Modelling reef fish connectivity: Investigating the biological mechanisms that influence connectivity patterns

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Anybody who has been seriously engaged in scientific work of any kind realises that over the entrance to the gates of the temple of science are written the words: Ye must have faith. It is a quality which the scientist cannot dispense with.

- Max Planck, 1932

"Either you decide to stay in the shallow end of the pool or you go out in the ocean."

- Christopher Reeve, n.d.

Statement of originality

This is to certify that to the best of my knowledge, the content of this thesis is my own work. This thesis has not been submitted for any degree or other purposes.

I certify that the intellectual content of this thesis is the product of my own work and that all the assistance received in preparing this thesis and sources have been acknowledged.

Steven Maxwell Hawes

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Abbreviations

ANOVA
Analysis of Variance

BDM
Biophysical Dispersal Modelling

CAP
Constrained Analysis of Principal Coordinates

CCA
Constrained Coordinates Analysis

DVM
Diel Vertical Migration

EAC
East Australian Current

EM Reefs
Elizabeth and Middleton Reefs

GIS
Geographic Information System

GPS
Global Positioning System

MPA
Marine Protected Area

NetCDF
Network Common Data Form

NMDS
Non-metric Multidimensional Scaling

NSW
New South Wales

OHS
Orientated Horizontal Swimming

OPeNDAP
Open-source Project for a Network Data Access Protocol

OVM
Ontogenetic Vertical Migration

PERMANOVA
Permutational Multivariate Analysis Of Variance

PLD
Pelagic Larval Duration

RFU
Relative Fluorescence Units

RK4
Runge-Kutta fourth-order integration

SE
Standard Error

SNK
Student Newman-Kuel's test

TRACE
Transparent and Comprehensive Model Evaluation

ZISSOU
Zooplankton interconnections and source-sink observation utility

VA
Vertical Advection

Abstract

Connectivity in marine systems is defined as the exchange of individuals between spatially distinct populations. For most marine populations, due to sedentary adults, connectivity occurs during the pelagic larval phase with prevailing currents can transporting larvae considerable distances to settle amongst other populations. Research has increasingly demonstrated that species-specific biological traits, e.g. vertical migration and sensory abilities, can influence where larvae settle. Biophysical dispersal models (BDMs) — a hydrodynamic model coupled with a biological model — lend themselves to inferring potential connectivity patterns, as experimental studies using current methods are inherently difficult over extended spatial and temporal scales. Biophysical dispersal models are complex whereby the combination of the two models produces many input parameters that can potentially affect the output of the BDM. Many studies now use a BDM approach to measure connectivity. Therefore, it is essential to understand how sensitivity of parameters in predicting dispersal patterns, to determine the traits modelers should include. Increasing the realism (and hopefully in turn the accuracy and precision of models leads to better understanding of the connectivity between marine populations, with significant conservation implications for the design of marine protected areas. This thesis explored the biological processes that affect the connectivity patterns of ichthyoplankton using four related data chapters. The first data chapter, a meta-analysis of connectivity studies using BDMs, investigated both trends and consequences of modelling choices on derived connectivity patterns. The four most common metrics were identified (i.e. local retention, self-recruitment, settlement success, and dispersal distance) were used to compare the influence of different parameters. Even though not all studies reported all or any of these metrics, considerable variation was found amongst the reported values. Some patterns for both physical and biological modelling choices were discerned despite challenges in comparing BDM studies to the high number of modelling choices and lack of identifiable standard amongst reported metrics of connectivity patterns. The results of this meta-analysis provide a useful framework on parameter choice for future consideration of connectivity studies. The second data chapter is an experiment measuring the ontogenetic vertical migration of reef fish off the coast of south-eastern Australia. The ichthyoplankton of seven reef-associated families were collected at three different depth ranges (0-1m, 5-50m, 50-100m), assessed for the ontogenetic stage (pre-flexion, flexion or post-flexion) and measured for total length (mm). Vertical migration patterns were found to differ between each family. The ichthyoplankton sampled demonstrated deeper migration with both increasing ontogenetic stage and length. The only family that displayed an opposite trend was Mullidae. There was no change in vertical ontogenetic distribution between coastal or eddy waters; however, eddies entrained more developed and longer larvae. The third data chapter is a theoretical modelling chapter that investigated the effect of different swimming behaviours (e.g. no swimming, diel vertical migration (DVM), ontogenetic vertical migration (OVM), and orientated horizontal swimming (OHS)) and differences in the parameterisation and implementation of OVM in a BDM. The most important behaviour on connectivity patterns along the coastline of south-eastern Australia was OHS. Differences in the implementation of OVM had a stronger effect on connectivity patterns than differences in the OVM strategies. The fourth data chapter synthesised the results from the previous three data chapters and explored the predicted connectivity patterns of an endemic and threatened Australian reef fish, the black cod (*Epinephelus daemelii*) using a BDM. *E. daemelii* larvae showed strong connections to both the natal and proximate regions. Four subpopulations were resolved, with three along the coast of New South Wales (NSW), separated by latitude, and an off-shore population comprising Elizabeth Reef, Middleton Reef, and Lord Howe Island. Within the context of the current marine protected area (MPA) network of NSW, strong settlement regions (released from both known regions of aggregation and across the known distribution) had only moderate or no sanctuary zone coverage (i.e. no-take areas). Settlement regions where additional protection could be beneficial to the recovery of the *E. daemelii* population were identified, e.g. Yamba. The results of this thesis increase our understanding of the influence of behaviour on connectivity patterns and identify methods for researchers to advancing BDM studies, with the aim engendering greater realism across derived connectivity patterns for marine larvae along the eastern Australian coast.

Contents

1 General Introduction

Marine populations are structurally different to terrestrial populations as the conditions of the fluid environment typically favour open populations (Caley *et al.* 1996; Figueira and Crowder 2006). The ocean is a dynamic system with currents dispersing eggs or larvae over potentially considerable distances, creating interconnected regions. Larval dispersal has been a topic of interest in marine ecology for over a century (Hjort 1914, 1926). Traditionally the focus has been on larval supply and recruitment dynamics (Victor 1983; Underwood and Denley 1984; Gaines and Roughgarden 1985; Doherty 1991), however, recent advancements in the field have allowed us to investigate the origin of recruited larvae, revealing these systems are not as open as previously thought (Swearer *et al.* 1999; Cowen *et al.* 2000; Jones *et al.* 2005). The spatial extent of this dispersal and the connectivity between areas are key questions within the field of marine ecology.

Connectivity, within the context of this thesis, is defined as the exchange of individuals between spatially discrete populations (Palumbi 2003; Cowen and Sponaugle 2009). A metapopulation is defined as the collection of connected populations (Hanski 1998). In the marine context, the primary mechanism of connectivity for metapopulations is via the processes of dispersal and recruitment of larvae (Sale *et al.* 2006). Connectivity within a metapopulation can be highly volatile due to events that are intrinsic (e.g. low exchange of individuals; Castorani *et al.* 2017) or extrinsic (e.g. natural variation in currents; Watson *et al.* 2012). The connectivity between populations is fundamental to community dynamics (local and metapopulation levels), genetic diversity and population persistence (Lowe and Allendorf 2010; Burgess *et al.* 2014; Lett *et al.* 2015). However, the influence of biological processes that contribute to this connectivity, the importance of variable connectivity on population dynamics, and the general dispersal patterns for many larval fishes are not fully understood (Cowen *et al.* 2007; Snyder *et al.* 2015; Giangrande *et al.* 2017)

The central aim of this thesis is to contribute to the understanding of the processes that influence the dispersal of larval fish and connectivity patterns between populations. The thesis has four parts:

- a meta-analysis comparing studies to assess the trends and influence of biophysical dispersal modelling (BDM) structure and parameters on resulting connectivity patterns.
- an empirical evaluation of ontogenetic vertical migration (OVM) patterns of larval fish, a key biological process known to influence connectivity.
- an investigation of the influences of different behaviours, strategies and modelling choices on connectivity patterns using a BDM.
- an application of a BDM, incorporating outcomes from previous chapters, to predict connectivity patterns and appropriateness of current marine protected area strategy for the threatened black cod (*Epinephelus daemelii*) of the temperate region of south-eastern Australia.

1.1 Larval fish dispersal

Many marine species, such as the archetypal example of reef fish, experience a two-stage lifecycle, initially in a pelagic larval stage and then transition into a sedentary adult stage (Sale 1991). The differences in morphology, habitat, and behaviour between these two stages of larval fish development can be striking (Leis and Carson-Ewart 2000; Leis and McCormick 2002). The sedentary nature of the adult stage for marine species with this dual lifecycle, results in connectivity between discrete populations (and within metapopulations) occurring predominantly during this pelagic larval phase (which can last from days to weeks), unlike terrestrial animals where this connectivity occurs more typically by adult migration (Cowen *et al.* 2007). Because pelagic larvae can disperse over vast distances of up to hundreds or even thousands of kilometres, rigorous quantification of connectivity patterns can be difficult (Levin 2006). The closest terrestrial example is seed dispersal, but unlike seeds, fish larvae have natural behaviours that can influence their dispersal (Cowen and Sponaugle 2009).

Most reef fish are oviparous — females either lay their eggs attached to a benthic substrate (e.g. rock or plant) or broadcast spawn them for males to fertilise. Fecundity can range from tens to thousands to millions of eggs per spawning event (Sadovy 1996), a strategy, which offsets the extremely high mortality rate for larval fish (i.e. estimated to range from above 85%; White *et al.* 2014; Johnson *et al.* 2015 to higher than 99.95%; McGurk 1986; Houde 1989a). Upon hatching, larval fish are not fully developed and undergo morphological changes before becoming a settlement stage juvenile (Leis and Carson-Ewart 2000). The ontogenetic stages of larval fish are described around the development of the caudal fin, a process called flexion. Flexion is defined as the point in development at which the notochord of a larval fish starts bending upwards at approximately 45 degrees to begin the formation of the caudal fin. The development of the caudal fin allows larvae to develop meaningful swimming abilities and transform from a planktonic to a nektonic state (Leis 2006). The period from hatching until flexion is defined as preflexion, and postflexion describes the period after the caudal fin has developed, but before the juvenile stage that starts when metamorphosis is complete. The period the fish spends in this larval stage is called the pelagic larval duration (PLD). The PLD ends when the larvae settlement occurs, which requires them to be developed enough to swim and sense suitable settlement habitat. The length of the PLD is species-specific, but despite some variability, there is typically similarity within the lower taxonomic level such as genus or family (Wilson and McCormick 1999; Victor and Wellington 2000). Variation within PLDs arises due to individual larva having flexibility in the timing of settlement, although there are certain physiological limitations (e.g. temperature or food availability) and genetic limitations on both the earliest and latest time a larva can settle. The settlement competencies required during this metamorphosis for larval fish to settle include the development of functioning fins, larger body size and increased muscle mass, and sensory abilities to allow for navigation and habitat selection (Leis 2006; Montgomery *et al.* 2006; Dixson *et al.* 2014).

Dispersal of larval fish, and the subsequent patterns of dispersal, are driven by the interface of a complex series of physical and biological processes. Dispersal begins with a spawning event, the timing and location of which are two strong drivers that influence the dispersal pattern (Puckett *et al.* 2014; Bauer *et al.* 2015; Donahue *et al.* 2015). The most significant process that contributes to the connectivity between discrete populations is the dispersal by ocean currents. Entrainment in oceanographic features, such as mesoscale eddies, can influence dispersal by changing the direction and increasing development of larvae (Graber and Limouzy-Paris 1997; Shulzitski *et al.* 2015). Dispersal can be driven by the length of the PLD by allowing larvae more time to decide where to settle; however, PLD has not been shown to be a strong predictor of dispersal distance (Mora *et al.* 2012; Treml *et al.* 2012; Koeck *et al.* 2015). It is now understood that fish larvae are not passively advected, and larval fish develop behaviours that can influence the pattern of dispersal once released into the pelagic environment. Potential evidence of active dispersal includes the ability of larval fish to recruit with siblings (Ottmann *et al.* 2016) and high self-recruitment and local retention (Jones *et al.* 1999; Swearer *et al.* 1999; Paris and Cowen 2004), even for larval fish with long PLDs. Vertical migration (diel and ontogenetic) is one such behaviour that allows larval fish to influence their dispersal distance by moving away from wind-driven surface currents (Paris and Cowen 2004). Reaching the developmental stage of flexion enables larvae to start swimming, often at speeds greater than the encompassing current advecting them (Fisher *et al.* 2000). Larval fish develop a suite of senses that allow them to detect and swim in the direction of settlement habitat (Gerlach *et al.* 2007; Bottesch *et al.* 2016). One thought is that larvae must be close to some available settlement habitat before the end of their pelagic larval duration or they die (Cowen and Sponaugle 2009), however, this is far from certain.

1.2 The importance of connectivity for fish populations

Alongside births and deaths, population connectivity is the process that defines the dynamics of both local and metapopulations (Figueira and Crowder 2006). Metapopulation persistence relies on a constant degree of connectivity to occur (Botsford and Hastings 2006). Local populations (discrete subpopulations within a metapopulation, ignoring the movement of adults; Grimm *et al.* 2003) that are demographically connected rely on stable connectivity from source populations to persist (Lowe and Allendorf 2010). Variability in connectivity between populations has long-term consequences for metapopulation growth (Watson *et al.* 2012; Williams and Hastings 2013). This thesis focuses on ecologically relevant connectivity, i.e. demographic connectivity whereby dispersal affects population growth and persistence (Gotelli 1991), and not genetic connectivity, which requires only a few individuals to be exchanged per generation (Slatkin 1993).

Understanding connectivity of marine systems is paramount for the conservation and management of metapopulations (Roberts 1997; Botsford and Hastings 2006; Crooks and Sanjayan 2006; Lester *et al.* 2009). An important instrument in the marine conservation toolbox is the marine protected area (MPA; Halpern 2003; Lubchenco *et al.* 2003; Gaines *et al.* 2010; Mellin *et al.* 2016), which can be effective if designed with clear conservation goals (Saarman *et al.* 2013). Marine protected area is a broad term that refers to conservation areas with potentially different spatial zoning, ranging from “no take areas” or marine reserves to mixed use zones that allow recreational fishing and boating activities (McCook *et al.* 2010).

Historically, habitat quality and habitat preservation have been the primary priorities for marine conservation and connectivity has often been overlooked (Crowder and Figueira 2006), habitat preservation does not provide the same ability as well-connected networks of protected areas for populations to recover from disturbance (Almany *et al.* 2009). Therefore, to address population persistence, connectivity is now considered an essential requirement when designing MPAs (Botsford *et al.* 2009; Christie *et al.* 2010; Abesamis *et al.* 2016; Bode *et al.* 2016; Jonsson *et al.* 2016; Smith and Metaxas 2018). The design and planning of marine protected areas is critical to their success (Botsford *et al.* 2001; Claudet *et al.* 2008) and as such, understanding the dispersal patterns of marine species across their entire life-cycle is critical for the design of MPA networks (Lockwood *et al.* 2002; Grüss *et al.* 2011; Breen *et al.* 2015; Weeks 2017). Dispersal information is essential in understanding the spatial connectivity between MPAs in a network (Warner *et al.* 2000; Shanks *et al.* 2003; Schill *et al.* 2015; Carr *et al.* 2017), and also to assess the connectivity to other non-protected marine areas (Pelc *et al.* 2010; Harrison *et al.* 2012). However, designing a unified network is not without its difficulty (Watson *et al.* 2012; Kendall *et al.* 2015; Coleman *et al.* 2017) or controversy (Roff 2014) as marine species have different dispersal distances and the natural variation of extrinsic factors, and carrying capacity has the potential to be more important than connectivity (Cabral *et al.* 2016). To address the temporal flux seen in connectivity patterns within MPAs (Fox *et al.* 2016), the conservation management paradigm of dynamic marine protected systems has also been considered (Smith *et al.* 2007; Soria *et al.* 2014). Dynamic protected areas are well established in some smaller artisanal fishing communities (Cinner *et al.* 2012) and can be effectively used to manage fisheries and increase populations of targeted species (Hobday and Hartmann 2006; Game *et al.* 2009; Ban *et al.* 2011).

