Coral reef fish larval connectivity in the Great Barrier Reef from biophysical modelling and genomics

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To my parents and grandparents

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ABSTRACT

The exchange of individuals among discrete habitat patches is indicative of population connectivity (or lack thereof). Knowledge about connectivity between reef habitats is essential for population persistence and recovery, population dynamics and management. On the Great Barrier Reef (GBR), most coral reef fish populations are connected via pelagic larvae, with dispersal by ocean currents linking populations. Advances in hydrodynamic modelling and understanding larval behaviour, along with our increased ability to generate genomic data, allows larval connectivity to be modelled at a range of spatial and temporal scales. Based on fish spawning activity and the influence of the physical environment on larval dispersal, I investigated: i) the interannual variation in larval connectivity over the entire GBR and the influence of El Niño Southern Oscillation (ENSO) events; ii) the connectivity of GBR fish populations at evolutionary timescales; and iii) the spawning timing effect on larval supply within spawning seasons. Biophysical modelling of larval dispersal was used to explore the effect of *Lutjanus carponotatus* (stripey snapper) spawning at annual, monthly and weekly timescales. Genomics of adults and recruits were used to examine genomic differentiation and selection potential across the GBR.

In the remainder of this thesis I present a review (**Chapter 2**) of the following: i) hydrodynamic and biophysical models used on the GBR to explore larval dispersal; ii) molecular tools and their application to genetic connectivity research; iii) information on population connectivity of fish species on the GBR; and iv) the combined use of novel biophysical modelling and genomic tools to inform multi-scale population connectivity. Subsequently, I present the connectivity results generated in this thesis as three individual data chapters (**Chapters 3-5**).

In **Chapter 3**, I explored interannual *L. carponotatus* larval connectivity patterns, together with wind and ocean circulation on the GBR, during a series of different ENSO events. Using biophysical modelling, I modelled *L. carponotatus* larval dispersal during the main spawning seasons from 2010 to 2017, by combining hydrodynamic models of the GBR with information obtained from larval tracking techniques. I calculated annual larval connectivity among regions distributed across the entire system. At

interannual scales, a well-connected network existed, although marked variation in annual connectivity values was exhibited. Generally, larval connections were stronger and more stable over shorter distances, but more variable at larger distances and during different ENSO conditions. ENSO-linked hydrodynamics enhanced multi-directional larval dispersal, although a southward larval dispersal was predominant, linking regions across the central and southern GBR, highlighting the East Australian Current (EAC) effect. This pattern was enhanced during El Niño events, when a strong North Vanuatu Jet (NVJ) bifurcation was exhibited. Contrarily, northward larval connectivity predominated during extreme La Niña events, with weaker NVJ and EAC, and stronger southeasterly winds and river discharge into the GBR.

Considering the larval dispersal patterns delineated in **Chapter 3**, I expected larvae to link adjacent island/reef groups on the GBR, with potential for high gene flow over the system after consecutive dispersal events. In **Chapter 4**, I analysed *L. carponotatus* genetic structure along the GBR, based on putatively non-adaptive and adaptive single nucleotide polymorphisms (SNPs). Additionally, I investigated the effect of isolation by distance (IBD) on genetic differentiation (where fish from closer regions would be genetically more similar than distant ones), and the potential for local adaptation to overcome gene flow. Adult and recruit fish tissue biopsies previously collected from five island groups along the central and southern GBR were genotyped and a total of 12,484 SNPs were retained for population genetic analysis. A weak genetic structure was found along the GBR based on non-adaptive loci, with a significant IBD effect. Adaptive loci revealed more differentiation, which increased with distance. Genetic differentiation from adaptive loci of recruit pulses was greater than that of adults and was spatially and temporally variable. Regions not inter-connected by larvae (according to biophysical modelling results from **Chapter 3**) presented significantly stronger genetic differences than inter-connected regions.

Following the GBR broad-scale connectivity analyses, I evaluated GBR fine-scale larval connectivity patterns in **Chapter 5**. I used a biophysical model validated for the southern GBR to explore the effect of timing of spawning, over the *L. carponotatus* spawning season, on larval supply to reefs in the Keppel Islands (southern GBR). I modelled the release and dispersal of larvae across a single spawning season, during different moon phases and months. I found significant larval

supply variation among spawning events, although spawning over multiple months and moon phases ensured a consistent larval supply to different reefs over local and regional scales.

In **Chapter 6**, I synthesise the findings and place these into the broader context of the literature and identify future directions and implications of this work.

Overall, findings reveal the importance of identifying consistent larval supply patterns, which are relevant for temporal stability in recruitment and population replenishment over time. Results highlight the influence of the physical environment on larval dispersal and survival over regional to local and temporal scales, including during different climate events and during intra-seasonal and lunar cycles. Further research is recommended on the effects of the time of spawning and selection on other fish species on the GBR, such as coral trout, and on fish larval survival at settlement/post-settlement stages.

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CHAPTER 1. GENERAL INTRODUCTION

Coral reef fish larval dispersal is facilitated by currents and larval behaviour, which are key processes for maintaining population connectivity, or exchange of organisms between populations, across space and over time (e.g. Cowen and Sponaugle 2009). Levels of larval exchange among coral reef fish populations have been debated, with more or less 'open' (i.e. highly connected) or 'closed' (i.e. showing limited exchange but high self-replenishment) populations, although these descriptions pertain to alternative perspectives on the subject (Mora and Sale 2002; van der Meer *et al*. 2015; Steinberg *et al*. 2016). Protecting population connectivity is fundamental to resilience and conservation, and similarly, understanding larval connectivity and retention patterns in marine reserve networks is key to achieve these objectives (Treml *et al*. 2008; Jones *et al*. 2009; McCook *et al*. 2009; Burgess *et al*. 2014). Self-recruitment (i.e. the fraction of larvae recruited into a population that is locally produced) has been proposed as the most common descriptor of larval dispersal (Burgess *et al*. 2014) (referred as the movement of larvae from the origin to the destination population; White *et al*. 2019). However, this measure is not as useful as local retention (i.e. the fraction of larvae produced by a population that settles back to their source population), which contains information on replacement and provides an estimate of population persistence (Botsford *et al*. 2009; Burgess *et al*. 2014). Reef fish populations may also depend substantially on externally supplied larvae, as shown for fish larval dispersal simulations on the northern Great Barrier Reef (GBR) (James *et al*. 2002), where information of regional ocean currents is incorporated in such simulations. Larval connectivity enhances gene flow and is important for maintaining genetic diversity and hence population resilience to change. Genetic similarities across space represent high levels of connectivity over time, while genetic differences suggest barriers to larval dispersal (Botsford *et al*. 2009). Better knowledge of population connectivity, at both ecological (i.e. the connectivity occurring at contemporary timescales) and evolutionary (historical timescales) timescales, would improve marine protected area design and fisheries management by informing on the degrees and patterns of connectivity across space and over time.

Directly tracking fish larvae in marine environments is challenging and impractical at the scales required to inform policies. However, a range of techniques are available to estimate larval connectivity, including biophysical modelling (coupling biological and physical models) of larval dispersal and analyzing genetic/genomic data (Leis *et al*. 2011). Numerous advances have been made in the numerical modelling field, including model resolution and particle number, computational power, validation of model assumptions, and incorporating larval behavioural capabilities (Jones *et al*. 2009; Paris *et al*. 2013; Bode *et al*. 2019; Swearer *et al*. 2019). Hydrodynamic/biophysical modelling have allowed us to better understand the dispersal processes and population connectivity across marine ecosystems, including the capacity of larvae to disperse and/or self-recruit and remain in the proximity of reefs (e.g. Black *et al*. 1991; Paris *et al*. 2005; Werner *et al*. 2007; Kininmonth *et al*. 2010, Wolanski and Kingsford 2014). Numerical modelling tools estimate contemporary larval dispersal informed by hydrodynamic and biotic processes and can be practical when accounting for larval supply patterns over multiple periods (e.g. interannual or inter-month variation). Population connectivity at historical timescales can be measured using neutral genetic markers like mitochondrial DNA (mtDNA) sequences and neutral single nucleotide polymorphism (SNP) loci, rather than outlier (putatively adaptive SNP loci – in this thesis) (see below). Using both biophysical modelling and genetics/genomics can help explain population structure informed by hydrodynamics and larval dispersal patterns (Teacher *et al*. 2013; Simpson *et al*. 2014; Klein *et al*. 2016; Lal *et al*. 2016; Truelove *et al*. 2017).

A range of genetic markers is available to analyse genetic connectivity on population genetic studies. The efficiency of genome-wide SNPs (i.e. genomics) for analyzing genetic structure is highlighted, since SNPs are highly abundant and widespread across the genome compared to alternatives (e.g. microsatellites or mtDNA sequences) (Morin *et al*. 2004). The use of SNPs also offers other advantages over microsatellites and mtDNA, such as presenting low genotyping error rates and segregating robustly between populations (Brumfield *et al*. 2003; Morin *et al*. 2004 Helyar *et al*. 2011). Genomics can improve genetic resolution for ecological and management related applications by genotyping 100s to 1000s of neutral and outlier (putatively under selection) SNP loci (Allendorf *et al*. 2010). Neutral loci provide genome-wide insights, whilst putatively adaptive outlier loci can effectively reveal

effects associated with divergent selection across different environments (André *et al*. 2011; Russello *et al*. 2012). Loci influenced by selection can therefore identify structure not evident from analyzing neutral loci, especially where high gene flow exists (Limborg *et al*. 2012; Milano *et al*. 2014; Gagnaire *et al*. 2015). Further, adaptive SNP loci can be useful for detecting temporal genetic differentiation in coral reef fish populations (Gould and Dunlap 2017). Together, these genetic tools provide good alternatives for conservation and effective fisheries management, for example to identify management units (e.g. as discrete genetic units) (Russello *et al*. 2012). Moreover, genomics can be integrated with oceanographic, geographic and modelling approaches to determine marine larval connectivity and adaptation patterns, dispersal barriers and source-sink dynamics (Selkoe *et al*. 2008; 2016).

The GBR is the world's largest coral reef ecosystem, with the Great Barrier Reef Marine Park extending across approximately 3,000 coral reefs distributed over 14 degrees of latitude (~10.7° S to 24.5° S). Reef habitat protection is established across the GBR through no-take marine reserves, which have significantly increased in area since 2004 to over 33% of the Great Barrier Reef Marine Park (Fernandes *et al*. 2005). On the GBR, inter-reef fish larval connectivity has been assessed by biophysical modelling, generally focusing on interannual variation and source-sink dynamics on the northern GBR (James *et al*. 2002; Bode *et al*. 2006; Kininmonth *et al*. 2010), inter-reef connectivity during particular spawning events in the southern GBR (Bode *et al*. 2019), and the influence of assumptions of larval behaviour on dispersal (Wolanski *et al*. 1997; Wolanski and Kingsford 2014). Research on genetic structure of fish populations on the GBR has focused on a range of species and generally concluded that no strong barriers to gene flow exist along the system for fishes with a pelagic larval dispersal phase, based on low genetic differentiation values from mtDNA and microsatellite markers (e.g. van Herwerden *et al*. 2009a; Jones *et al*. 2010). In contrast, parentage genetic studies have mainly focused on dispersal of some important fishery species, such as the coral reef groupers, *Plectropomus maculatus* and *Plectropomus leopardus*, and stripey snapper, *Lutjanus carponotatus*, demonstrating inter-reef larval connectivity at regional and local scales (Williamson *et al*. 2016; Bode *et al*. 2019), along with larval export from marine reserves towards other marine reserves and fished areas in the southern GBR (Harrison *et al*. 2012; 2020). Overall, the potential for fish larval dispersal from 10s to 100s of kilometres has been confirmed, at least in the

southern GBR, together with the capacity for fish populations to exhibit high levels of gene flow across the system. However, more research is needed to ascertain the variation in fish larval supply to reefs at a range of temporal scales and over the GBR, as well as the potential for natural selection to counteract gene flow on GBR fish populations.

On the GBR, winds and currents can experience fluctuations in direction, over periods of several days to several months and among seasons and years (Wolanski and Pickard 1985; Luick *et al*. 2007). The Gulf of Papua Current and East Australian Current (EAC) dominate offshore circulation on the northern, and central to southern GBR shelf edge, respectively (Ridgway *et al.* 2018). The EAC consists of a poleward flow along the continental slope and influences oceanic inflow from the Coral Sea onto the GBR (Brinkman *et al*. 2001). This flow, together with currents highly modulated by wind, residual tidal currents, oceanic inflow and river plumes, constitute the main factors influencing the low-frequency currents in the GBR. Interannual variability in circulation patterns on the GBR may be affected by changes in the El Niño Southern Oscillation (ENSO) (Wolanski and Pickard 1985), with large-scale current patterns associated with ENSO (Burrage *et al*. 1994). On the GBR, spatial patterns of synchrony of damselfish species' populations have been correlated with ENSO (Cheal *et al*. 2007). The influence of ENSO on ocean circulation and fish population fluctuations suggests that variation in these climate events may impact larval connectivity patterns in this system. Examining the relationships among interannual larval dispersal patterns and ENSO variability will inform the ecological implications thereof, as increased frequencies of future extreme El Niño and La Niña events are expected under future climate change scenarios (Cai *et al*. 2014; 2015).

At smaller (monthly or weekly) temporal scales, variability of the physical environment of the GBR may also influence fish larval dispersal and supply patterns to reefs. At this scale, spawning periodicity of species may be one of the most relevant factors influencing connectivity. In the Caribbean Sea region, spawning timing of fish species was shown to benefit larval replenishment (Donahue *et al*. 2015), while factors such as larval dispersal trajectories were significantly affected by the spawning timing around particular seasons and moon phases (Zeng *et al*. 2019). On the GBR, fish species have different, mainly seasonal spawning timings (Currey *et al*. 2013), e.g.

around austral spring, with many of these associated with lunar phases, e.g. coral trout and stripey snapper spawn around the new moon (Samoilys 1997; Kritzer 2004; Walshe and Slade 2009). Spawning by these and other species has also been documented over protracted seasons (extending to austral summer months) and other lunar phases (Kritzer 2004; Walshe and Slade 2009; Currey *et al*. 2013), with likely implications for larval dispersal outcomes.

The stripey snapper is a predatory reef fish ranging from India to northern Australia and Papua New Guinea (Allen 1985). The stripey snapper is an ecologically important species that displays a top down effect on reef fishes it preys on (Boaden and Kingsford 2015). It is also a secondary target commercial fishery species, dominant by-catch of coral reef grouper fisheries (*Plectropomus* spp.) and targeted by recreational fishers (Smith and McCormack 2007; Currey *et al*. 2010). Given this, informed management is appropriate to enhance resilience of the species and other species impacted by it on the GBR. Since stripey snapper is a widely distributed and abundant predator-prey species on the GBR, it represents a good study species to examine fish larval dispersal and population connectivity patterns over the GBR and at a range of temporal scales, including the effect of environmental variability. Current trends in climate change (involving disturbances such as coral bleaching and consequent prey species reductions) may affect stripey snapper more than other reef fish species, due to their trophic ecology, which is reliant on reef-based resources (Pratchett *et al*. 2008; Frisch *et al*. 2014). Stripey snapper has been considered a model reef-associated species in larval dispersal modelling studies in Western Australia due to its larval settlement behaviour and ecological similarities with other fishery relevant predatory species (DiBattista *et al*. 2017).

Research on stripey snapper on the GBR has included population biology (Newman *et al*. 2000; Kritzer 2002; 2004) and fecundity (Evans *et al*. 2008), effectiveness of marine reserves (Evans and Russ 2004; Williamson *et al*. 2004; Wen *et al*. 2013), reef use and recruitment patterns over local scales (Kingsford 2009), larval behavioural capabilities (Leis and Fisher 2006; Wright *et al*. 2010) and settlement behaviour (Quéré and Leis 2011). Further studies, included larval dispersal modelling in the Capricorn-Bunker Group in the southern GBR (Schlaefer *et al*. 2018), and population genetics along the GBR (Evans *et al*. 2010), as well as parentage studies

in the Keppel Islands in the southern GBR (Harrison *et al*. 2012). Studies using mtDNA from the control region identified high gene flow from the Palm Islands (central GBR) to the Capricorn-Bunkers, suggesting a single population stock for fisheries management (i.e. no genetic differentiation) along the GBR (Evans *et al*. 2010). The relatively long pelagic larval duration of *L. carponotatus* and extensive larval connectivity between reefs were the proposed causes for the lack of genetic structure. Around the Keppel Islands, parentage analysis using microsatellite markers indicated varying levels of local retention and connectivity among reefs during a particular spawning event (Harrison *et al*. 2012). Excluding the study by Harrison *et al*. (2012), no inter-reef *L. carponotatus* larval connectivity patterns have been estimated on the GBR. Moreover, mtDNA population genetic studies undertaken by Evans *et al*. (2010) need to be extended using genomic tools that can generate two orders of magnitude more neutral markers, along with many putatively adaptive loci (e.g. see DiBattista *et al*. 2017).

1.1 Aims and outline

In this thesis, I investigate population connectivity patterns of coral reef fish on the GBR, by applying both biophysical modelling of larval dispersal and population genomics approaches. I investigate connectivity of a reef fish predator and which is a fisheries target - *L. carponotatus*. I use this species to explore the influence of environmental factors on larval dispersal and connectivity over different spatial and temporal scales, which may also apply to other fishes with a pelagic larval phase on the GBR.

Accordingly, the main objectives of this thesis are to:

I) Estimate the interannual variation in larval connectivity over the entire GBR;

II) Assess the effect of multiple different ENSO events on interannual connectivity patterns;

III) Evaluate the population genetic structure along the GBR, based on both neutral and putatively adaptive loci;

IV) Evaluate the effects of geographic distance, larval connectivity, and local adaptation on genetic differentiation patterns;

V) Estimate fish larval connectivity patterns throughout a spawning season in the Keppel Islands; and

VI) Assess the effect periodic spawning has on larval supply patterns across a spawning season.

Chapter 2 describes the hydrodynamic and biophysical models applied to simulate larval dispersal in the GBR. The chapter summarises pertinent information available on fish genetic structure along the GBR according to genetic markers used and species-specific larval dispersal capabilities. This chapter provides a framework for the best available tools to estimate larval connectivity of the focal species, *L. carponotatus*, on the GBR, according to physical environment characteristics and the objectives of this thesis.

Chapter 3 is a temporal study of fish larval connectivity over the whole of the GBR based on biophysical modelling. In this study, modelled larvae were released over an 8-year period, covering different El Niño Southern Oscillation (ENSO) events. Modelled interannual connectivity patterns and variation were analysed for different El Niño, La Niña and neutral climatic events, including connectivity anomalies, as well as the relationship between modelled larval dispersal patterns and variation in ENSO intensity.

Chapter 4 examines the genetic connectivity of adults (constituting a mixed age cohort population) and recruits sampled over multiple recruitment seasons from the GBR, based on 1000s of neutral SNPs or multiple putatively adaptive (outlier) SNPs. Genetic differentiation patterns from neutral and outlier loci were determined within and among five island groups distributed along the system. Genetic distances were correlated with geographic distances, to test the effect of isolation by distance. The effect of larval connectivity patterns (from **Chapter 3**) on genetic distances was assessed.

Chapter 5 is a finer-resolution, temporal study on larval connectivity patterns simulating larval dispersal and supply to reefs in the Keppel Islands. Biophysically

modelled larvae were released throughout the lunar month over a protracted spawning season of *L. carponotatus* to test the effect of timing of spawning on supply patterns. A series of larval supply metrics (including external supply, retention and self-recruitment) were calculated over time, and estimated, together with measures of pelagic larval duration and dispersal distances, among: i) different moon phases, ii) different months, and iii) different reefs, within a spawning season.

Chapter 6 synthesises the findings of the thesis into a general discussion and draws conclusions from the main findings. Further work is proposed for particular areas of relevance according to larval connectivity and environmental variability identified on the GBR.

CHAPTER 2. THE USE OF BIOPHYSICAL MODELLING AND GENOMIC TOOLS TO EVALUATE CORAL REEF FISH POPULATION CONNECTIVITY IN THE GREAT BARRIER REEF

2.1 Abstract

Maintaining population connectivity is an essential process for population resilience, therefore assessing connectivity in marine ecosystems allows quantifying population exchange to better inform management activities. Several techniques, including numerical modelling and characterising genetic signatures, are applied to estimate connectivity in marine ecosystems. Here, I provide a review of: 1) hydrodynamic/biophysical models developed for the Great Barrier Reef (GBR) and their application to larval dispersal studies, 2) the use and advantages of accessing genetic and genomic data to measure connectivity, and 3) the combined use of modelling and genetic information to estimate connectivity. I also identify the next steps to better define population structure over space and time, using these different analytical approaches.

2.2 Introduction

The importance of marine population connectivity in conservation, design of marine reserve networks and fisheries management has led to an increase in coral reef connectivity research over recent decades (Almany *et al*. 2009; Jones *et al*. 2009; McCook *et al*. 2009). Challenges remain in how to combine findings from various connectivity techniques to better inform and achieve more effective management (Jones *et al*. 2009). Connectivity can be measured in several ways, with regional hydrodynamic ocean models and genetic markers proven useful for analysing population connectivity levels (e.g. Leis *et al*. 2011). However, each technique presents advantages and disadvantages over others and which is most appropriate depends on the research objectives. Connectivity studies integrating multiple data and approaches are generally most informative on assessing the spatial scales over which connectivity operates and management should be applied, and the factors influencing connectivity patterns (Selkoe *et al*. 2008).

The Great Barrier Reef (GBR) represents a highly flushed environment with inter-connected reefs (Harrison *et al*. 2012; Schiller *et al*. 2015; Williamson *et al*. 2016). However, informed connectivity related research is still relatively sparse for a system as large and complex as the GBR, which is facing increasing degradation from anthropogenic and climate change related pressures (Brodie and Pearson 2016). Great advances have been made on the hydrodynamic modelling of the GBR and its application to larval dispersal studies through biophysical models (see Table 2.1). Population genetics of fish populations and parentage studies, mostly based on mitochondrial DNA (mtDNA) and microsatellite markers, have revealed insights into GBR patterns of connectivity over regional scales (see Table 2.2). The present work aims to provide a review on the numerical models and genetic tools applied to GBR fish species, along with identifying the insights and advantages derived from using these tools to evaluate population connectivity patterns, causes and consequences.

2.3 Numerical modelling to predict larval dispersal on the GBR

On the GBR, a set of numerical hydrodynamic models has been used to model larval dispersal patterns in a range of organisms. Early research on modelling larval

dispersal and recruitment on the central GBR was conducted on crown-of-thorns starfish (CoTS) larvae, *Acanthaster planci* (Black *et al*. 1990; Bradbury 1990; Dight *et al*. 1990a; b; Black and Moran 1991; Black *et al*. 1991; Scandol and James 1992). Occurrence, distribution and larval dispersal patterns derived from two- and three-dimensional hydrodynamic modelling were greatly influenced by hydrodynamic patterns in the region.

Another early GBR study, undertaken by Oliver *et al*. (1992), analysed the relationship between model predictions and plankton distribution at Bowden Reef (central GBR) but found no correlation among them. Authors attributed their results to fine-scale circulation around reefs and suggested that 3-dimensional validated models with a small grid size should be used when analysing larval dispersal. Wolanski *et al*. (1989) studied the retention and dispersal of coral eggs around Bowden Reef and proposed that no reef should be considered in isolation within the GBR matrix, due to complex inter-reef circulation. Wolanski *et al*. (1997) found that the model reproduced field results for fish larval dispersal in the central GBR when appropriate larval behaviour was included, highlighting the importance of incorporating larval behavioural capabilities when modelling fish larval connectivity.

The previous modelling studies pioneered the study and importance of the physical environment on larval dispersal on the GBR. The following studies (further detailed in Table 2.1), expanded on the influence of hydrodynamics on larval dispersal and aimed to resolve some complex connectivity processes on the GBR, utilizing computational advances and finer resolution models. For example, reef fish larval connectivity (including self-recruitment) was investigated over many years over the Cairns sector in the northern GBR (James *et al*. 2002) (Table 2.1). By using connectivity patterns estimated by James *et al*. (2002), Bode *et al*. (2006) explored regional scale source-sink dynamics over the same GBR region (Table 2.1). James *et al*. (2002) used a hydrodynamic model from Bode and Mason (1994) to force regional winds, tides, and modelled boundary currents in the Coral Sea and included a parameterisation scheme for resolving reef geometry (Bode *et al*. 1997). The model's computational grid was based on the Arakawa "C" grid (Mesinger and Arakawa 1976) and was used with all available physical data for the region, including the Coral Sea, and a resolution scale of one nautical mile. The model was used to compute the two-

dimensional depth-integrated currents, with some larval behaviour aspects, such as mortality and settlement behaviour. A second-order Runge–Kutta algorithm was used to predict larval trajectories. Findings denoted an influence of southward currents on dispersing larvae, although northward flows alternated sporadically (James *et al*. 2002). These studies highlighted spatial and temporal variation in self-recruitment patterns, the importance of a few local populations to ensure the persistence of a metapopulation (James *et al*. 2002), along with identifying such key source-sink regions (Bode *et al*. 2006).

Simulations of seasonal particle dispersal along the inner GBR were described by Luick *et al*. (2007), after applying the hydrodynamic model described in Bode and Mason (1994), Bode and Mason (1995), and Mason and Bode (1995), along with incorporating a reef parameterisation scheme (Bode *et al*. 1997) (Table 2.1). Released particles displaced mostly northward, although with marked seasonal variation, with a "southwards season" identified in late August – December, when most southward and reef matrix dispersal occurred. Similarly, Kininmonth *et al*. (2010) applied the same hydrodynamic and particle tracking model used by James *et al*. (2002) to determine community structure and larval dispersal networks from coral species in the north-central GBR (Table 2.1). The GBR was defined as a small-world network with high connectivity levels and tight clustering (Kininmonth *et al*. 2010).

A number of studies on the GBR used SLIM (Second-generation Louvain-la-Neuve Ice-ocean Model), a finite element, vertically integrated, 2-dimensional hydrodynamic model presented by Lambrechts *et al*. (2008), which is based on an unstructured, variable-resolution grid (Legrand *et al*. 2006) (Table 2.1). The GBR SLIM model includes forcing such as wind stress, water circulation in the Coral Sea and tides, with the latter two applied along the open boundaries. The depth-integrated water equations of movement are discretised in space by means of a mixed finite element formulation, applying a third order explicit Adams-Bashforth integration scheme for the time-marching procedure. SLIM has been calibrated to model mixing processes (Andutta *et al*. 2013) and employed on the GBR to simulate dispersing marine turtle hatchlings (Hamann *et al*. 2011; Wildermann *et al*. 2017), seagrass propagules (Grech *et al*. 2016), and coral larvae (Thomas *et al*. 2014; 2015) (Table 2.1). In addition, SLIM was used to explore the effect of wind on *L. carponotatus* larval

dispersal patterns in the southern GBR by Schlaefer *et a*l. (2018) (Table 2.1), highlighting the influence of wind circulation on the species' recruitment patterns. The model domain covered the central and southern GBR and allowed high (< 1 km) to coarse (> 4 km) resolution under a Lagrangian advection-diffusion model (Spagnol *et al*. 2002) to track particles in most cases.

The Sparse Hydrodynamic Ocean Code (SHOC) is another model extensively used on the GBR in recent years. SHOC is a general purpose model (Herzfeld 2006) based on Blumberg and Herring (1987), developed by the Coastal Environmental Modelling Team (CEM) at the Commonwealth Scientific and Industrial Research Organisation (CSIRO). SHOC is applicable at a range of spatial scales, from coasts to regional ocean domains. SHOC is a finite-difference, 3-dimensional model based on equations of momentum, continuity and conservation of heat and salt and uses the Boussinesq and hydrostatic approximations. The equations are discretised in an Arakawa C grid, and SHOC uses a curvilinear orthogonal horizontal grid, with fixed or terrain following vertical coordinates (Herzfeld 2006). Forcing inputs include winds, bottom friction, surface heat and water fluxes, as well as sea-level, density and atmospheric pressure gradients, along with open-boundary conditions (e.g. tides and low frequency ocean currents).

SHOC is the model on which the hydrodynamic model of the eReefs project (http://ereefs.org.au/ereefs) is based. Commencing in January 2012, eReefs applies the latest in measurement technologies to provide an improved monitoring tool and a new set of integrated models across the GBR lagoon and ocean, including near real-time hydrodynamic models of the GBR. eReefs models include three-dimensional hydrodynamic, sediment, wave and biogeochemical models on high-resolution scales (1km and 4km) over a 300,000 km^2 area of the GBR, as well as a Relocatable Coastal Ocean Model (RECOM). RECOM allows a quick creation of higher-resolution models, with coarser resolution output from the eReefs model along the boundaries, in order to focus in more detail on local areas. Output from the hydrodynamic model includes three-dimensional velocity/temperature/salinity/density/passive tracers/sea-level/ mixing coefficients over the shelf from September 2010 to present. The hydrodynamic model developed for eReefs, was validated by Schiller *et al*. (2015). Many eReefs related papers have been published to date, including research on remote-sensing

reflectance and assessment of ocean colour (Baird *et al*. 2016; Jones *et al*. 2016), river discharge impacts (Robson *et al*. 2015), cross-shelf exchanges between the Coral Sea and the GBR (Schiller *et al*. 2015; Benthuysen *et al*. 2016), management of coral reefs (Weijerman *et al*. 2015), as well as GBR quality control monitoring (Steven *et al*. 2015), among others.

For studies of larval dispersal in the GBR, SHOC has proven useful for analysing larval retention around reefs (Cetina-Heredia and Connolly 2011) and connectivity of CoTS (Hock *et al*. 2014; 2017) and coral (Hock *et al*. 2019) populations (Table 2.1). In the former, a Lagrangian particle tracking algorithm, which is contained within SHOC, was employed to disperse particles. In the latter, Connie (Condie *et al*. 2012), an advection/diffusion hydrodynamic model of the entire GBR, was used. Connie has been broadly used to model particle dispersion around Australia (Condie *et al*. 2005; 2011; Condie and Andrewartha 2008; Berry *et al*. 2012a; b; Underwood *et al*. 2012; Aguilar *et al*. 2019), including the GBR (Feutry *et al*. 2013; Hock *et al*. 2014; 2017; 2019) (Table 2.1). Connie allows estimation of connectivity statistics between locations by simulating dispersal of particles by using high-resolution three-dimensional currents and particle tracking techniques. Particles are tracked using a fourth-order Runge-Kutta ODE solver that linearly interpolates in time and horizontal space to find the horizontal velocity at a determined depth and time. A wide range of larval features can be selected, including vertical depth, ontogenetic migration, swimming speed and mortality rates, for multiple developmental phases. Based on modelling the dispersal of coral larvae on the GBR, consecutive spawning events (rather than one main event) have been found to increase the reliability of larval supply and inter-reef connectivity, denoting the relevance of the GBR physical environment dynamics on larval dispersal and connectivity patterns (Hock *et al*. 2019).

In recent years, important advances have been made in the field of biophysical modelling on the GBR. For example, the GBR-Larvo model is a biophysical model of larval dispersal that has been validated using genetic parentage data of the coral trout (*Plectropomus maculatus*) on the southern GBR (Bode *et al*. 2019) (Table 2.1). This model uses the numerical scheme from James *et al*. (2002) and Luick *et al*. (2007) (for which the results were validated with current meter data), improving the resolution scale to 74 metres around reefs and tracking modelled spawned larvae with larval

behaviours based on an individual-based model (IBM). Their findings highlight the use of modelling and genetic methods (biophysical modelling and parentage data sets) to estimate more precise larval connectivity patterns, together with the application of biophysical models to produce larval dispersal estimates at relevant spatial and temporal management scales.

