changes on larval dispersal and connectivity of *A. millepora* in the southern GBR: an increase in water temperature and a change in westward water transport entering the GBR. The first of these changes was found to have a very significant effect on dispersal patterns, causing an increase in local retention of larvae, and a decrease in connectivity to other reefs. The change in the residual water transport onto the GBR shelf, on the other hand, was found to only have a marginal effect on larval dispersal, with changes in potential connectivity estimated to be about an order of magnitude smaller than those caused by the 2°C temperature increase.

6.4.1 Impact of increased inflow from the Coral Sea on connectivity patterns

The results of this study indicate that the projected changes in large-scale water circulation through the Coral Sea – specifically the expected change in the size of zonal transport impinging on the GBR shelf – are unlikely to have a significant effect on connectivity patterns in the GBR, at least if the changes that do occur are within the range of present model predictions. That the difference in the connectivity indicators was so limited, even for the more extreme scenario of a 28% increase in flow onto the shelf, can partly be explained by the fact that certain indicators, such as local retention and self-recruitment, are mostly affected by the flushing time of reefs, which is mainly controlled by tidal rather than Coral Sea-driven or wind-driven flows (see Andutta et al. 2012, Table 2; peak tidal currents at all mooring sites in the GBR are much greater than residual currents). Average dispersal distances on the other hand would be expected to be more strongly affected by low-frequency currents, since once larvae are flushed from a reef, it is the presence (or not) of a coherent low-frequency current which controls dispersal distances. Whilst changes in WCL were greater than changes in other indicators however, they remained small.

One way of interpreting the small variation in WCL for the future flow scenarios is by assuming that flow on the GBR shelf is already relatively energetic compared with the additional energy supplied by the increased inflow. The bottom friction stress term is a non-linear function of water velocity, so if energy is added to a shallow system in which flow speeds are already high, then a greater proportion of this additional energy is dissipated by bottom friction than if the same energy were added to a system with lower flow speeds (Wolanski and Spagnol 2000). The presence of strong tidal currents, as is the case on the southern GBR shelf, can therefore act to reduce the strength of less energetic low-frequency currents through tidal friction. Additionally, in reef-dense areas the widespread presence of secondary circulation features downstream of reefs can significantly increase energy dissipation and act to steer low-frequency currents around these areas (the so-called Sticky Water effect (Wolanski and Spagnol 2000)). This effect would

further attenuate the impact of stronger residual currents on larval dispersal, since many larvae enter the water column in these reef-dense areas. The combination of energy dissipation by tidal friction over the whole domain, and the Sticky Water effect further steering the strengthened low-frequency current away from reef areas, offers a plausible explanation for why modified Coral Sea inflow has a very limited effect on connectivity patterns. Additionally, whilst the net flow through the region was southward most of the time, during occasional prolonged periods of south-easterly trade winds it reversed direction, during which time the effects of the increased inflow onto the shelf would have been to reduce rather than enhance larval dispersal potential.

It is important to point out that we assumed that all other forcings of the hydrodynamic model would be the same as in the present day. Whilst this is a safe assumption to make for tides, it is possible that the wind field could change in the future. Many models predict a strengthening of large-scale south-easterly trade winds over the south-west Pacific Ocean (Sen Gupta et al. 2012), and this could also plausibly affect the currents directly on the GBR shelf. Given the lack of precise quantitative projections for any increase in wind strength however, or of any possible temporal shift in the season of stronger or weaker winds, it was not possible to take this effect into account in the model. It is also conceivable that the position of the Coral Sea inflow onto the GBR shelf could migrate northwards or southwards (Steinberg 2007). Such a change would likely have a significant impact on larval dispersal in the central GBR (Munday et al. 2009), though its impact on the southern GBR domain modelled in this study would likely be much more limited.

6.4.2 Impact of higher water temperature on connectivity patterns

Focusing next on the effects of the 2°C temperature increase, the results follow the observations of Figueiredo et al. (2014), who found that on reefs with a water residence time smaller than about 4 days, the temperature increase led to an increase in local retention of *A. millepora* larvae (due to the shorter larval mtc), whilst on reefs with longer residence times it led to a decrease in local retention (due to the higher mortality rate overcoming the effect of the increased mtc). The results of our study therefore suggest that most reefs in the southern GBR have water residence times smaller than 4 days, since most reefs underwent a significant increase in local retention. This result is not altogether surprising given the large tidal currents present throughout most of the region. Indeed, whilst some lagoons and atolls can have much longer water residence times, most reefs in the GBR would be expected to have residence times much lower than 4 days (see Andutta et al. 2012)³, as is also the case in many other coral reef ecosystems worldwide (Kraimes et al. 1998; Leis 1982; Paris and Cowen 2004). The large spatial variation in the change in local retention (Figure 6.2(b)) does however suggest that reefs with very different water residence times do co-exist in the southern GBR, not surprising given the large extent and diverse bathymetry of the region studied.

In addition to the general increase in local retention, larvae are predicted by the model to travel significantly shorter distances before settling, and reefs are expected to receive larvae from fewer other reefs. This general reduction in inter-reef connectivity may change the capacity of reefs to recover from disturbances such as bleaching events

³Readers of (Andutta et al. 2012) should account for the fact that most reefs in the GBR are actually much smaller than the 10 x 10 km precincts considered by the authors of that study to calculate residence times (which are even larger than the typical tidal excursion of 4–6 km). As such, individual reefs are likely to have much lower actual residence times than those reported in that study.

or tropical cyclones. Indeed, the results of the metapopulation model suggest this is the case, with reefs in different areas predicted to undergo significant positive or negative changes in recovery time, depending on their position in relation to other reefs, as well as on the water circulation patterns in their local area. Numerical models such as the one presented in this study can be used to predict which areas can potentially be most affected either way, though integrating such information for multiple species into effective marine management remains a key challenge (López-Duarte et al. 2012).

Despite the many difficulties inherent in transferring the results of numerical models into marine management strategies, some simple, practical considerations for MPA placement could be deduced from these models without extensive analysis. For example, if larvae of the main reef-building coral species are all found to exhibit reduced dispersal distances with a temperature increase, then it may be necessary to reduce MPA spacing in order to maintain an optimal level of inter-MPA connectivity, an important property for maintaining resilience in MPA networks (Almany et al. 2009; Green et al. 2014). Likewise, if local retention is also expected to increase for other coral species, then it may be reasonable to question whether the effectiveness of MPAs as sources of coral larvae to surrounding areas through spillover may be diminished. Whilst numerical models such as the one presented in this study cannot “prove” that such effects will occur, they can identify effects which may occur, and which merit further study with empirical means.