1.3 Measuring larval fish connectivity

Connectivity is one of the more challenging problems to study empirically in marine ecology (Cowen and Sponaugle 2009). Directly measuring larval fish connectivity with modern techniques is often challenging or impractical (and often impossible pending technological advancement in remote sensing; Witman *et al.* 2015). Larvae are minuscule (measured in mm) and exist within a vast oceanic environment. Larval fish are inherently difficult to track due to the combination of PLD ranging from weeks to months that allows them to disperse long distances (Victor and Wellington 2000) and high mortality rate — meaning only a fraction of the total spawned larvae will settle (Houde 1989a). Despite these difficulties, there are several direct and indirect methods for measuring dispersal using both natural and physical tags (Thorrold *et al.* 2007; Jones *et al.* 2009).

Natural markers are ubiquitous amongst larval fish (Kennedy *et al.* 1997; Campana and Thorrold 2001), which makes them experimentally advantageous. Genetic material is the most common natural marker used to measure connectivity (Hedgecock *et al.* 2007). There are several different methodologies for measuring dispersal using genetics, e.g. using genetic markers to compare gene flow between populations (Hepburn *et al.* 2009; Crandall *et al.* 2012; Serrano *et al.* 2016) or using parentage analysis to determine where progeny recruit (Jones *et al.* 2005; Planes *et al.* 2009; Berumen *et al.* 2012). Population-level gene flow is an indirect measure that requires less sampling effort, leading to a broader use amongst studies. Quantifying connectivity through gene flow involves comparing genetic microsatellite markers to determine if spatially discrete populations share genetic material (Doherty *et al.* 1995; Curley and Gillings 2009; Foster *et al.* 2012). The caveat to describing connectivity using gene flow is that only information on historical dispersal events (genetic connectivity) can be determined. Therefore, it is uncertain if larval connectivity occurred directly between two populations or indirectly through one or more connected populations. Parentage analysis, on the other hand, gives direct evidence of dispersal events but it requires onerous sampling of parents and progeny. This technique uses genetic markers to identify the natal population of new recruits giving estimates of dispersal distance (Planes *et al.* 2009; Berumen *et al.* 2012; Williamson *et al.* 2016), and with sufficient sampling can indicate the level of self-recruitment in populations (Jones *et al.* 2005; Herrera *et al.* 2016). The level of sampling difficulty increases when considering wider spatial or longer temporal extents. However, new methodologies have shown that dispersal kernels can be realistically estimated by sampling only 3% of the population (Bode *et al.* 2018). Determining connectivity through genetic markers is a continually changing field, with recent advancements giving the potential for greater insight into the dispersal movement between populations, e.g. genetic assignment tests on allele frequencies (Simpson *et al.* 2014).

A non-genetic natural marker for measuring the dispersal of larval fish is the elemental composition of an otolith, which can have markers of the surrounding chemical compositions of the water where the fish was spawned (Campana 1999; Swearer *et al.* 1999;

Thorrold *et al.* 2001). This technique has been used successfully to link adults with their juvenile nurseries in estuaries (Kennedy *et al.* 1997; Gillanders *et al.* 2003). For this technique to be useful, the spatial regions of interest must have identifiably different chemical signatures; otherwise, the exact birth location can be hard to ascertain (Thorrold *et al.* 2002). An inherent difficulty with this technique is that in marine and freshwater systems, the environmental markers are in constant flux (Swearer *et al.* 2003) and therefore constant monitoring must occur to confidently predict dispersal using otoliths (Gillanders 2002).

Techniques for physical markers on larval fish have developed in the last 15 years that allow direct measurement for connectivity (Cowen and Sponaugle 2009). Physical tagging can be applied using fluorescent chemical markers (Jones *et al.* 1999, 2005; Thorrold *et al.* 2002), staining clutches of eggs that provides information about the connectivity from a single location. Trans-generational marking, a technique less labour-intensive than fluorescent marking, involves injecting adult breeding females with enriched stable-isotopes (e.g. ^{137}Ba) that are passed onto each spawned egg and are incorporated into the otolith of the larvae (Thorrold *et al.* 2006). Dispersal can be measured by sampling recruits and detecting the stable isotope in the otolith. Studies have used this technique effectively to investigate connectivity of reef fish populations over small spatial scales (Almany *et al.* 2007) and comparing inter-annual variability (albeit with exhaustive sampling; Cuif *et al.* 2015). The advantages of trans-generational marking are that marking one female, in turn, tags each egg produced (for a period), reducing the number of adults required to mark, and that by using different concentrations of the stable-isotope, different locations can be discerned. The direct and indirect empirical methods described above can give accurate measurements of dispersal success and distance over smaller spatial scales but become almost impossible when considering long dispersal distances, e.g. coastal extents. Additionally, low sample sizes lead to a lot of uncertainty in the results of these empirical methods, although statistical tools have been developed to address these issues (Kaplan *et al.* 2017).

Biophysical dispersal models (BDM) are an alternative method to empirical measurement to predict potential connectivity patterns (Sponaugle *et al.* 2002; Paris *et al.* 2007). Consisting of coupled physical and biological models, BDMs reflect the complex interaction of processes on larval dispersal patterns. The physical model used in a BDM a numerical hydrodynamic model, often combined with data assimilation techniques of observation systems to resolve mesoscale and sub-mesoscale oceanographic processes, e.g., fronts and eddies. Open ocean circulation models are well understood; however, the near-shore dynamics (interaction of cross-shore and along-shore processes) are not as established due to their inherent complexity and variability (Largier 2003). Compared to our understanding of oceanographic processes, the fundamentals of many biological processes are not well understood. As our understanding of the early-life history of fishes (and other marine species) has progressed, the biological models in BDMs have increased in complexity. Individual-based models are the most common variant of BDMs, whereby the model advects individual larva encapsulating biological traits and behaviours through the hydrodynamic matrix. The biological models are often species-specific, using information gained from empirical studies of the early-life history for that particular species, but sometimes using general information to describe a suite of species. Studies using species-specific models are often difficult due to the lack of available information on the early-life history of many species, and often many assumptions must be made (Leis 2007). Therefore, identifying key biological processes influencing connectivity and information on larval fish behaviour are important areas of research.

Inferring patterns of larval dispersal using BDMs is a cost-effective tool compared to the empirical methods described above. Modelling provides the ability to manipulate parameters, and therefore ask questions that cannot be easily achieved with empirical methods, e.g. changing spatial extents ranging from localised reefs (Andutta *et al.* 2012) to global spatial scales (Wood *et al.* 2013; Treml *et al.* 2015) and changing temporal scales from intra-annual (Robins *et al.* 2013) to inter-annual (Young *et al.* 2012). Manipulating parameters allows for exploration of the influence of physical and biological processes and biological traits on connectivity, something that is difficult to measure empirically. These modelled patterns of connectivity, combined with other empirical measures of dispersal, provide a powerful tool for the inference of larval connectivity (Werner *et al.* 2007; Coscia *et al.* 2012; Foster *et al.* 2012; Crochelet *et al.* 2013). Studies measuring larval dispersal have been utilising BDMs for over three decades (Wroblewski 1982; Bartsch and Backhaus 1988), with increasing complexity being built into the models over time (Miller 2007; Werner *et al.* 2007; Cowen and Sponaugle 2009; Lett *et al.* 2009; Willis 2011). These models have been successfully used to assist in the design and planning of well-connected MPAs (Andrello *et al.* 2013; Jonsson *et al.* 2016; Coleman *et al.* 2017) and in understanding the larval dispersal of commercially important fisheries (Incze *et al.* 2010; Kough *et al.* 2013; García-García *et al.* 2016). The results of models are predictive only, and qualification on applications of these models is justified. Research must also focus on the validation of these models, considering the input parameters, the modelled processes, and the predicted connectivity patterns.

1.4 Thesis outline

The primary objective of this thesis was to investigate the processes, principally biological and behavioural, that influence the dispersal and connectivity patterns of larval fish. Three decades of research using BDMs have given many of examples of major findings and advances in connectivity research (Miller 2007; Cowen and Sponaugle 2009; Willis 2011). As with any cohesive field of research, there is a common aim to advance our overall understanding of the discipline finding generalities across studies, yet often results are conflicting (Leis 2010). This topic was explored using four interrelated data chapters. The first data chapter is a meta-analysis, evaluating published BDMs and identifying modelling decisions (both physical and biological), with the aim of building upon a previous review by Miller (2007). The first aim of the chapter was to identify trends in the inclusion and exclusion of modelling parameters, with the goal of understanding if there is a minimum suite of parameters that should be included in future BDM studies. More importantly, the second aim of the chapter was to understand the consequences of modelling choices on the resulting connectivity patterns. Common metrics were identified and compared across different parameter choices to understand the effects. These results provide a template for BDMs in the future by highlighting the outcomes of modelling choice and identifying knowledge gaps in important parameter choices.

The impetus for Chapter 3 was the knowledge gaps in the empirical data on the OVM patterns of larval fishes found along the eastern coast of Australia. Vertical migration, the ability of fish larvae to change position in the water column, is known to indirectly influence connectivity patterns by acting as a retention mechanism and limiting dispersal (Paris and Cowen 2004). Knowledge gaps on OVM patterns can hinder connectivity research on specific species, as BDMs can be forced to either exclude or at best use hypothetical OVM behaviour if no empirical information is available. Even with the information that is available on species, generalising within species, between species, and across regions is fraught with difficulties due to the variability in behavioural traits (Leis 2007). OVM is considered an important process in the dispersal of larval fish (Paris *et al.* 2007), and therefore I decided to gather data on these patterns for reef fish off the eastern coast of Australia. The experiment consisted of 16 sites, sampling larval fish at three different depths. Larval fish were identified down to the family level, and I analysed the seven reef-associated families with the largest sample sizes; Labridae, Mullidae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae, and Synodontidae. Larval fish at each depth were identified to the ontogenetic stages described above, and the length measured. While there have been many larval fish assemblage studies off the New South Wales (NSW) coast (Gray 1993; Dempster *et al.* 1997; Matis *et al.* 2014), only one study has specifically investigated the OVM patterns of some reef fish families (Leis *et al.* 2006). The effect of oceanographic features on connectivity pattern was another consideration, with the aim to see if the ontogenetic distribution changed when larval fish were in coastal waters entrained by the East Australia Current or within an eddy.

Chapter 4 is a theoretical modelling study, using a BDM to investigate the effect on connectivity patterns of several different behaviours: passive movement (restricted to the surface), vertical advection (passive movement with no vertical restriction; VA), diel vertical migration (DVM), OVM, and orientated horizontal swimming (OHS). I developed a BDM using the recommendations of North *et al.* (2009) and built upon other recent publications. Understanding which behaviours are important to connectivity allows us to focus empirical research on gathering information about these behaviours that can then be used in a modelling context. The second aim of this chapter was to gain an understanding of the sensitivity of larval fish behaviour (i.e. OVM) to different parameter values and methods of implementation. Gaining insight into the importance of parameter choice helps us understand the impacts of making assumptions to parameterise models when empirical knowledge of behaviour for a particular species is not available in from the literature.

The final chapter synthesised the results of each of the previous data chapters to investigate the connectivity of *E. daemelii*, a threatened reef fish endemic to NSW. I used the BDM developed for Chapter 3, configured to use the important behavioural traits for dispersal models identified in Chapters 2 and 4, and parameterised using the vertical distribution data gathered for Serranidae in Chapter 3. The larval dispersal patterns were generated during known spawning times across the eight-year period (2004-2011) and across the known distribution within Australia. Comparisons were made between the connectivity patterns seen with larvae spawned across the known distribution, and larvae spawned from only regions with known aggregating populations. Finally, these connectivity patterns were compared to the current legislated network of marine protected areas, both under state and federal jurisdiction, to identify if there are areas not currently protected that might assist *E. daemelii* in population recovery.

The oversimplified assumption that larval fish are passive actors to the surrounding oceanography during their pelagic larval stage has been debunked (Leis 2006). Furthering our understanding of larval fish behaviours and how much they affect connectivity is now a primary research focus. Through these four sections, this thesis endeavours to advance our understanding using a combination of experimental techniques to measure ontogenetic vertical migration distributions and theoretical modelling for assessing impacts of larval behaviours on connectivity patterns.

2 Making the right choices: understanding the impact of biophysical dispersal modelling on connectivity patterns

2.1 Abstract

Biophysical dispersal models (BDMs) are a tool for assessing both potential and realised connectivity of marine species with a pelagic larval phase. While BDM complexity is increasing as numerous parameters, including biological behaviours, are built into connectivity models there does not appear to be a consensus about the importance of these parameters. I synthesised 132 BDM studies (with 589 models) to investigate the parameter choices made, and collated common metrics from the resulting connectivity patterns. The first aim of this review was to examine the trends of these choices for BDMs, in particular which biological parameters studies are including in their models. The second aim was to assess the impact of different parameters on the resultant connectivity patterns, as represented by four commonly reported metrics; local retention, self-recruitment, settlement success, and dispersal distance. Due to the large variation in specific parameters included in each model, as well as differences in connectivity metrics reported, factorial comparisons of the effects of all relevant parameters on each metric were not possible. Interesting patterns emerged, such as model resolution not having a strong effect, mortality not greatly reducing settlement success and larval behaviour increasing the settlement success. To progress this field further I need to decide upon common metrics that allow meaningful comparisons between models, along with model validation against empirical results to start identifying the importance of different BDM parameters. This review should provide researchers with more context on what parameters are important to include in future BDM studies.

2.2 Introduction

Biophysical dispersal models (BDMs) have been used to investigate marine dispersal patterns for over three decades (Wroblewski and O'Brien 1981; Wroblewski 1982; Rothlisberg *et al.* 1983; Bartsch and Backhaus 1988) becoming increasingly common in the last 10-15 years to estimate marine larval connectivity. BDMs produce potential patterns of connectivity using a physical (i.e. hydrodynamic) model, coupled with a biological model, encapsulating the biology of a marine species, to move the larvae within the physical system (Cowen and

Sponaugle 2009). These models lend themselves to studies inferring distributional patterns for marine species with two distinct life stages, a pelagic larval stage and contrasting sedentary adult phase. BDMs allow us to investigate questions that are inherently difficult to ask *in situ* (Cowen and Sponaugle 2009), from allowing us to investigate potential connectivity patterns over wide spatial scales (Andrello *et al.* 2013; Treml *et al.* 2015) and long temporal scales (Berglund *et al.* 2012; Richar *et al.* 2015); to investigating how early-life history traits (e.g. spawning times, diel migration, and swimming abilities) affect connectivity patterns (Butler *et al.* 2011; Staaterman *et al.* 2012).