Table 2.1. Hydrodynamic and biophysical numerical modelling tools applied to the GBR to simulate dispersal and connectivity patterns of marine organisms.

Reference	Research	GBR region	Hydrodynamic/biophysical model	Particle tracking	Resolution scale	Behaviour
James *et al*. (2002); Bode *et al*. (2006)	Larval dispersal and retention patterns from reef fish	Central	Numerical hydrodynamic model (Bode and Mason 1994)	Second-order Runge-Kutta algorithm	1 nautical mile, and sub-grid scale (Bode *et al*. 1997)	Passive/ active phases, mortality, settlement behaviour
Gerlach *et al*. (2007); Wolanski and Kingsford (2014)	Effects of coral reef fish larvae behaviour on retention and homing; Fate of coral reef fish larvae	Southern	3DD (Black *et al*. 1991; Jenkins *et al*. 2000)	-	300 m; 200 m	Vertically well-mixed particles, swimming speed, olfactory cues
Luick *et al*. (2007)	Flow trajectories using tracer particles	Whole GBR	Finite hydrodynamic model (Bode and Mason 1994; 1995; Mason and Bode 1995)	Lagrangian particle tracking (Hardy *et al*. 2004; Mason *et al*. 2003)	~1.8 km to ~9 km, and reef parameterisation scheme (Bode *et al*. 1997)	Neutrally buoyant
Kininmoth *et al*. (2010)	Community structure and larval dispersal network from coral species	Northern and central	Hydrodynamic and Lagrangian particle model from James *et al*. (2002)	-	-	Mortality and settlement behaviour
Cetina-Heredia and Connolly (2011)	Larval retention variability according to reef shape and circulation features	-	SHOC	Lagrangian particle tracking algorithm from SHOC	~100 m	Passive
Hamann *et al*. (2011); Wildermann *et al*. (2017)	Dispersal of hatchling flatback turtles	Central and southern	SLIM	-	Unstructured grid - Varied; 150 m - 10 km	Hatchling's swimming (following the method of Wolanski and Kingsford 2014)

(Continued)

Table 2.1. (Continued) Hydrodynamic and biophysical numerical modelling tools applied to the GBR to simulate dispersal and connectivity patterns of marine organisms.

Reference	Research	GBR region	Hydrodynamic/biophysical model	Particle tracking	Resolution scale	Behaviour
Andutta *et al*. (2012)	Retention of larvae in a reef matrix	Southern	SLIM	Lagrangian advection-diffusion model (Spagnol *et al*. 2002)	~150 m to ~5 km	Passive
Thomas *et al*. (2014)	Inter-reef connectivity (coral larval dispersal)	Central and southern	SLIM	Individual-based model (IBM). Lagrangian advection-diffusion model (Spagnol *et al*. 2002; Hunter *et al*. 1993)	400 m - 10 km	Buoyant, passive, mortality and acquisition/ loss of competence (Connolly and Baird 2010)
Thomas *et al*. (2015)	Dispersal patterns and potential for depth of coral species	Central	SLIM	IBM from Thomas *et al*. (2014)	200 m - 5 km	Passive, larval competence and mortality rate (parameters in Figueiredo *et al*. 2013)
Grech *et al*. (2016)	Dispersal and settlement of seagrass (propagules)	Central	SLIM	Lagrangian advection-diffusion model (Spagnol *et al*. 2002)	200 m - 5 km	Passive
Hock *et al*. (2014); (2017)	Population connectivity of CoTS and systemic resilience	Along the GBR	eReefs/ Connie	Fourth-order Runge-Kutta algorithm	4 km	Buoyant and passive
Matz *et al*. (2018)	Migration between coral reef habitats	Along the GBR	Biophysical modelling from Treml *et al*. (2008; 2015), HYCOM+NCODA	Advection transport logarithm (Smolarkiewicz and Szmelter 2008)	8 km	Pre-competency and competency periods, mortality

(Continued)

Table 2.1. (Continued) Hydrodynamic and biophysical numerical modelling tools applied to the GBR to simulate dispersal and connectivity patterns of marine organisms.

Reference	Research	GBR region	Hydrodynamic/biophysical model	Particle tracking	Resolution scale	Behaviour
Schlaefer *et al*. (2018)	Wind influence on *Lutjanus carponotatus* recruitment	Southern	SLIM	Second-order Runge-Kutta algorithm	< 300 m - > 20 km	Passive and swimming
Bode *et al*. (2019)	Biophysical model validation	Southern	GBR-Larvo; numerical scheme developed from James *et al*. (2002) and Luick *et al*. (2007)	IBM	74 m - 1.85 km	Varied larval behavioural capabilities with ontogenetic variation
Hock *et al*. (2019)	Split spawning effect on coral larval connectivity	Along the GBR	eReefs/ Connie	Fourth-order Runge-Kutta algorithm	4 km	Upward swimming behaviour

2.4 Population structure of fish species on the GBR based on genetics

The degree of genetic connectivity between populations can be estimated by employing a range of genetic markers, including mtDNA, microsatellites and single nucleotide polymorphisms (SNPs). Mitochondrial DNA has been mostly employed to assess population genetic variation and demographic parameters (Moritz 1994). Microsatellites were proposed as the marker of choice in many studies, since they are both highly variable (polymorphic) and very informative molecular markers (DeWoody 2005; Hauser *et al*. 2011), however, the number of independent segregating loci that can be assessed is limited (Glaubitz *et al*. 2003). As an alternative to mtDNA and microsatellites, SNP genotyping provides high-density genome scans constituting an effective method to quantify genetic connectivity in marine organisms with high resolution (Gagnaire *et al*. 2015; Gaither *et al*. 2015; Lal *et al*. 2016; Pazmiño *et al*. 2017; DiBattista *et al*. 2017).

On the GBR, a number of studies have investigated genetic connectivity in marine fish populations (Table 2.2). Fish population structures, however, have been assessed based on a range of molecular methods, including mtDNA, microsatellites, inter-microsatellites (ISSR) and allozymes, but not SNPs (Table 2.2). Generally, studies show that fish species with a pelagic larval dispersal phase lack genetic structure along the GBR (Doherty *et al*. 1995; Dudgeon *et al*. 2000; van Herwerden *et al*. 2003, Bay *et al*. 2006; van Herwerden *et al*. 2009a; b; Evans *et al*. 2010; Farnsworth *et al*. 2010; Jones *et al*. 2010; Williamson *et al*. 2016; Ma *et al*. 2018) (Table 2.2). The opposite is evident in species that lack a larval phase, such as *Acanthochromis polyacanthus* (Doherty *et al*. 1994; 1995; Planes *et al*. 2001; van Herwerden and Doherty 2006; Bay *et al*. 2006; 2008) (Table 2.2). Parentage analyses based on microsatellite loci of coral reef groupers (*Plectropomus* spp.) determined larval dispersal with no genetic structure between the Percy, Keppel and Capricorn-Bunker Groups (Williamson *et al*. 2016). This study improved the understanding of larval connectivity patterns over regional scales and highlighted the relevance of multiple larval sources for population recovery and persistence after climatic disturbance events (Williamson *et al*. 2016). Population genetic patterns on the GBR may be shaped by a range of factors, including pelagic larval duration, spatial distribution (Riginos and Victor 2001), limited larval dispersal (and the presence of ‘stepping stone’

reefs along the system), genetic drift and migration (Doherty *et al*. 1995), ecological and biological traits (Bay *et al*. 2006; Farnsworth *et al*. 2010), and the variable and complex currents (Wolanski and Pickard 1985; Brinkman *et al*. 2001; Luick *et al*. 2007).

Table 2.2. Population genetic studies in marine fish species along the GBR. FN: Far North, N: North, C: central, S: South, I: inner, M: middle, O: outer. mtDNA: mitochondrial DNA, msat: microsatellites.

Study	Species	Early phase development	GBR Region							Molecular approach			Genetic structure
			FN	N	C	S	I	M	O	mtDNA	msat	enzymes/ proteins	
Doherty *et al*. 1994	*Acanthochromis polyacanthus*	Lacks pelagic larvae/ brood care			✓	✓		✓	✓			✓	Yes
Doherty *et al*. 1995	*Pterocaesio chrysozona*, *Ctenochaetus striatus*	Pelagic			✓	✓		✓	✓			✓	No
Doherty *et al*. 1995	*Acanthochromis polyacanthus*				✓	✓		✓	✓			✓	Yes
Doherty *et al*. 1995	*Amphiprion melanopus*, *Pomacentrus moluccensis, Chromis atripectoralis, Stegastes nigricans*	Benthic spawning/ pelagic larvae			✓	✓		✓	✓			✓	Some structure
Dudgeon *et al*. 2000	*Scarus frenatus*, *Chlorurus sordidus*	Pelagic		✓		✓		✓	✓	✓			No
Planes *et al*. 2001	*Acanthochromis polyacanthus*			✓	✓	✓		✓	✓	✓			Yes
van Herwerden *et al*. 2003	*Lethrinus miniatus*	Pelagic			✓	✓		✓	✓		✓		No
van Herwerden and Doherty 2006	*Acanthochromis polyacanthus*		✓		✓	✓		✓	✓	✓			Yes
Messmer *et al*. 2005	*Pseudochromis fuscus*	Benthic spawning		✓		✓			✓				Significant, but low genetic differentiation
Bay *et al*. 2006	*Acanthochromis polyacanthus*, *Amphiprion melanopus*, *Pomacentrus moluccensis*, *Pomacentrus amboinensis*,	Benthic spawning/ pelagic larvae		✓		✓		✓	✓	✓			No (except *Acanthochromis polyacanthus*). Some structure with ISSRs employed

(Continued)

Table 2.2. (Continued) Population genetic studies in marine fish species along the GBR. FN: Far North, N: North, C: central, S: South, I: inner, M: middle, O: outer. mtDNA: mitochondrial DNA, msat: microsatellites.

Study	Species	Early phase development	GBR Region							Molecular approach			Genetic structure
			FN	N	C	S	I	M	O	mtDNA	msat	enzymes/ proteins	
	Chromis atripectoralis, *Chrysiptera rex*, *Amblyglyphidodon curacao*, *Stegastes nigricans*												
Bay *et al*. 2008	*Acanthochromis polyacanthus*			✓	✓	✓	✓	✓	✓				Yes
van Herwerden *et al*. 2009a	*Lethrinus miniatus*				✓	✓			✓				No
van Herwerden *et al*. 2009a	*Lutjanus sebae*	Pelagic				✓	✓						No
van Herwerden *et al*. 2009b	*Plectropomus leopardus*	Pelagic	✓			✓							No
Evans *et al*. 2010	*Lutjanus carponotatus*	Pelagic			✓	✓	✓		✓				No
Farnsworth *et al*. 2010	*Eviota queenslandica*, *Eviota albolineata*	Benthic spawning/ pelagic larvae		✓				✓	✓				Genetic structure only within *E. queenslandica*
Jones *et al*. 2010	*Pomacentrus amboinensis*			✓	✓	✓	✓	✓	✓		✓		No
Williamson *et al*. 2016	*Plectropomus leopardus*					✓	✓		✓		✓		No
Williamson *et al*. 2016	*Plectropomus maculatus*	Pelagic				✓	✓		✓		✓		Some genetic diversity variation, but not ecologically significant
Ma *et al*. 2018	*Plectropomus leopardus*	Pelagic		✓	✓	✓			✓		✓		No genetic structure

2.5 Biophysical modelling and genomic applications for fish larval connectivity

In the last decade, application of numerical modelling, genomics and seascape genomics opened a new window into understanding the patterns of connectivity of marine organisms and spatial population ecology (Leis *et al*. 2011; Gagnaire *et al*. 2015; Riginos *et al*. 2016). We now have the tools to evaluate and understand connectivity patterns and generate accurate results to inform management of populations. However, to advance the field of connectivity, areas of future research include improving the hydrodynamic models' capacity to resolve realistic circulation patterns, understanding larval behavioural aspects to predict larval connectivity patterns more accurately, and applying genomics (together with parentage genetic analyses) to measure genetic connectivity and dispersal according to neutral and adaptive loci. A number of hydrodynamic/biophysical models are available for investigating connectivity patterns on the GBR (as previously discussed). Such data is available for different years allowing research at a range of temporal (and spatial) scales. Information on larval behaviour exists for a number of GBR fish species, including fishery species (e.g. Leis and Fisher 2006; Quéré and Leis 2011), even though further information is still required on more relevant traits for use in models, e.g. larval vertical migration, swimming capacity and sensory ability, in other species. Furthermore, the combination of SNP genotyping and Next Generation Sequencing platforms provides promising alternatives for assessing genetic connectivity at a high resolution in marine seascapes (e.g. Grewe *et al.* 2015; Pazmiño *et al.* 2018), including the GBR.

Seascape genetics/genomics is a growing field in ecology of marine populations, which aims to explain genetic connectivity patterns by ecological, oceanographic and geographic features (Liggins *et al*. 2016; Riginos *et al*. 2016; Selkoe *et al*. 2016). On the GBR, most studies have focused on one technique to evaluate population connectivity over the system, even though recent seascape genetic studies on coral species have revealed the importance of currents and larval dispersal patterns (i.e. by modelling larval connectivity) on gene flow patterns along the GBR (Riginos *et al*. 2019). Characterising the population genetic structure and evaluating the spatial larval connectivity (by biophysical modelling) can also provide insights into the patterns of larval dispersal and the importance of stepping stones in

marine connectivity (Davies *et al*. 2015). Monitoring reef fishes (*Plectropomus leopardus* and *L. carponotatus*) recruitment at the southern GBR over multiple years established that recruitment is highly variable, highlighting the importance of rare and large recruitment events in maintaining regional populations and commercial stocks (Kingsford 2009). Moreover, the importance of temporal fish larval supply fluctuations to reefs and stability via recruitment has been proved for the effectivity of GBR reserve networks (Harrison *et al*. 2020). Variability in fish species' recruitment patterns on the GBR highlights the necessity for better understanding of the larval dispersal dynamics in this system.

Genetic differentiation, including that from adaptive markers, can be explained by environmental features in marine seascapes, including environmental gradients (e.g. Nanninga *et al*. 2014; Jeffery *et al*. 2018). Changes in genetic differentiation patterns over different times and conditions can be influenced by changes in hydrodynamics (Klein *et al*. 2016) or differential survival of certain adaptive genetic variants (e.g. Momigliano *et al*. 2017; Coscia *et al*. 2020). Also, evaluation of recruit time series by genetics can provide insights into variability of spatial and temporal connectivity, owing to changes in source populations and oceanographic conditions (Selkoe *et al*. 2006). For example, the genetic differentiation from outlier SNPs of coral reef fish adults and recruits was measured during a 'marine heatwave' along Western Australia, highlighting the relevance of understanding larval dispersal and adaptive genetic signatures under particular climate events (Cure *et al*. 2017). Importantly, genetic connectivity in high gene flow species living in dynamic environments, e.g. many reef fishes in the GBR, including *L. carponotatus*, can be further assessed and/or re-evaluated by using genomics, ideally in a seascape genomics context (e.g. DiBattista *et al*. 2017). In the GBR, high population connectivity exhibited by reef fishes with pelagic larvae along the GBR is likely to be confirmed by neutral SNPs. However, adaptive markers may reveal finer scale population structure within the GBR spatially and temporally, particularly amongst recruitment cohorts sampled over time and space. Increasing efforts towards combined modelling of larval dispersal and genomic studies of ecologically and/or commercially relevant GBR species is strategically relevant to inform comprehensive larval connectivity patterns at a range of spatial (i.e. from regional to local) and temporal (i.e. from annual to weekly scales) scales.

In this thesis, I use and combine a series of approaches to determine population connectivity patterns in the GBR. I use biophysical modelling and genomics of adult and recruit reef fish to assess larval dispersal and genetic connectivity patterns over the system (regionally and locally) and over time (year-to-year and among different moon phases). The findings fulfill knowledge gaps and provide complementary information for better understanding of population connectivity in this complex ecosystem.

CHAPTER 3. ENSO EVENTS ENHANCE MULTIDIRECTIONAL INTER-REEF CONNECTIVITY

3.1 Abstract

Interannual variability in the Coral Sea circulation has been associated with El Niño Southern Oscillation (ENSO), while uncertainty remains regarding ENSO's influence on hydrodynamics and larval transport in the adjacent Great Barrier Reef (GBR). Here, fish larval connectivity was investigated during a series of ENSO events from 2010 to 2017 over the GBR, based on biophysical modelling of a widespread predatory reef fish, *Lutjanus carponotatus*. A well-connected system was evident, with along- and across-shelf larval connectivity differing at interannual scales. Generally, southward larval transport connected reefs in the central and southern regions of the GBR, highlighting the influence of the East Australian Current (EAC) along the continental shelf. This connectivity pattern was enhanced when the North Vanuatu Jet (NVJ) and EAC was strong during El Niño conditions. However, extreme ENSO events, such as the very strong 2010 La Niña, resulted in a predominant northward larval transport linking reefs. Increased larval supply to the north from southern regions was associated with weakened NVJ and EAC, strengthened southeasterly winds and greater river discharge into the GBR resulting in northward along-shore river plumes. This work highlights the potential effect of climate events on inter-GBR reef larval connectivity and identifies the variation experienced at interannual scales.

3.2 Introduction

Coral reef ecosystems such as the Great Barrier Reef (GBR) are naturally patchy, and the degree of connectivity between reefs is an important determinant of population dynamics at both local and regional scales (Sale 2004; Cowen and Sponaugle 2009). Larval connectivity is driven by both the physical processes in the ocean and the biological features of dispersing larvae in the seascape. Variability in ocean and wind circulation and larval transport characteristics (including spawning and larval behaviour) can generate a high degree of variability in dispersal and recruitment patterns of fish larvae (Schlaefer *et al*. 2018; Harrison *et al*. 2020). Empirical studies of larval connectivity demonstrate that larval fishes can disperse over several hundred kilometres (Simpson *et al*. 2014; Williamson *et al*. 2016), though studies of local recruitment suggest that this process is largely driven by local retention, whereby individual larvae only disperse short distances (Jones *et al*. 1999; Almany *et al*. 2017). Biophysical models that integrate the behaviour of larval offspring with their physical environment are increasingly used to investigate larval dispersal patterns and connectivity in marine seascapes (Swearer *et al*. 2019).

In the GBR, temporal variability in ocean currents can have important consequences for the spatial and temporal patterns of fish larval dispersal and connectivity between reefs. A fish larval dispersal network for the northern GBR sector suggested high connectivity and tight clustering (Kininmonth *et al*. 2010). The main direction of flow and residency time in the GBR lagoon changes seasonally which alters the fate of modelled particle dispersal (Luick *et al*. 2007). Further, modelled self-recruitment and inter-reef connectivity of fish larvae was shown to vary in the northern GBR at annual scales, with southward dispersal in some years and northward transport in others (James *et al*. 2002). Modelled coral reef fish larval recruitment in the southernmost GBR is also affected by variation of current circulation over years, with particular wind conditions favouring recruitment (Schlaefer *et al*. 2018).

El Niño Southern Oscillation (ENSO) is the strongest source of interannual global climate variability (Santoso *et al*. 2017). ENSO modifies the Walker Circulation, an integral component of ENSO, represented by a large-scale east-west atmospheric circulation along the equator (Julian and Chervin 1978). This circulation causes varying atmospheric and oceanic climate conditions in the tropical Pacific Ocean, represented

by warm El Niño or cold La Niña events (Santoso *et al*. 2017). Current trends in climate change suggest future extreme El Niño and La Niña events may increase in frequency due to greenhouse warming (Cai *et al*. 2014; 2015).

In the Coral Sea, ENSO dominates interannual transport variability of the South Equatorial Current (SEC), which strengthens or weakens a few months after El Niño or La Niña events, respectively (Kessler and Cravatte 2013). The SEC is composed of two Coral Sea branches, the North Vanuatu Jet (NVJ) and the North Caledonian Jet. The NVJ branch crosses the Coral Sea westwards, reaching the outer GBR and bifurcating northward, forming the Gulf of Papua Current (GPC) and southward, forming the East Australian Current (EAC), which flow along the east Australian continental shelf edge (Ridgway *et al*. 2018). Along the GBR shelf, ocean circulation is driven in part by cross-shelf pressure gradients associated with the EAC and Coral Sea intrusions (Brinkman *et al*. 2001; Luick *et al*. 2007; Benthuysen *et al.* 2016), with interannual fluctuations possibly modulated by ENSO events (Wolanski and Pickard 1985; Benthuysen *et al*. 2016). Simulations of sea-level differences between the central GBR and western Pacific islands identified strong southward flows across the GBR coinciding with El Niño events (Burrage *et al*. 1994). During El Niño and La Niña events, lower and higher river flow discharges have been found in the central and northern GBR (Lough *et al*. 2015; Reed *et al*. 2019), which can affect ocean circulation patterns (Furnas 2003).

The influence of ENSO events on fish larval dispersal and recruitment has been described across the Pacific Ocean. Fluctuations in fish larval supply, including larval dispersal trajectories and distances, have been linked to variable wind and current strength and direction, during either El Niño or La Niña events (Le Port *et al*. 2014; Mari *et al*. 2017; Hsiung *et al*. 2018), including strong ENSO events (Lo-Yat *et al*. 2011). Recruitment of tropical fishes off southwestern Australia has been positively correlated with the Southern Oscillation Index (SOI), an index that gauges ENSO's phase and strength (see Section 2 for more information about the SOI) (Wilson *et al*. 2017). Furthermore, population fluctuations of several damselfish species in the GBR synchronise during ENSO events (Cheal *et al*. 2007). However, the effect of ENSO phases on larval fish connectivity in the GBR is unknown.

This study uses a biophysical model to investigate larval connectivity patterns of a coral reef fish, *L. carponotatus*, throughout the GBR from 2010 to 2017. The study period spans an important time frame that captures four ENSO events, including one of the strongest La Niña events on record, a strong El Niño, and also neutral states. Specifically, the objectives are to: i) estimate the degree of larval connectivity between reefs in the GBR from 2010 to 2017; ii) identify fish larval connectivity anomalies during El Niño and La Niña events; iii) explore the relationship between GBR larval dispersal patterns and ENSO phases from 2010 to 2017; and iv) describe the large-scale ocean and wind circulation patterns during both El Niño and La Niña events. I hypothesise that interannual larval connectivity changes in the GBR due to ENSO phase changes, with either i) predominant southward larval connectivity associated with greater EAC transport, during El Niño conditions, or ii) predominant northward larval connectivity associated with stronger southeasterly winds and along-shore river plumes, during extreme La Niña phases.

3.3 Materials and Methods

3.3.1 ENSO events

The SOI, based on the Australian Bureau of Meteorology data (BOMa), was used to identify the ENSO phases for each larval dispersal event during October to January, between 2010 and 2017 inclusive, given stripey snapper spawning data (Table 3.1). The SOI data used to classify the different years according to ENSO events was obtained from the Australian Bureau of Meteorology at http://www.bom.gov.au/climate/enso/outlook/#tabs=ENSO-Outlook-history. Several other indices are also used to evaluate which ENSO phase is occurring, e.g. Niño3.4, based on SST anomalies averaged over the tropical Pacific Ocean (see for example http://www.bom.gov.au/climate/ahead/about-ENSO-outlooks.shtml). The SOI indicates the development and strength of El Niño or La Niña events in the Pacific Ocean, by measuring surface air pressure differences between Tahiti and Darwin (Australia) as an indicator of the intensity of the Walker Circulation (BOMb). The method the Australian Bureau of Meteorology uses to calculate the SOI is based on mean and standard deviation of the pressure differences with the climatology period

based on a dataset from 1933 to 1992 inclusive (BOMb). Sustained negative (below -7) or positive (above +7) SOI values typically indicate El Niño or La Niña events, respectively. The following ENSO events were identified within the study time frame: very strong 2010 La Niña (2010-2011), moderate 2011 La Niña (2011-2012), 2014 El Niño alert (2014-2015) and strong 2015 El Niño (2015-2016) (BOM 2012; Santoso *et al*. 2017; BOMa) (Table 3.1). ENSO events tend to decay by austral autumn of the following year (BOMa). During 2012 (2012-2013) and 2013 (2013-2014) neutral ENSO states prevailed, while 2016 (2016-2017) and 2017 (2017-2018) exhibited a mix of neutral and La Niña phases (BOMa) (Table 3.1). Watch and alert stages indicate that the tropical Pacific Ocean is showing signs that an ENSO event may occur in about 50 and 70% of cases, respectively (BOMc).

Table 3.1. Southern Oscillation Index values during *L. carponotatus* larval dispersal periods modelled. Data obtained from the Australian Bureau of Meteorology. The main ENSO phases during the eight year study period are indicated.

Year	October	November	December	January (next year)	Main ENSO phase
2010	18.3	16.4	27.1	19.9	Very strong La Niña
2011	7.3	13.8	23	9.4	Moderate La Niña
2012	2.4	3.9	-6	-1.1	Neutral
2013	-1.9	9.2	0.6	12.2	Neutral
2014	-8	-10	-5.5	-7.8	El Niño alert
2015	-20.2	-5.3	-9.1	-19.7	Strong El Niño
2016	-4.3	-0.7	2.6	1.3	Neutral-La Niña
2017	9.1	11.8	-1.4	8.9	Neutral-La Niña

ENSO development and strength in each month are represented by alternate shade styles: La Niña watch and La Niña (lighter to darker blue shades, respectively), El Niño watch, El Niño alert and El Niño (lighter to darker orange shades, respectively), and neutral (no shade).

3.3.2 Hydrodynamic model

Hydrodynamic data was provided through the eReefs project (http://ereefs.org.au) (Herzfeld *et al*. 2016), which includes a hydrodynamic model over a 300,000 km^2 area across the entire GBR. eReefs commenced in 2012 as a collaboration between the Great Barrier Reef Foundation, the Commonwealth

Scientific and Industrial Research Organization, the Australian Institute of Marine Science, Bureau of Meteorology, and Queensland Government, supported by funding from the Australian and Queensland Governments, the BHP Billiton Mitsubishi Alliance and the Science and Industry Endowment Fund. The eReefs hydrodynamic model is based on the Sparse Hydrodynamic Ocean Code (SHOC), which is a finite difference, three-dimensional model based on equations of momentum, continuity and conservation of heat and salt, which uses Boussinesq and hydrostatic approximations, discretised on an Arakawa C grid (Herzfeld 2006). The eReefs hydrodynamic model is forced by wind, surface heat and water fluxes provided by the Bureau of Meteorology's Australian Community Climate and Earth System Simulation (ACCESS-R; 12 km resolution). The ACCESS-R data are available through the Bureau of Meteorology (http://www.bom.gov.au/). The regional model is forced along the boundaries by low frequency ocean currents from the Bureau of Meteorology's Ocean Modelling Analysis and Prediction System (OceanMAPS), which is a global ocean model (Brassington *et al*. 2007). The tidal component is implemented from a global ocean tide model (Cartwright and Ray 1990; Eanes and Bettadpur 1995). Freshwater inputs to the GBR representing the major rivers are obtained from the Department of Natural Resources, Mines and Energy gauging network (Herzfeld *et al*. 2016). Model outputs include three-dimensional velocity, temperature, salinity, density and sea-level over the shelf, from September 2010 to present. The hydrodynamic model has been validated at key locations along the GBR and is a good indicator of currents in those regions (Schiller *et al*. 2015; Herzfeld *et al*. 2016).

Near-surface ocean currents and salinity (as a proxy of river discharge) from the eReefs hydrodynamic model (GBR4 v2) and wind data from ACCESS-R were accessed for stripey snapper larval dispersal periods (from October to January). Ocean current velocity (ms^{-1}) and salinity values were obtained at a depth of -1.5 m, and wind velocity (ms^{-1}) values at 10 m height. Ocean current, wind velocity and salinity were averaged in time (i.e. from October to January) for each of the years examined. The daily eReefs model current, wind and salinity data are available through the eReefs Catalog at http://data.aims.ereefs.org.au/thredds/catalog.html.

3.3.3 Study species

Stripey snapper, *L. carponotatus,* occurs from the Western Pacific Ocean to the northeastern Indian Ocean and is a widely distributed, dominant predatory fish in the GBR (Emslie *et al*. 2017). *Lutjanus carponotatus* has been used as a model reef species to investigate reef connectivity along the coast of northwestern Australia because of its relatively long pelagic larval dispersal phase and similar larval settlement behaviour and ecology to other fish predators (DiBattista *et al*. 2017). The spawning peak in the GBR occurs approximately from October to December (Kritzer 2004), and continuous spawning with at least weekly events has been recorded (H. B. Harrison unpublished data). The average pelagic larval duration (PLD) of *L. carponotatus* in the GBR was reported as 25 days (Schlaefer *et al*. 2018). Stripey snapper parentage studies confirmed that local larval dispersal occurs up to ~30 km (Harrison *et al*. 2012), although larvae may disperse further. Population genetic work on their population structure along the central and southern GBR, based on mitochondrial DNA, identified no population subdivision, suggesting that island groups are connected by larval dispersal (Evans *et al*. 2010).

3.3.4 Larval dispersal and connectivity modelling

Larval connectivity along the GBR was estimated using Connie 3.0, a high-resolution advection/diffusion model of the GBR (https://connie.csiro.au/) (Condie *et al*. 2012). Connie was used with the eReefs model velocity data at 4 km resolution scale and a fourth-order Runge-Kutta ordinary differential equation solver that subsequently tracked individual particles finding the horizontal velocity at the specified depth and time. Connie has been successfully used to model particle transport in the ocean, including (but not limited to) studies on relative particle retention and cross-shore transport at selected locations around Australia (Condie *et al*. 2011), larval dispersal potential of coral reef fish in northwestern Australia (Berry *et al*. 2012b), catadromous fish along the Queensland coast and Coral Sea (Feutry *et al*. 2013) and population connectivity patterns of crown-of-thorns starfish along the GBR (Hock *et al*. 2017; 2019).

GBR wide larval connectivity was investigated among 29 regions distributed along and across the GBR (Figure 3.1). These regions were chosen according to *L. carponotatus* occurrence records in the GBR (Atlas of Living Australia, http://www.ala.org.au). Regions referred as offshore included mid- to outer-shelf reefs. Modelled larvae were seeded from a number of locations within each region yearly, between 2010 and 2017. Larvae were released from October to December at a constant rate of 100 particles/grid cell/day to capture all possible spawning events and dispersed over a PLD of 25 days. Larval vertical distribution, based on larval development and behaviour data of *L. carponotatus* and other lutjanids (Miller and Cribb 2007; Leis *et al*. 2009; Quéré and Leis 2010; Leu and Liou 2013), occurred as follows: day 1 at 1 m, days 2 to 20 at 3 m, and days 21 to 25 at 6 m. Larval depth preferences were set to correspond with the depth distribution layers in Connie. Larval horizontal swimming velocity preferences were not included while dispersing, due to restricted access to proprietary code. Dispersing larvae were subjected to an 18% daily mortality rate, as proposed for marine pelagic larval mortality rates (Cowen *et al*. 2000; James *et al*. 2002).