6.4.3 Effect on recovery from disturbances

The time taken by a coral population on a given reef to recover from a disturbance depends on how many larval recruits it receives and on asexual growth rates, as well as on recruitment success. In the model used in this study, we have assumed that both asexual growth rates and recruitment success are unaffected by changes in water temperature. Whilst this assumption was driven by the lack of data available on this subject, it nonetheless allows us to isolate the response of recovery times to changes in larval dispersal alone. The results indicate that even with this simplification, the effect of the temperature increase on recovery times is complex. Local retention is expected to increase over most (but not all) reefs, and to differing extents. This should act to reduce recovery times over most reefs, but the advantage afforded by increased local retention depends on the extremity of the disturbance, since an event which destroys most of the coral on a reef will therefore also destroy most of the additional larval source. Higher local retention would therefore be expected to mainly aid recovery from minor disturbances, or during the latter stages of recovery from a major disturbance.

It seems logical to assume that a given reef would become better able to recover from disturbances if it gained more settlers from a larger number of reefs, preferably spread over a wide spatial area, to mitigate the effect of a disturbance wiping out a number of neighbouring coral populations. The temperature increase was found to cause an increase in the number of settlers on reefs in certain areas (Figure 6.2(c)). These reefs did indeed see decreases in recovery times for single-reef disturbances at 29°C (Figure 6.5(b)). However, larval dispersal distances were also found to decrease throughout the domain (Figure 6.2(a)), suggesting most reefs would have a reduced capacity to recover from disturbances affecting a wider area. The results of the metapopulation model support this hypothesis, as reefs affected by a wide-area disturbance saw a bigger jump in recovery times than when they were affected by a single-reef disturbance (+1% compared to +0.3%), despite the wide-area disturbance having an overall smaller impact than the

single-reef one (mean recovery time 16% smaller). These results suggest that in the future, reefs may have a similar capacity to recover from minor disturbances and small-area disturbances due to the increase in local retention and very short-distance connectivity offsetting the decrease in longer-distance connectivity, but a decreased capacity to recover from disturbances of greater severity and affecting a wider area due to the general decrease in inter-reef connectivity. Within this general trend the local picture is complex, with some patches of reefs possibly becoming more resilient to disturbances due to enhanced connectivity from neighbouring reefs (mainly located in areas of very high reef density) and others becoming much less resilient due to decreased connectivity from other reefs (mainly in areas with sparser reef distributions).

6.4.4 Other possible sources of change

In this study we have focused on the impacts of two specific effects driven by global climate change predicted to occur which we have considered as most likely to affect larval dispersal in the GBR; however other changes are also likely to occur to the GBR's environment over the next century, and these may also have an impact on larval dispersal and connectivity. A change in the local wind regime is possible for instance, and this could affect the wind-driven currents on the shelf (Sen Gupta et al. 2012). Exactly how the winds could change over the GBR during coral spawning periods in the austral summer is not yet clear however, and this is an issue which merits further study. Likewise any change in localised anthropogenic impacts not necessarily related to climate change, e.g. pollution from land or marine industry, could also have an impact on the health of coral larvae, though most such effects would be expected to be limited to the adult population rather than directly affecting larvae.

The modelling approach presented in this study makes use of a number of empirically-derived biological parameters to describe larval survival and competence acquisition/loss at different temperatures, with parameter values based on laboratory measurements of larvae. This is currently the best method available to replicate larval life history as accurately as possible, since equivalent measures for larvae in the open ocean do not exist. The upside of observing larvae in the laboratory is that it is possible to estimate biological parameters to a reasonably high level of accuracy, and this is shown in the model sensitivity analysis in Appendix 6.B which indicates that the uncertainty introduced by the biological parameters is relatively limited. The downside however is that various processes occurring on larvae in the ocean, such as predator mortality, are not accounted for. Likewise the possible effects of change in water quality or acidity on larvae are unknown. This should not affect the model predictions assuming these processes are not highly temperature-dependent. The extent to which larval mortality by predation is temperature-dependent is not an issue which has received much attention, and which may in particular merit further work.

It is worth keeping in mind that the present study has looked at potential connectivity assuming coral is present over all reefs in the domain. We have ignored direct impacts of climate change, and other stressors, on the health of adult coral and coral reef ecosystems as a whole, focusing solely on its effects on larval dispersal and potential connectivity. It is in fact probable that various stressors will act to dramatically reduce coral cover by the years 2080-2100 (Hoegh-Guldberg et al. 2007). This change in adult coral cover will necessarily affect connectivity in the GBR as the network will likely lose many sources of larvae. The extent to which any decline in coral population will vary spatially

is not known however, and it is not possible to account for spatial differences in coral cover in the model in the absence of spatially extensive, detailed data. We have therefore limited ourselves to describing “potential” connectivity, i.e. the potential connectivity network assuming equal coral density over all reefs. We can consider that we have assumed that concerted action to protect reefs from localised sources of stress, as well as from the effects of climate change, would have prevented a catastrophic decline in coral populations, and that dispersal of coral larvae would still be a key ecosystem process in the GBR.

APPENDIX

6.A Validation of hydrodynamics

Validation data for the hydrodynamic model are presented in this section. Tables 6.A.1-6.A.4 report observed and predicted depth-averaged current speeds and directions at different mooring sites in the GBR for each spawning season simulated. Observed data were obtained from the Great Barrier Reef Ocean Observing System (GBROOS; IMOS (2013)). Each table reports unfiltered values averaged over the length of the 35-day simulation indicated in the caption. These data showed good model performance in recreating realistic currents at the mooring locations, which included one site in an open-sea area (Capricorn Channel), where flow is relatively uniform in space, and 2 others close to an island (Heron Island North and South), where smaller-scale flow features become more important. In all cases the predicted current speeds and directions were close to the observed values, and within their standard deviations. Known biases include a tendency to underestimate current speed variability at the Capricorn Channel site, which may be due to inaccuracies in the wind forcing data, and a slight eastward bias in the current direction estimated at the Heron Island South site, which may well be due to inaccuracies in the local bathymetry dataset used: given the close proximity of the site to Heron Island, even a small misrepresentation of the topography could result in the current direction diverging from the observed values.