Complexity and realism in BDMs have increased progressively; likely driven in part by both reduced costs of high-performance computing and increasing open access to high resolution oceanographic flow models and dispersal models. Basic research is also fuelling this trend, as studies are increasingly demonstrating the nektonic ability of pelagic marine larvae (Leis 2010). Miller (2007) evinced this trend in the review of larval fish biophysical modelling (referred to by Miller as individual-level, coupled physical-biological models), where 43.3% of studies implemented behaviour, predominately age-dependent vertical migration behaviour. This increased focus on the importance of the biology in BDMs has led to important insights about the role of larval behaviour in dispersal. Spawning behaviour (along with the location of the natal site) influences dispersal patterns (Puckett *et al.* 2014), and vertical movement of larval fish increases retention near the natal site and affect connectivity patterns (Paris and Cowen 2004; Paris *et al.* 2007; Brochier *et al.* 2008; Robins *et al.* 2013). Horizontal swimming has not been specifically included in BDMs (commonly implemented as a random walk) to the same extent as vertical migration, although combined with the ability for larvae to orientate towards a source, it is expected to influence larval connectivity patterns (Leis *et al.* 2007). Directed swimming towards settlement sites increases settlement success, including settlement at or near the natal site (Staaterman *et al.* 2012; Wolanski and Kingsford 2014). From empirical studies it has been observed larval fish can achieve considerable swimming speeds, potentially giving the ability to out-swim the surrounding current, and it improves with growth (Leis and Fisher 2006).

This previous work has made it clear that the biological components of BDMs can strongly affect connectivity patterns; and this emphasis has been recognised in the ICES publication, “Manual of recommended practices for modelling physical-biological interactions during fish early life”, providing implementation guidance for researchers (North *et al.* 2009). Larval behaviour is prominent in published BDM tools, such as the Connectivity Modelling System (CMS; Paris *et al.* 2013) & Connie3 (http://www.csiro.au/connie/). But despite this increasing attention paid to the importance of the biological model, there remains little consensus on the relative importance of different biological parameters. For BDMs to be a robust tool in understanding the connectivity of marine populations (across similar taxonomic groups and oceanic regions), such a consensus of the minimum amount of biology to include is ultimately required is ultimately required. Considerable context dependence of the relative importance of some biological parameters may exist (i.e. the importance of horizontal swimming may depend on the strength of the flow regime or the length of the larval period), while the inclusion of others may always make a large difference to the resulting connectivity patterns.

In this study, I review the recent literature using BDMs to evaluate the ability of this collective body of work to provide insight into the ramifications of the choices made when attempting to include complexity and realism in models. I achieve this aim by firstly evaluating if the field is progressing in its inclusion of several distinct, but common biological parameters. I look at the collection of parameters included in BDMs, how this is changing over time, and if there are trends in how parameters are included (or excluded) based on the context of models. I define a model as a distinct collection of parameters for a BDM, and a study as a published collection of one or more models. Secondly, and most importantly, I investigate the consequences of including different parameters on model results. Here I assess if there are observable differences in key metrics of connectivity as a result of the inclusion of specific biological parameters. I also assess the degree to which the physical context of the models regulates any observed effect of biological parameters. This information will serve to guide the application of BDMs into the future and by highlighting the ramifications of the inclusion/exclusion of key biological parameters. It will also identify gaps in the implementation of these parameters which should serve to identify necessary empirical work needed to address these shortcomings.

2.3 Methods

2.3.1 Literature search

I searched for relevant studies (a non-exhaustive search) using the keywords; connectivity, model*, and larva*, querying the online search engines: ISI Web of Knowledge, SCOPUS, and Google Scholar. I found 132 published studies (with 589 distinctly parameterised models) matching these criteria, published in 50 journals (see the full list of references in Appendix A). I constrained the search criteria to after 2009, the publication date of the ICES manual recommending the way forward for biophysical connectivity models (North *et al.* 2009), and also close to the date of the last review in this area (Miller 2007). Whilst my primary research interest was the connectivity patterns of larval fish, I included connectivity studies modelling other marine species with a pelagic larval stage and sedentary adult phase (e.g. molluscs, crustaceans and corals), owing to often negligible differences in parameterised behaviours.

2.3.2 Data classification

Studies often performed multiple connectivity simulations (models) using variations of their BDM (involving different input values for one or more parameters), commonly undertaken to test the effect of different parameters (representing different species/taxa or variations in behaviours of the same species/taxa) on resulting connectivity patterns. In this review, I separately identify each of these scenarios within a study and refer to each as a model. The trends across studies are investigated when there are consistent common traits across models with a study (e.g. publication year, hydrodynamic model, and oceanographic region).

Each model was characterised by its traits, broadly grouped into three themes. The first theme looked at the context and the parameterisation of the physical model e.g. study location, specific particle tracking software, and hydrodynamic model used. To test an effect of the modelled geographical area on settlement, the regions were broadly categorised into open (i.e. coastal or island) or closed (i.e. bay or inland sea). The second theme considered the parameterised larval traits, i.e. pelagic larval duration, settlement competency (the time-period from when the larvae were allowed to settle to the end of the pelagic larval duration), spawning times, mortality, growth and movement behaviours. The third theme considered the metrics used to measure the connectivity patterns of the model and their specific values. In-excess of 20 different metrics were used to describe the patterns of connectivity predicted from BDMs. Several metrics were common amongst studies (i.e. dispersal kernels and connectivity matrices), while others were unique to a study. These metrics can be broadly categorised into two related classes. The first class included those metrics which summarised the dispersal kernel (mean, variance directionality) while the second captured metrics which identified connectivity pathways more explicitly (self-recruitment, local retention and settlement success; defined in Table 2.1). Specific values for every metric were not available from every study, and where possible, values were extracted from figures using GraphClick software (version 3.0.3; http://www.arizona-software.ch/graphclick/).

Table 2.1: *The definition of terms used when referring to the output of biophysical dispersal modelling studies in this review, definitions were adapted from Burgess et al. (2014), Cowen and Sponaugle (2009), Holstein et al. (2016)*

Term	Definition
Self-recruitment	The percentage of settlers to a site, regardless of their origin site, that were natal to that site.
Local retention	The percentage of the larvae natal to a site that recruited back to that site.
Settlement success	The percentage of recruits natal to a site that recruit to any site.
Dispersal kernel	The probability density function of the dispersal distance for the larvae released in the system.
Connectivity matrix	A matrix with columns specifying *i* natal sites and rows specifying *j* settlement sites, showing the probability of a larva spawned at site$_i$ that settles at site$_j$ at position$_{ij}$.

2.3.3 Data analysis

To address my aim of evaluating the application of biology in BDMs, I summarised model characteristics from my three themes and evaluated their relative occurrence and how this has changed over time. To address my aim of identifying the importance of including biological parameters on different metrics of connectivity as well as the context dependence of any such relationships, I compared each of the most commonly reported connectivity metrics (self-recruitment, local retention, settlement success and dispersal distance) amongst models including certain parameters. Due to differences in the metrics reported or obtained from studies, there is considerable variation in the sample sizes for each metric. I required there be at least five studies for a given metric within a parameter group to conduct a comparison. Linear regressions were used to compare the relationships of metrics and continuous model parameters and Student or Welch's t-tests (checking for equal variance using Bartlett's test) were used for comparisons between the metrics and categorical model parameters when there were only two levels. P-values were adjusted for multiple comparisons using false discovery rates (FDR; Pike 2011) using the *p.adjust* method in R (R Core Team 2018). To compare the influence of behaviours with the reported metrics, which was proportion data with heteroscedastic variation (using Barlett's test), I used beta regressions and used least squares means to conducted post-hoc pairwise analysis and corrected using FDR. I conducted all data analysis using the R programming language version 3.5.1 (R Core Team 2018).

2.4 Current trends in biophysical connectivity modelling

There was a mean of 19.3 BDM studies per year over the review period, peaking in 2012 (25 studies; Figure 2.1) — the last eight years of Miller's (2007) review averaged of 6.6 studies, demonstrating the increased prevalence of BDM studies as a research tool. In this section, I explore the current trends in both input parameters and output metrics of connectivity studies, using the four model characteristic themes of model context, biological model parameters, and the metrics of connectivity used.

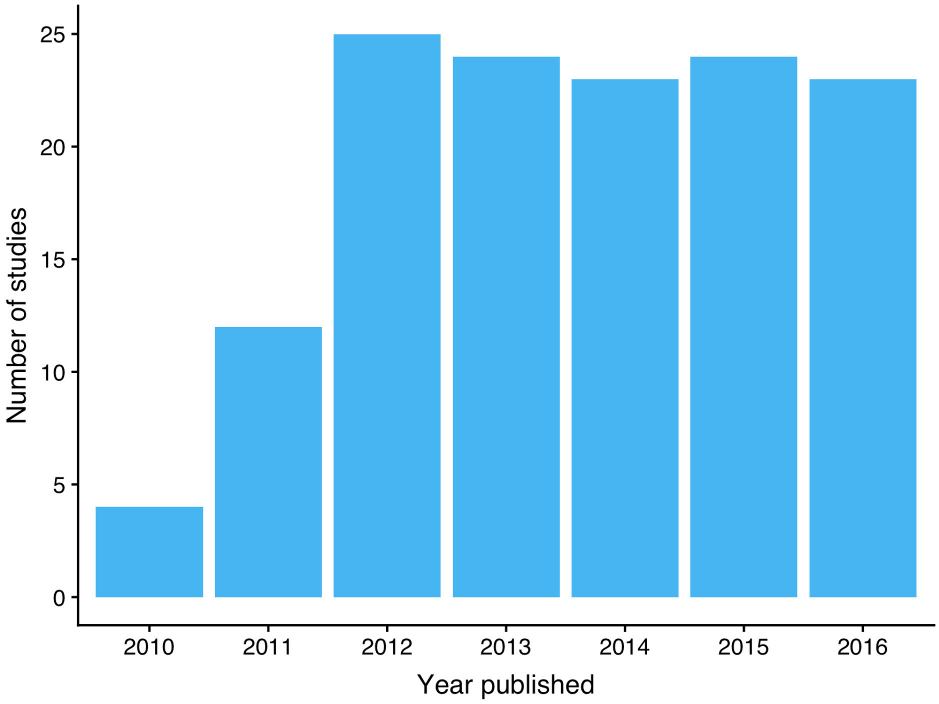

Figure 2.1: The number of studies using a biophysical dispersal model by publication year that were included in the review.

2.4.1 The model context

Most of the connectivity studies used an existing BDM (82.7%), the rest either built a BDM to answer the study question (15.8%) or specific information about the BDM was missing from the methods (1.5%). This high BDM reuse suggests increasing confidence in the output and ease of adoption for end-users — both essential for maturing the field. Although, whether this BDM reuse is based on evidence from partial model validation i.e. using genetic connectivity studies, or the reuse stems from other factors is hard to determine. Another benefit of reuse is that published BDMs have undergone the peer-review process, resulting in less onerous rationalisation of model methodology. Thirty-four different BDMs were used amongst the studies, although I was unable to identify the exact particle tracking model used for 24.8% of the studies. The three most popular BDMs were CMS (12.8%; Paris *et al.* 2013), Ichthyop (11.3%; Lett *et al.* 2008), and MGET (6.8%; Roberts *et al.* 2010). Every study used forecasting for their models, except for three hindcast solutions, where the larvae are initially tracked from settlement sites to determine their natal sites (Wren and Kobayashi 2016). The most popular hydrodynamic models used were ROMS (23.0%), the HYCOM (20.0%), and MARS3D (6.7%). Miller (2007) showed in his review the majority of studies used FEM (20%), HANSOM (12.9%), or ROMS in 7.1% of studies. It shows a current trend towards open-source models. The mean horizontal resolution of the hydrodynamic models was 5.2 km^2 (median of 3.7 km), ranging from finest (50 m; Brennan *et al.* 2014) to coarsest (33 km; Crochelet *et al.* 2013). In Miller (2007) the mean horizontal resolution was twice as coarse (10.8 km). Several BDMs nested hydrodynamic models (16.0%), to overcome issues of low resolution near coastal areas in modelling by using specific regional models. The hydrodynamic models covered over 20 different oceanographic regions across the world, of which three studies investigated connectivity patterns at a global scale. As observed in Miller (2007), modelling effort concentrated on highly industrialised fishing regions (i.e. the North-East Atlantic and Mediterranean Sea), and two-thirds were in temperate regions. Although, the number of studies in tropical regions increased to 36.0%, up from the 4.0% in Miller (2007). The behavioural aspects of early-life histories of tropical marine species (e.g. movement and orientation behaviours) are more commonly researched and thus increased focus on tropical connectivity patterns is not unexpected.

The studies used different time-scales of oceanographic data depending on the connectivity questions asked (inter- or intra-annual). Although studies trended towards running the BDM over a number of years (median = 3 years), one-quarter used only a single year (25.1%). One study used yearly average input data to interpret mean connectivity patterns (Feutry *et al.* 2013), accounting for variation, while also reducing the runtime of the model. Other outliers included studies investigating climate change scenarios, which used periods of 60 years (Aiken *et al.* 2011) and 130 years (Andrello *et al.* 2014) or a global connectivity study using 100 years (Jönsson and Watson 2016). Not all studies used a continuous period for the hydrodynamic forcing, choosing instead to use a suite of specific years. Knowing both that there is annual variation in the hydrodynamics of many oceanic regions (Pickard and Emery 2016) and that currents are a contributing factor to recruitment variation (Werner *et al.* 1997; Sale 2004); as high-powered computing becomes more readily available, the trend for BDMs should be towards using multiple years of oceanographic data. However, there is little evidence for this trend over the past 20 years based on Miller (2007) and this review. Modellers, particularly for studies focusing on demographic connectivity, should strive to include longer time frames, as this allows for inter-annual comparisons of connectivity patterns and accounts for natural variation in currents and allows us to infer how larval connectivity might differ with future climate change scenarios (Coleman *et al.* 2017). Although, it must be noted that predicted future dispersal scenarios can only be estimated using data from past observations, so caution has used when interpreting these dispersal patterns.

2.4.2 How connectivity studies are parametrising the biological model

Ten marine taxonomic groups, and one generic group, were identified from models parametrised using 83 specific species and 12 family level characteristics (Figure 2.2). The generic taxonomic group, applied in situations where a model used biological parameters that are applicable to multiple species, e.g. a specified pelagic larval duration. The most common taxonomic groups were either Generic or Fish (43.8% and 29.0% respectively; Figure 2.2), with the number of larval fish BDMs that were published each year consistent to that reported by Miller (2007) study. It must be noted, one study using generic species had 99 models (16.8% of the total models analysed in the review) implementing a suite of life history parameters (Treml *et al.* 2015). Using a generic taxon theoretically (provided dispersal patterns are not highly sensitive to a given trait) allows for more general interpretations (covering all species with similar traits) of the modelled dispersal patterns.