Sensory zones of 4 km surrounding reef habitats of the different regions examined were created, considering larval fish sensory capabilities (Leis 2007) and the applied model resolution scale (4 km). The buffer zone was created using a Geographic Information System, QGIS 2.18.0 (QGIS Development Team 2018). Larvae had to reach the reef sensory zones at the end of their PLD to be considered able to settle and were subjected to 13% mortality due to predation, as suggested for *L. carponotatus* while attempting to settle (Quéré and Leis 2010). Larvae that did not reach the sensory zones after the pelagic larval stage were not included in analyses.

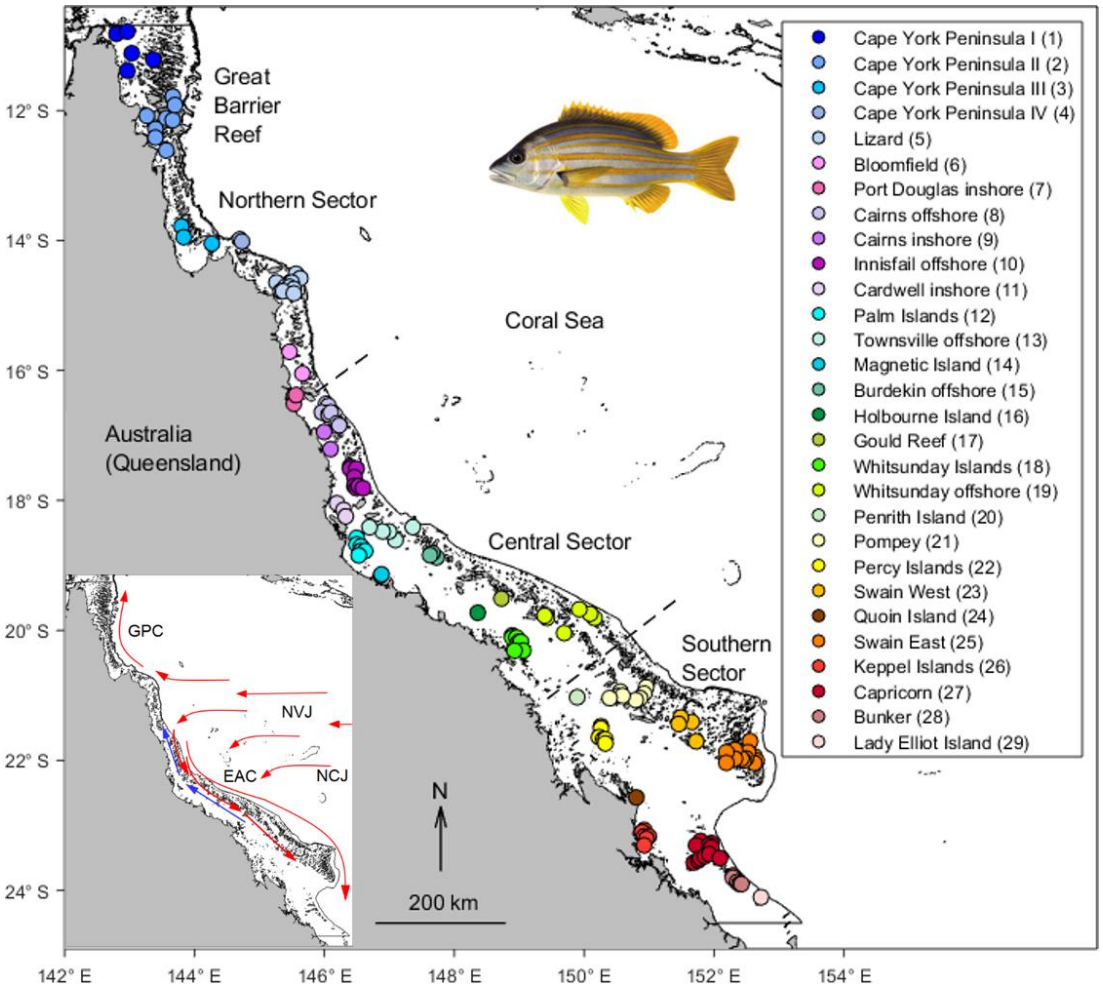

Figure 3.1. Regions of larval sources and destinations of modelled *L. carponotatus* larvae in the GBR. Each region is indicated by a colour (see inset colour key) and consists of a grouping of local populations. Region names in the legend are ordered from north to south (meridional axis), and the same order is used for representation of regions in the connectivity matrices. The black line offshore following the length of the coast delimits the GBR shelf and corresponds to the 100 m isobath. Northern, central and southern GBR sectors are divided by black dashed lines. *Inset:* Predominant and transient large-scale surface currents during the main spawning season of *L. carponotatus* are shown by red and blue arrows, respectively, in the inset panel. Western boundary currents: Gulf of Papua Current (GPC) and East Australian Current (EAC), and components of the westward flow of the South Equatorial Current (SEC): North Vanuatu Jet (NVJ) and North Caledonian Jet (NCJ). Illustration of *L. carponotatus* © R.Swainston/www.anima.net.au. The shapefile containing the reef habitats in the GBR (Lawrey and Stewart 2016) is available through the eAtlas server © Great Barrier Reef Marine Park Authority 2014.

3.3.5 Quantifying temporal patterns of connectivity

From 2010 to 2017, yearly connectivity values between 29 GBR regions were determined and eight connectivity matrices were created (Figure S3.1). Connectivity matrices show the probability that larvae spawned at a given origin (29 regions) disperse and recruit to a given destination (29 potential regions). Larval retention was defined as the fraction of larvae produced at a given region that settles into that region (Burgess *et al*. 2014). Larval connectivity was explored overall (averaged) from 2010 to 2017, and in each year separately. The coefficient of variation (CV) of yearly larval connectivity (from 2010 to 2017) between each pair of regions was calculated according to: CV = (standard deviation/mean). The positive anomalies in larval connectivity, indicating an increase in connectivity, referenced to the 2010-2017 mean, were calculated for the very strong 2010 La Niña, moderate 2011 La Niña, 2014 El Niño alert and strong 2015 El Niño events. In addition, the relationship between averaged larval connectivity and CV, and among larval dispersal patterns and the averaged SOI (obtained from values in Table 3.1), was explored over the study period, at a significance level of $p < 0.05$. Dispersal patterns were measured as northward, southward and across-shelf (from offshore towards the shore) larval connectivity, averaged over the central and southern GBR (excluding the southernmost inner islands and the adjacent Capricorn-Bunker to Lady Elliot regions, as connectivity patterns in this area were relatively different). The central-southern GBR sector was selected to show the connectivity variability according to the SOI as this region presented the greatest changes in larval dispersal patterns.

3.4 Results

3.4.1 Temporal patterns of larval connectivity

Larval connectivity values were obtained among 29 GBR regions from 2010 to 2017. Mean connectivity patterns during this period revealed multidirectional connectivity across the study region, with bi-directional larval dispersal along the latitudinal gradient of the GBR and cross-shelf transport (Figure 3.2a). Larval connectivity was predominantly southward in mid- to outer-shelf reefs in the central and southern GBR, although northward connectivity was also evident. Larvae sourced

from the far northern GBR (< 14° S) dispersed mostly northward. Cross-shelf connectivity in the central and southern GBR occurred mostly from offshore sectors towards the inner sector. The shelf widens in these regions, which is not the case for the northern GBR sector, where the GBR reefs are not separated into inshore and offshore sectors. Large-scale larval connectivity over hundreds of kilometres was identified in the GBR, although weaker connections occurred over large distances (from *ca*. 400 km) (Figure 3.2a).

GBR regions received and supplied larvae from and to multiple regions, respectively (Figure 3.2a). The region around Lizard Island, in the northern GBR, represented one of the smallest larval sinks (column 5; Figure 3.2a). The central sector of the GBR acted both as the most important larval source and sink (e.g. the offshore regions around Innisfail [column/row 10] and Townsville [column/row 13]) (Figure 3.2a). Particularly, the offshore regions between Cairns (row 8) and Burdekin (row 15) (i.e. between ~17 and 19° S) were relatively large larval sources. Larval retention was common in all GBR regions, although variable among regions (values along the diagonal; Figure 3.2a). Generally, greater retention occurred around central and southern island groups (e.g. Palm [row 12], Whitsunday [18] and Keppel [26] Islands) and southern reef groups (e.g. Swain [25] and Capricorn-Bunker [27] reef groups).

The degree of larval connectivity between reefs in the GBR was highly variable, both spatially and temporally. The CV in the degree of connectivity between sectors ranged from 0.07 (indicating a consistent level of exchange between sectors) to 2.83 (indicating a high level of temporal fluctuations from year to year). Overall, the median distribution of CV was 1.64 (Figure 3.2b), suggesting substantive temporal fluctuations in connectivity patterns between years. Higher CV values were identified northwards and over large distances southwards during the larval connectivity simulation period (Figure 3.2b). Generally, connectivity values were negatively correlated with CV (r = -0.76, p < 0.0001, exponential fit) (Figure S3.2), suggesting that connectivity patterns are consistent in time but events at the edges of the modelled larval dispersal distribution generate the greatest variability in the modelled dispersal patterns (i.e. the greatest larval connectivity variation is over longer distances away from a source region).

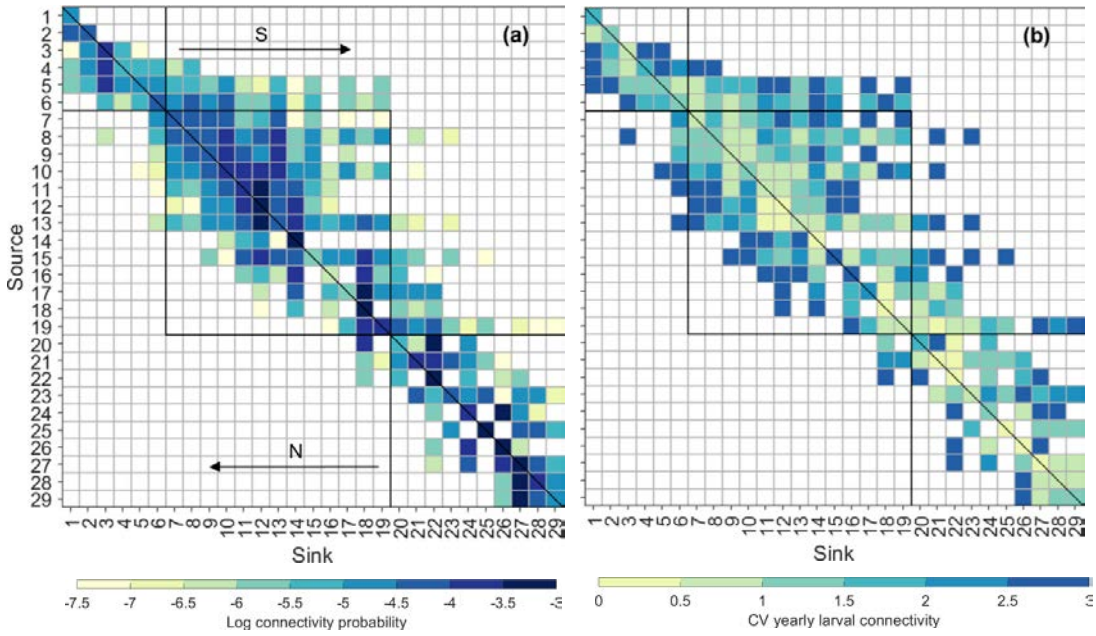

Figure 3.2. Averaged patterns of larval connectivity for *L. carponotatus* in the GBR during the period modelled. a) Larval connectivity matrix of *L. carponotatus* representing the average connectivity between regions of the GBR from 2010 to 2017. b) CV of annual larval connectivity from 2010 to 2017. Particles were released from October to December at source regions (rows) recruiting to sink regions (columns). Regions are ordered from north to south following the same order as in the legend of Figure 3.1. The northern, central and southern GBR sectors are bordered by black lined boxes. Values along the diagonal represent a) larvae settled into the same region and b) CV of larval retention, and values to the right or left of the diagonal indicate southward (S) or northward (N) connectivity, respectively.

3.4.1.1 The 2014 and 2015 El Niño events

Southward larval connectivity predominated in the GBR during the 2014 El Niño alert (Figure 3.3a) and during the strong 2015 El Niño (Figure 3.3b) events, identifying some of the strongest southward connectivity patterns over the central GBR to occur in 2014 (Figure 3.3e). In 2014, central and southern regions were sourced mostly by larvae transported from the north (i.e. columns 8 [Cairns region] to 29 [southernmost region]) (Figure 3.3a). In 2014, positive anomalies in larval source resulted mostly from larvae sourced from the north, particularly inner island regions (e.g. columns 9, 11-12, 14, 18) and offshore regions (e.g. the Whitsundays [column 19] and Swains [column 25] (Figure 3.3e). Higher southward larval connectivity towards particular central GBR

regions was present in 2015, including the Townsville offshore region, which also acted as a large larval source to other reefs (column/row 13) (Figure 3.3b,f). Northward inter-reef connectivity in the northern GBR (from the surroundings of the Lizard Island region at ~15° S to the far northern GBR) was strengthened in 2015 (row 5; Figure 3.3f).

3.4.1.2 The 2010 and 2011 La Niña events

Larval connectivity patterns during the very strong 2010 La Niña event were generally dominated by northward dispersal along the central and inner southern GBR sectors, in contrast to other ENSO events (Figure 3.3c,g). The furthest northward inter-reef connections were exhibited in 2010 (e.g. from Townsville offshore region [row 13]) (Figure 3.3c). Inner regions along the central GBR received the strongest larval supply from populations from the south in 2010 (columns 7, 9, 11-12, 14, 16, 18; Figure 3.3c,g). Some of these regions, including Port Douglas and Cardwell, were uniquely sourced by larvae released from the south (columns 7 and 11, respectively; Figure 3.3c). Offshore sectors, including those between Bloomfield and Townsville regions, received a higher than average larval supply from reefs to the south during 2010 (columns 6, 8, 10, 13; Figure 3.3g). Strong across-shelf larval connectivity along the southern GBR, from the Pompey region to the Percy and Whitsunday Islands regions (row 21, and columns 18, 22, respectively), and along the central GBR, between the Whitsunday and Burdekin offshore to the inner islands from the Whitsunday to Cardwell regions (rows 15, 17, 19, and columns 11-12, 14, 16, 18, respectively), was identified in 2010 (Figure 3.3c,g).

In the moderate 2011 La Niña event, southward larval connectivity predominated over the central and southern GBR, with relatively weak connections over large distances from offshore sectors (e.g. rows 8, 10, 13, 15, 19) (Figure 3.3d,h). Southward larval dispersal from the northern GBR, including Lizard and Bloomfield regions, increased towards the central GBR in 2011 (rows 5, 6) (Figure 3.3h). Particular central GBR regions, including the Innisfail and Burdekin offshore regions, acted as large larval sinks and sources of larvae in 2011 and 2010 La Niña events, respectively (columns/rows 10 and 15, respectively) (Figure 3.3g,h). In the southernmost half of the

southern GBR, cross-shelf larval connectivity from offshore sectors strengthened during the 2011 and 2010 La Niña events (rows 23, 25; Figure 3.3g,h).

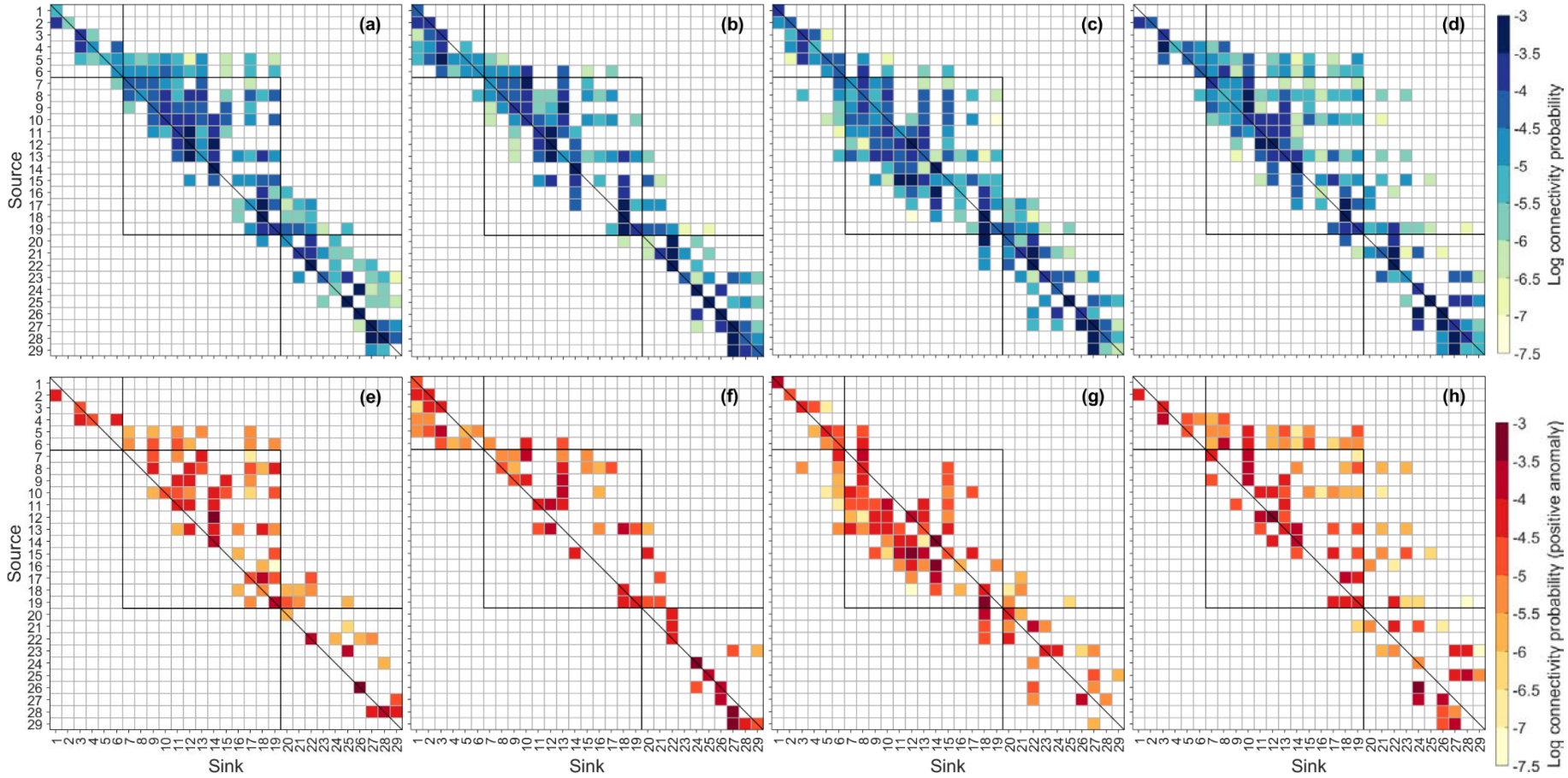

Figure 3.3. Larval connectivity matrices (top row) of *L. carponotatus* along the GBR, and positive connectivity anomalies (referenced to the 2010-2017 mean) (bottom row), for: a,e) 2014 El Niño alert; b,f) strong 2015 El Niño; c,g) very strong 2010 La Niña; d,h) moderate 2011 La Niña. Regions are ordered from north to south as in the Figure 3.1 legend. Northern, central and southern GBR sectors are bordered by black lined boxes. Values along the diagonal represent larval retention, and values to the right or left of the diagonal indicate southward or northward connectivity, respectively.

3.4.2 ENSO-linked connectivity dynamics

The relationship between interannual larval connectivity patterns in the central-southern GBR and the SOI was explored for a SOI range between -14 and 20. Generally, average southward or northward larval connectivity decreased or increased with an increase of SOI, respectively, particularly in very strong La Niña events (r^2 = 0.68 and r^2 = 0.78, respectively, $p < 0.05$ for both) (Figure 3.4a,b). In general, average cross-shelf larval connectivity increased at both lowest (El Niño) and highest (La Niña) SOI values, particularly during the latter conditions (r^2 = 0.76, $p < 0.05$) (Figure 3.4c).

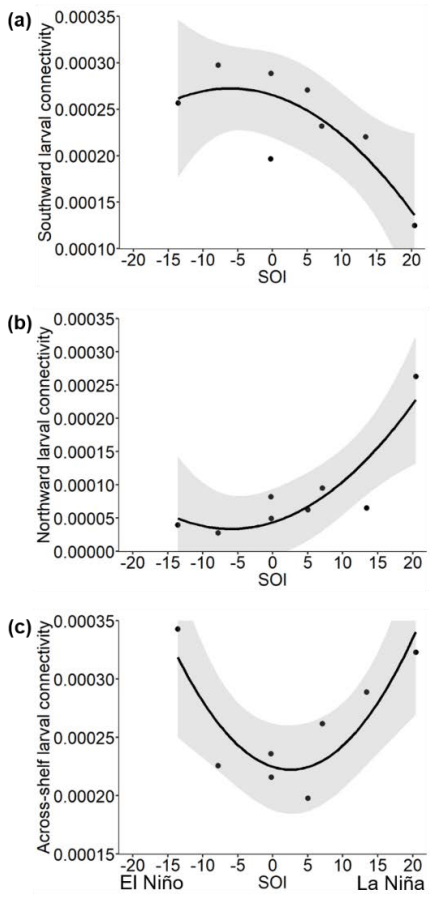

Figure 3.4. Relationship between the larval connectivity probability of stripey snapper and the Southern Oscillation Index (SOI) in the central GBR, according to: a) southward larval connectivity, b) northward larval connectivity, and c) across-shelf larval connectivity. The mean variables are calculated over the larval dispersal periods from 2010 to 2017. The grey bands show the 95% confidence intervals of the means. All relationships were statistically significant at a $p < 0.05$.

3.4.3 Ocean, wind and riverine discharge circulation patterns

Ocean and wind circulation patterns were investigated in the GBR and Coral Sea for the larval dispersal periods examined and their interannual changes associated with different ENSO events. The location of the NVJ bifurcation (into the equatorward GPC and poleward EAC) varied across the larval dispersal periods. In the very strong 2010 La Niña event, the NVJ bifurcation was positioned northmost at ~14.3° S and generally showed a gradual shift over time to the southernmost position (located at ~15° S) during the strong 2015 El Niño event (Figure S3.3). Ocean circulation in the far northern GBR followed a northward transport (adjacent to the GPC) over the study period, while GBR circulation around the NVJ bifurcation generally varied in the southward and northward directions according to the bifurcation latitude (Figure S3.3). The EAC was associated with oceanic inflow onto the GBR shelf at ~16.5° S and major oceanic inflow at ~18° S (central GBR), resulting in a predominant southward flow over the central and southern outer- and mid-shelf, in every study year, except during the very strong 2010 La Niña event (Figure 3.5a,b,S3.3). There was a strong onshore flow reflecting the surface wind-driven component resulting from southeasterly winds (Figure S3.3,S3.4).

3.4.3.1 El Niño conditions in 2014 and 2015

The NVJ bifurcation was strongest (i.e. the NVJ and GPC-EAC surface currents) during El Niño conditions, at which time an EAC speed of ~0.6 ms^{-1} occurred along the outside of the central and southern GBR (Figure 3.5a,S3.3). This circulation was associated with strengthened southward circulation along the central and southern GBR (up to ~0.15 ms^{-1}) (Figure 3.5a,S3.3). Generally, during El Niño conditions easterly-southeasterly and easterly-northeasterly winds of ~4-5 ms^{-1} winds developed across the GBR (Figure 3.5c,S3.4).

3.4.3.2 The 2010 and 2011 La Niña events

The NVJ and EAC were weakest during the very strong 2010 La Niña event (Figure 3.5b,S3.3). This circulation was associated with the strongest southeasterly winds of ~5-6 ms^{-1} in 2010 (Figure 3.5d,S3.4). River discharge into the GBR was low over the study period (including during the moderate 2011 La Niña event), except during 2010. In 2010, low-salinity along-shore northward plumes occurred along the inner- and mid-shelfs in the northern, central and southern GBR, notably from December (Figure 3.5e,f,S3.5). The highest river discharges included those from the Burdekin (19° 39' S, 147° 30' E) and Fitzroy (23° 31' S, 150° 53' E) Rivers. The effect of the Coral Sea circulation, winds and river flows in 2010 resulted in a predominantly northward circulation over much of the GBR (Figure 3.5b). Contrarily, during the moderate 2011 La Niña event, a strong EAC developed adjacent to the central GBR, although relatively weaker in the southernmost GBR when compared to other ENSO years (Figure S3.3). This circulation was associated with a predominant southward transport in the central GBR (Figure S3.3).

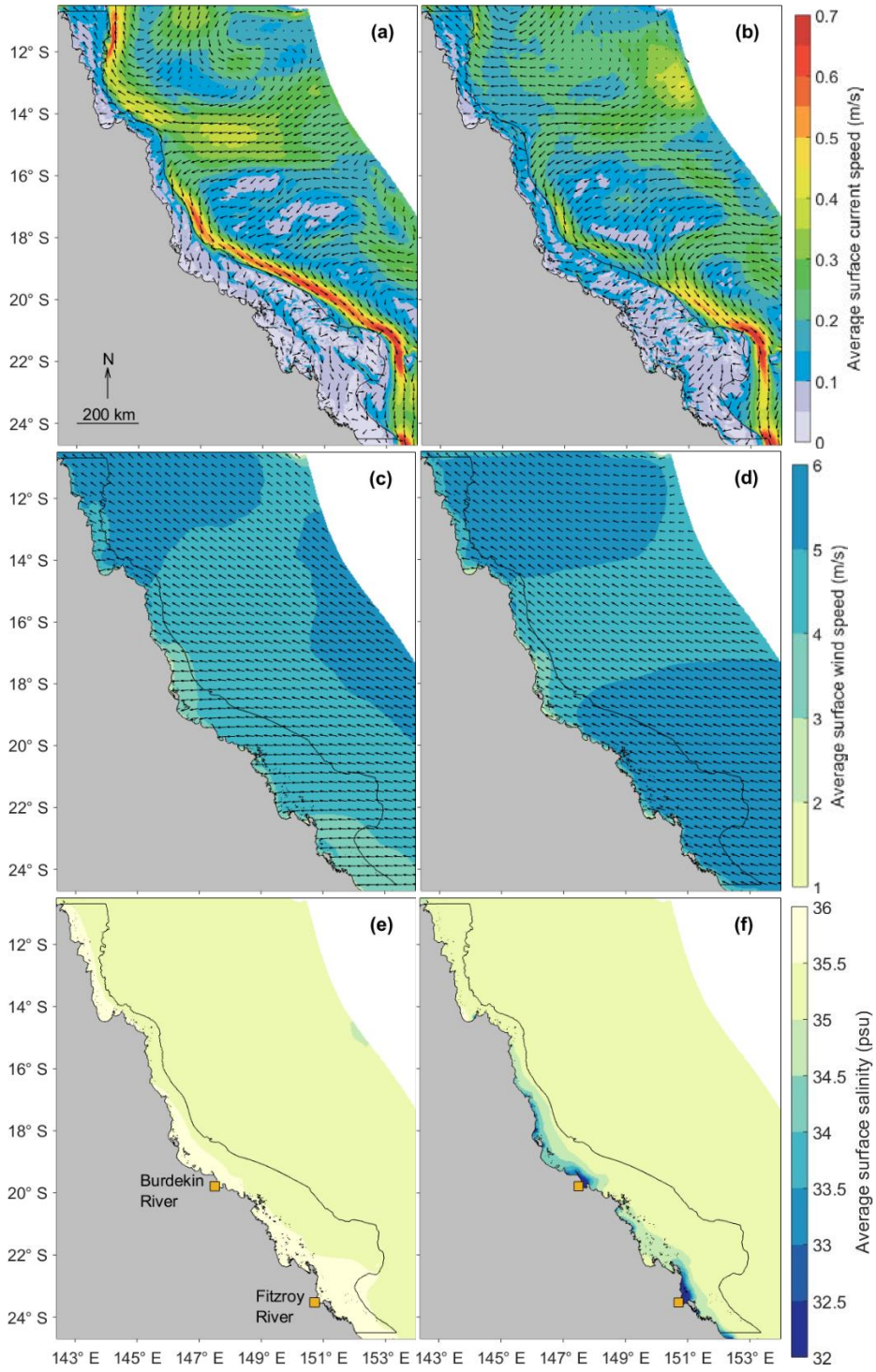

Figure 3.5. Average surface current velocity (ms^{-1}) (a,b), wind velocity (ms^{-1}) (c,d), and salinity (psu) (e,f) (October-January) over the GBR and Coral Sea for: a,c,e) averaged El Niño conditions during 2014 and 2015 (strong), and b,d,f) 2010 La Niña (very strong). Ocean current and wind directions are indicated by arrows and speeds are shaded (a-d). Locations of major river mouths (e,f) are indicated by orange squares. In all panels (a-f) the black line delimits the GBR shelf and corresponds to the 100 m isobath.

3.5 Discussion

The association between ENSO events and Coral Sea variation in ocean currents has been reported previously (Kessler and Cravatte 2013), as well as variability of fish larval dispersal and larval supply in the Pacific Ocean (Lo-Yat *et al*. 2011; Le Port *et al*. 2014; Hsiung *et al*. 2018). Here, I extend this work to investigate the effect of ENSO events on circulation patterns in the GBR and adjacent Coral Sea western boundary currents, and how the examined ENSO events affect fish larval dispersal and connectivity throughout the GBR. I found high interannual variation in the larval connectivity patterns in the GBR, during a series of El Niño and La Niña events and neutral states spanning eight years (2010 to 2017). ENSO linked hydrodynamic conditions in the GBR and Coral Sea, including those during extreme ENSO events, enhanced variations in the bi-directional larval dispersal along the latitudinal gradient and cross-shelf larval dispersal in the GBR.

The global impacts of ENSO extend to coral reef bleaching (Baker *et al*. 2008; McGowan and Theobald 2017), fisheries (Kumar *et al*. 2014; Ñiquen and Bouchon 2004; Arcos *et al*. 2001), rainfall variability (Vicente-Serrano *et al*. 2011) and river discharge (Lough 1994). ENSO-linked larval dispersal and recruitment dynamics have been documented for a range of marine organisms across the Pacific Ocean, e.g. oysters (Lal *et al*. 2020), corals (Treml *et al*. 2008; Wood *et al*. 2016; Romero-Torres *et al*. 2018; Thompson *et al*. 2018), fish (Mari *et al*. 2017), and crown-of-thorns starfish (CoTS) on the northern GBR (Wooldridge and Brodie 2015). A previous study found a strong association between ENSO and Australian climate, by estimating significant correlations between the SOI and climate-related variables (Power *et al*. 1999). In the present study, I found an association between ENSO intensity, i.e. by measuring the SOI, and fish larval dispersal patterns on the GBR, particularly when the effect of extreme events is pronounced.

Findings from hydrodynamic modelling suggest interannual variability in the Coral Sea and GBR circulation, potentially associated with ENSO. Changes in the Coral Sea westward transport were detected in previous studies following El Niño (increase) or La Niña (decrease) events (Kessler and Cravatte 2013), corresponding with the NVJ surface current strengthening and weakening during El Niño and La Niña

events, respectively, in the present study. During the 1982-83 El Niño event, the upper few hundred metres of the SEC at longitude 0° S - 10° S experienced a southward shift to 10° S - 20° S in the tropical Pacific Ocean (Meyers and Donguy 1984). In contrast, the SEC remained stable prior to this El Niño event (Meyers and Donguy 1984). In the present study, interannual changes in the location and strength of the surface NVJ bifurcation occurred, where its southernmost position occurred during the strong 2015 El Niño event. An along-shore surface (> 50 m) ocean circulation was described near Lizard Island in the northern GBR (near the NVJ bifurcation location) as displaying interannual variability in the northward and southward velocities over the period October-December between 2008 and 2013, with an increase in the northward component during the very strong 2010 La Niña event (Ridgway *et al*. 2018). ENSO may modulate other processes of the GBR circulation, such as intrusive upwelling events associated with weakening or reversal in the southeasterly winds (Benthuysen *et al*. 2016), including weakened wind speeds during the summer of 2015-2016 (Benthuysen *et al*. 2018).