Site	Lat (°S)	Lon (°E)	$ U _{Obs}$	$ U _{SLIM}$	α_{Obs}	α_{SLIM}
CCH	22.408	151.993	0.25 ± 0.12	0.25 ± 0.14	195.1 ± 80.1	198.1 ± 93.8
HIN	23.380	151.987	0.36 ± 0.17	0.33 ± 0.17	172.7 ± 97.4	169.6 ± 93.5
HIS	23.513	151.955	0.21 ± 0.10	0.21 ± 0.11	176.0 ± 106.1	$164.4.1 \pm 100.0$

Table 6.A.1: Observed (U_{Obs}) and simulated (U_{SLIM}) depth-averaged current speeds averaged in time over the length of the simulation for **2007**, reported in ms^{-1} with their standard deviations, at GBROOS mooring sites in the southern and central GBR. Average observed (α_{Obs}) and simulated (α_{SLIM}) current directions are also reported, in degrees relative to North, along with their standard deviations. Time-series plots of these data are shown in Figures 6.A.1-6.A.8 (with tides filtered out). CCH: Capricorn Channel; HIN: Heron Island North; HIS: Heron Island South.

Site	Lat (°S)	Lon (°E)	$ U _{Obs}$	$ U _{SLIM}$	α_{Obs}	α_{SLIM}
CCH	22.408	151.993	0.27 ± 0.11	0.26 ± 0.16	174.3 ± 71.1	186.4 ± 91.7
HIN	23.380	151.987	0.36 ± 0.17	0.34 ± 0.18	167.3 ± 90.2	167.9 ± 95.1
HIS	23.513	151.955	0.25 ± 0.13	0.21 ± 0.12	209.2 ± 81.2	170.2 ± 94.6

Table 6.A.2: Validation data for the **2008** simulation. See Table 6.A.1 caption for legend.

In order to assess the ability of the model to reproduce realistic flow over time-scales longer than the semi-diurnal tidal component (which dominates the variability in most places on the shelf), time-series plots of observed and predicted depth-averaged current speeds and directions, averaged over a 24-hour period, are shown in Figures 6.A.1-6.A.4 (speed) and 6.A.5-6.A.8 (direction). It is clear from these graphs that the predicted currents follow the same temporal patterns as the observed currents and always have similar values. The spring-neap tidal cycle is clearly visible in both observed and simulated curves. Whilst observed and predicted values occasionally diverge over time scales of 2-3 days, there are no prolonged or large-scale departures of predicted currents from observation which arouse concern. Overall, the model reproduced realistic current time series' at the mooring sites.

Further validation of the model in other parts of the GBR can be found in Thomas et al. (2014) and Thomas et al. (2015); Appendix S1.

Site	Lat (°S)	Lon (°E)	$ U _{Obs}$	$ U _{SLIM}$	α_{Obs}	α_{SLIM}
CCH	22.408	151.993	0.26 ± 0.09	0.25 ± 0.16	184.6 ± 68.7	190.4 ± 94.3
HIN	23.380	151.987	n/a	n/a	n/a	n/a
HIS	23.513	151.955	0.23 ± 0.12	0.21 ± 0.12	186.1 ± 88.5	162.3 ± 105.4

Table 6.A.3: Validation data for the **2009** simulation. Observed data for HIN were unavailable. See Table 6.A.1 caption for legend.

Site	Lat (°S)	Lon (°E)	$ U _{Obs}$	$ U _{SLIM}$	α_{Obs}	α_{SLIM}
CCH	22.408	151.993	0.25 ± 0.10	0.26 ± 0.16	190.9 ± 77.3	184.3 ± 91.6
HIN	23.380	151.987	0.34 ± 0.15	0.35 ± 0.20	175.4 ± 108.1	168.0 ± 96.6
HIS	23.513	151.955	0.23 ± 0.11	0.22 ± 0.12	188.2 ± 97.7	162.7 ± 104.7

Table 6.A.4: Validation data for the **2010** simulation. See Table 6.A.1 caption for legend.

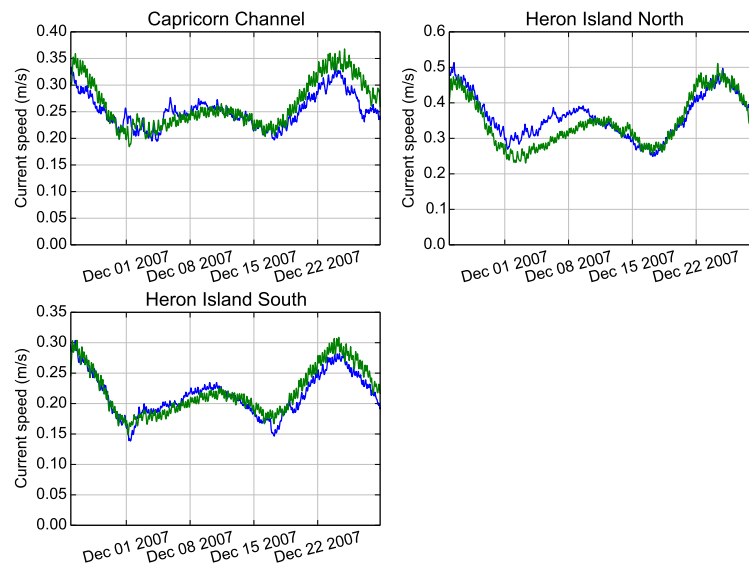


Figure 6.A.1: Time-series plot of observed (blue) and predicted (green) depth-averaged current **speed** at different mooring sites for the **2007** simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability.

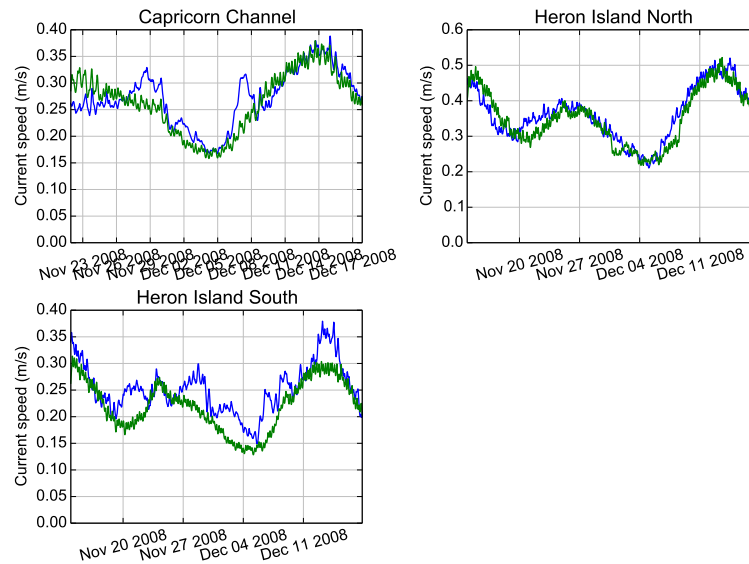


Figure 6.A.2: Time-series plot of observed (blue) and predicted (green) depth-averaged current **speed** at different mooring sites for the **2008** simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability.