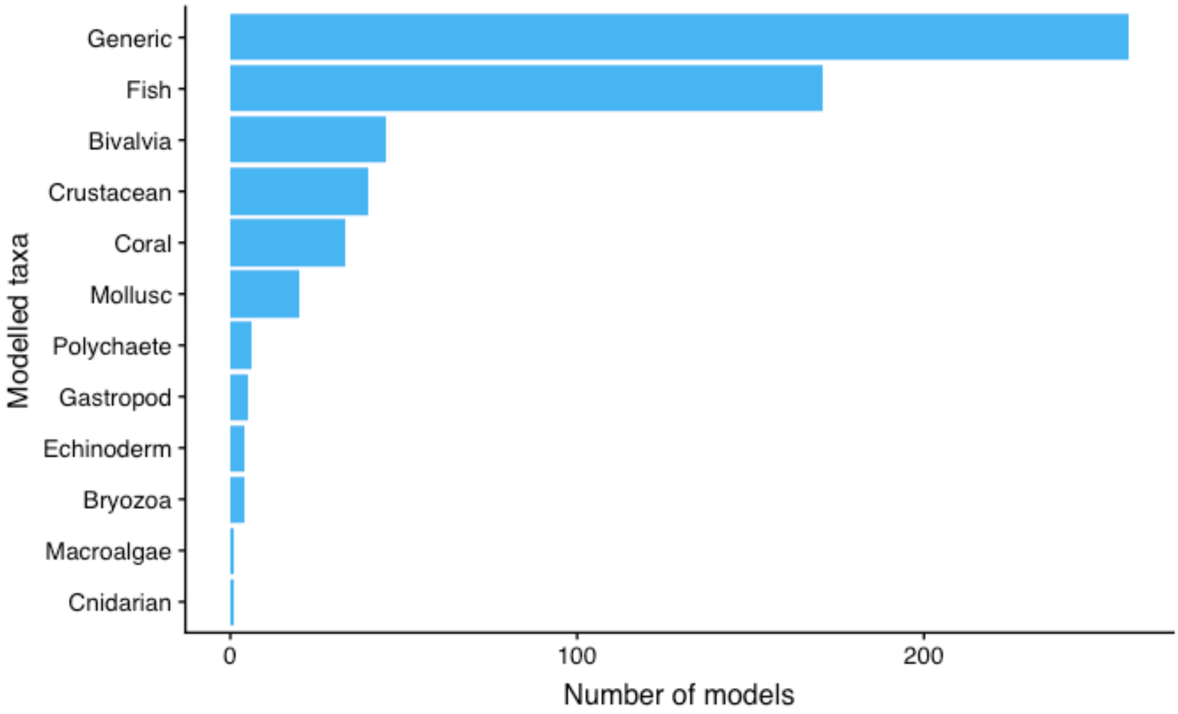

Figure 2.2: The identified taxonomic groups that were used to parameterise the biological model used in the biophysical dispersal modelling studies, from either species or family level attributes. The generic taxonomic group refers to models that used parameters values which were not specifically tied to a species, but rather could be shared across numerous species.

The biological parameters implemented were not consistent across studies, apart from: pelagic larval duration (PLD; 99.2%) that consisted of both fixed (91.1%), variable (6.0%; i.e. using a variable such as temperature), or a combination of both; and spawning behaviour (95.3%) that consisted of including information on timing, location, and amount of spawning larvae - as mentioned there was several models using a hindcast solution where spawning behaviour is not applicable (Table 2.2). These traits are fundamental to connectivity studies for marine larvae and these results were expected. The lack of consistent usage of other traits and behaviours could be attributed to a lack of concern that biology strongly influences patterns of connectivity. Given that recent publications do generally acknowledge the influence of behaviour on connectivity patterns however, it’s more likely this pattern can be attributed to gaps in biological knowledge about the early-life history of many marine species which makes biological parameterisation uncertain.

***Table 2.2**: The percentage of biological traits and behaviours that were implemented in the models of the reviewed biophysical dispersal modelling studies.*

Functionality	Implemented (%)
Pelagic larval duration	99.2
Spawning strategies	93.2
Settlement competency window	50.6
Sensory ability	46.3
Mortality	36.2
Movement	28.9
Growth	5.4
Orientation	4.4

The pelagic larval durations (PLD) ranged from 1-420 days, with a median of 30 days. The PLDs were taken from published values for species or taxonomic family where available, with the longest PLDs occurring for invertebrate species (e.g. the long duration ~400 days for the phyllosoma larval stage of lobsters; Butler *et al.* 2011; Kough *et al.* 2013). While these are the upper end for many zooplankton species, it is known that within a global context, planktonic species can follow larval duration paths measured in years or decades (Jönsson and Watson 2016). Approximately half the time PLDs were used in conjunction with a settlement competency window (50.6%; Table 2.2). The settlement competency window gives the marine larvae a period in which they are too young to settle, hence they become competent after a defined period. It is based on their known biology, where possible, incorporating the hypothesis that larvae must sufficiently develop morphological features before the pelagic larval stage can finish. The median start date when the larvae were considered developed enough to settle was nine days, which gave a period before the upper PLD day range was reached when the larvae could settle, creating a dynamic PLD for the larvae if suitable settlement habitat was found.

The spawning strategy was dependent on the biology of the modelled taxa and included pelagic eggs, demersal eggs, or brooding; implemented by changing the depth for the release of the larvae, e.g. demersal eggs were released on the bottom of the natal reef and pelagic eggs were released higher up the water column. The timing of when larvae were released varied from hourly intervals (Nilsson Jacobi and Jonsson 2011), daily (Kough *et al.* 2013), monthly (Staaterman *et al.* 2012), on lunar cycles (Davies *et al.* 2014) or a one-off spawning event (Huebert *et al.* 2011). Typically, the spawning events were pre-determined, but several studies using variable release times initiated by ocean temperature (Rochette *et al.* 2012; Andrello *et al.* 2014) or wave height — used by one study to spawn abalone larvae (Miyake *et al.* 2011). The number of release and settlement sites were different for nearly half of the studies (49.6%), often using a limited set of release sites with more available settlement sites to investigate the connectivity from known spawning areas. The number of larvae spawned varied considerably at each release site (10-10,000,000 larvae). The total larvae tracked in the system (spawning site multiplied by the number of sites, multiplied by the number of releases) had a similarly extended range of 328 in total to a sizeable 6.1 billion, with a median of 2.4 million. There can be an issue of not encapsulating the true estimate of dispersal patterns when BDM models use too few larvae (North *et al.* 2009; Willis 2011), however, the large median here suggests that for the most part computing power has lessened this consideration.

Larval mortality was implemented in only 36.2% of the models (Table 2.2), which was higher than the 30.8% in Miller's (2007) review. However, the implementation of mortality varied across the models, and the most common mortality function used was a constant function (82.1%), where a fixed percentage of the larvae were killed each day. The mean constant mortality rate used was 20.0%, ranging from 1.7% to 46.0%. Other mortality implementations were to use a decay function that decreased mortality based on age (8.2%), to kill the larvae based on a known temperature or salinity threshold (6.3%) or using a Weibull function (1.5%). Unlike in Miller's 2007 review, where growth was implemented in one-third of the studies, only a small number of the models reviewed had the ability for larvae to grow (Table 2.2). Growth rates of pelagic larvae are difficult to incorporate into a BDM where drivers of larval growth, e.g. environmental factors, temperature, and food availability are unknown (Metaxas and Saunders 2009).

The degree to which larvae can behave, specifically sense, orient and swim directionally (vertically or horizontally) is a fundamental concern in broader field of larval biology which has potentially important ramifications for connectivity. As discussed previously, this has been recognised in the world of BDMs, with general support for the inclusion of such behaviours. In this review, studies were classified according to which of the four-major larval behaviours were implemented; no movement (passive movement), movement (e.g. horizontal or vertical swimming, or vertical drift/buoyancy of larvae), orientation (ability to orientate towards a reef using sensory cues) and settlement (settle at a site using a sensory buffer or sticky zones). Larvae were given the ability to move in 28.9% of the studies (Table 2.2), conversely in 69.4% of the studies the larvae were assumed to be passive. Miller (2007) observed that 43% of the fish studies in the reviewed papers implemented movement behaviour, thus the percentage of BDM studies implementing larval behaviour is decreasing. Of the behaviours classified as movement, vertical migration using the Earth's rotation (diel) was the most commonly implemented behaviour (38.2%), with vertical migration synchronised with tides was also common (14.1%). Ontogenetic vertical migration, the idea that marine species change their vertical position in the water column dependent on their ontogeny, was used in 22.4% of the studies. Horizontal swimming was also implemented in 18.2% of the studies, although it must be mentioned that random walks to mimic turbulence does encapsulate undirected horizontal swimming and was used in almost all studies. A smaller number implemented vertical swimming in the larvae (11.2%). Some other movements included in studies were prompted by environmental conditions such as salinity (halocline migration; 0.6%) or migrating with the pycnocline (3.5%). The ability of the marine larvae to sense settlement habitat was implemented in 46.3% of the studies (Table 2.2). The common approach was to implement a buffer or sticky zone around the settlement site (91.2%). The mean size of this sensory zone was 10.7 (± 8.9) km. The other implementation gave the larvae a detection distance relative to the settlement site (Staaterman *et al.* 2012; Wolanski and Kingsford 2014). This settlement cue was used to allow the larvae to orientate towards, and thus swim in the direction of the reef if the larvae was within the cue distance ranging between 1-10 km (mean distance was 3.5 km), with a combination of early and late onset orientating abilities.

I compared the modelling of behaviours between two taxa groups, fish and invertebrates, for the reason that fish tend to have move swimming behaviour implemented based on their biology (ignoring generic taxa and non-animal models). Surprisingly movement was more consistently implemented in invertebrate studies than fish, where 2010 and 2011 only had studies with passive larvae and settlement behaviour (Figure 2.3 a, b). The proportion of fish models with passive larvae trended downwards over the course of the review, with movement included in more than half of all models in 2016 (Figure 2.3 c). For invertebrates, the proportions of actively moving to passive larvae occurred in fairly equal proportions, except for 2014, when the majority were passive moving studies (Figure 2.3 d). Orientated swimming was only implemented in the fish models, and in low numbers (Figure 2.3 a). For both fish and invertebrates, the proportion of models implementing the ability to sense settlement habitat remained constant, although this proportion was higher in fish models (Figure 2.3 c, a).

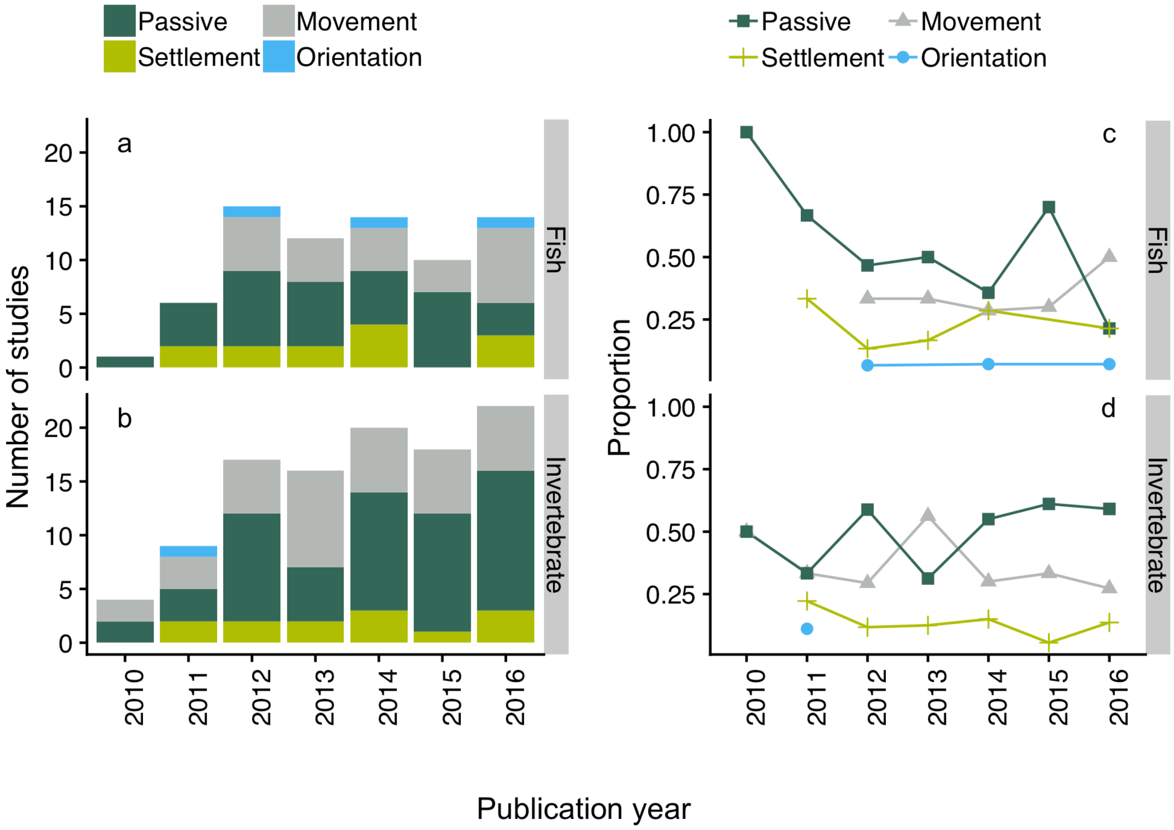

Figure 2.3: The total number of studies using biophysical dispersal models implementing behaviours for fish (a) and invertebrates (b) and the proportion of the published studies for fish (c) and invertebrates (d) by the publication year. The behaviours are passive = passive movement of the larvae; movement = the ability of the larvae to move, settlement = larvae can sense suitable habitats for settlement using a "sticky" zone; and orientation = larvae can orientate and swim towards settlement habitats. Note that a study can be counted for each behaviour if it contains models that include that behaviour.

There is growing empirical knowledge of larval fish behaviour influencing the outcome of connectivity (Leis 2006; Cowen and Sponaugle 2009), and also BDM studies demonstrating that connectivity changes with the implementation of behaviour, suggesting the way forward is to include behaviour in connectivity models (North *et al.* 2009; Staaterman and Paris 2014). Therefore, this finding is interesting from a biological viewpoint, as the results show the majority of studies are not including any behaviour at all in their models; 73.9% of models implemented passive larvae, although it must be noted this trend was decreasing for larval fish BDMs (less than a quarter used passive larvae in 2016, Figure 2.3 c). There is also a well-established body of empirical literature which highlights the often-extensive swimming abilities of larval fish (Leis 2006, 2010). Even where horizontal swimming is not considered biologically important, it is well understood zooplankton exhibit diel vertical migration patterns, migrating below the mixed layer, hypothesised due to predator avoidance (Lampert 1989). The importance of vertical position is that the larvae are exposed to different current velocities at different depths in the water column. Several studies in the review showed that vertical migration (either diel or ontogenetic) increased self-recruitment and limited the dispersal kernel (Aiken *et al.* 2011; Young *et al.* 2012). Orientation was only implemented in a small number of models, yet there is an increasing body of research in the last decade regarding the ability of reef fish larvae to orientate towards natal reefs using olfactory mechanisms (Gerlach *et al.* 2007), celestial cues (Leis *et al.* 2014; Faillettaz *et al.* 2015) and a magnetic compass (Bottesch *et al.* 2016).

One possible reason for not implementing behaviour is that the complete (or even partial) early life history is often unknown for many species and researchers are trying to avoid using any conjectural behaviour assumptions in their models. Fish larval behaviour is known to be species specific, yet many models are limited to using known data from the family taxonomic level due to the lack of specific knowledge for the species of interest. It has been argued that this approach is fraught with danger, as behaviour can vary widely amongst species within a family taxonomic grouping (Leis 2010). Performing sensitivity analyses on modelled parameters is a worthwhile strategy to determine the sensitivity of the BDM output to a behaviour with limited species-specific data. This lack of species-specific knowledge poses the question, especially for sensitive input parameters, can I only model species where I fully understand the early life history, or is there a degree of assumption that is deemed to still be scientifically valid to answer the study question? It also emphasises the empirical work that is still required to better understand fish early-life history.

2.4.3 The metrics used to describe connectivity

There were more than 30 different measures used to describe the patterns of dispersal and settlement amongst the models. The three main approaches were to use combinations of dispersal kernels (58.7%), connectivity matrices (realised or potential; 56.5%) and graph theory (21.6%). Less common measures of model output were analyses using larval centre of mass (average geographical position of the larvae; Miyake *et al.* 2011, Lacroix *et al.* 2013), isotropy (describes the inertia around the centre of mass; Ayata *et al.* 2010), positive area (number of areas that had larvae in them; Puckett *et al.* 2014), and proportion of sites settled (Robins *et al.* 2013).