The influence of oceanic inflow from the Coral Sea on the central GBR circulation has been described during the austral winter, suggesting an effect on along- and across-shelf dispersal of spawn material from reefs (Brinkman *et al*. 2001). Here, I show oceanic inflow from the EAC onto the GBR shelf in the central and southern GBR over the study period. The inflow enhanced southward dispersal of larvae, including larval dispersal between offshore regions. There was also a strong onshore flow which enhanced cross-shelf larval connections from offshore sectors. Predominantly southward dispersal in the GBR lagoon is controlled by the cross-shelf geostrophic pressure gradient attributed to the combined effect of the EAC and the opposing forces from river discharge and southeasterly winds (Luick *et al*. 2007). The present study indicated strengthened southward transport and larval connectivity during El Niño conditions, which was associated with strengthened EAC surface current and weakened southeasterly winds. Contrarily, a weak EAC surface transport and strong southeasterly winds during the very strong 2010 La Niña event led to predominantly northward flow and larval connectivity. The very strong 2010 La Niña year was associated with record rainfall in Australia (BOM 2012), producing large river plumes along the coast with predominantly along-shore northward flow, as suggested during strong southeasterly trades (Furnas 2003). Interannual variability in the GBR

has been indicated by sea surface salinity changes during the 2008-2015 summer season, with some of the greatest negative salinity anomalies identified during 2010 (Ridgway *et al*. 2018). Moreover, extreme southward or northward flows across the GBR have coincided with El Niño events or intense regional cyclone activity, respectively (Burrage *et al*. 1994). In the present work, no cyclones occurred in the region during the study period, however, strong northward flows occurred during very strong La Niña events, when cyclones normally develop across the region (BOM 2012).

Major coastal discharge events into the GBR relate to low-salinity plume waters along the coast and onto the shelf, mostly over inshore reefs but also extending to mid-shelf reefs (Devlin and Brodie 2005), both of which constitute the preferred *L. carponotatus* habitats (particularly the former) (Emslie *et al*. 2017). Extreme La Niña years, such as the very strong 2010 La Niña event can result in stronger river discharges with an overall extent of surface plume waters over much of the northern and central GBR (Devlin *et al*. 2012). Chlorophyll a, zooplankton and fish larvae can overlap in river plumes with potentially favourable feeding environments in space and time (Swieca *et al*. 2020) and larval survival benefits by providing protection against visual predators due to turbid plumes (Carreon-Martinez *et al*. 2014). However, higher prey concentrations of fish larvae in river plumes is not necessarily associated with better larval growth and condition, and factors such as intensity of river discharge and winds, and turbulence (as well as visibility), may affect larval feeding success (Axler *et al*. 2020a), resulting in more or less favourable environments for larval fishes and their prey and predator distributions (Axler *et al*. 2020b). On the central GBR, very high zooplankton biomass and copepod egg production rate were documented within a riverine plume in coastal waters as a consequence of freshwater run-off following flooding events (McKinnon and Thorrold 1993), together with changes on larval fish community structure and abundance, potentially affecting larval survival and recruitment (Thorrold and McKinnon 1995). In this study, I associate strong northward larval dispersal to river plumes during particular ENSO events along the GBR, however whether *L. carponotatus* larval survival is enhanced or diminished in the vicinity of river plumes, and therefore larval recruitment favoured during northward (or even southward) dispersals associated with plumes, remains unknown. The potential effect of flooding events and plumes on the GBR as a driver of fish larval survival and mortality needs to be analysed for specific GBR species and environmental conditions,

particularly during ENSO-linked conditions and during the wet season (October-March).

Genetic studies have estimated weak barriers to gene flow between populations of fish species with a pelagic larval dispersal phase, along the GBR, with no genetic differentiation among northern, central and southern sectors (Dudgeon *et al*. 2000; van Herwerden *et al*. 2009a; Jones *et al*. 2010). This broad-scale genetic connectivity pattern is attributed to larval dispersal by currents, contrarily to the genetically differentiated populations at regional scales expected for GBR fishes that lacks larval dispersal (Doherty *et al.* 1994). Genetic studies on *L. carponotatus* and a coral reef grouper, *Plectropomus maculatus*, found high levels of gene flow across the GBR, between the Palm, Whitsunday, Keppel and Capricorn-Bunker regions (Evans *et al*. 2010). Findings in the present modelling study support the extensive connectivity displayed by fish genetics over the GBR, also suggesting that gene flow between most distant reefs is favoured mostly by larval exchange through intermediate reefs, and longest connections (those over several 100s of kilometres) are potentially more variable. Modelled larval connectivity in the present study supports the idea that genetic exchange can at least occur at contemporary (ecological) timescales on the GBR.

Parentage genetic analyses of *P. maculatus* and *Plectropomus leopardus* confirmed bi-directional larval dispersal in the southern GBR, among the Percy, Keppel and Capricorn-Bunker regions, identifying short-distance (up to ~50 km) and long-distance (up to ~250 km) dispersal (Williamson *et al*. 2016). Implications of the southward and northward transport detected in the present modelling study have also been extended to dispersal of other GBR organisms, e.g. corals (Riginos *et al*. 2019). Biophysical dispersal models and spatial genetic structure in GBR broadcasting corals inferred asymmetric larval dispersal across this system, with more prevalent north-to-south connections, although strong northward dispersals were also present (Riginos *et al*. 2019). Favourable hydrodynamic conditions may also enhance long-distance dispersal (> 100 km) of brooding corals in the GBR, as shown by genetic analysis and suggested to be caused by dispersal of asexual larvae, polyp bail-out or rafting of small colonies between reefs (van Oppen *et al*. 2008). The importance of southward larval connections (and gene flow) on sustaining GBR coral populations, are also highlighted

for coral reef fish populations, as shown by the presented modelling results, and other modelling works in the northern GBR (James *et al*. 2002).

Determining interannual fish larval recruitment patterns in the GBR is important for understanding population replenishment dynamics. The relevance of annual *L. carponotatus* recruitment pulses around One Tree Island (southern GBR) has been emphasised as these can greatly influence population size and sustainability of the adult population (Kingsford 2009). This finding denotes the significance of understanding interannual recruitment patterns in GBR fish populations, including rare replenishment events, for supporting total abundance of fish populations. Modelled fish larval dispersal limited to the northern-central GBR indicated a predominantly southward larval dispersal, emphasising the dependence of southernmost populations on larval supply from northernmost regions (Bode *et al*. 2006). In the present study, southward larval dispersals were more prevalent, including long-distance pulses, however, during particular ENSO events, such as during the very strong 2010 La Niña event, strong northward larval dispersal was particularly relevant for supplying larvae, especially to central reefs. Importantly, I associate the ENSO-linked larval dispersal variability with regional larval replenishment from multiple reefs over time, highlighting the potential of interannual larval connectivity dynamics for GBR populations' persistence and recovery.

The extent to which reef fish populations are intra- (self-recruitment of larvae) and inter-connected (larval exchange) is an important ecological factor to consider in marine reserve network design (Abesamis *et al*. 2017) and metapopulation dynamics (Treml *et al*. 2015), including metapopulation persistence in the GBR (James *et al*. 2002). Multiple and single larval sources for damselfish populations in the Capricorn-Bunker (southern GBR) and Lizard Island (northern GBR) regions have been suggested, respectively, according to pre-settlement otolith chemistry conditions (Patterson *et al*. 2005). In addition, large self-recruitment levels has been documented for damselfish fish around Lizard Island (up to 60%) (Jones *et al*. 1999), and relatively high self-recruitment has been estimated at the same region in relation to other northern reefs according to larval connectivity modelling (James *et al*. 2002). Also, modelled self-recruitment of fish populations is highly variable at interannual scales in the northern GBR, and the importance of external larval pulses (i.e. not related to local

larval retention) on larval replenishment at the reef level has been highlighted (James *et al*. 2002). Accordingly, larval modelling in the present study identified the Lizard Island region as one of the least seeded by external larvae, associated with its proximity to the NVJ bifurcation, with an important fraction of locally settled larvae originating in the same region. The presented modelling suggests that certain GBR regions rely more on self-recruitment than others, and that multi-directional larval pulses can potentially supply reefs at a GBR regional scale (especially those in the central sector). Self-recruitment of *L. carponotatus* and *P. maculatus* was documented for marine reserves in the Keppel Islands (Harrison *et al*. 2012), while self-recruitment and larval connectivity of *P. maculatus* and *P. leopardus* were shown to vary at GBR regional scales based on parentage studies (Williamson *et al*. 2016). Inter-reef larval connectivity patterns in the GBR, including interannual connectivity changes, as supported by the present study, should be considered in ecological and management studies.

A number of recommendations are suggested for future fish larval connectivity studies in the GBR. The use of fine-scale hydrodynamic models is recommended since poorly flushed areas, such as those of closely aggregated reefs, may affect larval retention (Andutta *et al*. 2012). The inclusion of species-specific larval behaviour in biophysical models, such as swimming performance and orientation, is advised as it can provide more realistic connectivity (Bode *et al*. 2019), retention and self-recruitment (Wolanski *et al*. 1997; Wolanski and Kingsford 2014) estimates.

In conclusion, this study demonstrates the influence of ENSO on GBR larval connectivity on interannual timescales. A well-connected system is maintained over time, given the variability of interannual connectivity between regions. Bi-directional larval connectivity is exhibited not only between regions, but also among GBR sectors, with changes in dispersal patterns and increased distance connections associated with different ENSO events. A predominant, although variable southward, connectivity is exhibited over the central and southern GBR. However extreme ENSO events, e.g. the very strong 2010 La Niña event in this study, can promote stronger larval dispersal from southern regions, particularly when southward dispersal is limited. Larval connectivity in the far northern GBR is predominantly northward, although larval supply from reefs to the south of this sector increases with particular ENSO events. Inter-

regional modelled connectivity in the GBR emphasises the need to understand the annual stability of the interconnections between reefs within and between the surrounding regions.

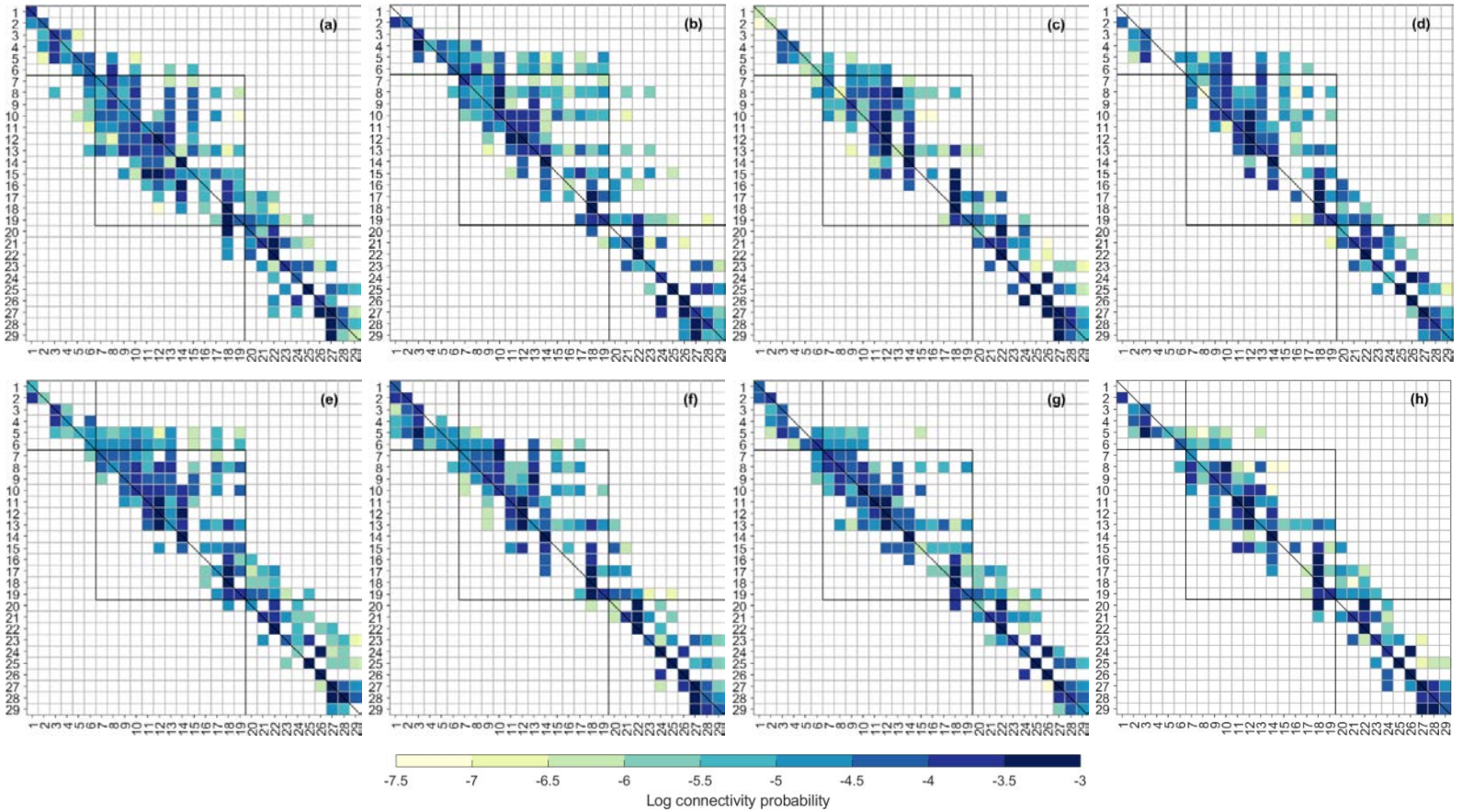

Figure S3.1. Larval connectivity matrices of *L. carponotatus* along the GBR for: a) very strong 2010 La Niña, b) moderate 2011 La Niña, c) 2012 neutral, d) 2013 neutral, e) 2014 El Niño alert, f) strong 2015 El Niño, g) 2016 neutral-La Niña, and h) 2017 neutral-La Niña. Regions are ordered from north to south as in the Figure 3.1 legend. Northern, central and southern GBR sectors are bordered by black lined boxes. Values along the diagonal represent larval retention, and values to the right or left of the diagonal indicate southward or northward connectivity, respectively.

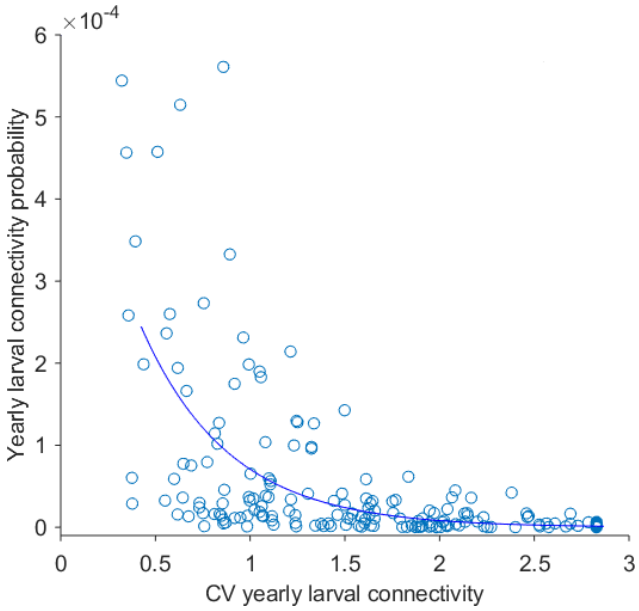

Figure S3.2. Relation between inter-regional larval connectivity probabilities (averaged for *L. carponotatus* main spawning seasons, from 2010 to 2017) and the coefficient of variation (CV) of those connections, on the GBR. The probability corresponds to Figure 3.2a and CV in connectivity corresponds to Figure 3.2b. The locations of the regions from which modelled larvae was released are shown in Figure 3.1.

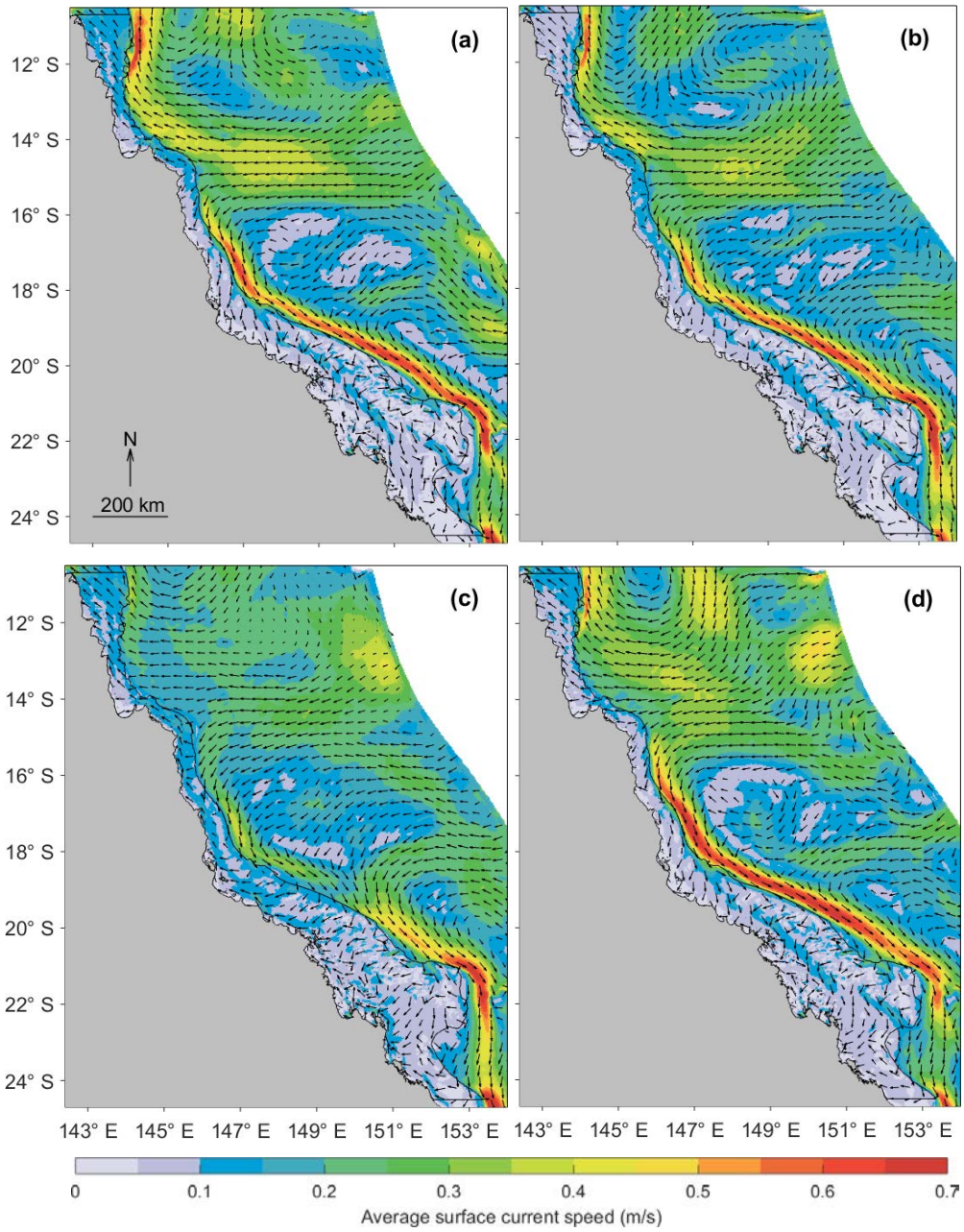

Figure S3.3. Average surface current velocity (ms^{-1}) (October-January) over the GBR and Coral Sea for: a) 2014 El Niño alert, b) strong 2015 El Niño, c) very strong 2010 La Niña and d) moderate 2011 La Niña. Current directions are indicated by arrows and speeds are shaded. The black line delimits the GBR shelf and corresponds to the 100 m isobath.

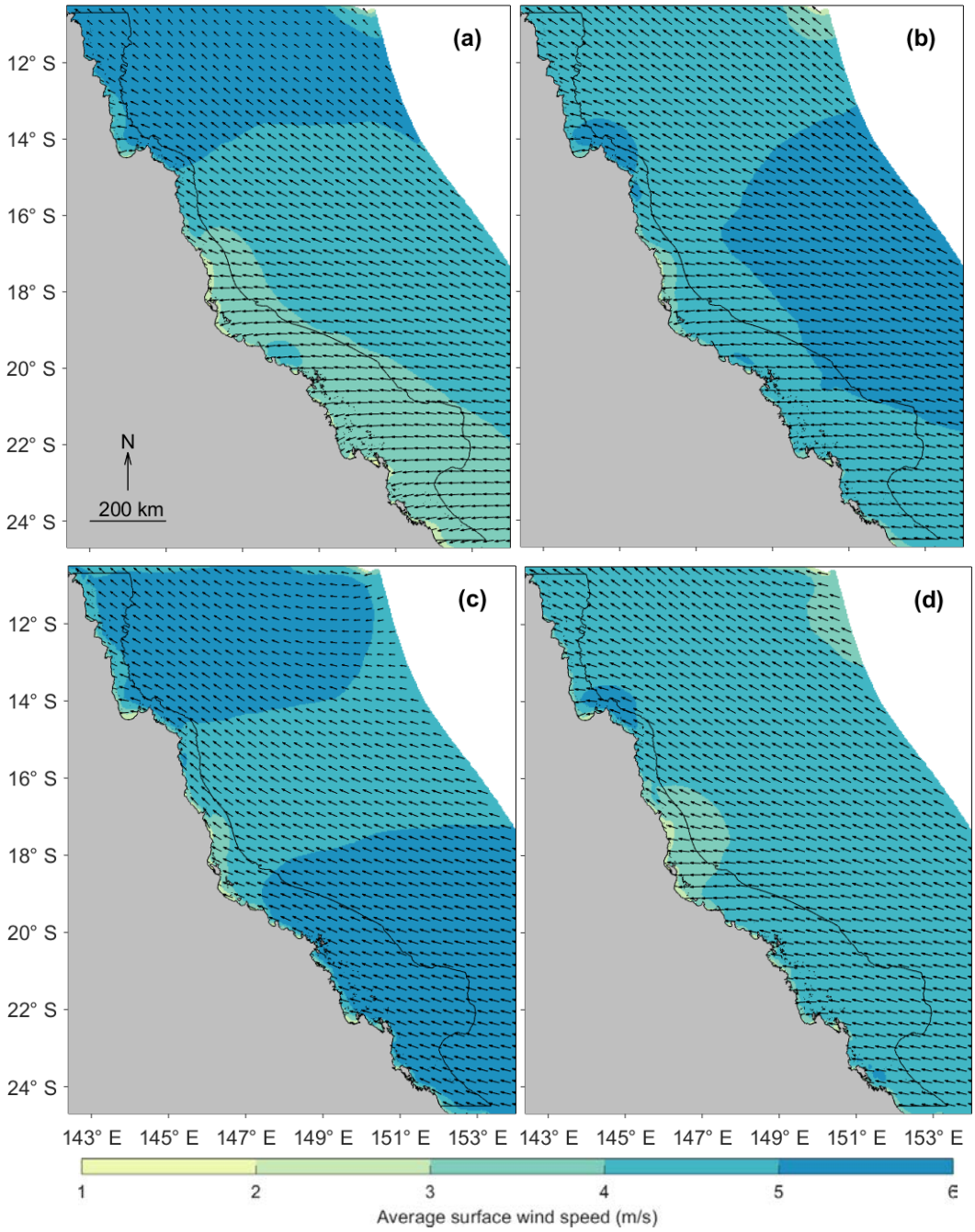

Figure S3.4. Average surface wind velocity (ms^{-1}) (October-January) over the GBR and Coral Sea for: a) 2014 El Niño alert, b) strong 2015 El Niño, c) very strong 2010 La Niña and d) moderate 2011 La Niña. Current directions are indicated by arrows and speeds are shaded. The black line delimits the GBR shelf and corresponds to the 100 m isobath.

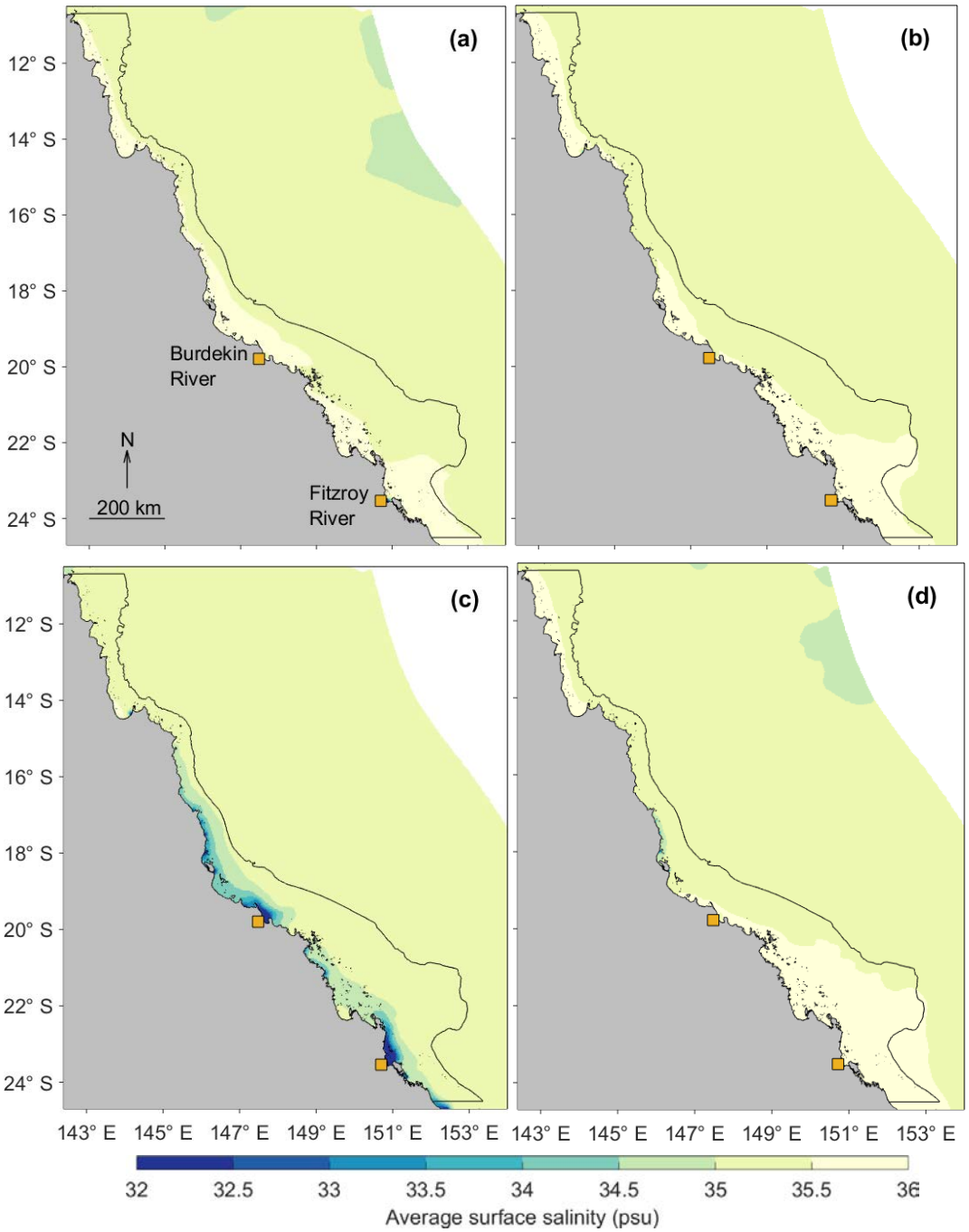

Figure S3.5. Average surface salinity (psu) (October-January) over the GBR and Coral Sea for: a) 2014 El Niño alert, b) strong 2015 El Niño, c) very strong 2010 La Niña and d) moderate 2011 La Niña. The black line delimits the GBR shelf and corresponds to the 100 m isobath.

CHAPTER 4. BROAD-SCALE GENOMIC STRUCTURE AND ISOLATION BY DISTANCE IN A HIGH GENE FLOW CORAL REEF FISH

4.1 Abstract

Marine fish populations exhibit varied degrees of genetic differentiation across space and over time, since where and when spawning occurs affects population connectivity levels, due to variability in environmental factors. In the Great Barrier Reef (GBR), high gene flow is reportedly common among spatially distributed fish populations based on previous studies using putatively neutral mitochondrial DNA sequence data. However, our understanding of the potential for local adaptation based on genomic differentiation between GBR fish populations remains largely unexamined. Here, I evaluated the population genomic structure of an abundant predatory fish in the GBR, *Lutjanus carponotatus*, based on putatively non-adaptive and adaptive SNP loci from adult and recruit samples from the central to southern GBR. Additionally, I assessed the effect of geographic distance and larval connectivity on genomic variation. Genomic structure of adult populations based on 12,440 neutral loci was weak (range F_{ST}-values = 0.0017 – 0.0023), albeit significant between most islands, following an isolation by distance pattern (Mantel's r = 0.65, p < 0.01). Putatively adaptive loci (n = 22) revealed greater genomic divergence, which increased with distance (Mantel's r = 0.76, p < 0.001). High heterozygosity levels occurred amongst populations for both neutral (H_e range = 0.281 – 0.288) and adaptive (H_e range = 0.321 – 0.347) loci. Northernmost adults and southernmost recruits presented the highest genomic divergences among the respective regions, with spatial and temporal genomic variation between recruitment events. Within the same GBR sector, genomic differentiation of recruits was more prominent than that of adults. Biophysical modelled larval connectivity confirmed that islands lacking connectivity also presented significantly more genomic differentiation than inter-connected islands, for both neutral (average F_{ST}-values = 0.0021 to 0.0017, respectively; ANOVA, p < 0.01) and outlier (average F_{ST}-values = 0.059 to 0.016, respectively; ANOVA, p < 0.05) loci. Connectivity of GBR fish populations is more restricted than previously thought. Genomics identified previously undetected limited coral reef fish larval dispersal over

large distances with patterns of genetic structure identified amongst recruitment cohorts, suggesting an effect of selection on early-life stages.

4.2 Introduction

Seascape genetics constitutes an informative approach to investigate the spatial ecology of marine populations by integrating molecular studies with geographical and environmental features, especially when genetic signals are relatively weak (Selkoe *et al.* 2008). Coral reef fish species can be geographically widespread with varying degrees of exchange among populations (Mora and Sale 2002), making it challenging to effectively manage these resources. Most coral reef fishes have a pelagic larval dispersal phase which may experience larval connectivity between populations tens (Almany *et al.* 2017) to hundreds (Williamson *et al.* 2016) of kilometres apart. Estimating genetic differentiation between populations of a species can inform their connectivity patterns based on levels of gene flow. Marine fishes, including coral reef fishes, can experience restricted gene flow, with variation either attributed to isolation by distance (IBD) (Planes and Fauvelot 2002; Beltrán *et al.* 2017; Ackiss *et al.* 2018), environmental gradients (Milano *et al.* 2014; Nanninga *et al.* 2014), and/or oceanographic barriers to dispersal (Teacher *et al.* 2013; Saenz-Agudelo *et al.* 2015; Torrado *et al*. 2020).