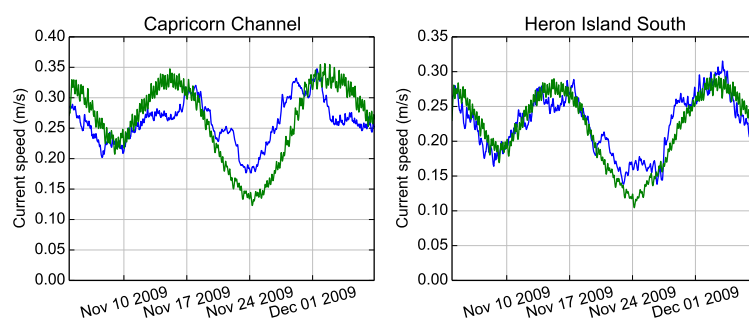


Figure 6.A.3: Time-series plot of observed (blue) and predicted (green) depth-averaged current **speed** at different mooring sites for the **2009** simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability. Observed data for Heron Island North were unavailable.

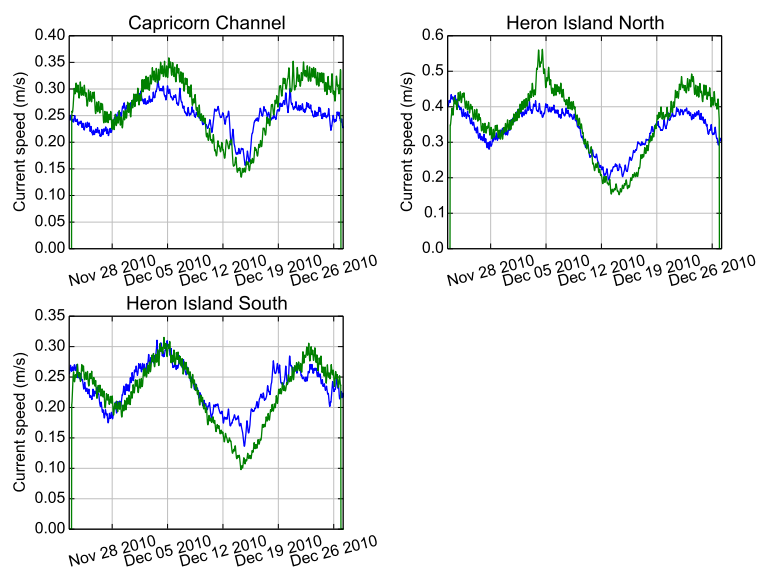


Figure 6.A.4: Time-series plot of observed (blue) and predicted (green) depth-averaged current **speed** at different mooring sites for the **2010** simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability.

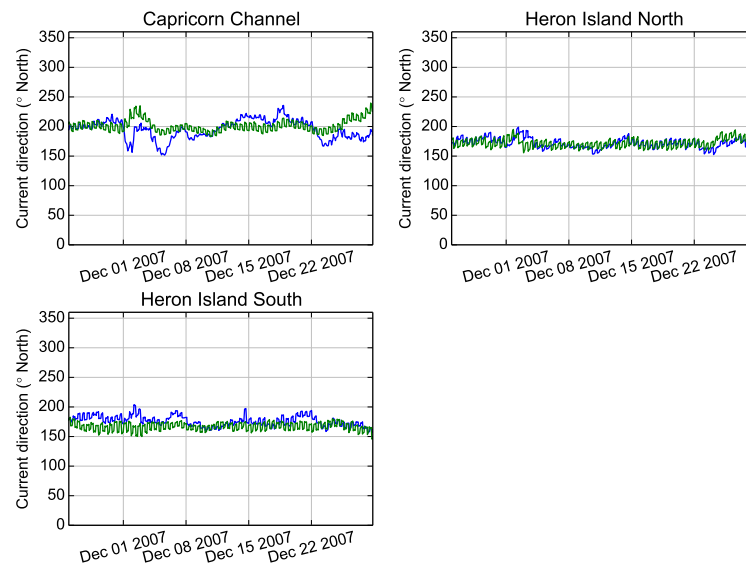


Figure 6.A.5: Time-series plot of observed (blue) and predicted (green) depth-averaged current **direction** at different mooring sites for the **2007** simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability.

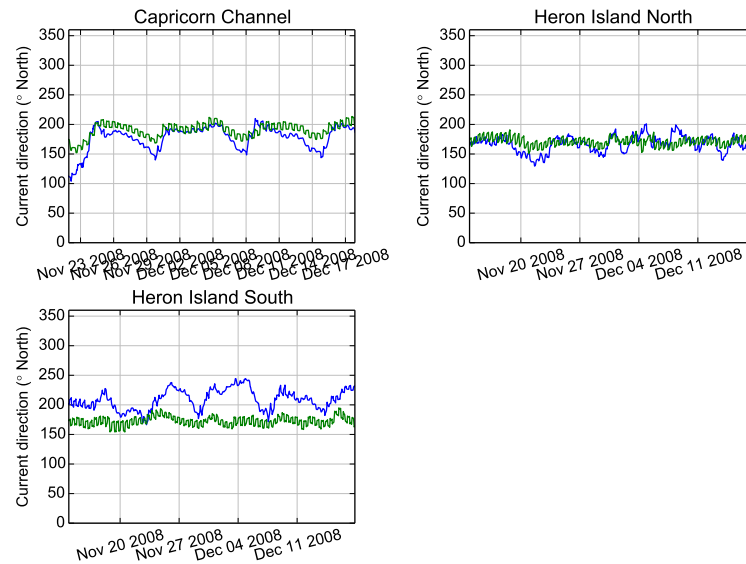


Figure 6.A.6: Time-series plot of observed (blue) and predicted (green) depth-averaged current **direction** at different mooring sites for the **2008** simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability.

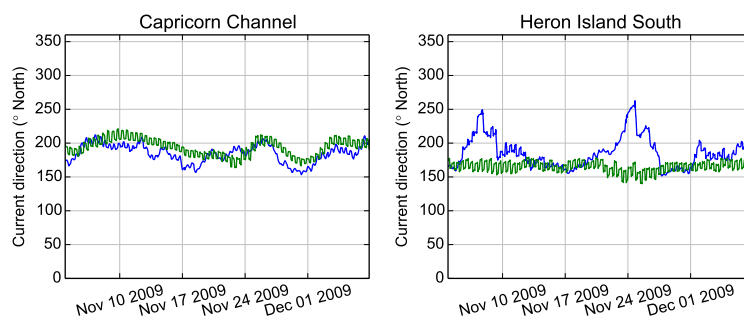


Figure 6.A.7: Time-series plot of observed (blue) and predicted (green) depth-averaged current **direction** at different mooring sites for the **2009** simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability. Observed data for Heron Island North were unavailable.