The trend in biophysical modelling is to present data using visual techniques such as heat maps, which, while being effective tools for visually communicating complex patterns qualitatively, are not amenable to the extraction of exact metric values. When a dispersal kernel was used, 36.4% of the time, the mean dispersal distance was reported. The most common connectivity values reported in the reviewed studies—when a connectivity matrix was presented—were local retention (58.6%), self-recruitment (50.8%), and global settlement success of larvae (42.3%). However, whilst these response metrics were explicitly described, I was only able to extract actual values from 14.4%, 21.3%, and 32.1% of the studies in which connectivity matrices were described for local-retention, self-recruitment, and settlement success respectively. Based on the extracted data, there was a large spread of the mean self-recruitment amongst the models, ranging from 0-98%, depending on the study, with a median self-recruitment percentage of 13.0%. Local retention had mean values ranging between 0.3% to 46.7% and a median of 8.9%. Mean settlement success of the larvae (available for 18.0% of the studies), ranged from 0.1% to 80.0% successful settlement rates, with a median of 16.7%. Mean dispersal distance had a median value of 77.3 km (range of 9-668 km).

The high percentage of successfully settled larvae per model seems atypical for connectivity models. It was expected that the overall settlement success would be lower, even without mortality, due to the tendency of oceanographic currents to move larvae off-shore. There are caveats to this, size of settlement patch, topography of the modelled domain, size of grid hydrodynamic grid used (ability to capture inshore processes), and how the model handles larvae at boundary conditions - a modelling choice that was rarely reported. Also keeping in mind that settlement success in these models does not reflect post-settlement processes and therefore at best dispersal and not true connectivity is predicted from the modelled output. One other explanation could be in the implementation of these models, and how larvae are handled when they try and move on land - do they sit where they are and wait until a current velocity can move them offshore (often assisted by larval behaviour, i.e. swimming) or do they die? The first option could artificially increase settlement near source regions for hydrodynamic models that do not capture inshore processes correctly. The large ranges for the metrics of self-recruitment, local retention, and settlement success were unexpected—perhaps combinations of the geographical location and many studies reporting potential connectivity instead of realised connectivity (realised is a more accurate measure offset by biological processes such as estimated egg production and/or mortality). However, the large range of input parameters must be responsible for such variations - in the next section how these modelling decisions effect these common metrics is explored.

2.5 Influence of modelling decisions on connectivity metrics

As indicated above, much of the variation observed in connectivity values and patterns across the reviewed studies will be driven by modelling environments, specifically parameter decisions. The reviewed literature is used to assess the impact of various model and parameter choices on resulting connectivity values. Consideration was restricted to models characteristics/input parameters and output connectivity metrics that were shared amongst the majority of studies, as described in the methods section. Specifically, investigating the impact of four characteristics of modelling environment (choice of model, model resolution, model design and study system) and four biological parameterisation decisions (larval duration, competency window, larval mortality and movement behaviour) on the key common metrics of connectivity (self-recruitment, local retention, settlement success & dispersal distance). Other important biological decisions, i.e. spawning spatial and temporal patterns, were left out due to the inherent complexities in comparing between study regions, even though they were seen in the reviewed studies to influence dispersal (Drake *et al.* 2011; Moksnes *et al.* 2014; Kool *et al.* 2015). Note there are situations where there were not enough data points to make valid comparison of specific connectivity metrics and there are uneven sample sizes between the groups. Discussed below are the various components of models, outlining expected influences of each side on the identified response metrics and comparing this to what has been observed in the models summarised here:

2.5.1 Modelling environment

The oceanographic systems were described as either open or closed, based on their geography (see methods). Logically, if the scale of the systems are equal, closed systems are predicted to increase both local retention and settlement success, as closed systems should lead to decreased rates of larval loss and increased chances of settlement. Self-recruitment is expected to either be lower or equal in a closed system compared to an open system of comparable size, as while more larvae will settle back to their natal patch, there will be more recruits from other patches. Dispersal distance is expected to increase within an open system, as currents can take larvae further off-shore or alongshore. I found self-recruitment and settlement success tended to be higher in a closed system (39% and 12% higher respectively), although the differences were not significant (self-recruitment: $t = 1.18$, $df = 22.7$, $p_{adjusted} = 0.335$; settlement success: $t = 0.55$, $df = 126$, $p_{adjusted} = 0.471$). The mean local retention in open systems (10.1%) was not significantly higher than in closed system (16.8%; $t = -1.60$, $df = 52$, $p_{adjusted} = 0.229$), contrary to the prediction. Dispersal distance was 2.7 times greater in open systems, compared to closed ($t = -3.29$, $df = 65.1$, $p_{adjusted} = 0.006$). Only dispersal distance behaved as hypothesised, with the result of local retention being most unexpected. This could be indicative of researchers appropriately choosing the boundaries of the modelled systems based on the biology of the modelled taxa. In this case, even seemingly open systems, may in fact be demographically closed ones. This can be explained by the geographical nature of an open system, potentially allowing more larvae to be dispersed away from natal sites and towards more distant settlement sites or into large oceanic features, there are many more dispersal permutations in open systems.

There is no clear effect of particle-tracking model choice on the resulting connectivity metrics (Appendix A; Figure A1). In general, model choices produced less variability for metrics of local retention and dispersal distance and more variability within measures of settlement success and self-recruitment. Although this trend was not consistent, for example within the choice of particle tracking model, the Connectivity Modelling System (CMS) had relatively consistent predicted values of self-recruitment, but rather variable local retention, settlement success and dispersal distance. Without knowing the specifics of various BDMs, it was expected that there would be inherent variation due to the different implementations. However, any strong trends seen here could be due to the specific code of a model biasing towards a particular metric, e.g. an unreported bug. For hydrodynamic model choice, studies using more generalised hydrodynamic models (e.g. HYCOM, ROMS, and POM) had the largest ranges amongst the metrics for hydrodynamic models, while more specific models (e.g. MARS-3D and HANSOM) had the least variation (Appendix A; Figure A2). However, for both BDM and hydrodynamic models, the largest variation was seen for the models that were most common amongst studies.

Nested hydrodynamic models (i.e. sub-models with higher resolution to capture coastal dynamics), used in more complex BDMs to capture small scale regional processes, are expected to give more realistic and accurate connectivity patterns. Another less common option is to use unstructured grids, that allow for meshes to be smaller near coastal regions and larger for open water (Sundelöf and Jonsson 2012; Puckett *et al.* 2014). Following from this, hydrodynamic models with finer resolution should also produce more realistic connectivity patterns, and model resolution is thought to be a defining characteristic of model variability (Hufnagl *et al.* 2017). It must be noted that this is not an option for many BDMs, where the choice of hydrodynamic model can be limited for the study area. Finer resolution of the general spatial domain or from using nested models to capture small scale coastal dynamics such as eddies and topographic effects, should in theory influence dispersal (Pineda *et al.* 2007). If small-scale processes do indeed retain larvae closer to their natal site (Gawarkiewicz *et al.* 2007), then it is predicted local retention and settlement success would increase, and dispersal distance would be reduced. Self-recruitment is more complex due to the connectedness of the system — if there are strong transport links with other non-natal source regions, then the effect of the predicted increase in local retention will be potentially counter-balanced by an increase in settlement from non-natal larvae, a process seen in systems where near-shore processes were captured on a finer scale (Teske *et al.* 2016). Therefore, the simplest prediction being that there will be no change in self-recruitment due to steady increase of local and external settlement. I found only one significant positive predictive relationship between the resolution of the hydrodynamic model and the metrics; local retention (a relationship driven by limited data points, $r^2 = 0.27$, $F(1,47) = 17.76$, $p_{adjusted} = 0.000$; Figure 2.4 a), the rest were not significant; self-recruitment ($r^2 = 0.05$, $F(1,71) = 3.51$, $p_{adjusted} = 0.130$; Figure 2.4 b), settlement success ($r^2 = 0.01$, $F(1,121) = 0.17$, $p_{adjusted} = 0.680$; Figure 2.4 c), or dispersal distance ($r^2 = 0.03$, $F(1,62) = 1.83$, $p_{adjusted} = 0.242$; Figure 2.4 d). When using nested hydrodynamic models, the self-recruitment significantly reduced (36.5% versus 0.9%; $t = 9.17$, $df = 65.2$, $p<0.05$). However, caution should be used when evaluating this result due to the large unbalanced samples between the groups (only 10 models reporting self-recruitment had nested designs, whereas 65 did not). Similar to model resolution, there was no significant difference in the settlement success or dispersal distance when using nested models, and there were no studies using nested models where I was able to get local retention values. Counter-intuitively to the prediction, local retention was found to significantly increase as the resolution gets coarser, although it is a relationship driven by two data points at 10 and 15 km (Figure 2.4 a). One possible explanation is that models with coarser resolutions often are over larger spatial scales and therefore use larger settlement habitats, which could increase local retention. Self-recruitment was found to decrease when nested models were utilised, but did not change with global model resolution, demonstrating the complexity of the metric and its relationship to the connectedness of the region. The results of settlement success and dispersal distance not changing with finer resolution models, also ran counter to predictions. This suggests that coarser models might not change the prediction of dispersal distance, but the settlement metrics might be influenced by the model resolution. The only study within the review to investigate the effect of model resolution found that dispersal distance did not change, but settlement success increased as the model resolution got coarser (Garavelli *et al.* 2014). Studies outside the scope of the review period have found coarser model resolution decreased the overall settlement success (Huret *et al.* 2007; Putman and He 2013) or not while not specifically influencing local retention, changes in resolution did vary the dispersal patterns (Kvile *et al.* 2018). In addition to this increased spatial resolution, the temporal resolution of the models is also important. Finer temporal scales allow for increased accuracy in resolving oceanic circulation. However, finer temporal scales are often compromised for memory requirements in storing large volumes of oceanographic data. Many studies within this review also did not clarify the time scales of both the hydrodynamic model and the BDM, often only reporting one value.

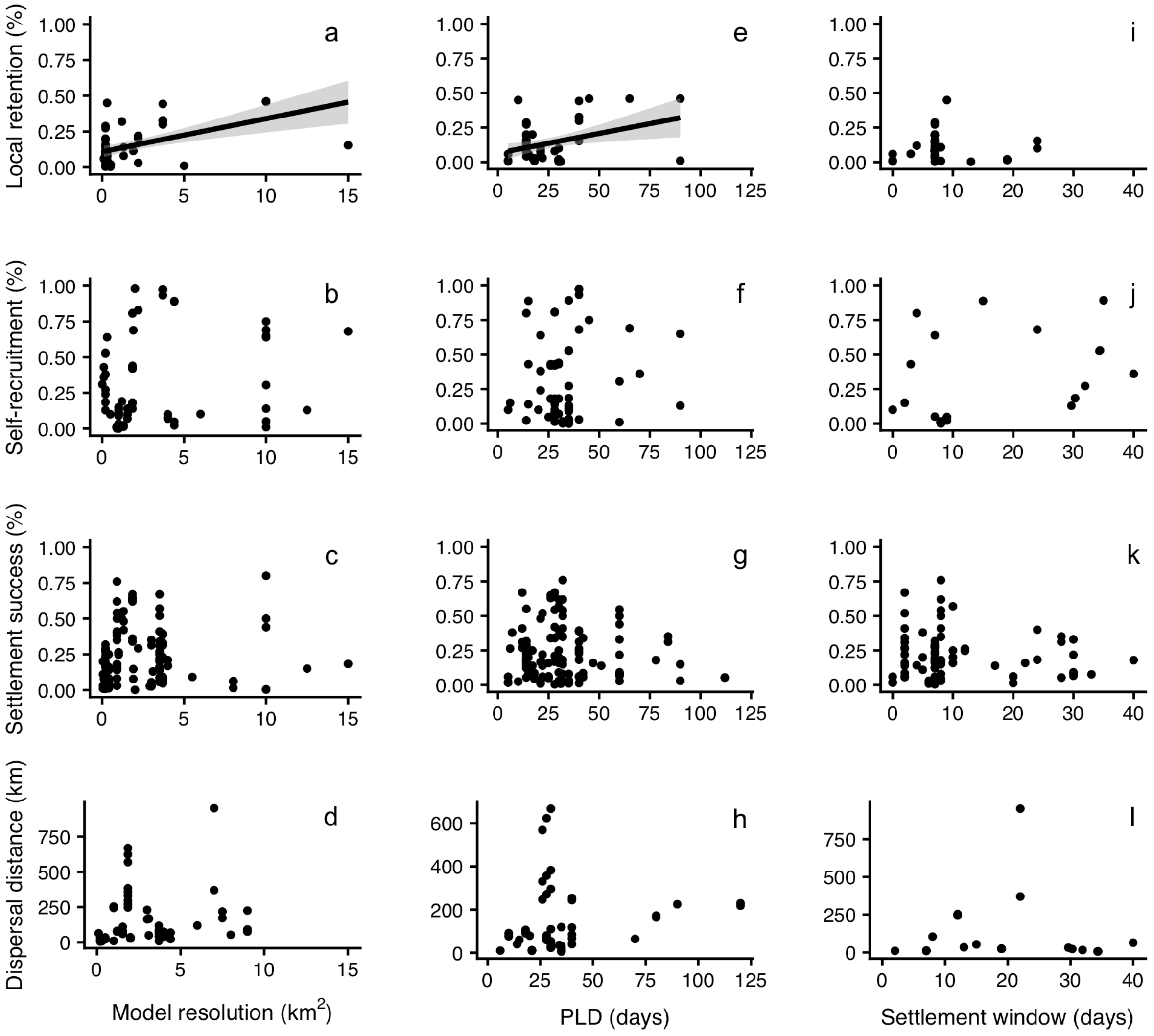

Figure 2.4: Comparison of the relationship between three input parameters for biophysical dispersal models; model resolution (km^2; a-d), pelagic larval duration (days; e-h), and settlement competency window (days; i-l), with four common metrics of connectivity; local retention (%), self-recruitment (%), settlement success (%), and dispersal distance (km). Significant linear regressions are shown with 95% confidence intervals.

2.5.2 Biological parameterisation

As indicated above, the length of the larval period (PLD) was one of only a few biological parameters implemented in every model. Given its fundamental importance in the modelling process (the general basis for the duration of any given model run) it would be expected to have impacts on foremost the dispersal distance as larvae can spend more time in the water. A longer PLD increases the potential for long-distance dispersal and therefore local retention is expected to be lower (Kendall *et al.* 2016). Most likely self-recruitment will not change with PLD due to decreases in local retention being offset by fewer particles from neighbouring source regions settling (although it relies on the connectedness of the region, as larvae from more distant source regions could start settling and driving down self-recruitment). It is predicted that, in general, settlement success will not change, as increasing the PLD might reduce local settlement, but open up new potential areas of settlement away from the natal reef. However, settlement success relies on the context of the model domain and the amount of off-shore drift, or nearshore dynamics drifting larvae in-shore (Moksnes *et al.* 2014). There was a weak relationship with local retention ($r^2 = 0.13$, $F(1,48) = 7.41$, $p_{adjusted} = 0.036$; Figure 2.4 e) and no relationship with any of the other common metrics and the length of the PLD; self-recruitment ($r^2 = 0.03$, $F(1,67) = 2.48$, $p_{adjusted} = 0.402$; Figure 2.4 f), settlement success ($r^2 = 0.01$, $F(1,79) = 1.91$, $p_{adjusted} = 0.529$; Figure 2.4 g), and dispersal distance ($r^2 = 0.05$, $F(1,60) = 2.93$, $p_{adjusted} = 0.402$; Figure 2.4 h). Increasing the length of the PLD had the opposite effect on local retention as predicted, appearing to slightly increase the longer the dispersal, although it is a very weak relationship. The hypothesis that longer PLDs would increase dispersal distance was not supported when considering the metrics between studies. Several studies within this review did specifically assess the effect of PLD and found it to be positively related to dispersal distance (Robins *et al.* 2013; Soria *et al.* 2014; Treml *et al.* 2015; Abesamis *et al.* 2016; Jönsson and Watson 2016) and only one study found no relationship (Mora *et al.* 2012). Thus, the lack of a relationship for most of the metrics highlights the important role of other factors (either behaviour or physical modelling environment) in driving dispersal characteristics. Any relationship between dispersal distance and PLD would affect the settlement success, dependent on the geographic location of available settlement sites. Settlement success and self-recruitment behaved as predicted, showing no relationship with PLD. Although, many studies in the review did find that within their domain, increasing the PLD reduced the overall settlement success (Drake *et al.* 2011; Bidegain *et al.* 2013; Kendall *et al.* 2013; Cetina-Heredia *et al.* 2015).