Conservation and fisheries management need to account for marine population connectivity to identify inter-connected populations and restricted exchange of individuals or adaptive connectivity (Gagnaire *et al.* 2015). Marine populations may be connected by dispersing larvae, however, gene flow may exist between distant populations in a stepping-stone manner (Davies *et al*. 2015). In addition, genetic differences among populations may be enhanced by larval dispersal limitations and/or by local adaptation (Teacher *et al.* 2013; Ackiss *et al.* 2018). Combining both genomics and biophysical modelling of larval dispersal is therefore important to identify and inform underlying causes of potential genetic differentiation and to comprehensively examine connectivity patterns in space and over time. This will enable managers to better incorporate population dynamics along with informing about population persistence and recovery times (Leis *et al.* 2011; Burgess *et al*. 2014).

Single nucleotide polymorphisms (SNPs) are relatively novel markers for evaluating population genetic structure since they are more abundant and widely dispersed across the genome than either microsatellite or mitochondrial DNA (mtDNA) markers (Morin *et al.* 2004). One of the advantages of using genomics relies on their capacity to investigate population genetic connectivity based on loci putatively either unaffected by natural selection (i.e. neutral loci) or under selection (i.e. outlier loci) (Grewe *et al.* 2015; Pazmiño *et al.* 2018). Population structure patterns may differ between neutral and adaptive loci, even in high gene flow marine fish species, with genetic variation among outlier loci reflecting local environmental adaptations (Limborg *et al.* 2012; Torrado *et al*. 2020) and/or limited dispersal (DiBattista *et al.* 2017; Salas *et al.* 2019). Larval dispersal into a population increases gene flow and can impose a limit on local adaptation, although under limited connectivity and with environment playing a role on the organisms' fitness, selection may counteract the effects of gene flow (Lenormand 2002). Selection may act on early-life stages, with different conditions potentially enhancing or limiting survival of the dispersing larvae or recruits.

Genetic studies analyzing loci from both adults, and temporally and spatially collected recruits, allow better understanding of population connectivity patterns in marine environments (Thia *et al*. 2021). Comparing genetic variation from adult and recruit groups of fish populations can inform of ecologically relevant processes such as self-recruitment and connectivity (Christie *et al.* 2010). Recruit samples not genetically differentiated from the co-located adults suggests that connectivity is maintained at local and regional scales, whilst gene flow can be limited at larger spatial scales among coral reef fishes (Priest *et al.* 2012; Horne *et al.* 2013). Source-sink dynamics of coral reef fish populations have been assessed using genomics in Western Australia, identifying the likely source population for recruitment events (Cure *et al.* 2017). Furthermore, the ability of high gene flow species to cope with changing oceanographic conditions, including possible environmental extremes, can be deducted from outlier analysis of adult versus recruit stages, as adults constitute mixed cohort populations while recruits represent survival under certain environmental conditions at the time of recruitment (Cure *et al.* 2017).

Along the Great Barrier Reef (GBR) off northeastern Australia, the stripey snapper, *Lutjanus carponotatus*, is a widely dispersed predatory fish with an average pelagic larval dispersal phase of 25 days (Schlaefer *et al.* 2018). Detailed parentage

studies confirmed that *L. carponotatus* larvae disperse locally up to ~30 km (Harrison *et al.* 2012), although likely further, as no restrictions to gene flow were identified between populations over 800 km apart along the GBR, based on mtDNA (Evans *et al.* 2010). This apparent lack of genetic differentiation is also reported for other coral reef fish species in the region (Doherty *et al.* 1995; Dudgeon *et al.* 2000; van Herwerden *et al.* 2003; 2009a; Jones *et al.* 2010). High genetic connectivity of *L. carponotatus* along the GBR was proposed to result from larval dispersal between islands (Evans *et al.* 2010), with low stock differentiation of other reef fishes among central and southern GBR regions suggested to be a consequence of intermediate stepping stones mediating connectivity without strong selection (Doherty *et al.* 1995). A recent genomic study of *L. carponotatus* along northwestern Australia, across substantial environmental gradients, identified an IBD effect, together with several genetic breaks, likely representing restricted larval dispersal over long distances (DiBattista *et al.* 2017). Additionally, 66 outlier SNP loci indicated regional stripey snapper groups between northeastern and southwestern populations, which were less clear using neutral SNPs (DiBattista *et al.* 2017). Along the GBR, weaker larval connections of stripey snapper were identified over long distances by biophysical modelling of larval dispersal (**Chapter 3**) and environmental gradients exist along the latitudinal gradient. However, the potential for genomic differentiation at the scale of larval connectivity or local adaptation of fish populations is yet to be examined.

Here, I assess potentially restricted or putatively adaptive connectivity of stripey snapper population from the central to the southern GBR using genomic tools to evaluate the hypotheses that *L. carponotatus* population connectivity is restricted between: a) geographically distant island groups, and b) different cohorts, in some cases. This was done using neutral and putatively adaptive SNPs. Putatively adaptive SNPs may identify significant genetic differentiation patterns if they exist, unlike neutral SNPs that generally do not resolve significant genetic structure. To test these hypotheses, genomic analyses were conducted on both neutral and putatively adaptive SNP loci generated for *L. carponotatus* as follows: 1) Adult and juvenile samples from five island groups distributed along the GBR study area during different seasons and years were genotyped, 2) *L. carponotatus* larval connectivity was biophysically modelled across the same GBR study area, and 3) Correlations between the genetic and geographic distances were evaluated to determine if there is an IBD effect on the

population structure examined, and if intermediate reefs mediate gene flow along the GBR. This enabled me to establish whether: i) putatively adaptive SNP loci elucidate significant genetic differences in the study system, but neutral SNP loci do not; ii) adults and different cohorts of recruits are genetically more similar within than between island groups; iii) differentiation amongst recruit pulses is more prominent than it is amongst adult populations from the same regions; iv) neutral and putatively outlier SNP based genetic distances increase with geographic distances; v) there is a correlation between observed neutral and outlier SNP genetic differentiation patterns; and vi) islands not inter-connected by larval dispersal display greater genetic differentiation than those inter-connected by larvae.

4.3 Materials and Methods

4.3.1 Sample collection

Tissue samples of adult and juvenile *L. carponotatus* were collected over 800 km along the GBR. In the northern and central GBR, *L. carponotatus* mature on average at 190 mm fork length (FL) and 2 years of age (with juvenile and adult fish represented by immature and mature individuals, respectively), and can live up to 15-20 years (Kritzer 2004). Mature fish first appear in the 160-179 mm FL size class, with 50% maturity attained in the 180-199 mm FL size class, and 93-100% maturation at the 220-239 mm FL size class by age 4 (Kritzer 2004). A total of 219 adults were sampled from nine locations in the central GBR, across the Palm (Pelorus Island, n = 20; Fantome Island, n = 15) and Whitsunday (Hook Island, n = 26; Whitsunday Island, n = 19) Islands, and in the southern GBR, across the Percy (South Island, n = 44), Keppel (Middle Island, n = 22; Halfway Island, n = 23) and Capricorn (Polmaise Reef, n = 24; Mast Head Island, n = 23) Islands (Figure 4.1). A total of 181 juveniles were sampled within the southern GBR, across the Percy Islands (n = 42), Keppel Islands (n = 94) and Capricorn Island Group (n = 45) (Figure 4.1). Sampling was by divers using biopsy probes mounted on spear guns or using hook-and-line or fish traps. Adults from the Palm, Whitsunday, and Capricorn (Mast Head Island) groups, were collected between March 2006 and October 2007, and from the Percy, Keppel and Capricorn (Polmaise Reef) groups, from September 2011 to June 2012. Juveniles were collected

between February and March 2009 (Keppel Islands), and from March 2012 to June 2012 (Percy, Keppel and Capricorn groups). Either fin or muscle was sampled via hook and line fishing or biopsy probe (Evans 2008) and immediately preserved in 80 or 95% ethanol.

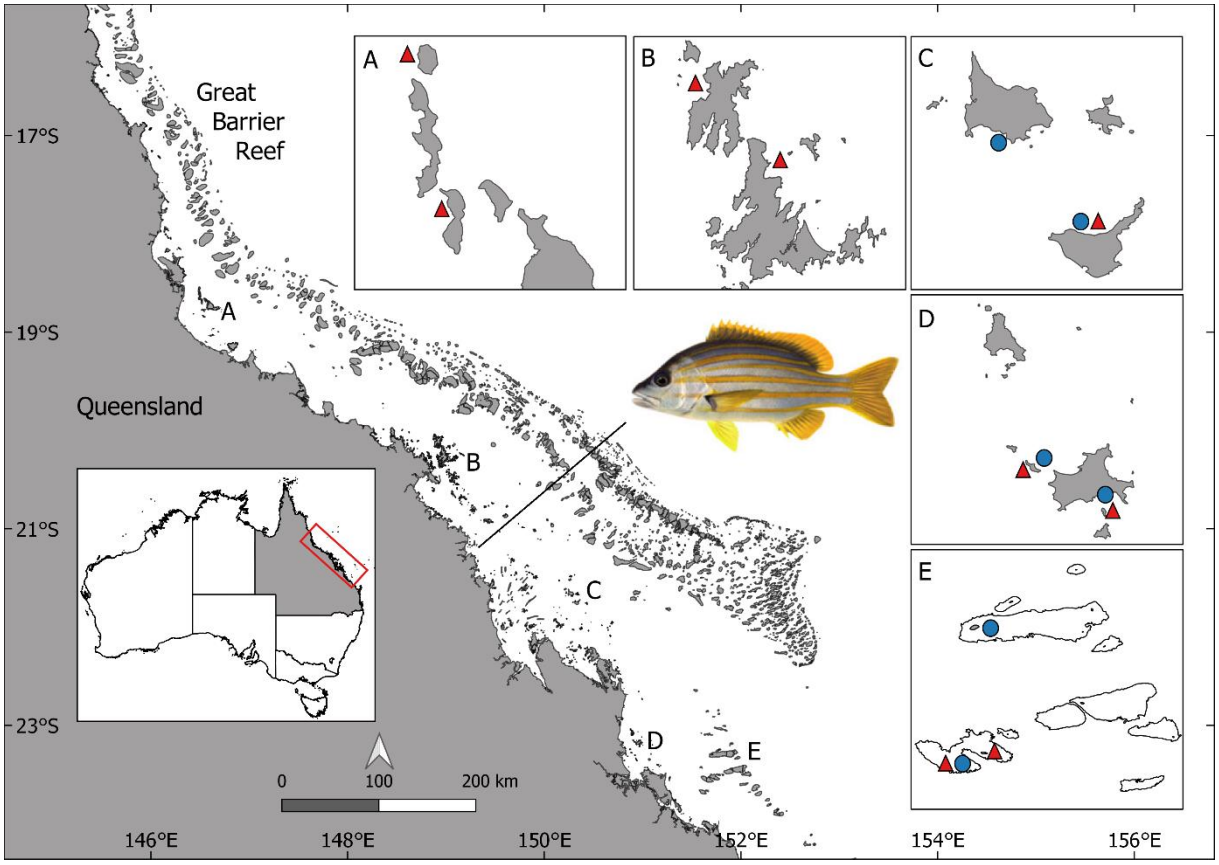

Figure 4.1. Sampling locations of *L. carponotatus* adults (red triangles) and juveniles (blue circles) in the following island groups along the GBR: A) Palms, B) Whitsundays, C) Percys, D) Keppels and E) Capricorns. Central and southern GBR sectors are divided by a black line. In the Capricorn Group the lines around the islands (dark grey) represent coral reef areas. Illustration of *L. carponotatus* © R.Swainston/www.anima.net.au.

4.3.2 Sample preparation and DArTseq

Genome-wide SNPs were inferred by Diversity Arrays Technology (DArT), as per Sansaloni *et al*. (2010) and (2011). The success of DArT for genome-wide, high throughput and highly informative DNA genotyping has been demonstrated in

numerous organisms (Kilian *et al.* 2012). Rapid SNP discovery is now possible due to the combination of DArT complexity reduction with sequencing on the Next Generation Sequencing (NGS) platforms, i.e. DArTseq (Sansaloni *et al.* 2011). Recent studies successfully applied DArTseq to develop thousands of SNPs for population genetic studies (e.g. Grewe *et al.* 2015; DiBattista *et al.* 2017).

Lutjanus carponotatus tissue samples were placed into individual wells in fully skirted V-shaped 96-well PCR plates according to DArT instructions (www.diversityarrays.com), containing no more than 20 mg of tissue per sample, fully submerged in no more than 100ul of 70 to 100% ethanol, and plates thoroughly sealed with PCR strip caps. Plates were packed in sturdy containers with padding between container and plates, and shipped to DArT in Canberra, Australia, for automated plate processing. Prior to shipping, test samples were controlled for DNA quality by extracting the DNA using a salting out protocol (Sunnucks and Hales 1996) and verifying DNA integrity electrophoretically using 0.8% agarose gel in 1x TAE buffer, after which the molecular weight of the bands was inspected under fluorescence. A second quality control step was undertaken by DArT and samples not meeting the quality test were excluded from analysis. DArT methods provide an intelligent selection of genome fraction corresponding predominantly to active genes by using a combination of restriction enzymes which separate low copy sequences from the repetitive fraction of the genome. DArTseq 1.0 was applied for marker discovery and genotyping of SNPs. This procedure assays approximately 50,000 DNA fragments from DArT representations for polymorphism (Sansaloni *et al.* 2011; Kilian *et al.* 2012). A total of 31,121 *L. carponotatus* SNPs were identified by DArTseq.

4.3.3 SNP filtering

SNPs were quality control evaluated using DartQC (a command line pipeline, https://github.com/esteinig/dartQC) and the genome association analysis toolset PLINK v1.90 (Chang *et al.* 2015). Low quality SNP data was discarded. An average of 17 ± 2% of missing data was found across the data set. Samples with > 30% missing information were excluded from analysis. SNPs were filtered out by minor allele frequency < 1%, call rate < 85%, read depth < 5, reproducibility < 95%, and duplicates

of the same locus and any clusters of linked loci. SNPs in linkage disequilibrium (r^2 > 0.3), and out of Hardy-Weinberg equilibrium across populations after a false discovery rate of 0.05, were excluded. After filtering, a total of 12,484 SNPs remained for population genetic analysis. The resulting PLINK formatted files were converted into other program specific input files using the data conversion tool PGDSpider v2.1.0.3 (Lischer and Excoffier 2012).

4.3.4 Identification of neutral and outlier loci

Following data filtering, I proceeded to identify loci putatively under selection in order to create both neutral and outlier data sets for population analysis. Identification of outlier SNPs consisted of two independent outlier detection methods applied to the SNP data set from adults and juveniles between sampling locations. First, a Bayesian approach implemented in BayeScan v2.1 (Foll 2012) was used. A total of 100,000 iterations were run by the program consisting of 5,000 iterations wrote out with 20 pilot runs of the 5,000 iterations each, before starting the calculation. These were used for sample size estimation, with 10 iterations between two samples (thinning interval), and a burn-in of 50,000 to attain convergence before starting the sampling. The prior odds for the neutral model were set to 50. BayeScan was also run with the prior odds set to 75 and 100, returning the same set of outliers for all three sets of prior odds (50, 75 or 100). However, a few extra outliers were detected by the prior odds of 50 (due to an increase in the power to detect markers under selection), which were effectively identified as strong outliers by the second outlier detection method (FDist2). Loci were classified as potential outliers when a posterior probability of > 0.76, a Bayes Factor (BF) in the range of 3 to infinity, and a log10(BF) between 0.5 and infinity were detected and considered “substantial” to “decisive” evidence for selection, based on Jeffrey’s scale of evidence for Bayes factors (Jeffreys 1961; Foll 2012). This approach coincided with a false discovery rate of < 0.1. A total of 22 putative outlier loci under divergent selection were detected in BayeScan. Second, FDist2 methodology, following an FDist approach (Beaumont and Nichols 1996), was implemented in Arlequin v3.5.2.2 (Excoffier and Lischer 2010) and independently applied to the SNP data set. This approach assumed a non-hierarchical finite island model, where the number of simulations and demes to simulate were set to 20,000 and 100, respectively. Putative

outlier loci identified using both methods were compared by setting the false discovery rate threshold from BayeScan, resulting in the same 22 outliers detected in both BayeScan and Arlequin, which were thereby confirmed as potential true outliers for further analysis. However, an extra 22 putative outliers were only detected in Arlequin, with a total 44 outliers under divergent selection detected by this method. Finally, the 44 putative outliers detected by either Bayescan or Arlequin from the total SNP dataset were removed to produce two separate datasets for further population analysis: 1) a total of 12,440 neutral SNPs data set, and 2) a 22 putative outlier dataset.

4.3.5 Identification of recruitment groups

Lutjanus carponotatus juveniles were collected in the southern GBR to select a series of seasonal recruitment pulses for spatial and temporal genomic analysis. First, the age versus FL relationship of *L. carponotatus* was estimated from 85 juvenile fish, ranging from 22 mm to 183 mm, collected in the Keppel Islands between 2004 and 2007. The age of each fish was estimated from the juvenile otolith daily rings. The length at age equation was defined as: age = $0.6504*FL^{1.1994}$. Second, a larger data set consisting of > 1,800 *L. carponotatus* juveniles collected in the southern GBR was used to estimate the main spawning peaks of the species by back dating to the spawning date according to the age-length relationship. Third, juveniles used in this study were selected from the main spawning peaks over time in the Percy and Keppel Islands and Capricorn Group, coinciding with the sampling of adults within the southern GBR during 2012. An extra recruitment period was included in the Keppel Islands during 2009. The selection process resulted in the following recruit groups included in the present study: PER_I: October to November 2011; PER_II: December 2011 to February 2012; KEP_I: March to May 2008; KEP_II: October to December 2008; KEP_III: January to March 2012; CAP_I: July to September 2011; CAP_II: December 2011 to February 2012 (see Table 4.1 for sample numbers).

4.3.6 Genetic diversity and differentiation

The genetic diversity within *L. carponotatus* adult and recruit groups was evaluated by calculating the observed (H_o) and expected (H_e) heterozygosity for loci, using Arlequin v3.5.2.2. The genetic differentiation between both islands and locations within islands was measured as pairwise F_{ST}-values (Weir and Cockerham 1984), in both the neutral and outlier data sets, using Arlequin. In addition, Arlequin was used to estimate the amount of genetic variation among island groups by an analysis of molecular variance (AMOVA) and to estimate the inbreeding coefficient, F_{IS}, within populations.

4.3.7 Genetic structuring patterns

The population genetic structure in 12,440 neutral loci along the GBR was investigated using fastSTRUCTURE v1.0 (Raj *et al.* 2014). fastSTRUCTURE is a fast algorithm using a variational Bayesian framework for inferring population structure from large SNP genotype data, based on the simplest, independent-loci, admixture model. I used fastSTRUCTURE because variational algorithms are almost two orders of magnitude faster than STRUCTURE, achieving accuracies comparable to those of ADMIXTURE (Raj *et al.* 2014). The algorithm was run from K = 1 to K = 9, where K denotes the number of populations. Values for the model complexity required to explain structure in the dataset were obtained from fastSTRUCTURE.

Population genetic structure in 22 outlier loci along the GBR was explored in STRUCTURE v2.3.4 (Pritchard *et al.* 2000; Falush *et al.* 2003), as previously reported for outlier loci of fish populations in other marine environments (Milano *et al.* 2014; Cure *et al.* 2017; DiBattista *et al.* 2017; Diopere *et al.* 2018; Salas *et al.* 2019). STRUCTURE uses Bayesian clustering algorithms based on pre-defined population genetic models, and assumes a model in which individuals, based on their genotypes, are probabilistically assigned to K populations, each of them presenting an allele frequency set at each locus. The length of burn-in period was set at 150,000 before the start of data collection, as this represented an acceptable rate of convergence of the summary statistics values, followed by 300,000 Markov chain Monte Carlo repetitions. The admixture (ancestry model) and correlated frequencies model (allele

frequency model) were applied. STRUCTURE was run under the LOCPRIOR model (Hubisz *et al.* 2009), which is recommended when the amount of available data is limited, including data sets with a few genetic markers. LOCPRIOR models do not tend to find structure when none is present, and they are able to ignore the sampling information when the ancestry of individuals is uncorrelated with sampling locations (Pritchard *et al.* 2000). The algorithm was run from K = 1 to K = 9 and 10 iterations were run. The output files from STRUCTURE were used in conjunction with the software Structure Harvester v0.6.94, which implemented the Evanno method to detect the number of genetic groups, K, which best fit the data (Earl and von Holdt 2012).

The between-population differentiation in neutral and outlier loci was also assessed using a multivariate method, the Discriminant Analysis of Principal Components (DAPC), implemented in the R package, adegenet 2.1.1 (Jombart 2008). DAPC is a supervised method, which unravels complex population structures (Jombart *et al.* 2010). The optimal number of retained principal components was identified by optimizing the a-score.

4.3.8 IBD and neutral vs. outlier differentiation patterns

The correlation between linearized genetic ($F_{ST}/(1-F_{ST})$) and geographic (km) distances along the GBR was tested applying a Mantel test. Mantel tests were based on 10,000 permutations and implemented in the R package, ade4 v1.7.13 (Dray and Dufour 2007). The geographic distance between both island groups and between locations within island groups (where present) was measured as the shortest distance between sampled sites. IBD was tested for neutral loci, evaluating two genetic data sets, one considering inter-island F_{ST}-values, i.e. grouping individuals per island group or 'inter-island group', and another one considering inter-location F_{ST}-values, i.e. grouping individuals per sampling location or 'inter-location', regardless of island group. The relationship between genetic differentiation from outlier loci and geographic distance was tested to discern spatial genetic differentiation patterns. In addition, Mantel tests were applied to analyse the correlation between the genetic differentiation patterns from outlier and neutral loci for potential effects of gene flow on the outlier based genomic structure.

4.3.9 Biophysical modelling of larval connectivity

Larval connectivity between GBR island groups was estimated by biophysical modelling (data from **Chapter 3**) to infer the potential for larval dispersal to mediate gene flow, using the dispersal modelling and visualisation tool, Connie3 (CSIRO Connectivity Interface, https://connie.csiro.au/). Connie3 uses the three-dimensional, 4km resolution eReefs hydrodynamic model data (Herzfeld *et al.* 2016), based on the Sparse Hydrodynamic Ocean Code (Herzfeld 2006), by tracking modelled larval dispersal with a fourth-order Runge-Kutta ordinary differential equation solver. Modelled *L. carponotatus* larvae were seeded daily between 2010 and 2017, from the Palm, Whitsunday, Percy, Keppel and Capricorn groups, during the main spawning season (October to December; Kritzer 2004). Seeding was at a rate of 100 particles per grid cell per day. Larvae were dispersed for 25 days, with a vertical distribution from 1 m (day 1) to 3 m (day 2 to 20) and 6 m (day 21 to 25), which accommodates changes in larval behaviour over time, according to development and behaviour information of larvae of *L. carponotatus* and other lutjanids (Miller and Cribb 2007; Leis *et al.* 2009; Quéré and Leis 2010; Leu and Liou 2013). Larval depth preferences were set to match with the depth distribution layers in Connie3. Larval horizontal swimming velocity preferences were not included while dispersing, due to restricted access to proprietary code for Connie3 at the time of the study. Dispersing larvae were subjected to an 18% daily mortality rate (Cowen *et al.* 2000; James *et al.* 2002). Larvae released from one island were considered to have reached a different island if they were within a 4 km sensory zone from the surrounding reef habitats following the dispersal phase, according to larval sensory capabilities (Leis 2007) and the model's horizontal resolution. Mean connectivity probability between any two island groups was calculated by averaging yearly connectivity results between each of the paired groups. Mantel tests were run with 10,000 permutations between the larval connectivity values and genetic distances from both neutral and outlier loci. In addition, to test potential genetic differentiation due to differences in larval connectivity, islands were grouped into those exhibiting larval connectivity between them and those not exhibiting larval connectivity between them, based on prior biophysical modelling. Average and standard deviation of the F_{ST}-values based on both neutral and outlier loci were

calculated for each of the groups, and differences between them tested by one-way analysis of variance (ANOVA), after confirming normally distributed data.

4.4 Results

4.4.1 Genetic differentiation patterns along the GBR

All populations presented observed heterozygosities significantly lower than expected for both neutral (H_o range = 0.239 – 0.275, H_e range = 0.281 – 0.309) and outlier loci (H_o range = 0.166 – 0.263, H_e range = 0.307 – 0.383) (t test, $p < 0.01$) (Table 4.1). Genetic diversity of neutral loci from adult *L. carponotatus* showed little variation over 800 km along the GBR, although the Whitsunday (H_o = 0.265) and Palm (H_o = 0.249) Islands in the central GBR showed marginally higher heterozygosities than the other island groups (Table 4.1). Heterozygosity from outlier loci was highest in the northernmost region (Palm Islands, H_o = 0.233) and lowest in the southernmost region (Capricorn Group, H_o = 0.207). Inbreeding coefficients within populations were relatively lower in the central GBR (F_{IS} range = 0.047 – 0.101) compared to the southern GBR (F_{IS} range = 0.103 – 0.126). Within recruit groups observed heterozygosities from neutral loci varied between 0.249 and 0.275 in the Percy and Capricorn groups, and from outlier loci these observed heterozygosities varied between 0.166 and 0.263 among the Capricorn and Keppel groups, respectively (Table 4.1).

Genetic differentiation of adults sampled along the GBR based on neutral *L. carponotatus* loci (n = 12,440) revealed little spatial population structure (F_{ST} range = 0.0017 – 0.0023). However, significant inter-island differences were evident, except for the Percy Islands compared with Capricorn and Keppel groups (Table 4.2). AMOVA revealed that most of the overall genetic variation was accounted for within populations (> 99%, $p < 0.05$), with < 1 % explained within ($p > 0.05$) and among ($p < 0.05$) regions. Mean patterns of genetic differentiation identified the Palm and Percy Islands presented the highest (mean F_{ST}-value = 0.0021 ± 0.0001) and lowest (mean F_{ST} = 0.0018 ± 0.0002) F_{ST}-values, respectively. Highest pairwise differentiation was identified between the most distant island groups, i.e. Palm and Keppel (F_{ST} = 0.0023); Palm and Capricorn (F_{ST} = 0.0022) (Table 4.2). Inter-location pairwise differentiation

was not significant within island groups along the GBR, except for the Palm Islands (F_{ST} = 0.0048) (Table S4.1). However, relatively higher inter-island F_{ST}-values were estimated when treating each sampling location per island group as a population (F_{ST} range = 0.0017 – 0.0057), indicating low inter-location structure (Table S4.1).

Table 4.1. Genetic diversity metrics: expected and observed heterozygosities (H_e, H_o) and inbreeding coefficients (F_{IS}) for *L. carponotatus* sampled along the GBR, based on 12,440 neutral and 22 outlier SNPs. N denotes population sizes; temporal recruitment group codes are indicated in parentheses as follows: Per_I - October to November 2011; Per_II - December 2011 to February 2012; Kep_I - March to May 2008; Kep_II - October to December 2008; Kep_III - January to March 2012; Cap_I - July to September 2011; Cap_II - December 2011 to February 2012. Per, Kep, and Cap represent Percy, Keppel and Capricorn groups, respectively. * denotes significant differences between observed and expected heterozygosities ($p < 0.05$). SD: standard deviation.

Group	N	Stage	H_o (±SD)	H_e (±SD)	H_o (±SD)	H_e (±SD)	F_{IS}
			neutral		outlier		
PALM	35	Adult	0.249 (±0.159)	0.286 (±0.157)	0.233 (±0.133)	0.347 (±0.155)	0.101*
WHITSUNDAY	45	Adult	0.265 (±0.167)	0.288 (±0.156)	0.226 (±0.140)	0.329 (±0.157)	0.047*
PERCY	44	Adult	0.239 (±0.151)	0.281 (±0.158)	0.214 (±0.135)	0.324 (±0.152)	0.126*
KEPPEL	45	Adult	0.241 (±0.151)	0.281 (±0.157)	0.228 (±0.124)	0.34 (±0.150)	0.12*
CAPRICORN	47	Adult	0.246 (±0.157)	0.283 (±0.158)	0.207 (±0.109)	0.321 (±0.150)	0.103*
PERCY	16	Juvenile (Per_I)	0.272 (±0.167)	0.304 (±0.153)	0.243 (±0.162)	0.325 (±0.141)	0.088*
PERCY	26	Juvenile (Per_II)	0.249 (±0.157)	0.289 (±0.156)	0.206 (±0.159)	0.362 (±0.137)	0.117*
KEPPEL	32	Juvenile (Kep_I)	0.253 (±0.155)	0.286 (±0.156)	0.263 (±0.150)	0.369 (±0.147)	0.095*
KEPPEL	17	Juvenile (Kep_II)	0.266 (±0.164)	0.303 (±0.154)	0.242 (±0.139)	0.383 (±0.122)	0.106*
KEPPEL	45	Juvenile (Kep_III)	0.256 (±0.163)	0.284 (±0.157)	0.234 (±0.134)	0.364 (±0.144)	0.078*
CAPRICORN	16	Juvenile (Cap_I)	0.275 (±0.173)	0.309 (±0.154)	0.166 (±0.150)	0.307 (±0.158)	0.083*
CAPRICORN	29	Juvenile (Cap_II)	0.257 (±0.162)	0.289 (±0.157)	0.199 (±0.143)	0.309 (±0.188)	0.093*

Genetic structure from *L. carponotatus* adult outlier loci (n = 22) along the GBR was stronger than neutral loci, showing one and two orders of magnitude greater F_{ST}-values. Between-island differentiation accounted for low but significant overall genetic variation (AMOVA, 3.28%, $p < 0.05$). Geographically distant groups presented the highest pairwise F_{ST}-values, i.e. Palm - Capricorn ($F_{ST} = 0.108$) and Palm - Keppel ($F_{ST} = 0.071$) (Table 4.2). Northernmost (Palm) and southernmost (Capricorn) regions presented the greatest averaged F_{ST}-values, ranging from 0.068 (± 0.03) to 0.055 (± 0.038), respectively. Genetic differentiation was weakest in the Percy Islands, presenting non-significant pairwise genetic differentiation against the Keppel ($F_{ST} = 0.001$) and Whitsunday ($F_{ST} = 0.008$) Islands.

Genetic structure between adult populations and recruitment groups from neutral loci was relatively low, varying from 0.0013 within the southern GBR (between Capricorn adults and recruits in the Keppel Islands [Kep I]), to 0.0043 among central and southern GBR (between the Palm adults and recruits to the Capricorn Group [Cap I]) (Table 4.2). Significant pairwise differentiation was detected between adults and recruits, varying according to the different islands and recruitment groups (Table 4.2). The Percy adult population had the fewest significant differences from recruits in the southern GBR. Genetic differentiation based on outlier loci was stronger than that of neutral loci, with the Palm adults significantly differentiating from all recruits in the southern GBR (Table 4.2). Temporal genetic differentiation of recruit groups was variable within islands, with non-significant variation in the Percy Islands (based on both neutral and outlier loci), but significant pairwise differentiation in the Keppel Islands (based on neutral loci) and Capricorn Group (based on outlier loci) (Table 4.2). Spatially, recruit samples differed significantly from each other in 8 and 11 of 16 tests of neutral and outlier loci, respectively (Table 4.2). Overall, Capricorn recruits (particularly Cap I) differed from the rest of the recruit locations sampled based on outlier loci. Within the southern GBR, genetic differentiation within recruits was greater than within adults for both putatively non-adaptive (F_{ST}-values range: 0.0019 – 0.0044 and 0.0017 – 0.0017, respectively) and adaptive (F_{ST}-values range: 0.0003 – 0.1130 and 0.0005 – 0.0308, respectively) loci (Table 4.2).