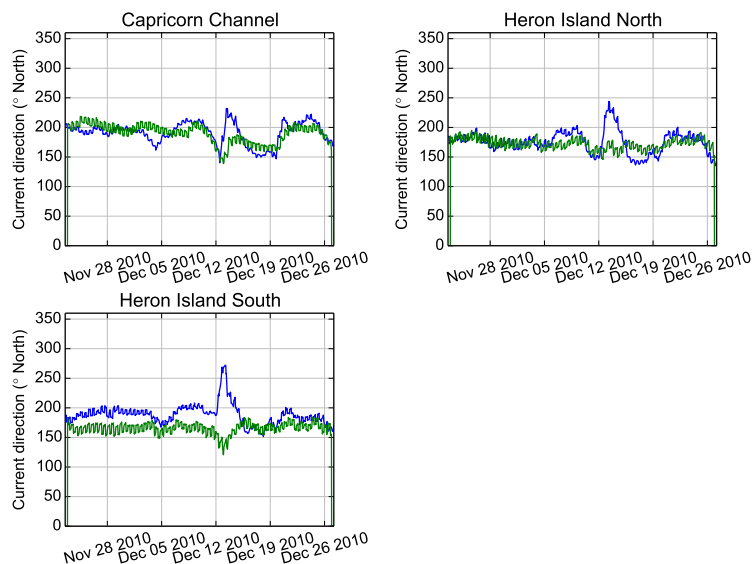


Figure 6.A.8: Time-series plot of observed (blue) and predicted (green) depth-averaged current **direction** at different mooring sites for the **2010** simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability.

6.B Sensitivity of results to larval biology parameters

In order to gauge the sensitivity of the model to uncertainties in the larval biological parameters, the larval dispersal module was run using upper and lower uncertainty estimates for the temperature-dependent biological. Changes in connectivity due to parameter uncertainty were then compared to the change in connectivity caused by the 2°C temperature increase from 27°C to 29°C.

As mentioned in the Methods section of this chapter, larval mortality and competence acquisition and loss were accounted for using the model of Connolly and Baird (2010), with parameter values supplied by J. Figueiredo (pers. comm.) based on experimental data from laboratory observations of *A. millepora* coral larvae at different temperatures. Larval survival probability was modelled using a generalised Weibull distribution:

$$s_T(t) = [1 - \sigma_T(\lambda_T t)^{v_T}]^{1/\sigma_T} \quad (6.2)$$

where $s_T(t)$ is the proportion of the initial larval cohort still alive at time t , and λ_T , v_T and σ_T are independent parameters whose values were obtained by fitting the model to experimental data. The subscript T denotes temperature dependence. The above survival model results in an instantaneous mortality rate of:

$$\mu_T(t) = \frac{\lambda_T v_T (\lambda_T t)^{v_T-1}}{1 - \sigma_T(\lambda_T t)^{v_T}}. \quad (6.3)$$

Experimental estimates of the three parameters λ_T , v_T and σ_T for *A. millepora* in water at 27°C, along with their uncertainties, are reproduced in Table 6.B.1.

The process of larvae acquiring and losing competence was modelled in a similar, though not identical, way. Larvae were considered to undergo an initial time period after spawning, $t_{c,T}$, during which they were unable to acquire competence, and after this period they acquired competence at a constant stochastic rate a . Competence loss was then modelled using a standard Weibull distribution, with the instantaneous competence loss rate being:

$$\beta_T(t) = b_T \eta_T (b_T t)^{\eta_T-1} \quad (6.4)$$

where b_T , η_T and ω_T are independent parameters whose values were obtained by fitting the model to experimental data. Estimates of these parameters for *A. millepora* in water at 27°C, along with their uncertainties, are shown in Table 6.B.2.

Parameter	Value
$\lambda_{27^\circ\text{C}}$ (day ⁻¹)	1.38 x 10 ⁻⁴ (2 x 10 ⁻⁶ – 2.31 x 10 ⁻³)
$v_{27^\circ\text{C}}$	0.2069 (0.1340 – 0.3070)
$\sigma_{27^\circ\text{C}}$	2.0824 (1.6623 – 2.1634)

Table 6.B.1: Estimates of mortality parameters for *A. millepora* at 27°C. Values in parentheses indicate lower and upper 95% confidence intervals.

Parameter	Value
$t_{c,27^{\circ}\text{C}}$ (days)	4.89 (4.77 – 5.01)
a (day^{-1})	0.4497 (0.3672 – 0.5497)
$b_{27^{\circ}\text{C}}$ (day^{-1})	0.02669 (0.01847 – 0.03770)
η	0.3981 (0.3236 – 0.4988)
$\omega_{27^{\circ}\text{C}}$	2.0824 (1.6623 – 2.1634)

Table 6.B.2: Estimates of mortality parameters for *A. millepora* at 27°C. Values in parentheses indicate lower and upper 95% confidence intervals. Note that parameters without the subscript 27°C were not found to be temperature-dependent.

Table 6.B.3 shows the sensitivity of the model to each mortality and competence parameter. Specifically, the table reports the change to 2 connectivity indicators – self-recruitment and mean dispersal distances – caused by varying each parameter to its upper and lower 95% confidence intervals, with respect to the baseline simulation in which all parameters were kept at their normal values. The differences in these indicators between the baseline 27°C simulation and the 29°C simulation are included for comparison. Each parameter was varied individually, with all other parameters kept at their normal values. Only parameters which varied with temperature were changed. The simulations were run during the period following the coral mass spawning of 2008 (chosen as it was considered to be an “average” year for larval dispersal), for *A. millepora* coral at 27°C.

The results show that the uncertainties in the competence parameters have a very small effect on the values of the connectivity indicators, with changes of between 1% and 4% relative to the baseline simulation, well below the difference between the 27°C and 29°C simulations. The same is also true for the uncertainties in the mortality parameters, with the single exception of λ , whose upper confidence interval was sufficiently high that changes relative to the baseline simulation at 27°C were comparable to those between the 27°C and 29°C simulations. Decreasing this upper uncertainty should therefore be the focus of future experimental work, in order to decrease the uncertainty in the model estimates. Given the low effects of uncertainty on the other parameters however, the results appear to be relatively robust to the expected levels of uncertainty in the biological parameters.