A settlement competency window (the length of which is constrained by the pelagic larval duration), was implemented in about half of the models and lengthening this window is postulated to increase settlement success by increasing the probability of finding suitable settlement habitat (Metaxas and Saunders 2009). The shorter the pre-competency period (the period when the larvae cannot settle, the end this period denotes the start of the settlement competency window) the earlier larvae can settle if the habitat is conducive and theoretically closer to the natal habitat. Therefore, I predicted that local retention and self-recruitment would both increase while average dispersal distance would decrease. The length of the settlement competency window, dependent on the pelagic larval duration, was found to have no relationship with any of the common metrics; self-recruitment ($r^2 = 0.18$, $F(1,25) = 5.38$, $p_{adjusted} = 0.115$), local retention ($r^2 = 0.04$, $F(1,32) = 1.32$, $p_{adjusted} = 0.520$), settlement success ($r^2 = 0.01$, $F(1,73) = 1.02$, $p_{adjusted} = 0.520$) or dispersal distance ($r^2 = 0.00$, $F(1,21) = 0.00$, $p_{adjusted} = 0.984$). An increase in self-recruitment with the size of the settlement window was as predicted, although this same relationship was not seen in local retention. Of studies in this review that specifically increased the size of the competency window (allowed larvae to settle earlier), all reported settlement success and local retention (Wolanski and Kingsford 2014), along with self-recruitment (Sanvicente-Añorve *et al.* 2014) increased. Other results where the competency window size was altered within a study produced no clear pattern, possibly due to changing multiple parameters (Holstein *et al.* 2014). The size of the settlement competency window should be tightly linked to probability of settlement success and dispersal distance for an individual larva. However here I saw neither of these, perhaps any observable relationships are masked by the impact of parameterisation decisions made by these models which may have stronger effects on settlement success (e.g. mortality, see below).

Mortality is a great unknown factor in pelagic larval life stages, except that it is presumed to be high (Houde 1989a; Pepin 1991; White *et al.* 2014; Johnson *et al.* 2015). It is difficult to quantify larval mortality, but modelling can be a key tool in understanding the processes driving this high mortality (Peck and Hufnagl 2012). Mortality was implemented in more than one-third of models. Implementing mortality (along with known spawning output) assists in changing derived connectivity patterns from mere potential to more realised patterns of connectivity (although ignoring post-settlement processes), whereby high mortality in early stages of ontogeny limits the tails of the dispersal kernel and flattens the peak. Although there are many factors of mortality that are often ignored when modelling mortality in BDMs, from predator-prey interactions to food availability. Therefore, logically it follows that including mortality will greatly reduce the settlement success and local-retention of larvae, along with reducing the dispersal distance. Self-recruitment should remain constant or slightly increase due to a restricted dispersal kernel when a constant rate of mortality is used. Local retention increased when mortality was applied ($t = -3.04$, $df = 10.3$, $p_{adjusted} = 0.048$; Figure 2.5 a). It was found that models which included mortality had similar levels of self-recruitment ($t = -0.75$, $df = 74$, $p_{adjusted} = 0.701$; Figure 2.5 b) and settlement success ($t = -$

0.02, df = 126, $p_{adjusted}$ = 0.983; Figure 2.5 c) to models run without mortality. Including mortality also had no effect on the dispersal distance of the marine larvae (t = -0.65, df = 17.2, $p_{adjusted}$ = 0.701; Figure 2.5 d). Neither settlement success nor dispersal distance lessened with mortality as predicted, but mortality did reduce the variation of the settlement success and the dispersal distance (apart from two outliers). The fact the settlement success values did not change is a strange result, as several BDM studies in the review found increasing mortality reduced settlement success (Chassé and Miller 2010; Kendall *et al.* 2013; Neo *et al.* 2013). Another study within the review found increasing mortality reduced the dispersal kernel (Treml *et al.* 2015), contrasting these results, again suggesting a multitude of other factor are involved. Self-recruitment behaved as expected, and the variation increased, which would occur if settlement success also decreased, as fewer larvae would be arriving from other sites. Local retention behaved the opposite to expectations, the mean local retention doubled when mortality was included in a BDM, however the degrees of freedom for interpreting this result are low due to the unbalanced sample sizes. The high values for both local retention and settlement success when mortality is included in the model are curious, as intuitively the high mortality rates of larvae (average values used were 10% per day), should greatly lower both these metrics.

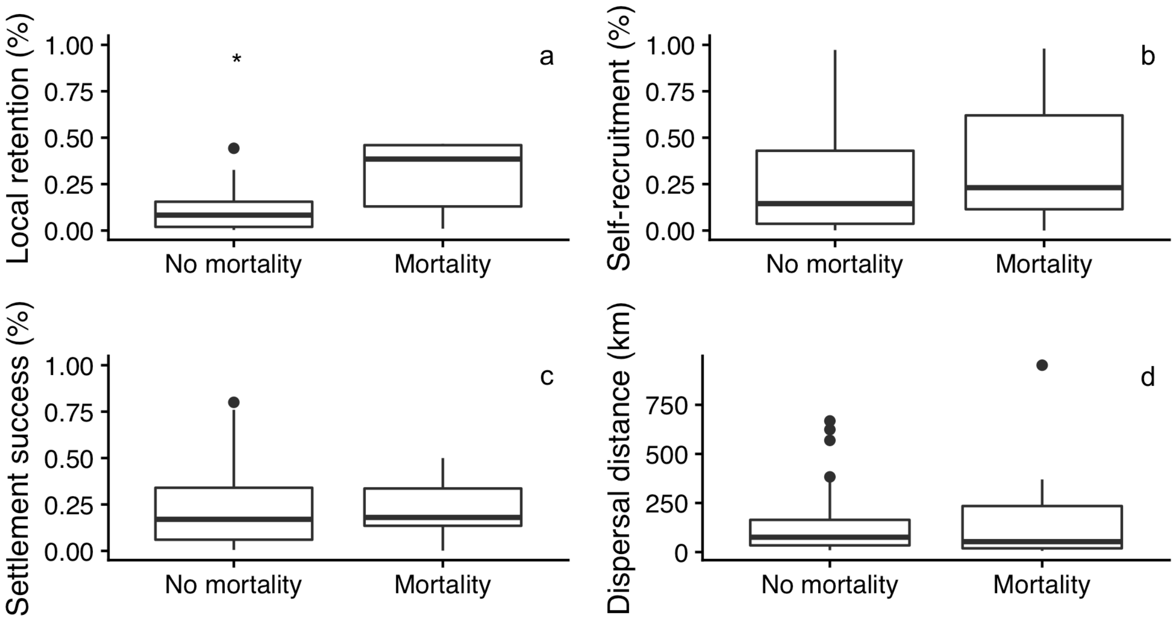

Figure 2.5: Comparing biophysical dispersal models that implemented mortality with the metrics of local retention (%; a), self-recruitment (%; b), settlement success (%; c) and dispersal distance (km; d). Asterisk indicates statistically significant differences.

Behaviour of marine larvae, was classified into four areas for this review, as specified earlier. I compared the metrics against passive larvae, larvae that can swim (undirected horizontal and vertical), sense settlement habitats (using a buffer or sticky zones), and orientation (directed swimming towards settlement habitats). While I also looked at a combination of these behaviours, only the combination of movement and sensing settlement behaviours had enough models and reported values for comparisons. Local retention was expected to increase when movement behaviour was implemented, based on previous results (Paris and Cowen 2004; Cowen and Sponaugle 2009; Moksnes *et al.* 2014). However, settlement sensory behaviour or orientation are predicted to lower, but not have a discernible effect on local retention. It is unclear how self-recruitment should be affected by behaviour, as local retention increases, self-recruitment would also increase, unless movement also increases long-distance dispersal by exposing larvae to currents with different velocities, which would in turn reduce self-recruitment as more external recruits settle to a patch. Settlement success should increase with behaviour, as movement increases the ability to find settlement patches, settlement buffer and orientation allows larvae to find patches easier when they are competent to settle. Dispersal distance is hypothesised to decrease with behaviour, as for many species with buoyant eggs and larvae, passive larvae are exposed to the strongest surface currents and settlement buffer and orientation both allow for larvae to settle earlier by navigating to suitable habitats. Even though it was strongly expected, no effect of behaviour on local retention could be found from the reviewed studies due to the limited data, there was no data to contrast settlement or movement and settlement behaviours (Figure 2.6 a). Even though the mean local retention for passive larvae moderately increased with movement and to a lesser extent with orientation, there were no differences found between the groups. The only behaviour that produced self-recruitment values that differed significantly from passive larvae was orientation (with limited values for orientation; estimate = 0.29, SE = 0.06, z-ratio = 4.00, $p_{adjusted} = 0.000$; Figure 2.6 b). Orientation also produced significantly lower self-recruitment (38% less) compared to settlement sensory behaviour (estimate = 0.20, SE = 0.07, z-ratio = 3.01, $p_{adjusted} = 0.007$), movement (34%; estimate = 0.23, SE = 0.08, z-ratio = 3.09, $p_{adjusted} = 0.007$), and compared to movement and settlement buffer combined (22% less; estimate = 0.42, SE = 0.10, z-ratio = 4.65, $p_{adjusted} = 0.000$). The highest values of settlement success (mean of 50.2%) were achieved when combining movement and settlement buffer

(Figure 2.6 c) and greater than the mean settlement success the other behaviours; passive (estimate = 0.29, SE = 0.08, z-ratio = 3.55, $p_{adjusted}$ = 0.004), movement (estimate = 0.26, SE = 0.09, z-ratio = 3.11, $p_{adjusted}$ = 0.009), settlement (estimate = 0.26, SE = 0.09, z-ratio = 2.72, $p_{adjusted}$ = 0.022), and orientation (estimate = 0.21, SE = 0.09, z-ratio = 2.45, $p_{adjusted}$ = 0.035). The rest of the behaviours did not produce significantly different values of settlement success to each other. Dispersal distance significantly increased by over 300 km when settlement sensory behaviour was combined with movement (estimate = 0.29, SE = 0.12, z-ratio = -3.05, $p_{adjusted}$ = 0.013) was included in the model compared to passive larvae (Figure 2.6 d). The variation when including only settlement behaviours was extreme compared to the other behaviours. There were no reported values for models that included orientation.

The hypothesis of increased local retention with behaviour was not supported. A number of the studies in the review found that including behaviour increased local retention compared to passive larvae (Ewers-Saucedo *et al.* 2016; Klein *et al.* 2016). The low number of data points for local retention could have led to this unexpected result — I have few data points for either settlement sensory or the combination of movement and settlement sensory. The surprising result for self-recruitment was that combining settlement sensory behaviours and movement increased the proportion so greatly as compared to implementing only movement. The logic behind this is puzzling, as settlement sensory should increase settlement success overall, but evenly across all the habitats. Including movement, settlement sensory or a combination of the two over passive behaviour, while reducing variation, did not produce significantly different self-recruitment values as predicted. For movement and settlement sensory, values tended to be lower suggesting more long-distance transport, yet each had outliers of reported high self-recruitment rates (Figure 2.6 b). As hypothesised, there was a clear trend that including behaviour increased the settlement success of larvae in a model, also seen in models where increasing buffer size (Kendall *et al.* 2013) or adding movement increased settlement success (Moksnes *et al.* 2014; Hubbard and Reidenbach 2015; Klein *et al.* 2016). However, vertical movement was not always seen to have an effect on settlement success within the reviewed studies (Adams *et al.* 2014; Neo *et al.* 2015). The only behaviour to not fit into the trend was orientation, which still trended to higher values, but the low number of reported results did not allow for meaningful results. When orientation ability was altered within a study, it was found to increase local retention, self-recruitment, and settlement success (Staaterman *et al.* 2012; Wolanski and Kingsford 2014). In the meta-analysis dispersal distance behaved the opposite of predicted, increased significantly when settlement sensory behaviour and settlement sensory and movement behaviour was included. The variation of dispersal distance for models including settlement sensory models was extreme compared to other behaviours. Behaviour has been demonstrated to both limit (Butler *et al.* 2011; Adams *et al.* 2014; Moksnes *et al.* 2014) and increase (Corell *et al.* 2012; Criales *et al.* 2015) the dispersal distance of pelagic larvae, suggesting how the behaviour is parameterised, as well as interactions between parameters is important.