Table 4.2. Population genetic differentiation, measured as pairwise F_{ST}-values, between *L. carponotatus* adult populations (capital letters and pale fill) and between different groups of recruits (medium grey fill) along the GBR, based on 12,440 neutral SNPs (below diagonal) and 22 outlier SNPs (above diagonal). Significant differences after *Benjamini-Hochberg* correction ($p < 0.05$) are in bold. Per, Kep, and Cap represent Percy, Keppel and Capricorn groups, respectively, for different recruitment periods as detailed in Table 4.1. Pairwise inter-island larval connectivity, between the sampled island groups, is identified if evident ($^{+}$) or not (^{Ø}) based on biophysical modelling.

	PALM	WHITSUNDAY	PERCY	KEPPEL	CAPRICORN	Per_I	Per_II	Kep_I	Kep_II	Kep_III	Cap_I	Cap_II
PALM	-	**0.0391**	**0.0523**	**0.0712**	**0.108**	**0.083**	**0.0566**	**0.0318**	**0.0599**	**0.0685**	**0.1434**	**0.0604**
WHITSUNDAY	**0.00203**^{Ø}	-	0.0076	**0.0271**	**0.0557**	**0.034**	0.0052	0.0109	0.0059	**0.0224**	**0.0776**	0.0151
PERCY	**0.00201**^{Ø}	**0.00181**$^{+}$	-	0.0005	**0.0308**	0.0214	0.0054	0.0156	0.0112	**0.0364**	**0.0614**	0.0158
KEPPEL	**0.0023**^{Ø}	**0.00199**^{Ø}	0.00169^{+}	-	**0.0236**	0.0277	0.0125	0.0067	0.0064	**0.0332**	**0.056**	**0.0279**
CAPRICORN	**0.00222**^{Ø}	**0.00177**^{Ø}	0.00166^{+}	**0.00172**$^{+}$	-	**0.0768**	**0.0366**	**0.0247**	**0.0466**	**0.0389**	0.0277	**0.0257**
Per_I	0.00315	0.00264	0.00273	**0.00341**	**0.00325**	-	0.0033	**0.0372**	0.0396	**0.0461**	**0.113**	**0.0557**
Per_II	0.00241	**0.00213**	0.00205	0.00245	**0.00234**	0.00325	-	0.007	0.017	0.0155	**0.0631**	0.0158
Kep_I	0.00178	0.00145	0.00191	0.00177	0.00132	**0.00332**	0.00246	-	0.0116	0.0003	**0.0563**	**0.0219**
Kep_II	0.00296	0.00238	0.00322	0.00308	0.00279	**0.00436**	**0.00399**	0.00294	-	0.0142	**0.0501**	**0.0389**
Kep_III	**0.00239**	**0.00243**	**0.00181**	**0.00208**	**0.00171**	**0.00296**	**0.00278**	**0.00206**	**0.00356**	-	**0.0568**	**0.0211**
Cap_I	**0.00428**	**0.00327**	0.00310	0.00319	**0.00313**	0.00406	**0.00430**	0.00316	0.00412	**0.00317**	**-**	**0.0381**
Cap_II	0.00221	0.00171	0.00152	0.00177	0.00189	0.00317	0.00223	0.00191	0.00301	**0.00206**	0.00213	-

4.4.2 Genetic structuring patterns using clustering methods

Bayesian analysis using fastSTRUCTURE to analyse population genetic structure based on 12,440 neutral loci identified one population (K=1) along the examined 800 km of the GBR. This suggests high genetic connectivity between island groups. However, Bayesian clustering analysis using STRUCTURE based on 22 outlier loci suggested that two genetic groups (K=2) best fit the data along the 800 km of the GBR examined here, based on the Evanno method (ΔK = 26.91). Populations were grouped into central (Palm and Whitsunday) and southern (Percy, Keppel and Capricorn) GBR sectors. There was a transition zone from northwest to southeast GBR, represented as a clear gradient of change in SNP allele frequencies between the central GBR regions (Palm and Whitsunday) and the southern GBR regions (Percy, Keppel and Capricorn). The Percy population was placed as having an intermediate outlier SNPs allele frequency relative to allele frequencies of the adjacent northernmost (Palm and Whitsunday) and southernmost (Keppel and Capricorn) populations (Figure 4.2).

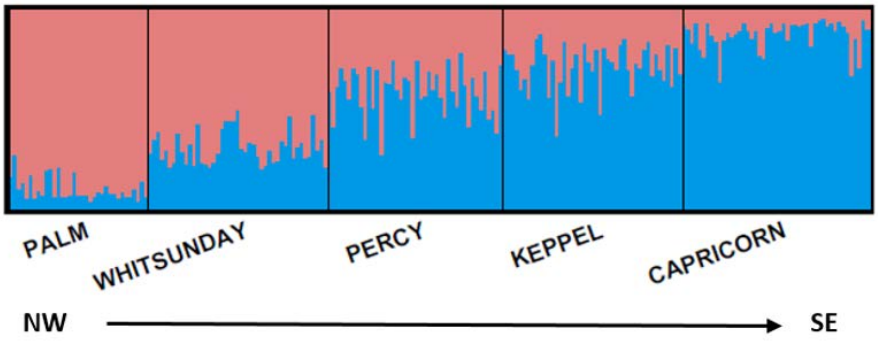

Figure 4.2. Bayesian clustering analysis in STRUCTURE (K = 2) for adult *L. carponotatus* populations along the GBR, based on 22 outlier SNPs. Individuals sampled in the different island groups are represented by vertical bars, and the probability of assignment to one of the clusters is shown by proportionally varying bars of two colours (representing changes in the 22 biallelic allele frequencies [ranging between 1 and 0 in each population] in each sampled location), indicative of possible different stocks. Groups are ordered from northwest to southeast according to their position over 800 km along the GBR.

Overlapping populations (i.e. greatest mixing) was most evident in the center of the DAPC diagram, based on neutral loci, consistent with STRUCTURE results for a single genetic stock. However, the clusters representing adult populations collected from (i) the Palm and Whitsunday Islands, (ii) Percy Islands, and (iii) Keppel Islands and Capricorn Group were separated to some degree (Figure 4.3a). Generally, recruitment groups in the southern GBR were grouped closer to adult populations within this sector than to central GBR regions, suggesting greater genetic similarities among them (Figure 4.3a). Recruits within the Percy Islands were clustered closer to each other and to the Percy adult population, similarly to one of the Capricorn recruit groups (Cap I). Likewise, Keppel recruits were relatively more closely distributed among the Keppel and Capricorn groups, potentially indicating retention and inter-island connectivity.

Genetic clustering based on potentially adaptive outlier loci in DAPC identified similarities among populations (Figure 4.3b). However, a left to right pattern was consistent with a northwest to southeast direction of central and southern GBR sampled regions (Figure 4.3b). Recruits within the Capricorn and Keppel islands showed greater genetic similarities to the Capricorn adults, and those within the Percy Islands to the Percy adults (Figure 4.3b). Recruits in the Percy Islands (austral spring-summer pulses) were clustered together, while Capricorn and Keppel recruits were relatively more separated from each other, especially one of the Capricorn pulses (austral winter pulse, Cap I), suggesting stronger and weaker genetic similarities among different recruit cohorts, respectively.

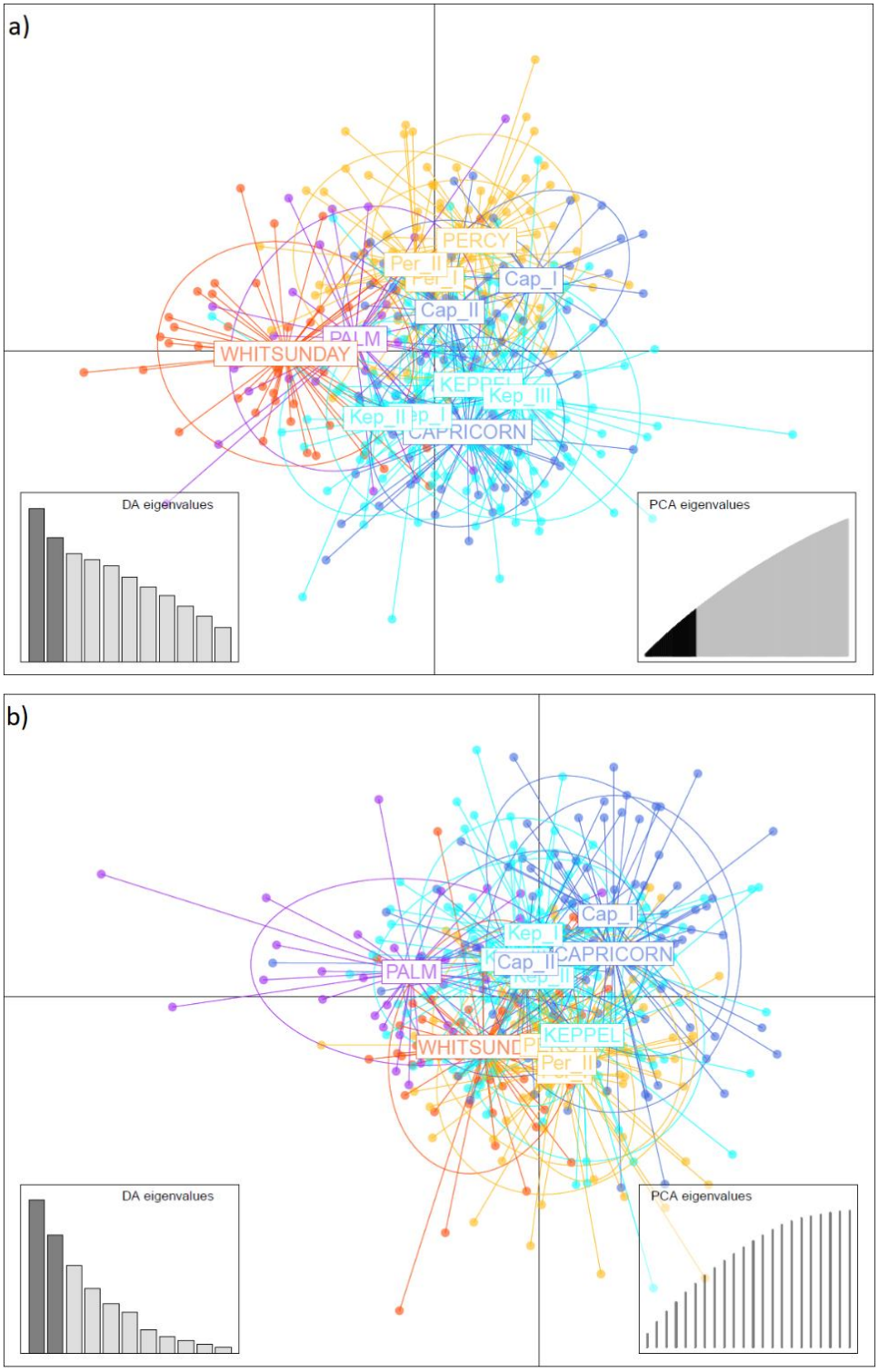

Figure 4.3. Discriminant analysis of principal components for *L. carponotatus* populations along the GBR, based on a) 12,440 neutral SNPs, and b) 22 outlier SNPs. Island adult population samples are indicated in capital letters, whilst Per, Kep and Cap indicate Percy, Keppel and Capricorn island samples of recruits, respectively. I, II, and III indicate different recruitment periods within islands as detailed in Table 4.1.

4.4.3 Isolation by distance effect along the GBR

Genetic differentiation based on neutral loci and geographic distance along the GBR followed an IBD pattern, with a significant and positive correlation when analyzing inter-island group (individuals grouped per island group) and inter-location (individuals grouped per sampling location within islands) F_{ST}-values (Mantel test, r = 0.65, p < 0.01; Mantel test, r = 0.23, p < 0.01, respectively) (Figure 4.4a). Likewise, genetic differentiation from outlier loci was significant and positively correlated with geographic distance for both data sets (Mantel test, r = 0.76, p < 0.001; Mantel test, r = 0.43, p < 0.001, respectively) (Figure 4.4b).

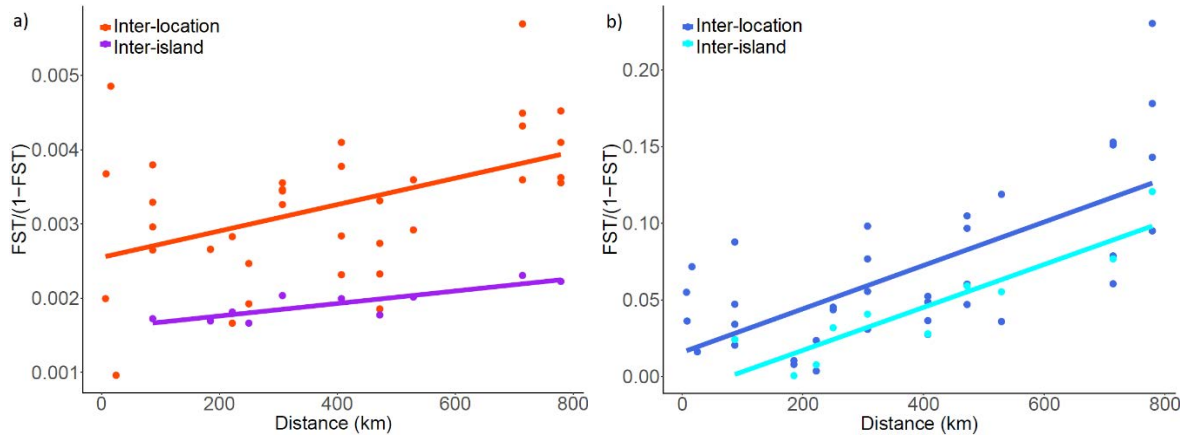

Figure 4.4. Relationship between genetic differentiation and geographic distance depicting isolation by distance patterns along the GBR for the coral reef fish *L. carponotatus*, based on a) 12,440 neutral loci, and b) 22 outlier loci.

Variation in pairwise genetic differentiation based on outlier loci along the GBR was significant and positively correlated with genetic differentiation based on neutral loci, considering both inter-island group (Mantel test, r = 0.46, p < 0.05) (Figure 4.5a), and inter-location F_{ST}-values (Mantel test, r = 0.25, p < 0.05) (Figure 4.5b).

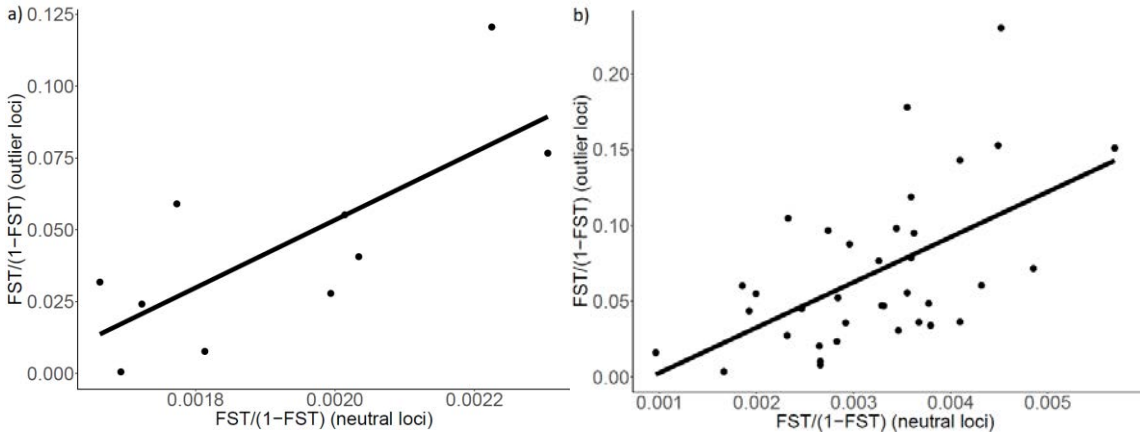

Figure 4.5. Relationship between a) inter-island group and b) inter-location genetic differentiation patterns based on the correlation between outlier (Y-axis) and neutral loci (X-axis) for the coral reef fish *L. carponotatus* along the GBR.

4.4.4 Limited larval dispersal revealed by biophysical modelling

Biophysical modelling of larval dispersal identified potential bi-directional larval connectivity between Whitsunday – Percy, Percy – Capricorn, Percy – Keppel, and Keppel – Capricorn groups (Table 4.2). Larval connectivity was not achieved among the Palm Islands and other groups, nor between the Whitsunday Islands and both Keppel Islands and Capricorn Group. Mantel tests revealed no significant correlation between inter-island genetic differentiation and larval connectivity values for the neutral (Mantel test, r = -0.06, p > 0.05) or outlier loci (Mantel test, r = -0.15, p > 0.05). However, pairwise genetic differentiation of *L. carponotatus* was significantly greater among islands that did not experience larval inter-connectivity (islands separated by approximately > 300 km) compared to those which did (islands separated by approximately < 250 km), for either neutral (average F_{ST}-values = 0.0017 (± 0.0001) and 0.0021 (± 0.0002); ANOVA, p < 0.01) or outlier (average F_{ST}-values = 0.016 (± 0.014) and 0.059 (± 0.028); ANOVA, p < 0.05) loci, respectively (Figure 4.6).

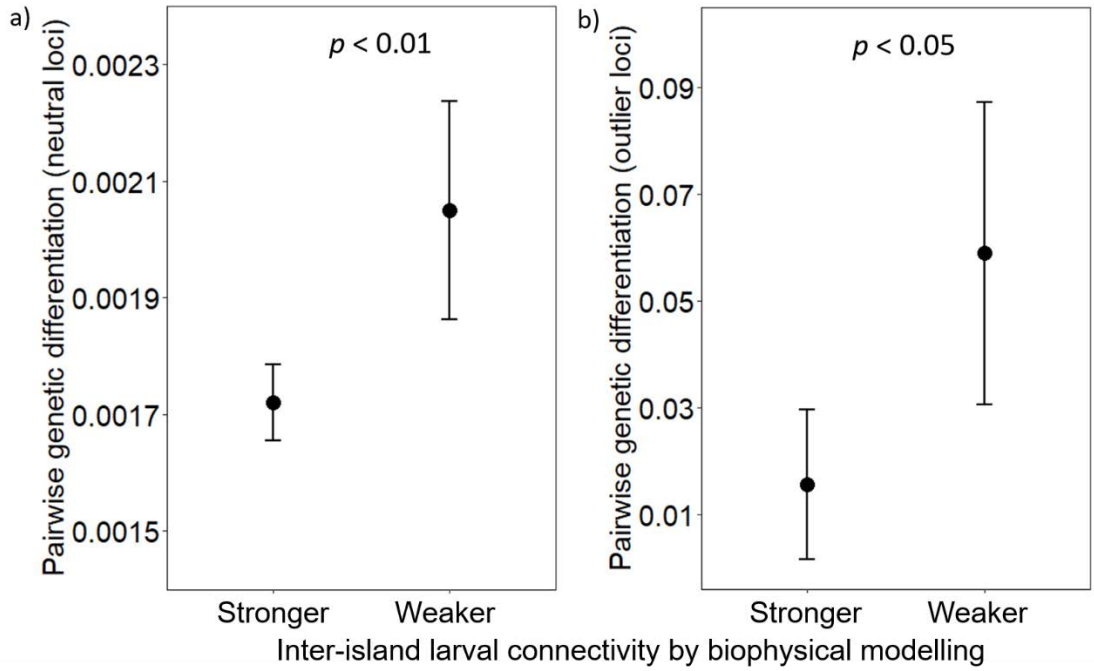

Figure 4.6. Average (± SD) pairwise genetic differentiation values (measured as F_{ST}-values), based on a) neutral and b) outlier loci of the coral reef fish *L. carponotatus* from islands along the GBR (including Palm, Whitsunday, Percy, Keppel and Capricorn islands) that exhibited stronger or weaker inter-island larval connectivity, based on biophysical modelling.

4.5 Discussion

The present study provided evidence for subtle genomic structure in the stripey snapper population along an 800 km span of the GBR. As hypothesised, greater genomic divergence was revealed by outlier loci, with restricted connectivity among geographically distant islands, likely representing limited larval dispersal over large distances and suggesting a potential role of selection. Outlier SNP loci identified restricted spatial and temporal connectivity between recruitment events, and greater genetic differentiation amongst recruit pulses than in adult populations, as recruits represent a range of temporally distinct dispersal events, with survival under potentially different environmental conditions. Gene flow levels based on neutral loci combined with biophysical modelling of larval dispersal provided support for the potential of intermediate reefs to mediate connectivity across the GBR in a stepping-stone manner over time.

Genetic differentiation between *L*. *carponotatus* populations was weak based on neutral loci, supporting evidence of no genetic structure identified for this and other coral reef fish species in the GBR, including species from Lutjanidae and Lethrinidae families with similar life-history characteristics (van Herwerden *et al.* 2003; 2009a; Evans *et al*. 2010). Genetic diversity levels within *L*. *carponotatus* populations in the GBR were similar to those described for *L*. *carponotatus* over 2,500 km along the Northwest Australian coast, where little variation was presumed to be due to pelagic larval duration and inter-reef connectivity (DiBattista *et al.* 2017). High abundance and fecundity of *L*. *carponotatus*, together with a relatively long pelagic larval phase, large number of reefs and limited physical barriers to larval dispersal, constitute relevant factors for establishing good levels of gene flow in the GBR. Hydrodynamics in the GBR are affected by oceanic inflows, winds and across-shelf pressure gradients, which produce currents that affect particle dispersal within the study region (Brinkman *et al.* 2001; Luick *et al.* 2007; **Chapter 3**).

IBD patterns were evident in genetic variation from neutral *L*. *carponotatus* loci along the GBR. Similarly, *L*. *carponotatus* pairwise genetic differentiation patterns were associated with an IBD trend in Northwest Australia, although a weak correlation was attributed to the species abundance and high larval dispersal potential (DiBattista *et al.* 2017). Significant IBD trends along the GBR have also been reported in corals (Lukoschek *et al.* 2016). Genetic differentiation of coral reef fish species has been correlated with an IBD pattern in other coral reef ecosystems, covering a range of geographic distances: from relatively short (200–500 km) (Beltrán *et al.* 2017) to over 1,500 km (Nanninga *et al.* 2014) and 7,000 km scales, across the Pacific Ocean (Planes and Fauvelot 2002). The range of F_{ST}-values in these studies were higher than those for *L*. *carponotatus* on the GBR based on neutral loci, although larger spatial scales and larval dispersal capabilities of species represent likely causes for this discrepancy. Results from biophysical modelling support the IBD concept by providing evidence of no direct larval connectivity between the more distant islands for which low levels of genetic structure were estimated. Thus, these findings are consistent with Doherty *et al*. (1995), which suggested that high gene flow via a stepping-stone process links distant regions and homogenizes the genetic structure of fish populations along the GBR. However, islands that were not directly inter-connected by larval dispersal based on biophysical modelling presented a significantly greater level of

genetic differentiation, which coincided with geographic distances of > 300 km. These results suggest that genetic drift effects might overcome those of gene flow at these spatial scales (> 300 km), as suggested for the same species along the northwestern Australia shelf (DiBattista *et al.* 2017).

Seascape genetics constitutes a growing discipline that can provide important insights into ecological and oceanographic drivers of genetic patterns (Schultz *et al.* 2008; Selkoe *et al.* 2010; D'Aloia *et al.* 2014). In the present study, biophysical modelling results were not significantly correlated with inter-island genetic differentiation between sampled adult populations. However, the observed larval dispersal patterns based on modelling revealed that less inter-connected islands presented significantly greater genetic differentiation. A larval tracking model for *L. carponotatus* along the northwestern shelf of Australia did not predict the genetic partitioning among regions, suggesting that larval behaviour and physical environment characteristics play an important role in larval dispersal (DiBattista *et al.* 2017). Similarly, the complexities of *L. carponotatus* larval behavioural capabilities should be resolved to obtain more precise inter-reef connectivity values when modelling biophysical larval dispersal. Another aspect to take into consideration here is the indirect, but potentially high gene flow, effect in a stepping-stone manner along the GBR. Additionally, if adaptive divergence limits gene flow in marine fish populations, genetic structure might be poorly predicted from larval tracking patterns and be more related to environmental variation (Limborg *et al.* 2012).

The potential role of environmental variables on shaping marine fish genetic structuring patterns based on neutral and/or outlier loci has been highlighted (Vandamme *et al*. 2021), including latitudinal differences on temperature and salinity, as they may be a good indicator of adaptive variation among populations (Milano *et al.* 2014). Stronger differences in coral reef fish genetic structure derived from outlier loci compared to neutral loci has been suggested as a consequence of isolation, adaptation or both (Salas *et al.* 2019). In the present study, genetic divergence was found between warmer northernmost and cooler southernmost sampled GBR populations. This variation, although based on relatively few outlier loci (n = 22), coincided with limited larval dispersal results and was consistent with thermal gradients and regional thermal regimes (warmest monthly-averages) (Wooldridge and Done

2004). Similarly, although on corals, moderate levels of gene flow were found among southern and central or northern GBR regions, hypothesising that selection influenced the coral population structure along the temperature differential of reefs (Smith-Keune and van Oppen 2006). Genetics and biophysical modelling of corals along the GBR highlighted the importance of larval dispersal, particularly southward pulses, on gene flow, suggesting that northward dispersal pulses may present low fitness and do not contribute substantially to gene flow (Riginos *et al*. 2019).

In addition, here, genetic differentiation from recruits' outlier loci was generally greater among the Capricorn Group (southernmost part of the GBR) and the rest of the recruit locations sampled. Additionally, genetic divergence from recruits' outlier loci was reduced within islands of similar recruitment periods, including the Percy Islands (seasonal recruitments distributed among austral spring and the following summer), whilst greater variation was evident from recruits between austral winter and summer events within the Capricorn Group. Genetic differentiation of outlier loci increased with geographic distance, and structuring patterns correlated significantly with those from neutral loci, although moderately. Isolation seems to be playing a role on the outlier genomic structure of GBR fish, although I cannot confirm whether there is a role for local adaptation in shaping the genomic structure. However, the influence of drastically changed oceanographic conditions, such as those experienced during marine heatwaves, extreme ENSO events or future climate change scenarios, could affect larval dispersal and survival, as suggested from outlier loci structure in a high gene flow fish in Western Australia (Cure *et al*. 2017).

In conclusion, population connectivity constitutes an essential process in marine ecology and evolution, and using both genomic and larval connectivity approaches can help better inform fisheries management and conservation of species (Leis *et al.* 2011; Russello *et al.* 2012; van Wyngaarden *et al.* 2017). Findings in this study extended those of previous genetic work on *L. carponotatus* along the GBR, which suggested that populations may be managed as a single stock (Evans *et al.* 2010). Evidence in this study, however, indicates that whilst variation amongst neutral loci may indicate high gene flow across this area (which is relevant for resilience after disturbances), larval and adaptive connectivity may be restricted among distant regions (e.g. northernmost and southernmost populations) thus limiting demographic connectivity

and having implications for effective resource management. Expanding the genomic analysis to the whole GBR, and including species with different life-history and larval behaviour characteristics, would allow a more comprehensive understanding of potential restrictions to connectivity in this large coral reef ecosystem. Further research into potential mechanisms of selection in fish populations, e.g. sampling at larger spatial scales and including many recruitment cohorts at contrasting recruitment events (see Benestan *et al.* 2016; Jeffery *et al.* 2018; Diopere *et al.* 2018; Liggins *et al*. 2019, for further details on seascape genetics), including extreme climate conditions, would improve our understanding of patterns of adaptation to regional and local conditions in the GBR. In this study, the use of SNP genotyping and NGS enhanced our capacity to identify gene flow limitations in GBR fish species, highlighting its application to re-assess population connectivity in other species.

Table S4.1. Population genetic differentiation, measured as pairwise F_{ST}-values, between *L. carponotatus* adult populations sampled from nine locations along the GBR, based on 12,440 neutral SNPs (below diagonal) and 22 outlier SNPs (above diagonal). Significant differences after *Benjamini-Hochberg* correction ($p < 0.05$) are in bold. Island groups are: PAL: PaIm Islands; WHI: Whitsunday Islands; PER: Percy Islands, KEP: Keppel Islands; CAP: Capricorn Group. Localities within the aforementioned main groups are: Pel: Pelorus Island; Fan: Fantome Island; Hook: Hook Island; Whi: Whitsunday Island; Sth: South Island; Mid: Middle Island; Half: Halfway Island; Pol: Polmaise Reef; MHe: Mast Head Island.

	PAL_Pel	PAL_Fan	WHI_Hook	WHI_Whi	PER_Sth	KEP_Mid	KEP_Half	CAP_Pol	CAP_MHe
PAL_Pel	-	**0.0668**	**0.0298**	**0.0525**	**0.0346**	**0.057**	**0.0729**	**0.0867**	**0.1251**
PAL_Fan	**0.00483**	-	**0.0893**	**0.0712**	**0.1062**	**0.1312**	**0.1325**	**0.1511**	**0.1871**
WHI_Hook	0.00345	0.00343	-	0.0158	0.0036	0.0267	**0.0497**	**0.0568**	**0.0881**
WHI_Whi	**0.00354**	**0.00325**	0.00096	-	**0.0229**	**0.0351**	**0.0463**	**0.0448**	**0.0948**
PER_Sth	0.00291	**0.00358**	0.00166	**0.00282**	-	0.0078	0.0102	**0.0417**	**0.0432**
KEP_Mid	**0.0043**	**0.00566**	0.00231	**0.00408**	0.00265	-	**0.0349**	0.02	**0.0329**
KEP_Half	0.00358	**0.00447**	0.00283	**0.00376**	0.00265	0.00366	-	**0.0806**	**0.045**
CAP_Pol	0.00361	0.00354	0.00185	**0.0033**	0.00192	0.00264	0.00295	-	**0.0521**
CAP_MHe	**0.00408**	**0.0045**	0.00273	0.00232	0.00246	**0.00378**	**0.00328**	0.00199	-

CHAPTER 5. HIGH TEMPORAL FLUCTUATIONS IN FISH LARVAL SUPPLY FROM FINE-SCALE BIOPHYSICAL MODELLING OF DISPERSAL PATTERNS

5.1 Abstract

Reef fishes exhibit a range of spawning strategies often associated with lunar cycles. Biophysical modelling studies of fish larval dispersal generally focus on annual or seasonal connectivity dynamics. In this study, I evaluate how the timing of spawning affects larval supply to reefs at sub-seasonal timescales. I use a high-resolution biophysical model to simulate the release and dispersal of *Lutjanus carponotatus* larvae over 20 successive moon phases within the Keppel Islands, in the southern Great Barrier Reef. Models included species-specific larval biology and behaviour. Spawning during new or quarter moon phases, or during the first half of the spawning season (October-November), significantly enhanced local larval supply to nearby reefs. Contrarily, spawning at full moon phases, or during the second half of the spawning season (December-February), supplied fewer larvae and with longer pelagic phases. Dispersal distances were significantly shorter during first quarter moon phases, and at the beginning of the spawning season. Most larvae released from reefs in the Keppel Islands settled beyond the island group. Spawning over multiple months and moons across the spawning season increased larval arrival success to different reefs over local and regional scales. This study underscores the importance of understanding fine-scale temporal patterns of spawning in reef fishes to improve modelling of larval dispersal which can, in turn, better inform species management.