Parameter changed	Upper/lower value	Self-recruitment	Mean dispersal distance (km)
Mortality parameters			
ν	lower	+8.2%	-5.6%
	upper	-2.4%	+1.2%
σ	lower	-0.5%	+0.5%
	upper	-0.2%	+0.0%
λ	lower	-2.3%	+1.6%
	upper	+30.2%	-12.0%
Competency parameters			
t_c	lower	+3.8%	-1.0%
	upper	-2.9%	+1.0%
b	lower	-1.7%	+1.1%
	upper	+1.2%	-1.0%
29°C		+39.5%	-10.6%

Table 6.B.3: Change in connectivity indicators (self-recruitment and mean dispersal distance), with respect to the baseline simulation for 27°C. 'Upper/lower' refers to parameter values at upper and lower 95% confidence intervals, respectively.

CONCLUSIONS AND PERSPECTIVES

Conclusions

The previous chapters of this thesis have presented an effort to build and apply a realistic model of coral larval dispersal in the Great Barrier Reef (GBR). The model had to fulfil a number of requirements, discussed in Chapters 2 and 3. These related mainly to the topographic intricacy of the region, which necessitated the use of a multi-scale model, the complexity of the water currents, which necessitated a careful model calibration and validation, and the nature of larval biology, which necessitated the use of an Individual Based Model (IBM) accounting for various biological traits. The result is an integrated biophysical model based on a finite element ocean model, SLIM, to resolve the hydrodynamics, coupled to a Lagrangian particle tracking module to simulate larval trajectories and settlement – the first such model capable of simulating larval dispersal down to the reef scale over a wide expanse of the GBR.

The particle tracker generated a huge amount of information. With millions of particles released over more than a thousand reefs, the resulting connectivity network had more than a million potential connections. A strategy was needed to extract useful information from the connectivity matrix. One approach explored was to identify spatial patterns in the connectivity network; this is presented in Chapter 4. In particular, tools from graph theory were applied to detect the presence of clusters of highly connected reefs in the network. A novel community detection approach was employed to partition the reef network into such clusters (termed “reef communities”), and to infer the presence of dispersal boundaries between regions poorly connected to each other. This was one of the first attempts to transfer clustering tools from graph theory into the domain of marine connectivity, and the first known ecological application of this particular community detection method.

Adapting a relatively abstract mathematical tool, such as a community detection algorithm, for use in a real ecological application requires careful consideration. The physical meaning of how the tool works, and what its results mean, must be deduced and ex-

plored, and this is not always a trivial matter. The algorithm used to find communities of reefs lends itself well to this task due to its use of a single resolution parameter with a precise mathematical definition. By additionally creating an indicator with a precise ecological significance, namely the proportion of inter-community connectivity in the network, a physically intuitive measure can be associated with every set of communities generated. This measure in essence describes what proportion of larval exchange occurs between reefs in different communities, an indicator which captures the ecological relevance of the partitioning configuration. This indicator was used to identify community configurations at different levels of isolation. Some possible uses of this method to inform marine planning were also discussed.

The model was then applied to explore the potential connectivity between reefs of two morphologies: near-sea-surface reefs (NSS), whose upper reaches approach the sea surface, and submerged reefs, whose shallowest parts do not come as close to the surface. The locations of reefs of this latter type have only very recently been mapped in the GBR, and as such they have received very little attention. Given their different spatial distribution compared to NSS reefs, larvae released over these reefs could be expected to have differing dispersal characteristics. Focusing on the central part of the GBR, where their locations have been most accurately mapped, the biophysical model was used to simulate larval dispersal from both NSS and submerged reefs, and quantify the potential of each reef type to supply larvae to each other; this study is described in Chapter 5. Submerged reefs were found to potentially constitute a significant source of larvae to NSS reefs, a factor which should be accounted for in marine management strategies. Furthermore, the model was used to locate shallow reef areas which rely most on other shallow areas for their larvae; these reefs are suggested to be more vulnerable to the effects of disturbances such as bleaching events or cyclones, as their sources of larvae are more precarious. These areas were found to have undergone larger real decreases in coral cover than other reefs during the period between 1986 and 2004. This study was amongst the first to estimate the connectivity potential of submerged reefs, and the first to simulate larval dispersal from them in the GBR.

The model was also used to quantify spatial gradients in potential larval dispersal in the region for the first time, and identified some clear trends. A significant cross-shelf gradient was found, with self-recruitment being very high in nearshore reefs and lower in mid-shelf reefs, a result of the stronger currents in mid-shelf areas. Furthermore, a clear along-shelf pattern in self-recruitment was identified, with reefs in the northern part of the central GBR, where the continental shelf is thinner, having higher self recruitment than those in the south, where the continental shelf is wider. This was ascribed to differences in the strength of tidal currents caused by the variation in the width of the shelf. In addition to these spatial differences in larval dispersal, the model indicated that inter-annual differences can also be important, with dispersal distances in particular being prone to notable inter-annual fluctuations across the four spawning periods modelled. These results suggest that further work is needed to properly assess the extent of inter-annual variations in connectivity patterns in the GBR.

Climate change is expected to bring many important changes to coral reef ecosystems worldwide. Chapter 6 investigates some possible effects of climate change on coral connectivity in the GBR. By simulating the effects of two major changes projected to occur by the years 2081-2100 – an increase in water temperature and a change in water circulation patterns in the Coral Sea – the model was used to estimate the possible impact of each change on connectivity patterns. Increased coral temperatures were found to have

a much greater effect than the change in water transport entering the shelf (by about an order of magnitude). The increased water temperature was also predicted to have a very spatially heterogeneous effect on recovery times from disturbances, with some reefs predicted to undergo large increases, potentially leaving them more vulnerable to damage from bleaching and/or cyclones, whilst others may instead have faster recoveries. This work, building on the speculative study of Munday et al. (2009), was the first known attempt to make spatially explicit estimates of connectivity for a future scenario in the GBR, by using output data from the latest generation of global climate models to downscale regional effects (in the Coral Sea) to the GBR shelf, in conjunction with new biological data on the effect of temperature on coral larvae.

Perspectives for future work

Improving the model

As discussed in Chapter 3, alongside its many advantages the biophysical model has a few important limitations. The model as it is presented in this thesis represents, to the best of my knowledge, the most complete model of larval dispersal in the GBR¹, however both its accuracy and its ability to model different areas could be improved if these limitations are tackled. These issues will now be discussed in turn.