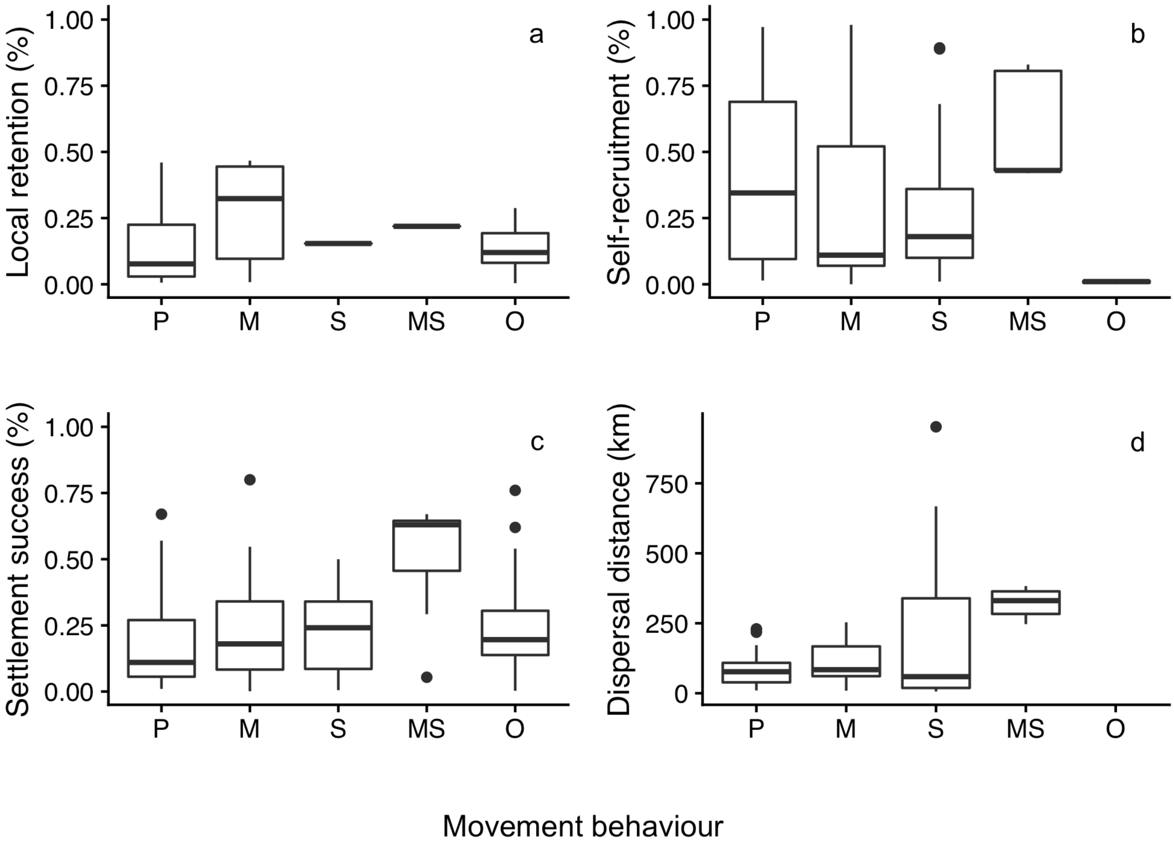

Figure 2.6: The effect of larval behaviour (P=passive, M=movement, O=orientation, S=settlement buffer, MO=movement and orientation, MS=movement and settlement buffer, OS=orientation and settlement buffer) on the mean local retention (%; a), self-recruitment (%; b), settlement success (%; c), and distance travelled (km; d) in the reviewed biophysical dispersal modelling studies

2.6 Conclusion and recommendations

The current state of the field does not give the impression it is moving forward as coherently as it should be in the eight years since the ICES manual of recommended practices was published (North *et al.* 2009). A significant reason for this is likely the absence of published behavioural data on the early-life history of many marine species, highlighting a key area of required future research. Without this species-specific early-life history data, it can be difficult to justify introducing behaviour into models, as robust models aim to minimise assumptions. On the contrary, it is much harder to defend BDMs that do not include behaviour that is understood to be important to dispersal and the specific empirical data is accessible. The popularity of BDMs as a connectivity research tool has been consistent since 2012 and implementations of these models are getting more complex in recent years, especially for larval fish with the proportion implementing movement behaviours increasing. Other behaviours of settlement sensory strategies and orientation were consistently (or sporadically in the case of orientation) implemented across the review period for models of either fish or invertebrate species, not reflecting the trend of movement. From a biological viewpoint this is encouraging, as it is in keeping with the research showing that biology matters in dispersal and studies appear to be including it when the relevant data is available in the literature.

The most surprising result from the modelling environment parameters was that the model resolution (either global resolution or through nested models) had no strong effect on the common metrics investigated, as model resolution (spatial and temporal) is naturally important. This result does not mean modellers should not aim for better precision in hydrodynamic models, but perhaps it does give confidence that when using a BDM to investigate connectivity within regions where only coarser (but well validated) hydrodynamic models are available, that other modelling choices (e.g. including vertical migration) can mitigate the effect of coarseness on dispersal. Choice of hydrodynamic model is based on regional availability, model resolution, and validation, whereas the decision on which particle tracking models to use can be down to other tangible choices e.g. user experience, native operating system, or required computing power. The effect of open and closed systems was not as strong as expected either, suggesting perhaps open systems are not as “open” as believed (conversely closed are also not as “closed” as supposed) and they still exhibit strong levels of settlement success and self-recruitment (Cowen *et al.* 2000; Giangrande *et al.* 2017).

No relationship between the length of pelagic larval duration and the four common metrics was found. This suggests that the model context also has a large influence on metrics, as a longer PLD is expected to decrease local retention and self-recruitment and lengthen the dispersal distance. The size of the settlement competency window had unexpected results, having no effect on settlement success, local retention and dispersal distance. These results provide increased confidence that the potential connectivity patterns of studies parameterising their BDMs with PLD and settlement windows using limited known data for their species of interest. It was surprising to see such high levels of settlement success and that these values were not affected by the inclusion of mortality in models. This may be due to unrealistically high levels of habitat homing or “sticky” settlement zones and certainly warrants further attention as some form of realistic mortality must be applied in order to capture realised connectivity patterns, instead of potential patterns. The mean settlement success and dispersal distance of the larvae was increased when combining movement with settlement sensory. The dispersal distance results are unexpected, perhaps a result of increased settlement success at more distant settlement sites. Behaviour also decreases self-recruitment, except when movement and settlement were combined. Therefore, implementing larval behaviour would seem to produce different (and likely more realistic) metrics to using passive larvae in a BDM study, and at least needs to be considered when generating connectivity patterns. Obviously parametrising some of these behaviours can be difficult due to the lack of information, however even a simple sensory system can have a strong effect on the metrics considered. Although, in the absence of empirical data and model validation, there is no way to be certain if this is an undue effect or not.

The large variation seen in both the model inputs and the connectivity metrics produced from these BDMs was unexpected. Variability of metrics is likely driven by the non-trivial number of parameter choices made, both physical and biological, in BDMs, many of which are optional or species specific. There is a grey area when determining what information to include in a model and what level of accuracy and precision is required for biological inputs. Connectivity metrics of self-recruitment, local-retention, and settlement success appear to be affected by different model inputs, which underscores the inherent complexity of these systems. Admittedly, it is difficult to undertake a comparative meta-analysis of BDMs such as this due to the numerous parameters involved. Even within the four chosen common metrics there can be different definitions (which were often difficult to tease out) that can lead to more noise within the results. For example, dispersal distance could refer to the geographical distance between the natal and the settlement site or it could be the distance the larvae travelled before it settled. Historically, local retention and self-recruitment have often been used, if not interchangeably, then used assuming one can infer the other as the numerators are the same, leading to some potential ambiguity about the reported values - obtaining values from connectivity matrices resolves this uncertainty.

A caveat to the analysis of the biological behavioural traits focused on in this review is that the underlying implementations were ignored (Table 2.2). There are a multitude of approaches that can be taken when including behaviours in a model, some will be more realistic than others and the effect of this different implementations on dispersal is essentially unknown. The sheer number of parameters will inevitably generate a lot of noise in the metrics that could hide relationship that do exist. Unlike sensitivity studies, where parameter choice can be limited and/or controlled, comparing across studies introduces complexity. In addition, the connectivity metrics will be closely aligned with model domain choices, for example the number of settlement patches in the model and the size of these settlement patches will have an effect on these connectivity metrics — accounting for the large variation. This variation could create too much noise to determine general patterns with physical and biological parameters even though there could be a potential relationship. A next step would be to standardise these connectivity metrics using features of the model domain to provide more revealing comparisons. This complexity within BDMs makes it difficult to learn and move forward using the model outputs, ultimately limiting the capacity for making more informed decisions with respect to BDMs. The way forward is through devising an unbiased technique for model validation and then utilising validated models as a baseline for understanding the parameters that are important.

This review has also highlighted the lack of unity in both input parameters and metrics to describe the output of the BDMs. There is no consensus on what biological parameters to choose when implementing a model, i.e. what behaviours are required in a BDM to accurately estimate the connectivity for a reef fish species. BDMs are non-trivial models, making it difficult to standardise the output in order to produce simple comparisons. Although agreement about common metrics and consistent metrics reporting would help alleviate these issues. Standardisation of metrics will also assist in validating the estimated patterns of connectivity with empirical studies (e.g. genetic studies, comparisons long-term known recruitment data and other techniques where appropriate), providing important model validation. This would provide a formal framework to validate BDMs against empirical studies that have measured some or all of these metrics and allow us to fine tune the importance of required parameters. The inherent difficulty of course lies in empirical studies being able to measure these metrics, and to begin with it will only be possible for small scale studies. Model validation should be an ultimate goal of BDM studies, especially as understanding connectivity is a central tenet of applied marine ecology, including designing marine reserves (Almany *et al.* 2009; Bode *et al.* 2016).

In conclusion, I believe in order for this field to progress further, we need to better understand the relative importance of different behaviours on the dispersal of marine larvae (potentially species/taxa specific). This understanding will enable modellers to generate baseline models for connectivity and highlight areas of knowledge gaps in early-life history that need to be addressed so I can confidently parametrise these BDMs and generate better outcomes.

3 Size and stage-dependent vertical migration patterns in the larval fish of temperate reef-associated fishes and the effects of entrainment in cold-core eddies off the coast off New South Wales, Australia

3.1 Abstract

Larval fish have been shown to vertically migrate with ontogeny, a behaviour that influences their dispersal through exposing the larvae to currents with different velocities at different stages of development. Most studies have focused on studying the vertical migration of tropical reef fishes, that have been shown in general to migrate downwards with ontogeny. This chapter aimed to investigate if similar ontogenetic vertical migration patterns also occur for temperate reef fish along the eastern coast of Australia. The vertical distribution was sampled at three depth ranges (0-1 m, 5-50 m, 50-100 m) using MOCNESS and Neuston nets. Sixteen stations were sampled at night over the period 2-18 June 2015; eight along the continental shelf, and eight within cold-core eddies. Larval fish were identified to the lowest taxonomic level possible, their length measured and classified as either preflexion, flexion or postflexion based on their developmental stage. Generalised linear models were used to determine if the larval fish exhibited patterns of vertical migration with ontogeny and length. Four families (Labridae, Serranidae, Scorpaenidae, and Synodontidae) exhibited a downwards migration with ontogeny, Mullidae migrated upwards with ontogeny, and two families showed no ontogenetic vertical migration (Pomacentridae and Scaridae). The amount of vertical migration varied between taxonomic families. There was no effect of eddy on ontogenetic vertical migration but for any family except Scaridae, the larvae inside an eddy were longer, suggesting retention. Environmental variables explained only some of the variance, and it was not consistent between taxonomic families. The vertical migration patterns observed, while varying between taxa, provide the ability for larval fish to influence their dispersal through ontogeny. These results of this study will be useful in parameterising connectivity modelling studies for these temperate reef-associated families.

3.2 Introduction

Larval fish generally begin life with a limited behavioural set of capabilities after hatching from eggs, but with the onset of ontogenetic development they increase their competency to swim, sense and orientate over a short period of time (days to weeks; Leis 2006). Historically, larval dispersal was thought to be driven predominately by ocean currents and the length of pelagic larval duration of the species (Williams *et al.* 1984). Other effects were considered negligible due to the weak swimming ability of larvae. Subsequent research has found out that behaviour plays a big part in the dispersal of larval fish. The capability of larval fish to change their vertical position in the water column increases local retention (Paris *et al.* 2007). Larval fish can often sustain horizontal swimming speeds higher than the prevailing currents, allowing them to influence their path of dispersal (Fisher *et al.* 2000; Leis and Fisher 2006). Furthermore, the larvae of many species can also detect and orientate towards settlement habitat using their senses to detect water chemistry, sound, and visual cues (Kingsford *et al.* 2002; Leis 2010). These factors in combination enable larvae to choose between reefs, i.e. search for higher quality habitat or evince a preference to settle close to the natal reef (Jones *et al.* 2005; Gerlach *et al.* 2007). Behavioural traits influencing dispersal are particularly important for the many reef fish species with bipartite life histories: a pelagic larval phase and sessile adult phase. The dispersal, and thus connectivity between populations, occurs during its pelagic larval stage.

One commonly observed behavioural trait of fish is the tendency to migrate vertically through the water column (Leis 1986, 1991; Boehlert *et al.* 1992; Rodríguez *et al.* 2006). These movement patterns might be in response to their development (ontogenetic vertical migration, OVM), to daily light/dark cycles (diel vertical migration, DVM), or an evolutionary advantage to reduce mortality due to either predator avoidance (especially visual predators in the case of diel vertical migration; Lampert 1989) or in search of potential prey (Pearre 2003; Irisson *et al.* 2010). The ability of larvae to regulate their depth from the time of hatching is dependent on their ability to sense, orientate, and swim (behaviours that are well development by settlement age; Leis 2010). The vertical distribution patterns of diel (Lampert 1989; Sabatés 2004) and ontogenetic (Boehlert *et al.* 1992; Grønkjær and Wieland 1997) vertical migration are well represented in the literature. It has also been hypothesised that vertical migration provides metabolic advantages by allowing larval fish to change their thermal environment (Wurtsbaugh and Neverman 1988) due to changes in diet with ontogeny (Llopiz and Cowen 2009). Larvae changing their position in the water column allow for indirectly affecting dispersal due to changes in current velocities (Paris and Cowen 2004; Paris *et al.* 2007), either through physical processes such as Ekman transport (Sponaugle *et al.* 2002) or by selective tidal transport in and out of estuaries (Grioche *et al.* 2000; Hare *et al.* 2005). Turbulent surface waters have also been seen to induce ontogenetic shifts in vertical distribution, with preflexion larvae migrating away from turbulent waters (Hernandez *et al.* 2009). Different patterns between taxa can be driven by the differences in diets (Llopiz and Hobday 2015).

While it is increasingly acknowledged that vertical migration affects dispersal and population connectivity, general patterns of OVM are not well understood. It has been suggested that the overall biomass of larval reef fish tends to get deeper in the water column with ontogeny (Paris and Cowen 2004; Irisson *et al.* 2010). Species-specific ontogenetic vertical migration patterns are relatively unknown due to the variation between and within species, and over spatial contexts (Leis 2010). Therefore, localised studies are required to determine the vertical migration patterns of larval fish. This study focuses on investigating the ontogenetic vertical migration patterns of larval reef fish off the coast of New South Wales (NSW), Australia. While there have been many studies on the vertical distribution of larval assemblages off the NSW coast (Dempster *et al.* 1997; Gray and Miskiewicz 2000; Keane and Neira 2008), changes in vertical distribution with development are less studied. OVM has been investigated for some commercially valuable species off the coast of NSW (Smith 2003), along with more general relationships between length and depth, comparing surface to deeper off-shore waters (Gray 1993) and DVM patterns between preflexion and postflexion larval fish (Gray 1998). Understanding this early-life history aspect of larval fish is important for parameterising biophysical models since reducing the number of assumptions improves the accuracy of a model (Leis 2007).

The eastern coast of Australia has complex ocean conditions, a rugged coastline with a narrow continental shelf and a strong near-shore boundary current (the East Australian Current, EAC). Previous studies have suggested that over short time periods, passive advection can explain observed dispersal patterns (Smith *et al.* 1999). However, it is hypothesised that vertical migration behaviour can strongly influence dispersal in the region by assisting larval fish in avoiding the strong EAC surface currents (Paris *et al.* 2007). The EAC often spawns warm-core and cold-core eddies off the coast of New South Wales at any latitude, though they tend to be concentrated below 32°S (Suthers *et al.* 2011; Everett *et al.* 2012). These mesoscale eddies entrain continental shelf waters, bringing with them both pelagic eggs and newly hatched larval fish and providing nutrient rich environments for them to develop and potentially reducing predation (Syahailatua *et al.* 2011; Mullaney and Suthers 2013; Matis *et al.* 2014; Shulzitski *et al.* 2015). Simulation studies have shown that eddy speed, fish swimming speed (Chang *et al.* 2017), and the vertical distribution of fish (Condie and Condie 2016) can influence the retention time within an eddy. Mesoscale cyclonic eddies, with their nutrient rich waters, have increased phytoplankton production (McGillicuddy *et al.* 1999; Waite *et al.* 2007), leading to increased zooplankton abundance as an eddy grows older (Govoni *et al.* 2010). This potential for eddies to act as a planktonic incubator (Bakun 2006) could drive changes in the vertical patterns of larval fish compared to that observed in coastal waters if the plankton are located at different depths to coastal waters due to the structure of the eddy — the fish larvae will migrate to where the zooplankton are located in the water column (Govoni *et al.* 2010). Depth distributions of fish larvae assemblages have been seen have different patterns between cold-core and warm-core eddies (Muhling *et al.* 2007). There is no reason to expect that eddies would drive differences in patterns of ontogenetic vertical migration, however, to my knowledge no studies have empirically investigated whether or not this is the case.