5.2 Introduction

Reef fish populations need a supply of larvae to persist and recover from disturbance events over time. Specifically, population persistence on particular reefs depends on both retention of locally produced larvae and larval supply from other reefs (Leis *et al*. 2011; Burgess *et al*. 2014). Inter-reef connectivity and larval retention are important in ensuring the persistence of reef metapopulations (Treml *et al*. 2015), including reef fish metapopulations in the Great Barrier Reef (GBR) (James *et al*. 2002). In fact, temporal variation in coral reef fish larval dispersal can have important consequences for metapopulation dynamics (Catalano *et al*. 2020). In the GBR, modelled self-recruitment of reef fish has been shown to change over time (James *et al*. 2002). Empirical observations of coral reef fish larval dispersal in the GBR proposed that dispersal can be highly variable over space and time (Harrison *et al*. 2012; 2020), and these dynamics can result in stability in the overall recruitment to island groups (Harrison *et al*. 2020). However, little is known of the biological and physical processes that shape recruitment dynamics in marine ecosystems (Cowen *et al*. 2007; Cowen and Sponaugle 2009).

Biophysical models of larval dispersal represent a relatively practical way to explore how fish larval dispersal patterns vary spatially and temporally in marine seascapes. Biophysical modelling advances in the last three decades revealed the importance of incorporating larval behavioural capabilities (e.g. swimming behaviour and response to auditory cues) when modelling fish larval dispersal, since they can impact retention, self-recruitment and connectivity patterns (Wolanski *et al*. 1997; Wolanski and Kingsford 2014; Faillettaz *et al*. 2018). Moreover, the connectivity structure of marine reef populations is primarily influenced not only by larval behaviour, pelagic larval duration (PLD) and mortality, but also by the larval release timing (Treml *et al*. 2015). Knowledge on the effect of the timing of spawning of reef fish populations on larval connectivity is therefore crucial to further understand the drivers of spatial and temporal variation in dispersal patterns.

Marine fishes exhibit a number of spawning strategies, including temporal patterns of reproduction over the year (Lowerre-Barbieri *et al*. 2011). The time of spawning is a critical moment in the life of marine fishes, including coral reef fishes, because it determines the physical environment under which the released larvae is

exposed, influencing the larval dispersal and survivorship, and population connectivity and dynamics (Claydon 2004; Shanks and Eckert 2005; Shanks 2009; Lowerre-Barbieri *et al*. 2011; Wong-Ala *et al*. 2018). Furthermore, larval dispersal would spread the risk of offspring failure, in a patchy, uncertain environment (Doherty *et al*. 1985).

Spawning timing may be related to larval replenishment success, as suggested for modelling of reef fish larvae (Donahue *et al*. 2015). Modelled fish larvae released during the observed aggregation period near the full moon increased settlement success, with earlier ages of settlement and shorter distances, compared to those larvae released at other times (Donahue *et al*. 2015). This variability was associated with mesoscale oceanographic conditions over the lunar month enhancing larval success or advection. In addition, shifting patterns in the synchrony of coral reef fish larval replenishment can vary depending on the oceanographic conditions encountered by larvae over the lunar cycle, with variation in pelagic conditions potentially contributing to the plasticity in reproduction and larval growth in marine species (Sponaugle and Pinkard 2004). Another study analysing larval settling dynamics of a highly iteroparous coral reef fish found that settling larvae arising from spawning near full moons were both younger and more numerous (Shima *et al*. 2020). Contrarily, larvae arising from spawning closer to new moons were both less abundant, older and larger, with post-settlement selection favouring these individuals (Shima *et al*. 2020).

Marine fish larval modelling highlighted the importance of resolving multiscale temporal variability in larval dispersal and connectivity, by finding differences in modelled larval dispersal and trajectory distances between seasons and between new and full moon phases (Zeng *et al*. 2019). In the GBR, water currents are modulated by tides, wind and oceanic influences of the East Australian Current, with variation over monthly and weekly scales (Wolanski and Pickard 1985). Larval dispersal modelling of coral species in the GBR determined that split spawning, i.e. simulating consecutive spawning events rather than only one, benefits corals by strengthening the external larval supply to reefs (i.e. larvae supplied by other reefs) and inter-reef connectivity (Hock *et al*. 2019). This finding emphasised the relevance of successive spawning events for larval supply success because of the high fluctuations found in ocean conditions over time in the GBR. Lunar periodicity in spawning activity is

recognised for many GBR fish species, with reproductive activity occurring seasonally over many months (Walshe and Slade 2009). Due to uncertainty in the effect of the time of spawning of coral reef fishes on larval recruitment success to reefs in the GBR, I address this effect by applying biophysical modelling of larval dispersal of a multiple spawner fish.

Here, I assess how the timing of fish spawning in the GBR affects variation in larval supply patterns to reefs in the Keppel Islands (ca 23° S, southern GBR) (Figure 5.1), by using a validated high-resolution biophysical model for the southern GBR (Bode *et al*. 2019). Hydrodynamic simulations of tracer dispersals in the Keppel Bay showed differences in tracer fluxes among seasons (Luick *et al*. 2007). My study species is the stripey snapper, *Lutjanus carponotatus*, for which inter-reef connectivity and local retention of larvae have been confirmed based on genetic parentage data across the Keppel Islands (Harrison *et al*. 2012). Stripey snapper are widespread in the Indo-West Pacific and are abundant in the GBR, where they can form spawning aggregations (Claydon 2004) and spawn multiple times over the austral spring-summer seasons (Kritzer 2004). Stripey snapper may spawn near the new (Kritzer 2004) and third quarter moon phases on the GBR (G. P. Jones and D. Williamson unpublished data), although otolith data from recruits in the southern GBR (collected between 2012 and 2013) suggest that they can spawn weekly across the austral spring-summer (Figure S5.1) potentially near every moon phase. Stripey snapper larvae are pelagic, dispersed by currents for 21 to 38 days (Harrison 2012; G. P. Jones and D. Williamson unpublished data) and are behaviourally capable, including swimming (Quéré and Leis 2011; Leis and Fisher 2006) and auditory (Wright *et al*. 2010) capacities.

In the present study, models incorporated the role of both the physical environment and larval biology and behaviour on larval supply potential. The numerical scheme was developed from the models of James *et al*. (2002) and Luick *et al*. (2007), with a fine-scale resolution that has been implemented to resolve hydrodynamics around reefs and islands. In the present study, *L*. *carponotatus* larval dispersal simulations were performed for spawning events during every lunar phase between October and February (defined as a spawning season). Specifically, the objectives are to: i) determine the spatial larval dispersal patterns in the Keppel Islands; ii) determine

the temporal larval supply patterns to reefs in the Keppel Islands; and iii) evaluate the effects of timing of spawning on larval supply. I test the null hypothesis that for *L. carponotatus* there is no variation in larval supply success among spawning events within a spawning season, i.e. during different moon phases or different months. Findings provide important insights into the temporal connectivity dynamics of coral reef ecosystems and the effect of spawning timing on larval success.

5.3 Material and Methods

5.3.1 Biophysical model and larval dispersal simulations

The biophysical model was recently validated using genetic parentage data of the coral trout (*Plectropomus maculatus*) in the southern GBR (Bode *et al*. 2019). I modelled releasing *L*. *carponotatus* larvae from all reefs in the Keppel Islands, an inshore island group of the southern GBR (Figure 5.1). When islands were relatively large, such as North Keppel and Great Keppel Islands, larvae were sourced from a number of reefs around each island. Current flow variability, including tides and northward-southward reversals, influenced mostly by trade winds, and low-frequency currents, is captured by the model hydrodynamic component. The model uses a sigma transformation in the vertical, where (six) layers represent a fixed proportion of the water column, and vertical eddy viscosities and length scales of vertical diffusivity are provided. The model is based on a temporally implicit three-dimensional barotropic scheme, and its grid resolutions are 1.85 km for the GBR, 370 m for the Keppels, and 74 m around focal reefs (Bode *et al*. 2019), making it suitable to capture both eddy formation and horizontal mixing in the proximity of reefs. Currents were determined hourly between October 2011 and February 2012, covering spawning events during a typical *L. carponotatus* spawning season.

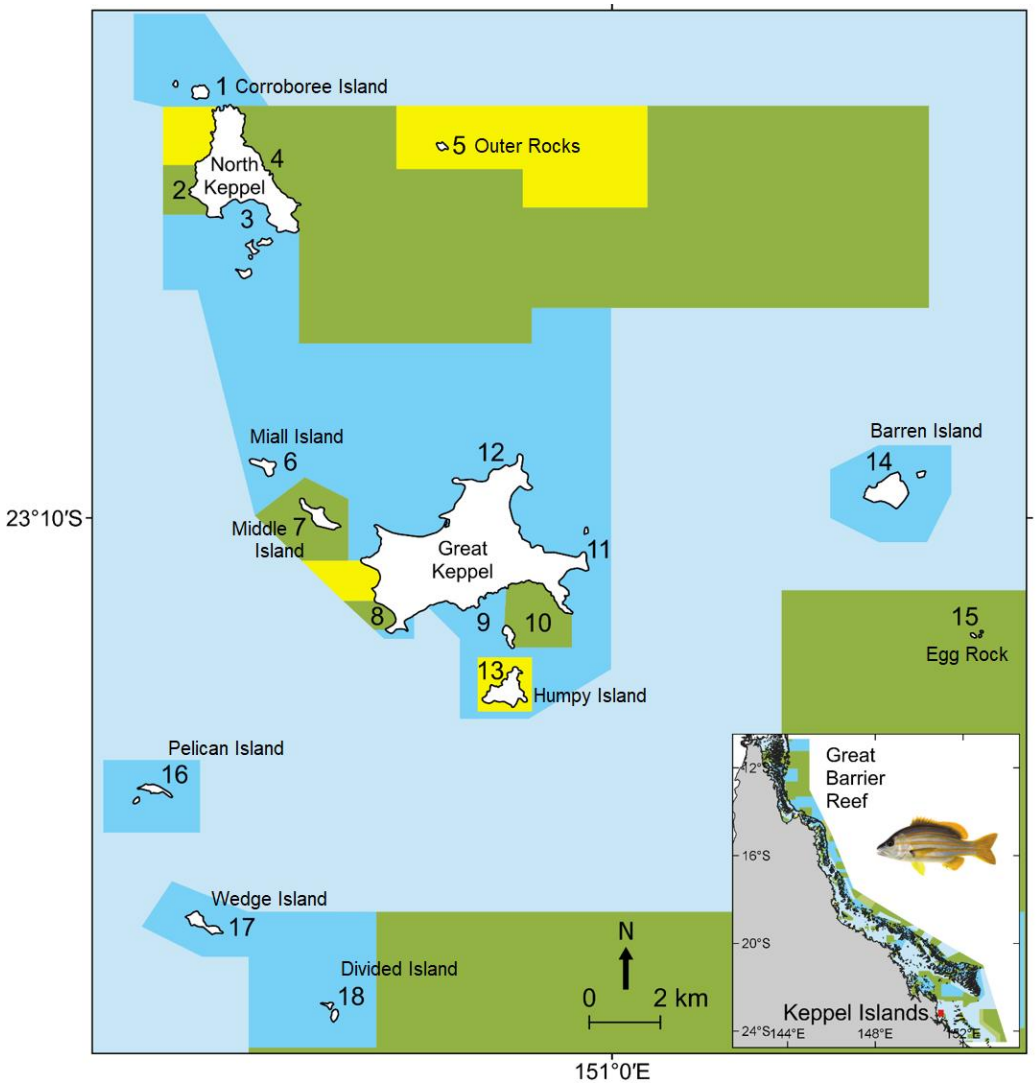

Figure 5.1. The Keppel Islands are part of the Great Barrier Reef Marine Park. Reefs included as spawning locations in the biophysical modelling of fish larval connectivity are numbered from 1 through 18. Reefs coincide with Marine National Park (green - non-fished areas), Conservation Parks (yellow - fished), Habitat Protection (darker blue - fished) areas and General Use (lightest blue - fished) areas (Great Barrier Reef Marine Park Authority - Produced December 2016 by Spatial Data Centre - Edition V. Commonwealth of Australia [GBRMPA]. Inset shows the extent of the GBR along the Northeast Australian coast, with a red dot marking the position of the Keppel Islands in the southern GBR.

An individual-based model was used in 5-minute time steps to track each larva from the spawning source and throughout the pelagic larval dispersal phase. The behavioural component of the model included egg buoyancy, larval sensory ability and behaviour (i.e. capacity of larvae to swim, undertake ontogenetic vertical migration,

and orientate), pelagic larval duration (PLD), and mortality, with behaviours experiencing diel, spatial and ontogenetic changes, along with individual variation (Bode *et al*. 2019). Larval behavioural characteristics are based on *L. carponotatus* and the related lutjanid species, *L. malabaricus*, for which empirical data is available. Approximately 600 larvae were released daily per kilometre of reef slope at the selected reefs (Figure 5.1). Releases were modelled during the new, first quarter, full and third quarter moons from October 2011 to February 2012, resulting in a total of 20 spawning events (Table S5.1) and 20 connectivity matrices (Figure S5.2). Since spawning frequency information around moon phases is unavailable for *L. carponotatus*, I released larvae one day on each side of moon phases, which assumes a resting period between spawning events over a protracted spawning season (Figure S5.1). Spawning was modelled at high/ebbing tides, which may facilitate transport off-reef (e.g. Johannes 1978; James *et al*. 2002), and during daylight hours. A total of 2,641,419 larvae were released per spawning event across the Keppel Islands.

The number of released larvae per reef was proportional to the reef slope size of each reef and therefore calculations of larval supply to reefs were based on fractions of arriving larvae relative to the total number of larvae released according to each source reef, making supply values comparable among reefs. Dispersing larvae were subjected to an 18% mortality per day, as suggested for pelagic larvae in marine environments (Cowen *et al*. 2000; James *et al*. 2002). Larval dispersal was modelled for a total period of between 21 to 38 days (PLD), considered as the active larval settlement period for *L. carponotatus*. Sensory zones of 6 km were created around every reef based on settlement habitat preferences (Kingsford 2009; Quéré and Leis 2010) and auditory sensitivity in settlement-stage *L*. *carponotatus* larvae (Wright *et al*. 2010). Larvae were assumed as able to settle if within a reef sensory zone between days 21 and 38 of the dispersal phase, otherwise larvae were not included in the analyses. The sensory zones were created using a Geographic Information System, QGIS 2.18.0 (QGIS Development Team 2018). Additionally, settling larvae were subjected to 13% mortality due to predation at settlement, as suggested for *L. carponotatus* (Quéré and Leis 2010).

5.3.2 Larval supply metrics and data analysis

I measured larval connectivity patterns between reefs in the Keppel Islands as the number of modelled larvae that dispersed from one reef to another and quantified the overall larval supply, the duration particles remained in the water column (PLD), and the total distance travelled during this period (Euclidean distance between source and settlement reef). For each reef in the study region (1-18), I distinguished between larval supply that was generated from endogenous recruitment, or the degree of local retention (i.e. the fraction of larvae produced by a population that settles into that population; Burgess *et al*. 2014), and exogenous recruitment, defined as external larval supply from other reefs in the island group. Also, I estimated self-recruitment levels as the fraction of larvae recruited into a population (i.e. including supply coming from other populations) that is locally produced (Burgess *et al*. 2014). The variability of larval supply between spawning events was measured as the coefficient of variation (CV) across all spawning events, calculated as the standard deviation of larval supply over the temporal mean. Since little is known about the impact temporal variation has on larval supply among different reefs in the island group, I also calculated the correlation among larval supply to reefs over time by measuring Spearman's correlation. In addition, I estimated the probability of larval dispersal from each reef in the Keppel Islands to reefs beyond the island group.

In order to evaluate the effect of the time of spawning on larval supply I tested statistical significant differences in modelled larval supply to reefs, PLD, larval dispersal distance and larval export between moon phases, and among months. Statistical significances were tested by parametric ANOVA or non-parametric Kruskal-Wallis tests, following normality or non-normality distribution of the data, respectively, at a significance level of 0.05. Larval supply metrics were displayed as boxplots to depict data distribution and variability among different moon phases or months during the modelled spawning period. Boxplots were constructed with mean values over time of larval supply metrics at each modelled reef (i.e. each boxplot is composed of 18 values) in the Keppel Islands.

5.4 Results

5.4.1 Spatial larval dispersal patterns

Larval dispersal simulations spanning 20 spawning events over a 5-month period showed extensive connectivity throughout the Keppel Island region. Self-recruitment was relatively low (< 10%) on most reefs, although substantial variability was observed between reefs (averaged self-recruitment values ranged from < 1% to > 20%) (Table S5.2). Larval dispersal was predominantly northward and eastward, resulting in a relatively strong larval supply towards North Keppel Island and surrounding islands (reefs 1 to 5), particularly from central reefs adjacent to Great Keppel Island (reefs 6 to 13), but also from southernmost reefs (reefs 16 to 18) (Figure 5.1,5.2). However, northernmost reefs [reefs 1 to 5] were a poor source of larvae to southernmost reefs. The easternmost reef (reef 15) also acted as a relatively important larval source to other reefs in the region (Figure 5.1,5.2). The other eastern reef in this region (reef 14), was relatively important as a sink reef. Larval connectivity was also substantial within northern (vicinity of North Keppel Island) and central (vicinity of Great Keppel Island) regions (Figure 5.1,5.2).

Reef-to-reef connectivity, larval retention and self-recruitment exhibited large variation among spawning events, with a CV median distribution of 1.86 (range: 0.43 to 3.54) (Figure S5.3), 2.12 (range: 1.18 to 3.06) (Figure S5.3) and 0.64 (range: 0.36 to 2.40) (Table S5.2), respectively. The CV of larval retention and self-recruitment presented significant negative correlations with the area of reef slope for source reefs (r = -0.47, p < 0.05; r = -0.55, p < 0.05, respectively). In general, larval retention and self-recruitment were more variable over time where the area of reef slope was small, with reefs from North Keppel Island (western no-take area, reef 2), Great Keppel Island (western no-take area, reef 8), easternmost no-take (reef 15) and southernmost fished (reefs 16, 17 and 18) areas, showing self-recruitment CV values > 1 (Table S5.2). Reef-to-reef larval supply correlations over time in the island group ranged from relatively weak (r = 0.29) to very strong (r = 0.95) (Figure S5.4).

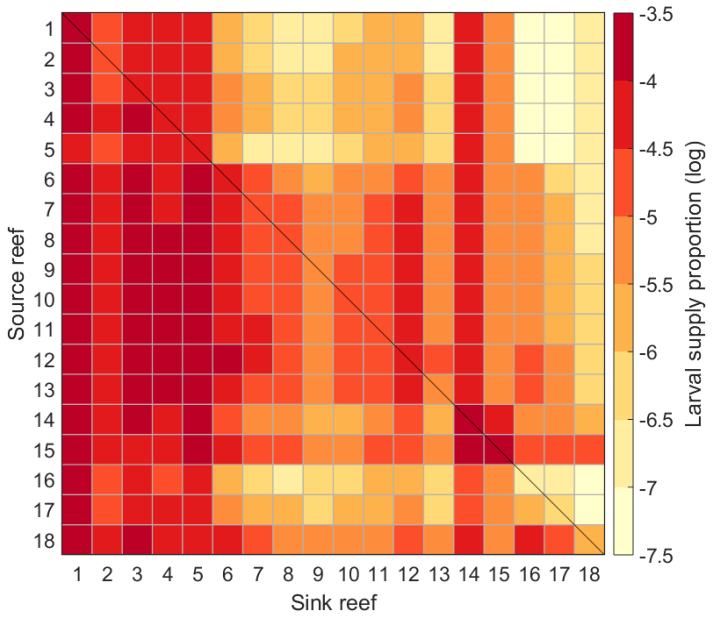

Figure 5.2. Modelled larval connectivity of *L. carponotatus* in the Keppel Islands (southern GBR). Modelled larvae were released from 18 reefs around each of four moon phases from October 2011 to February 2012. Values represent the probabilities of larval connectivity from source reefs to sink reefs as a log of the probability of larvae supplied. Values along the diagonal represent larval retention (referred as larvae spawned and settled at the same reef). The positions of the 18 reefs are shown in Figure 5.1.

5.4.2 Temporal larval supply patterns

The timing of spawning events resulted in highly variable patterns of larval supply, PLDs and dispersal distances over the full spawning season of *L. carponotatus* in the Keppel Islands (Figure 5.3,5.4). Both mean external larval supply to reefs and mean larval retention within reefs varied between moon phases (Figure 5.3a,b). Median values of external larval and larval retention were stronger in the first quarter moon spawning events, progressively diminishing during the new, third quarter and full moon phases (Figure 5.3a,b). Significant differences in mean larval supply were evident between spawning events around the new and first quarter moons compared to spawning around the full moon, for both external larval supply (Kruskal-Wallis, $p < 0.05$) and larval retention (Kruskal-Wallis, $p < 0.05$). Testing for differences in total larval supply to reefs (i.e. adding together both external larval supply and retention)

between moons provided the same results. Mean PLD values for larvae spawned over the different moon phases followed an opposite trend to that of larval supply, and were significantly different from each other for all phases (ANOVA, $p < 0.05$), although greater differences occurred between the largest PLDs around the full moon, compared to the lowest PLDs over the new and first quarter moons (ANOVA, $p < 0.05$) (Figure 5.3c).

At monthly scales, modelled external larval supply to the reefs was significantly higher in the first phase of the spawning season (October and November) compared to the second phase (December, January and February) (Kruskal-Wallis, $p < 0.05$) (Figure 5.3d). Similarly, reefs significantly retained more modelled larvae during the early (October and November) than the mid-late spawning season (December, January and February) (Kruskal-Wallis, $p < 0.05$) (Figure 5.3e). Testing for differences in the total modelled larval supply to reefs (i.e. adding together both external larval supply and retention) between different moon phases provided the same results. Median values of average larval retention were higher than those of external larval supply for every month (Figure 5.3d,e). When considering the time that larvae spent in the water column before settling, significant differences were found between all months (ANOVA, $p < 0.05$), except at the beginning of the spawning season (i.e. October vs. November), when PLD values were lowest (Figure 5.3f).

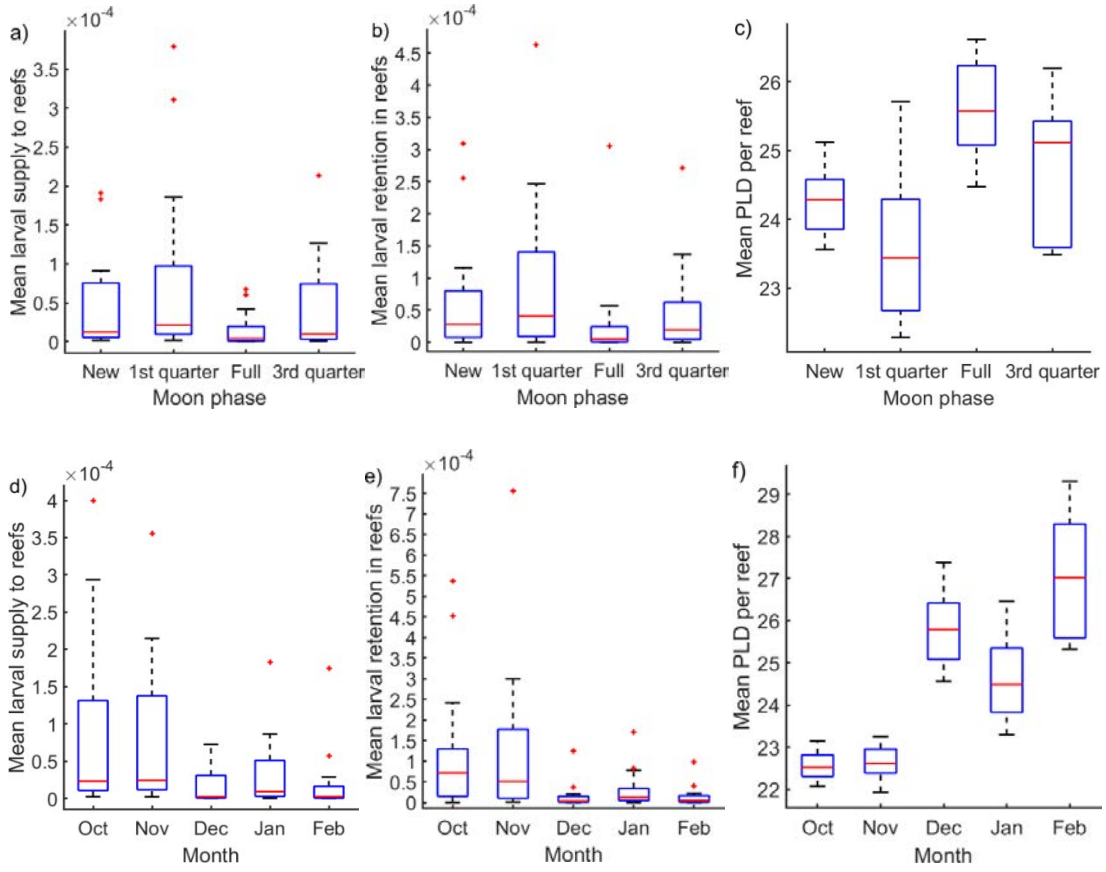

Figure 5.3. Boxplots of the average larval supply from external sources and larval retention probabilities between October 2011 and February 2012 for reefs in the Keppel Islands (southern GBR). Releases were modelled from 18 source reefs (Figure 5.1) around each moon phase (new, first quarter, full and third quarter) (a, b) or for each month during the spawning period modelled - from October 2011 (Oct) to February 2012 (Feb) (d-e). The mean pelagic larval durations (PLD, days) of settling larvae per reef are shown for each release period (c,f). In boxplots, the box shows interquartile range (IQR) - representing 50% of the data and contains the median value (centre line), the 25th and the 75th percentiles (bottom and top edges, respectively). Whiskers extend up to 1.5 times the IQR, and outliers are represented by red crosses.

Mean modelled larval dispersal distances from reefs in the Keppel Islands varied among spawning periods (Figure 5.4). Contrary to larval supply patterns, the least distance in larval dispersal was achieved during the first quarter moon and was significantly different to larval dispersal during all other moon phases, with a median dispersal distance of around 50 km (Figure 5.4a, ANOVA, $p < 0.05$). In contrast,

maximum dispersal distances were achieved following new and full moon spawning events, with median values approximating 80 km (Figure 5.4a). Monthly larval dispersal had the smallest distances during the first half of the spawning season (i.e. October and November), with dispersal distances increasing significantly from December onwards (ANOVA, $p < 0.05$) (Figure 5.4b). Mean larval dispersal distances varied greatly between reefs within spawning events, with differences of up to approximately 30 - 40 km among outliers (Figure 5.4a,b).

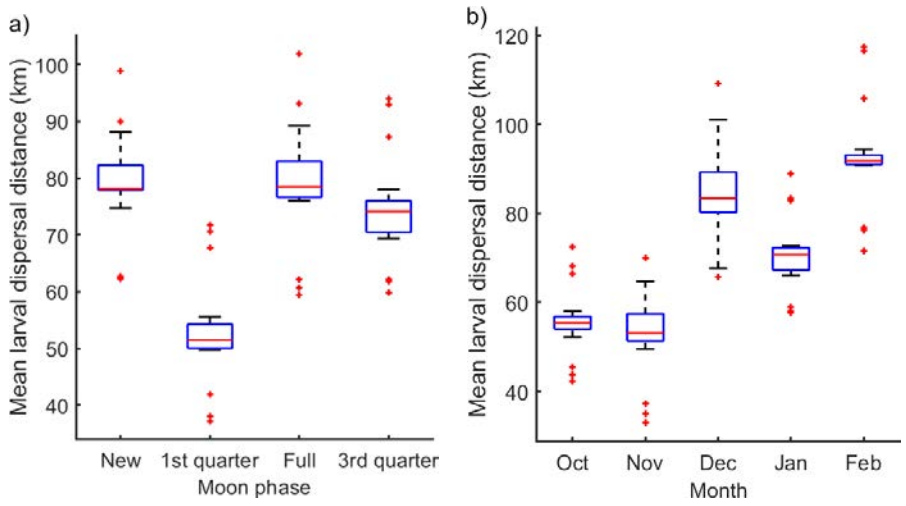

Figure 5.4. Distribution of the average larval dispersal distance from source reefs in the Keppel Islands during modelled spawning events between October 2011 and February 2012. Larvae were sourced from 18 reefs (Figure 5.1) amongst (a) moon phases (new, first quarter, full and third quarter moon phases) and (b) months examined - from October 2011 (Oct) to February 2012 (Feb). In boxplots, the box shows interquartile range (IQR) - representing 50% of the data - and contains the median value (centre line), the 25th and the 75th percentiles (bottom and top edges, respectively). Whiskers extend up to 1.5 times the IQR, and outliers are represented by red crosses.

In addition to the modelled larval supply to reefs within the Keppel Islands, I calculated larval export from each reef to GBR reefs outside the Keppel Islands. Results suggest that most larvae produced by fish populations within the Keppel Islands settle outside the system (Figure 5.5a,b). Great variability exists in the mean

reef-to-reef contribution of exported larvae within moon phases and months (Figure 5.5a,b). Larval export from the Keppel Islands to GBR reefs was relatively stable among spawning events, even though significant differences existed between the full and third quarter moon phases (Kruskal-Wallis, $p < 0.05$), and among February and the rest of the months (Kruskal-Wallis, $p < 0.05$). Reef-to-reef larval export to the GBR from the full moon and December spawns was the least variable, presenting the largest median values (consistent with the smallest larval supply values within the Keppel Islands during these periods) (Figure 5.5a,b).

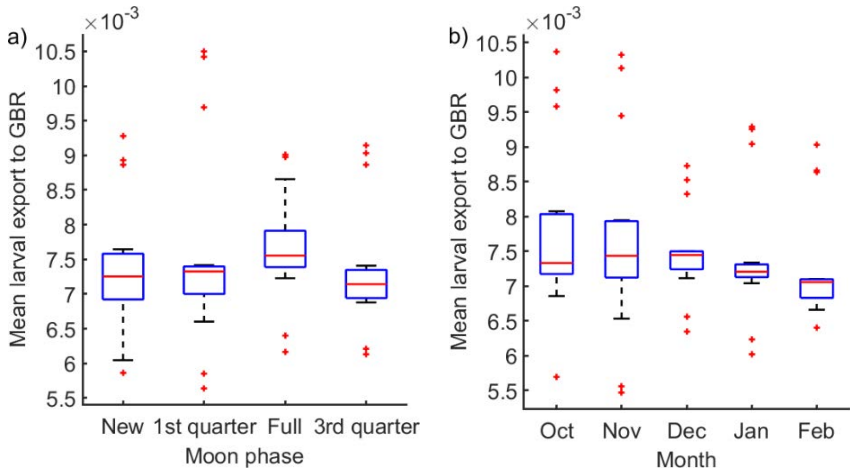

Figure 5.5. Boxplots of mean probability of modelled patterns of fish larvae exported from reefs in the Keppel Islands beyond the island group to the GBR. Larvae were sourced from 18 reefs (Figure 5.1), a) around every moon phase (new, first quarter, full and third quarter) and b) during every month for which it was modelled - from October 2011 (Oct) to February 2012 (Feb). In boxplots, the box shows interquartile range (IQR) - representing 50% of the data - and contains the median value (centre line), the 25th and the 75th percentiles (bottom and top edges, respectively). Whiskers extend up to 1.5 times the IQR, and outliers are represented by red crosses.