Focusing first on the hydrodynamical model, one of its limitations is represented by the external forcings used to drive it, due to the time-consuming process of calibrating Coral Sea inflow currents, and the fact that calibrating the model adequately for the entire GBR at the same time remains very challenging with the existing set-up. A possible avenue for improvement could be to couple the GBR shelf model to a large-scale circulation model by using the output of such a model to force the shelf model at the boundaries. Tentative efforts to force SLIM with the output of the HYCOM Reanalysis dataset resulted in worse results than those obtained with the more fiddly setup used in this study (see §3.2.5), however a more promising avenue may be to couple it to the newly-developed, higher resolution SHOC model. In any case, the present setup, whilst offering a high degree of flexibility and a good agreement with observed currents for periods of about a month, is very resource-intensive to set up and use, and moving towards a coupling with a larger model could notably facilitate its continued use, as well as allowing larger parts of the GBR to be modelled at the same time, and over longer periods of time.

There is some uncertainty about the impact of not including waves in the model; whilst on the one hand they can dominate flow over fringing reefs exposed to the Coral Sea (particularly reefs with back-reef lagoons), these reefs do constitute a relatively small minority of the total number of reefs in the domain so their global impact is likely to be limited (Monismith 2007). On the other hand, studies of larval dispersal over a small set of reefs including fringing reefs may necessitate a wave breaking component. Further work should be carried out to verify the impact of wave breaking over reefs on reef-scale and regional circulation.

The model presented in this study is two-dimensional; the choice to use a 2D rather than 3D model was motivated by the need to obtain a very high horizontal resolution in the vicinity of reefs. This condition has been shown to be essential if we are to realistically

¹ See §2.2.4.4 for a review of previous models

model the water circulation and the dispersal of larvae in the GBR (this point is hopefully clear from the literature review in Chapter 2; see also Burgess et al. (2007) and Wolanski and Spagnol (2000)). Obtaining reef-scale resolution (i.e. in the order of 100 m) was too computationally demanding with a 3D model, so a 2D model was therefore employed, a choice considered appropriate for the GBR given the well-mixed nature of waters on the GBR shelf (see §2.1.6 and references therein). The good performance of previous 2D models of flow on the GBR shelf compared to equivalent 3D models appears to support this choice (e.g. see Black et al. 1991; Luick et al. 2007). However, it is clear that using a full 3D model could not only improve the ability of the hydrodynamic model to realistically simulate circulation susceptible to affect larval dispersal, for instance by resolving 3D effects such as up/downwelling in the wakes of reefs (Deleersnijder et al. 1992), but could also allow the particle tracker to account for the effects of vertical movement of larvae, a factor which could be crucial in affecting dispersal of many reef fish larvae (Leis 2007; Paris et al. 2007).

It is vital that a 3D model of the region retain the same horizontal resolution as the model presented in this thesis. Given the high computational cost of achieving this over the entire GBR shelf however, an alternative solution may be to couple a smaller-scale full 3D model of a given study region with a larger-scale 2D model of the entire GBR shelf such as the one presented in this study. Recent advances in the 3D version of SLIM have improved its speed and stability, and it has been shown to be an effective tool in studying 3D flow effects in the GBR over an area of roughly 200 x 50 km (Delandmeter et al. 2015). By coupling this model with the 2D whole-shelf model, it would be possible to simulate larval dispersal over a specific group of reefs in 3D. Whilst such a model could not be used to study long-distance connectivity, it could be very useful in estimating local retention of larvae by their natal reef in different parts of the GBR, a measure which could be useful for estimating the persistence of different populations, and thus be used to inform marine management (Botsford et al. 2009b; Burgess et al. 2014). Such a model could also be used to estimate connectivity patterns within an isolated set of reefs, for instance a cluster of reefs identified with the community detection method in Chapter 4. A further interesting study would be to compare the performance of the 2D and 3D models over a given study area in simulating horizontal currents and larval dispersal, in order to more quantitatively assess the benefits that a 3D model could bring to modelling connectivity in the GBR.

The sensitivity of the results of the biophysical model to the various forcings, assumptions and parameterisations which went into it is also an issue that merits further attention. During the course of this study, some sensitivity tests were carried out on separate parts of the model (e.g. the sensitivity of residual water currents on the mesh resolution and the Manning coefficient in the hydrodynamic model, cf. §3.2, and the sensitivity of connectivity indicators on the biological parameters in the Lagrangian model, cf. §6.A), and modelling the sensitivity of larval dispersal to changes in Coral Sea inflow was the focus of Chapter 6. However, it would also be useful to carry out a more holistic sensitivity analysis comparing the sensitivity of a set of final connectivity indicators to various changes in the model. These changes could be related to: a) the model setup (e.g. mesh resolution and generation fields, diffusivity parameterisation in the hydrodynamic model, diffusivity coefficient in the Lagrangian model), b) uncertainties in the external forcings and parameters (e.g. wind field and tides in the hydrodynamic model, larval biological parameters in the Lagrangian model) and c) assumptions made about larval behaviour (e.g. settling behaviour). Carrying out such an analysis would allow us to see

which factors the model is particularly sensitive to, and which thus require particular care and potentially further work to optimise them.

Model applications

In this study I have focused solely on one type of marine organism: coral. This choice was motivated partly because coral is of great importance to coral reef ecosystems, and partly because of the simplicity of coral larval behaviour, which renders it easier to model. A more complete model of larval dispersal dynamics should additionally consider a range of species important to the ecosystem. A first tentative effort towards doing this was made by implementing active swimming behaviour into the Lagrangian module, allowing for the simulation of species with directed swimming; however this avenue was not pursued, owing partly to the lack of precise data on larval swimming cues and characteristics, and, mainly, to the fact that the behaviour of many types of fish larvae appears to be intrinsically three dimensional (Paris et al. 2007; Wolanski and Kingsford 2014) so a full 3D model is probably needed to treat them correctly.

Questions of temporal variability in connectivity in the GBR have not been extensively addressed in the published literature, however as discussed in §2.1 the currents on the GBR shelf are potentially prone to seasonal, annual and multi-annual fluctuations due to variability in the wind field and in water exchanges with the Coral Sea. The issue of inter-annual changes in connectivity was touched upon in Chapter 5, but this topic has not been the main focus of this thesis. The approach adopted in Chapters 5 and 6 was to implicitly account for inter-annual variations in connectivity by averaging connectivity indicators over 4 spawning events in separate years, however further work is needed to shed light on the extent of inter-annual variations over a longer period, for instance addressing questions such as: are multi-annual or decadal trends apparent in connectivity? How many years do we need to simulate to capture the full range of temporal variability? More specifically, can temporal changes be linked with large-scale phenomena such as ENSO events? Also, does the community structure in the connectivity network change significantly from one year to the next?

The answers to these question could help to inform marine management strategies. For instance if dispersal distances are shown to vary in a cyclical way, it may be acceptable for MPA spacing to reflect dispersal in years with highest dispersal distances, rather than the average dispersal distances. Likewise the issue of whether dynamic MPA placement could offer greater benefits (for connectivity) than the present static approach is also a topic which could be tackled, for instance by assessing whether it would make sense to change MPA spacing in years where dispersal distances are expected to be greater or smaller than normal, perhaps using meteorological indicators, or measures such as the Southern Oscillation Index.

Further work could also help to shed more light on the possible impacts of climate change on coral connectivity. For instance a change in the regional wind field could lead to altered connectivity patterns, or altered inter-annual variability. More precise projections for the evolution of regional wind patterns in the future are needed to investigate this. Climate change may also have a direct impact on corals and fishes inhabiting the GBR, for instance higher water temperatures and increased acidity are already acting as additional stressors on the ecosystem and in the future this could lead to a significant decline in coral cover (Hoegh-Guldberg et al. 2007). This could be accounted for in the

model by reducing coral cover over areas expected to be most vulnerable to these impacts, but precise spatial projections would be needed, and are currently lacking.

The focus in this study has been on estimating potential connectivity between habitats, limiting our focus solely to the larval dispersal process. A more complete ecological picture could be generated by estimating realised connectivity, which encompasses not only larval dispersal but also pre- and post-dispersal processes such as larval production and recruitment into the destination population. A first step in building such a model is presented in the metapopulation model in §6.2.3 of Chapter 6. The next step could be to incorporate multiple species, or to incorporate connectivity matrices from successive years' larval dispersal simulations. Such a model could be used to study the response of various species to disturbances such as bleaching events or cyclones, as well to inform marine management by identifying habitats which most influence population persistence in other habitats (e.g. see Guizien et al. 2012). Additionally, accounting for the increased larval production capabilities of some populations over others (for example populations empirically found to be healthier or larger, or located inside marine reserves) could improve the accuracy of the model.

A goal of larval dispersal models has long been to generate results which can be validated by empirical studies. Whilst the individual components of the model presented in this study are either based on published data from laboratory experiments (larval biology component) or have been validated using observed data (hydrodynamic component), the end estimates of connectivity produced by the model have not been quantitatively validated with empirical data owing to the complexity of comparing estimates of larval dispersal with empirical measures of connectivity. These latter measures generally account for pre- and post-dispersal processes, which larval dispersal models do not, and have a much “coarser” temporal and spatial resolution (cf. discussion in §2.2.4). This is particularly the case for coral. Obtaining results detailed enough to allow comparison with simulations could therefore be very resource-intensive. At present, very few biophysical models have been validated with empirical observations (Burgess et al. 2014). Despite these challenges however, finding a way to compare model predictions with empirical measurements would be very useful in confirming the validity of such models (Sponaugle et al. 2012). Possible strategies include comparing the output of metapopulation models, rather than simply dispersal models, to observed data (to account for pre- and post-settlement processes), and building stronger collaborations between modelling teams and experimentalists to allow closer coordination.

It is important to bear in mind that whilst the present study is specific to the Great Barrier Reef, the techniques explored could equally be applied to gain insights into marine connectivity in many other parts of the world. The GBR represents one of the toughest tests in multi-scale coastal marine modelling on Earth due to the large range of time- and space-scales over which important hydrodynamic phenomena occur (Wolanski et al. 2003). Indeed the difficulty inherent in modelling the water circulation, and larval dispersal, in the GBR was one of the main motivations for focusing on this region using the multi-scale SLIM model, given the limitations of previous studies using standard structured-grid modelling approaches. However, there are also many other topographically complex, multi-scale coral reef ecosystems in the world, and the modelling approaches presented in this thesis could be equally useful in studying these regions. In addition to the biophysical dispersal model itself, the community detection method presented in Chapter 4 could be used to gain insights into the network structure of many other large coral reef ecosystems. The inherent flexibility of this method means it can be

used to reveal connectivity network structure over a wide range of spatial scales – from large-scale divisions of the network into, say, a handful of clusters, to the smaller-scale subdivision of these clusters into smaller, but still clearly distinct units. It could therefore be employed to study connectivity networks of various shapes and sizes around the world.

Throughout the different chapters of this thesis, I have touched on a number of different ways in which the modelling results could be used to inform marine planning. For example knowing the community structure of the connectivity network could allow MPAs to be distributed more evenly across areas which are ecologically isolated from each other in terms of larval exchange (Chapter 4). If we also know the characteristics of larval dispersal in each community, for instance how far away from their natal reef larvae settle, then the average MPA-to-MPA spacing in each community could be adjusted to reflect the dispersal potential of larvae in that specific area. The potential benefits to this approach are significant, as it could result in MPAs being better connected amongst themselves, and also able to reach greater numbers of other reefs. The results presented in Chapter 5, showing the importance of submerged reefs in larval connectivity networks, are also relevant to marine planning as they emphasize how planners should not only consider near-sea-surface reefs in their analyses. Whilst these conclusions were obtained from modelling of the GBR, they could equally be used to inform marine planning in other parts of the world. Even the work presented in Chapter 6, exploring the possible effects of climate change on connectivity in the GBR, deals with issues which are likely to affect connectivity in many other coral reef ecosystems around the world, such as higher water temperatures and changes in water circulation.

The work presented in this thesis has demonstrated some of the capabilities of numerical modelling tools to study coral connectivity. In order to translate this work into practical findings which could be directly used to inform marine management or coral reefs, a systematic approach is now needed to generate enough data to represent a robust set of findings. A greater number of years' spawning events should be modelled in order to capture the full range of inter-annual variability present in the GBR; a larger number of coral species should also be modelled – and these should represent a selection of the most important reef-building corals present in the regions under study; and empirical measurements of species-specific coral cover on different reefs should also ideally be used to inform where larvae are released in the model and in what numbers. All of this will require a certain investment in time and resources, both to run the model over and over for different years and different coral species (though some of the model improvements discussed above could greatly reduce the computational resources needed), and to collect the empirical data needed to inform the model, for instance biological survival and competence acquisition/loss parameters for all the coral species, and spatial coral cover data. Given the potential of the numerical model to yield useful results however, as demonstrated in this thesis, a further research effort in this direction may well yield results which could directly be used to better manage the coral reef environment for the future.

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