5.5 Discussion

In this study of fine-scale larval dispersal patterns, I found that the timing of spawning events are an important determinant of patterns of larval supply and recruitment dynamics in coral reef seascapes. Larval dispersal simulations using a

high-resolution biophysical model showed that larval retention was common for most reefs in the Keppel Island region. However, incoming larvae from surrounding reefs was a more important source of larval supply than retention. Sub-seasonal fluctuations in larval supply were evident across the five-month period of the study. Larval release simulations around different moon phases and months within a spawning season influenced larval arrival success, with temporal releases providing benefits at both local and regional scales.

Previous studies analysing the effect of temporal spawning on fish larval connectivity focused mostly on annual scales (e.g. Kough *et al*. 2016; **Chapter 3**). Analysis on the benefit of timing of fish spawning aggregations on larval replenishment were undertaken in the Caribbean (Donahue *et al*. 2015). However, this study contrasted the benefits of spawning during a confirmed spawning window as opposed to outside this window by estimating larval replenishment success in the region but not considering reef-to-reef supply patterns (Donahue *et al*. 2015). In addition, modelled fish larval dispersal distances among new and full moons and between spring and winter were investigated in the Caribbean and the northwest Atlantic (Zeng *et al*. 2019), showing that spawning at different times within the spawning season may generate dispersal differences. The present study builds on previous studies to explore the effect of reef fish spawning timing within a spawning season on larval supply patterns. The patterns of larval supply observed in the present study suggest that over time, there is a minimum guaranteed larval supply to reefs. These results expand on empirical observations of larval dispersal for *P. maculatus* in the Keppel Islands whereby the recruitment contributions from individual reefs were found to be highly variable though the contributions from multiple source reefs generated stability in the overall recruitment to the island group (Harrison *et al*. 2020). In addition, I found that multiple spawning events enhance the larval dispersal to a range of different reefs (over local and regional scales). Spawning at different times has different and uncertain survivorship and spawning multiple times may spread the risk of failure and balance larval supply, in variable environments such as the one found in the GBR, as a diversified bet-hedging strategy (Wilbur and Rudolf 2006).

Larval dispersal simulations in the present study reveal the potential importance of larval recruitment pulses, including both incoming larvae from external reefs and

retained larvae, over local scales. I showed that inter-reef larval connectivity links many reefs in the Keppel Islands, while larvae are also retained on reefs during a single *L. carponotatus* spawning season. The modelled reefs coincided with reefs from marine reserves sampled for genetic parentage analysis of *L. carponotatus* and *P. maculatus* by Harrison *et al*. (2012), confirming inter-reef connectivity and local retention of larvae, albeit during a different spawning period to the present study. My modelling, however, did not include data on fish larval density per area, and results therefore represent the propensity of areas to supply and/or receive larvae according to the physical environment and the dispersive capabilities of larval offspring. Here, simulations of larval export for *L. carponotatus* from the Keppels further support the potential for this system to export larvae to other reef groups in the GBR. Parentage studies of *P. maculatus* at a regional scale confirmed the potential for larvae produced in the Keppel Islands to disperse towards other GBR regions - including the Percy Islands and the Capricorn Group (Williamson *et al*. 2016).

Here, modelled larval supply patterns revealed the importance of source and sink dynamics over local scales. Northern and central reefs acted as relatively stronger larval sinks, with an apparent predominant northward larval flow in the study region. In addition, I found that multiple external larval pulses may be more important than retention at reef scales, and that large temporal and spatial variation in recruitment - including both external supply, retention, and self-recruitment - is common. The high variability in reef fish larval recruitment processes and the relevance of external pulses has also previously been revealed at regional scales in the northern GBR, covering many years of spawning seasons (James *et al*. 2002). Additionally, interannual *L. carponotatus* connectivity over the entire GBR identified high coefficient of variation levels (**Chapter 3**). Here, larval supply levels were variable across one spawning season of *L. carponotatus*, which together with the great changes in interannual larval connectivity identified in **Chapter 3**, suggest that fine-scale sub-seasonal connectivity patterns may vary from year to year within the Keppels. Moreover, genetic parentage analyses of *P. maculatus* in the Keppels identified variable inter-reef larval dispersal levels over years (Harrison *et al*. 2020). Studies on coral connectivity in the GBR also estimated large interannual fluctuations in potential larval supply (Hock *et al*. 2019). Collectively, these results suggest high levels of variability in larval supply of spawning fishes and corals in the GBR - from annual to weekly scales.

Here, findings also suggest that larvae experience different PLDs according to the timing of spawning, which may have further relevant implications for the survival of larvae. Higher arrival success rates by younger larvae (shorter PLDs) found in the present modelling study, may indicate greater post-settlement mortality, while lower success of older larvae (longer PLDs), may represent greater post-settlement survival, as previously suggested for older (and larger) reef fish larvae settling (Shima *et al*. 2020). Variation in offspring size of marine fish has been proposed as a bet-hedging strategy to cope with environmental uncertainty (Shama 2015). Recruitment of reef fish in the GBR varies over time, with significant mortality differences among cohorts of the same species (Eckert 1987), and demographic consequences (Doherty and Fowler 1994). Strong settling cohorts can substantially affect abundance of GBR local populations, including *P. leopardus* (Russ *et al*. 1996). These findings indicate the importance of considering both PLD and the ecology of larval survival, based on the timing of spawning and behaviour, when investigating larval connectivity dynamics.

Management of fish populations often includes protecting spawning aggregations according to spawning timing, e.g. coral reef fin fish closures in the southern GBR around new moons in November and December (Russell 2001). These closures aim to protect fishes during the spawning season and are mainly focused on coral trout but are also expected to benefit other fish species with overlapping spawning seasons, such as *L. carponotatus* (Russell 2001; Walshe and Slade 2009). Although the main objective of fish closures relies on protecting the spawning aggregations, the fate of the larvae produced and their recruitment success across the spawning season remains unknown. The present study, even though focused on a single spawning season and a single species (stripey snapper), provided evidence suggesting variation in larval recruitment success among moon phases and among months at local spatial scales. Although, stripey snapper (and coral trout) spawn from October to December around the new moon, they also spawn outside these times, including other moon phases and other months. Therefore, further protecting spawning aggregations over consecutive spawning events may be beneficial to the fishes and their fisheries, based on this and other studies reported herein, and a single closure may not necessarily capture the most important spawning event every year. Results suggest, however, that the November-December closures around the new moon may remain as one of the best strategies to protect fish and their offspring, due

to a balance among larval supply success at local and regional scales. Knowledge of the timing of coral reef fish species spawning is important for managing and modelling their connectivity, since larval supply patterns likely vary significantly over the spawning season.

In conclusion, the physical environment of the GBR is highly dynamic, affecting larval supply patterns of reef fish populations to reefs over a range of temporal and spatial scales. Spawning at particular times over the spawning season may represent higher chances of survival and recruitment success. Multiple spawning may benefit larval supply success over time in variable environments, where recruitment failure may be more variable.

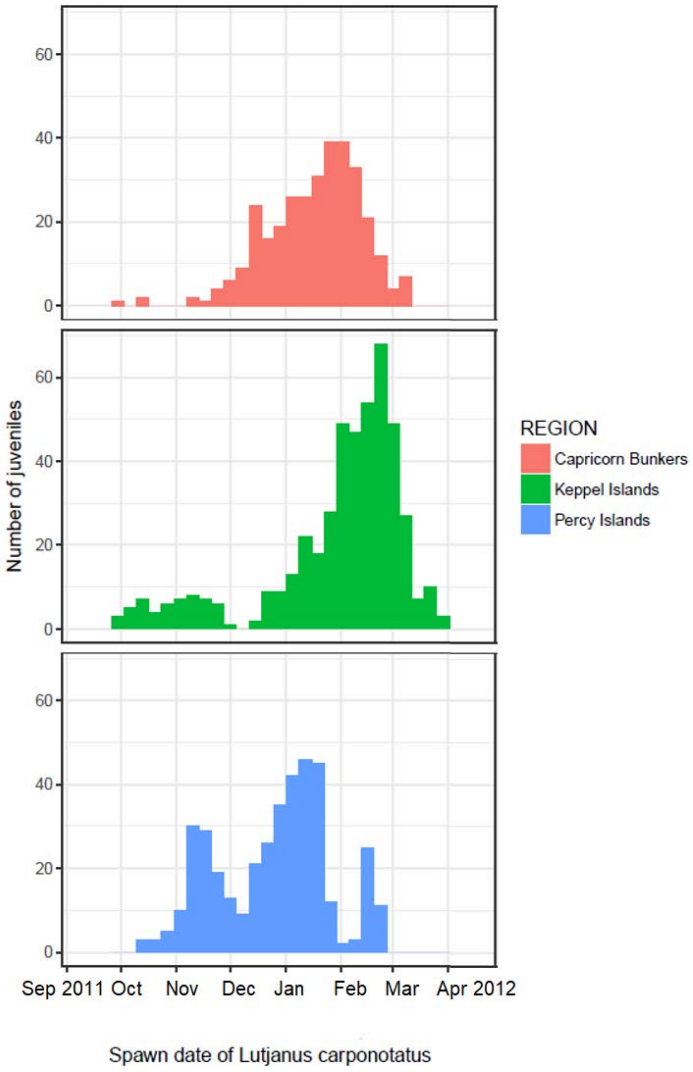

Figure S5.1. Time of spawn of collected *L. carponotatus* juveniles in the southern GBR, including the Capricorn-Bunker Group, and Keppel and Percy Islands. Spawning time was estimated from daily ring counts of otoliths, suggesting multiple spawning events across the austral spring-summer months (between September 2011 and March 2012).

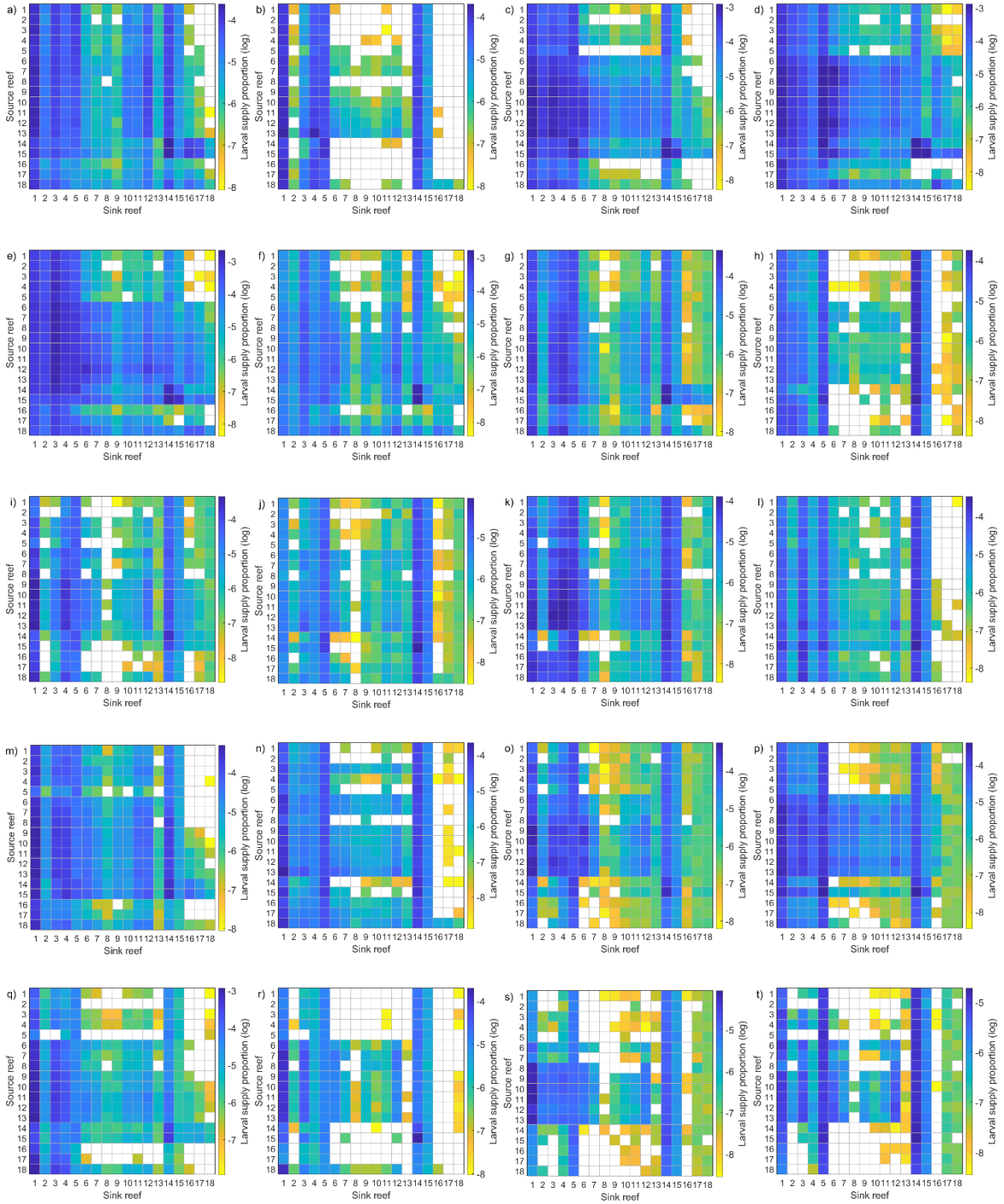

Figure S5.2. Biophysical modelled fish larval connectivity for spawning events around the first quarter, full, third quarter and new moons, from October 2011 to February 2012 (consecutive from a) [first quarter phase in the beginning of October 2011] to t) [new moon phase in the end of February 2012]), in the Keppel Islands (southern GBR). Values represent the probabilities of larval connectivity from source reefs (Y-axis) to sink reefs (X-axis). Reefs included in the modelling (1 - 18) are shown in Figure 5.1.

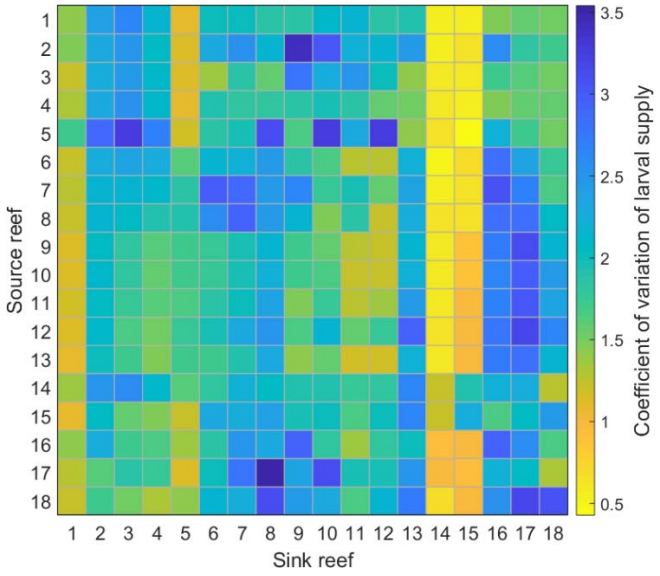

Figure S5.3. Coefficient of variation of the biophysical modelled fish larval connectivity (not log transformed) identified in the Keppel Islands (southern GBR). Values are based on 20 spawning events, corresponding to the larval release from 18 reefs (shown in Figure 5.1) around every moon phase between October 2011 and February 2012.

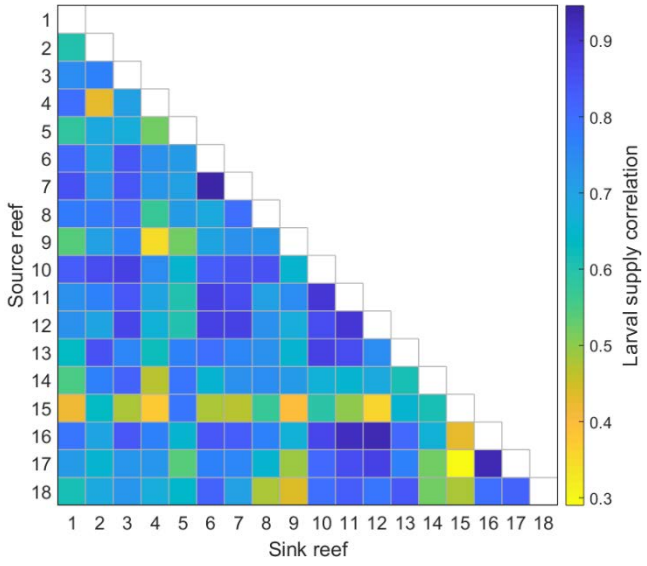

Figure S5.4. Correlation values (Spearman) of the larval supply to reefs over time, based on releases of larvae around every moon phase between October 2011 and February 2012, from 18 reefs in the Keppel Islands (southern GBR) (shown in Figure 5.1).

Table S5.1. Modelled spawning dates of *L. carponotatus* in the Keppel Islands (southern GBR).

Moon phase			
First quarter	Full moon	Third quarter	New moon
04/10/2011	12/10/2011	20/10/2011	27/10/2011
03/11/2011	11/11/2011	19/11/2011	25/11/2011
02/12/2011	11/12/2011	18/12/2011	25/12/2011
01/01/2012	09/01/2012	16/01/2012	23/01/2012
31/01/2012	08/02/2012	15/02/2012	22/02/2012

Table S5.2. Mean self-recruitment (%) across the 18 reefs modelled in the Keppel Islands (southern GBR) for larvae released around every moon phase from October 2011 to February 2012. Coefficient of variation of self-recruitment over the spawning period is also presented.

Reef	Self-recruitment (%)	Coefficient of variation
1	2.96	0.5
2	2.17	1.6
3	2.86	0.58
4	3.81	0.39
5	5.62	0.36
6	5.88	0.48
7	8.23	0.98
8	2.32	2.13
9	10.62	0.71
10	9.52	0.41
11	10.74	0.41
12	15.38	0.36
13	12.58	0.67
14	14.94	0.6
15	22.25	1.12
16	0.24	2.4
17	1.99	1.27
18	13.85	2.03

CHAPTER 6. GENERAL DISCUSSION

In this thesis, I estimated population connectivity of fish on the GBR, by simulating the release and dispersal of *Lutjanus carponotatus* larvae and assessing genetic differentiation of *L. carponotatus* adults and recruits independently. Larval connectivity among reefs is well established over the eight years examined (2010 to 2017), with interannual variations in connectivity patterns associated with the El Niño Southern Oscillation (ENSO). Larval supply to reefs largely depends on variable external supplies from a number of reef sources, although local recruitment also relies on larvae retained and returning to their source reefs. Larval supply strength, together with larval age at settlement, and dispersal distances significantly vary over the lunar month and between months during the spawning season. Genetic analyses confirmed extensive larval connectivity within and among island/reef groups, although subtle genetic differences are evident among distant reefs (i.e. over 100s of kilometres), potentially influenced by dispersal limitations and/or local adaptation. Larval dispersal capacity is consistent with the dispersal potential of coral reef fish larvae found on the GBR and other marine environments (van Herwerden *et al*. 2003; DiBattista *et al*. 2017; Salas *et al.* 2019). Larval connectivity in the GBR ecosystem is extensive due to the dynamic along- and across-shelf currents linking the myriad of well distributed reefs across the largest present day coral reef system in the world.

Measuring marine connectivity is an essential, yet complex issue to resolve in order to achieve a better understanding of the spatial ecology of populations. Therefore, using multiple approaches and examining temporal variation over years (when variable ENSO conditions existed) or over multiple months (during the main spawning season) is advantageous (Leis *et al*. 2011). Approaches to estimate population connectivity include numerical models, genetic/genomic tools and otolith chemistry, each with different advantages depending on the spatial and temporal scales applicable to the purposes of the research (Jones *et al*. 2009). In this thesis, I measured connectivity using two different, yet complementary approaches: 1) biophysical modelling (**Chapters 3, 5**), resulting in a number of connectivity metrics, including external larval supply and retention, along with larval dispersal distances,

and 2) genetic techniques (**Chapter 4**), based on population genomics. Another approach, which is critical to inform and confirm direct connectivity patterns, is parentage genetic analysis. Whilst parentage analysis was not undertaken in this thesis, previous studies relevant to the species as well as to the temporal and spatial scales examined in the present study were completed for *L. carponotatus*, *Plectropomus maculatus* and *Plectropomus leopardus* in the GBR (Harrison *et al*. 2012; Williamson *et al*. 2016; Harrison *et al*. 2020), and confirmed inter-reef larval exchange across study regions/locations. The abovementioned published results from parentage analyses, alongside the genomics and modelling of larval recruitment examined in my thesis, are further discussed herein.

As an initial part of the connectivity study in this thesis, I investigated larval dispersal and variation along the whole of the GBR over multiple years (across eight years, **Chapter 3**). These larval dispersal analyses were centred on reliable hydrodynamic models for the GBR. Some of the advantages of using numerical models relied on their ability to concurrently simulate ocean currents and fish spawning over the GBR during different ENSO phases and at different times during a given spawning season. I subsequently measured larval supply variability at a smaller temporal scale, by examining multiple larval dispersal periods associated with a series of spawning events across multiple lunar months (during the austral spring and summer - from October to February, **Chapter 5**). Findings allowed me to explore the degree of multi-scale larval connectivity on the GBR, including particular complexities in the physical and biological (such as larval behavioural capabilities) factors affecting dispersal.

Larval dispersal predictions suggested a high level of connectivity and supply variation on the GBR, which was enhanced by extreme climate events, although temporal changes in fish larval connectivity have not yet been tested by parentage studies in this system. Parentage analyses over time would be helpful to confirm the observed temporal changes in connectivity patterns (e.g. Harrison *et al*. 2020). Biophysical dispersal models can then be used to assess the expected degree of connectivity variation in particular regions at different times and under different climate states. Biophysical modelling of dispersal patterns can be used to identify reefs that may be more connected by larvae over regional scales across the GBR (i.e. probably

at the earliest PLDs when larvae are competent to settle onto a reef). Therefore, models could identify those regions more likely to show parent-offspring relationships when sampling for parentage studies to confirm the ratio of larval export (e.g. from marine reserves) to retention (e.g. within marine reserves). Recruitment benefits of marine reserves for fishes have been identified in the southern GBR (Harrison *et al*. 2012), however such benefits should be tested across other GBR regions as well, in order to have a more comprehensive perspective of recruitment benefits in the GBR.

The use of single nucleotide polymorphisms (SNPs) for analysing genetic connectivity along the GBR in this thesis extended previous genetic work on *L. carponotatus* that used mitochondrial DNA (Evans *et al*. 2010), supporting the extensive levels of gene flow of reef fish along this system and the potential for both regional and local inter-reef larval supply. The use of outlier SNPs (those putatively affected by selection) indicated stronger levels of population differentiation, especially among the most distant island groups examined (i.e. over approximately 800 km). These findings, together with those from neutral SNPs and larval dispersal modelling (indicating greater differentiation at more than 300 km) suggest increasingly limited larval dispersal over distances of more than 300 km and up to 800 km in the study area, highlighting an isolation by distance (IBD) effect on genetic differentiation. Moreover, results from outlier SNPs suggest a potential effect of selection on restricting the extent of larval dispersal. Findings from Evans *et al*. (2010) suggest that *L. carponotatus* should be managed as a single (panmictic) stock on the GBR. Findings in this thesis highlight the ability of SNP markers to identify potential restrictions to the extent of connectivity of spawning marine organisms. Using SNPs should therefore enable better informed management of stocks on the GBR. Regional larval dispersal and a stepping-stone effect along the GBR suggest that effective regional scale management of *L. carponotatus* may benefit populations in this system.

Although relatively few outlier markers were identified in the genomic study of *L. carponotatus* along 800 km of the GBR (**Chapter 4**), this number is comparable to the number of outliers employed in genomic connectivity studies of fish populations across the world for population genetics. For example, Limborg *et al*. (2012) detected 16 outlier SNPs in the high gene flow marine fish *Clupea harengus* in the northeast Atlantic, and Milano *et al*. (2014) identified 17 outlier SNPs for *Merluccius merluccius*

across European populations, both spanning 1000s of kilometres. Cure *et al*. (2017) detected 9 – 22 outlier SNPs for *Choerodon rubescens* populations along approximately 600 km of Western Australia, while DiBattista *et al*. (2017) found 66 outlier SNPs for *L. carponotatus* populations along approximately 2,500 km of Northwestern Australia. The number of identified outlier SNPs, however, varies according to the methodology applied and how stringent the detection threshold is, i.e. the relationship between false positives and the power to detect markers under selection. A number of programs using different methods have been used for outlier detection, including Bayescan, Arlequin and Outflank (e.g. Benestan *et al.* 2016; van Wyngaarden *et al.* 2017). In the genomic study of this thesis, stringent methods, including Bayescan and Arlequin, were used to identify outlier SNP markers in *L. carponotatus* along the GBR.

The genomic data (**Chapter 4**) revealed that subtle genetic structure is evident among adults from some of the most distant (and environmentally contrasting) GBR regions (e.g. the Palm and Capricorn-Bunker Islands). Additionally, genetic structure is also evident among adult and recruitment pulse cohorts (e.g. the Palm Island adults and Capricorn-Bunker Islands' recruits), and among recruit pulses (specifically, among recruit pulses from the Percy and Capricorn-Bunker Group Islands), with all the above-mentioned relationships exhibiting significant F_{ST}-values > 0.1. Interestingly, variability was even found in the genetic differentiation among adult populations (e.g. in the Palms) and recruits in the southern GBR, as well as among recruitment cohorts within the southern sector, suggesting temporal variability in genetic differentiation and the potential for environmental variability to determine larval survival. Extreme climate events (such as El Niño and La Niña), and projected climate change scenarios on the GBR, including projected ocean warming (see for example Done *et al*. 2003), may significantly affect survival and connectivity patterns of reef fish larvae across this system, and only the 'fittest' larvae may prevail. It has been hypothesised for GBR coral larvae under global warming, that migrant larvae genotypes from lower to higher latitudes would be expected to survive better than migrants in the opposite direction due to higher tolerance of lower latitude than higher latitude larvae to warm waters (Matz *et al*. 2018). This is particularly relevant to larval survival when considering that reef fish larval dispersal patterns on the GBR vary at interannual scales and this has been associated with differences between extreme ENSO events (as shown in

Chapter 3), with predominantly southward or northward dispersal pulses associated with either El Niño or La Niña events, respectively.

Further research using genomics on GBR fish populations could explore sampling cohorts of larval recruits from contrasting environmental conditions, such as during extreme El Niño/La Niña climate events, different seasons and/or different regions in order to identify potential signals for selection on recruitment cohorts. However, not only environmental factors may be playing a role in reef fish larval survival, also post-settlement selection events are important to examine, for example, according to age/size of settling larvae, where older/larger larvae may survive better (Shima *et al*. 2020). This behavioural aspect may be particularly relevant in traditionally cooler, southern parts of the range, if associated with an extreme El Niño event. Findings from observed larval dispersal patterns during fine-scale biophysical modelling (**Chapter 5**) suggest that PLD of settling larvae differs among spawning events at sub-seasonal scales, and therefore suggest an indirect effect of timing of spawning and larval age on larval survival. Further studies on GBR fishes may reveal the potential for biological and physical interactions to affect larval survival at settlement and post-settlement periods.

Biophysical modelling revealed that large fluctuations in dispersal patterns occur: a) at interannual scales among GBR regions (**Chapter 3**), and b) at monthly scales and between moon phases among locations (**Chapter 5**). Results from regional biophysical modelling highlight the importance of both common (over shorter distances among closest regions) and rare (longer distance - related to interannual variability of the physical environment and climate events) larval pulses on the distribution of settled recruitment cohorts on the GBR. Local modelling (in the Keppel Islands) suggests the presence of relatively common inter-reef larval supply patterns, with particular islands being more inter-connected than others. This pattern is consistent with observed differences in source-sink dynamics. Inter-reef variability in larval supply parameters - such as self-recruitment - is very variable, highlighting the importance of resolving local scale hydrodynamics when modelling variability in larval dispersal. Another relevant aspect emerging from reef fish recruitment studies on *L. carponotatus* and *P. leopardus* at particular islands on the GBR (specifically in the Capricorn-Bunker Group; Kingsford 2009), supported by the biophysical modelling in this thesis, is the

variation in larval supply pulses. In particular, certain GBR regions may be more likely to retain larvae (for example the Keppel Islands, findings in this thesis; Harrison *et al*. 2012; Williamson *et al*. 2016), compared to other GBR regions that may rely more on external larval supply from surrounding regions: for example, the Percy Islands and Capricorn-Bunker Group (Williamson *et al*. 2016). This variation, influenced by regional and local hydrodynamics, may alter the benefits that marine reserves provide via the supply of larvae.

The relevance of marine reserves in the GBR for increasing the fish density, biomass and batch fecundity, along with a longer spawning period and greater potential for larval supply, has been shown for target fishery species such as *L. carponotatus*, *P. maculatus* and *P. leopardus* (Williamson *et al*. 2004; Evans and Russ 2004; Evans *et al*. 2008; Boaden and Kingsford 2015; Carter *et al*. 2017). Marine reserve benefits also extend to adjacent marine reserves and fished areas by supplying larval pulses (Evans and Russ 2004; Berumen *et al*. 2012), and different island/reef groups may experience greater or lesser benefits from locally retained or externally supplied larvae. Therefore, understanding larval dispersal patterns of abundant and well distributed species, such as *L. carponotatus* on the GBR, will help optimise larval supply benefits amongst MPAs and from MPAs to fished areas, thus informing/improving MPA placement and MPA network design.

A number of recommendations emerge that can be applied to inform future reef fish connectivity research in order to refine larval supply measures and local adaptation effects, including the incorporation of larval behavioural characteristics, spawning timing information and larval survival differences in space and time, depending on environmental conditions. Survival conditions may depend on differences in spawning time, environmental differences experienced during the larval phase and age/size at settlement/post-settlement stages. Other complexities, such as the influence of spatially different sensory zones (e.g. as a function of coral coverage) on larval connectivity could also be incorporated. Additionally, we need the observations for calibration and validation of hydrodynamic models and also for modelling larval dispersal, in order to improve modelling results.

In conclusion, this thesis represents one of the first attempts to examine reef fish larval connectivity patterns at a range of spatial and temporal scales on the GBR,

by combining biophysical modelling and genomics. Further, similar studies (using a combination of approaches and data used in this thesis) on other coral reef organisms with different characteristics will be very insightful. The use of novel hydrodynamic and biophysical models of the GBR ecosystem predicted a highly dynamic physical environment and associated variability in larval dispersal. A potential effect of selection on reef fish larvae and recruits was revealed. However, the effect selection may have on larval survival and population connectivity, particularly under GBR warming events and extreme climate conditions, requires further study. Overall, there is potential for regional and local larval supply to reefs on the GBR, and findings denote the relevance of considering temporal fluctuations (from annual to weekly scales) in larval dispersal when assessing connectivity and recovery of populations.

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