In this study, I investigated the vertical distribution of larvae in different oceanographic features (eddy versus no-eddy) off the coast of New South Wales (NSW), Australia using depth-stratified plankton tows. It must be noted that the sampling method only infers the vertical distribution and does not inform about the specific behaviour leading to these patterns (Pearre 1979). I aimed to determine the patterns of ontogenetic vertical distribution of temperate reef fish families off NSW (estimated both by fish length and ontogenetic stage), and if the nature of these patterns are dependent on the surrounding oceanography (entrained in an eddy).

3.3 Methods

Sampling was undertaken along the eastern coast of Australia aboard the Australian Marine National Facility's RV *Investigator* (2-18 June 2015, voyage number IN2015_V03). Sixteen stations were sampled across two coastal regions and two cold core eddies (one frontal ~7 days old and one mesoscale ~26 days old; Roughan *et al.* 2017) in the Eastern Australian Current (EAC; Figure 3.1; Figure 3.2). The location of the eddies was calculated onboard using real-time data and novel techniques (Roughan *et al.* 2017). At each station, larval fish were sampled using two different net types, a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) and a Neuston net. Both nets had a 1 m^2 mouth area and 500 µm mesh. The MOCNESS system sampled over two different depth ranges, 5-50 m and 50-100 m, conducting two 10-minute tows over each depth range. The Neuston net captured larval fish at the near surface level (0-1 m) and was deployed for two 10-minute tows per station. For the rest of this chapter, the depths will be referred to as surface (0-1 m), middle (5-50 m; the thermocline occurred at ~50 m across all stations), and deep (50-100 m). Neuston and MOCNESS nets were deployed at the same time and all tows were conducted between sunset and sunrise to remove any confounding effect of diel vertical migration.

Conductivity, temperature, and depth (CTD) measurements (including dissolved oxygen and fluorescence) were recorded at each station using the Seabird SE911 CTD system and Aquatracker fluorometer. Each net had a flow sensor, enabling concentrations of larval fish per cubic metre to be calculated. For each sample pair per station, each sample was preserved in 10% buffered formalin solution. But for one sample per net, larger fish that could be easily identified in the sample by eye were removed before formalin fixation and preserved in 70% ethanol solution. In total, 36.4% of the larval fish was preserved in ethanol, with a bias towards postflexion fish (postflexion fish made up 59.0% of the larval fish preserved in ethanol and only 20.7% of the fish preserved in formalin). The ad hoc selection process for ethanol preservation was used at all stations. Both samples were used in the analyses and no correction for shrinkage was made for the ethanol samples. Therefore, the measurements of postflexion larvae could be biased towards under-measurement of length (the exact level of shrinkage is species and even individual specific; Pepin *et al.* 1998), but comparisons were not made across groups and the effect on the results is predicted to be minimal. Total lengths of postflexion larvae preserved in either formalin or ethanol only differed for two families; Labridae ($p < 0.001$) and Scaridae ($p < 0.05$). In these cases, the smaller larvae preserved in formalin is likely due to the selection of larger larvae for ethanol preservation.

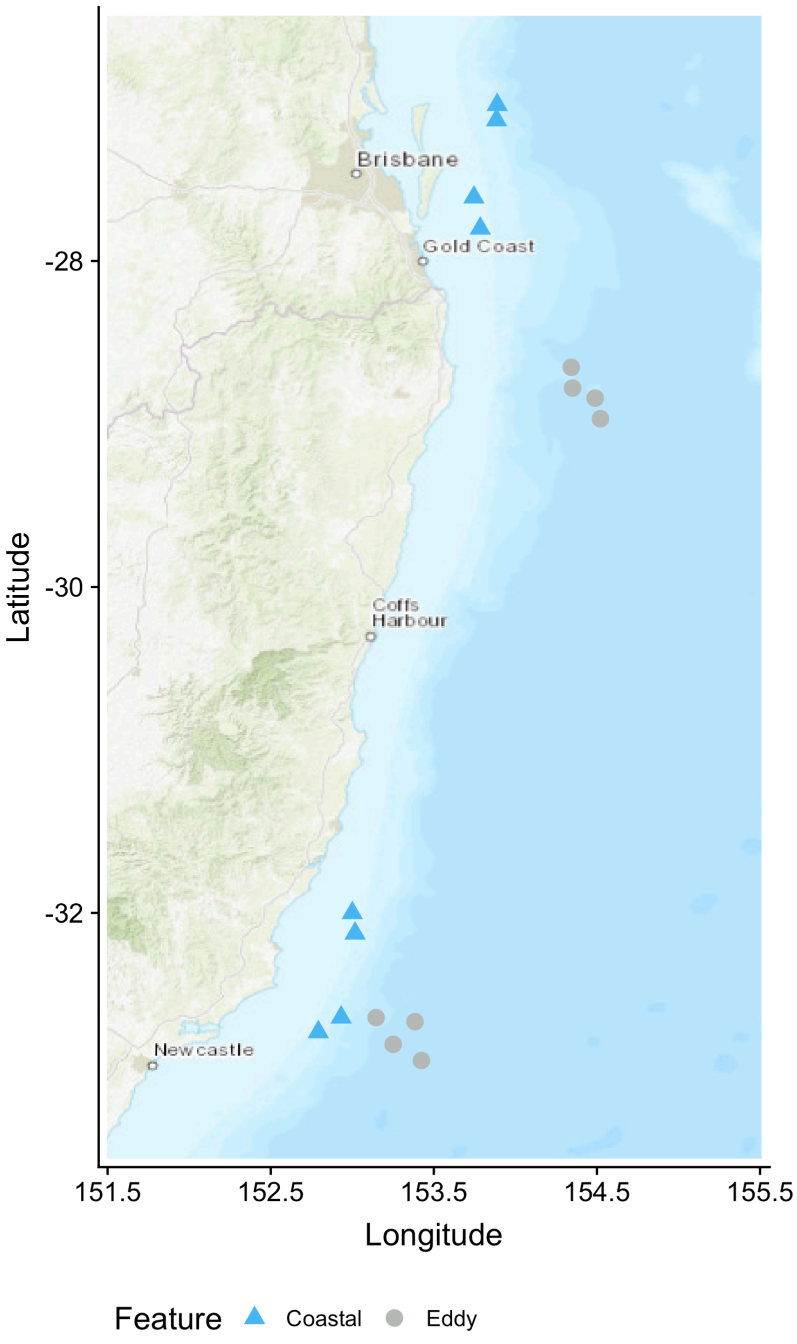

Figure 3.1: The sixteen stations sampled off the eastern coast of Australia during 2-18 June 2015. Circles denote the coastal water stations and triangles denote the eddy water stations.

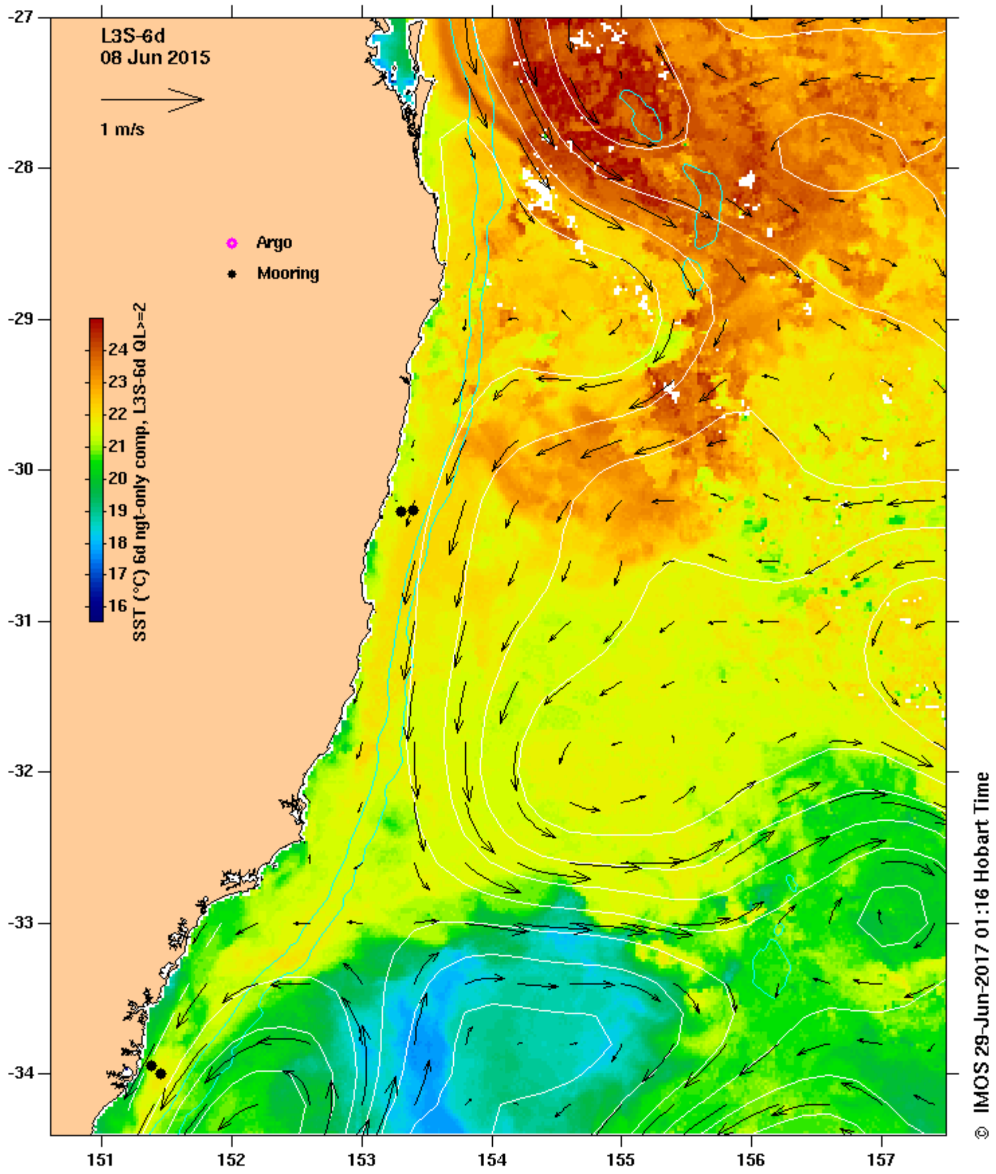

Figure 3.2: Indicates the current velocities of the same region on June 9th, halfway through the sampling effort (data was sourced from the Integrated Marine Observing System (IMOS) - IMOS is a national collaborative research infrastructure, supported by Australian Government.)

3.3.1 Data processing

In the laboratory, each zooplankton sample was sorted to separate out the larval fish. The samples were rinsed to remove excess formalin and preserved in 70% ethanol solutions. The larval fish were then sorted by morphological features and identified to the family taxonomic level where possible, utilising reference guides and expert help where appropriate (Moser 1996; Neira *et al.* 1998; Leis and Carson-Ewart 2000). For the analysis, the most abundant (greater than 100 captured) reef-associated fish families were identified from the samples, which were the family groups: Labridae, Mullidae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae, and Synodontidae. For larval fish, ontogenetic stages can be broadly defined relative to the developmental hallmark of flexion, marked by the beginning of the development of the caudal fin when the notochord bends upwards and fin rays start to develop. For the analysis, the larval fish were classified into three categories of ontogenetic stage, i.e. preflexion, flexion, or postflexion (Figure 3.3). Each fish was photographed using a calibrated stereo microscope and the standard length (SL) was measured to the nearest μm using the image acquisition software Media Cybernetics Image-Pro Insight Version 8.

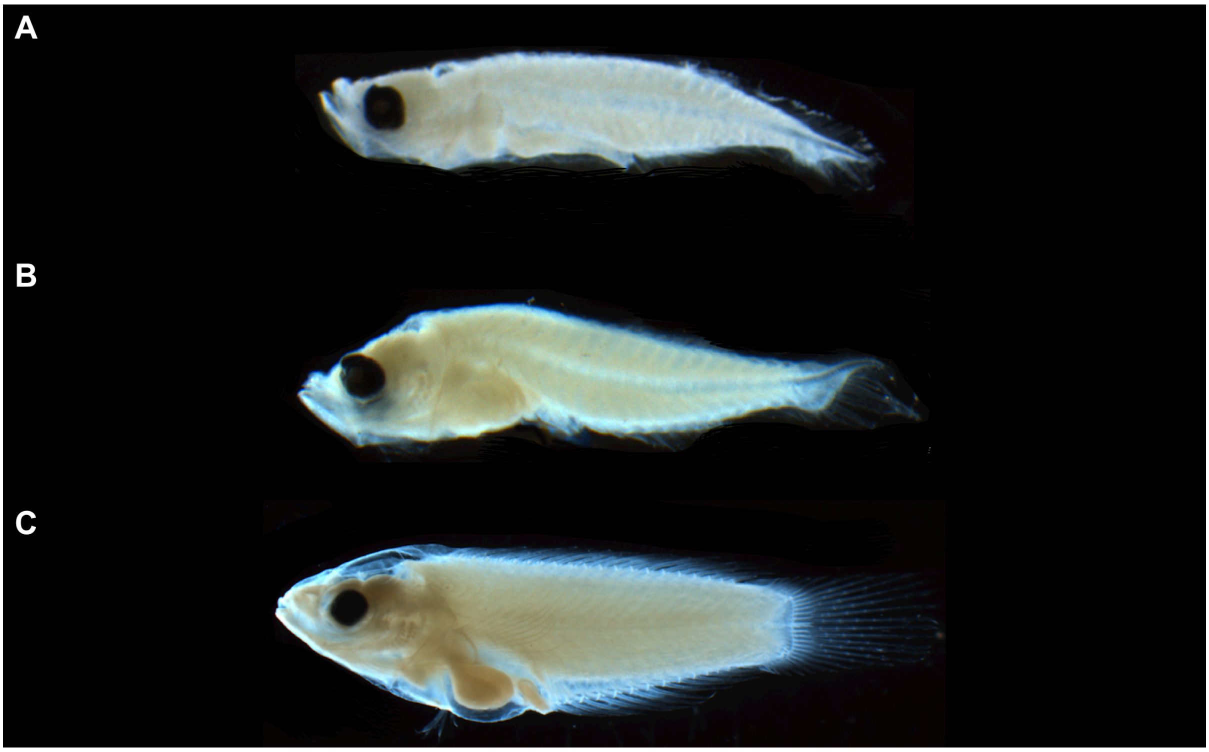

Figure 3.3: The three stages of ontogeny as seen in Labridae larvae; preflexion where the notochord is straight, and no fin rays are present (SL 3.69 mm) (A), flexion (SL 4.17 mm) where the notochord flexes upwards at a 45-degree angle (B), and postflexion (SL 9.34 mm) where the caudal fin has developed (C).

3.3.2 Data analysis

To evaluate the effect of depth and oceanographic feature on OVM patterns, I used general linear models (GLMs) with either length or concentration as the response variable (Table 3.1). A separate GLM was constructed for each of the seven families and the two response variables (length and abundance), using the independent factors of feature (levels: eddy or coastal), and depth (levels: surface, middle, deep). The stage-abundance data was analysed with concentration (individuals per 1000 m^3) as the response variable and using ontogenetic stage (levels: preflexion, flexion, postflexion) as a factor. For visualising the stage-abundance, the depth of the centre of mass for each ontogenetic stage of each family was calculated by weighting the mean depth of an interval by the proportion of larvae of each stage which occurred within that interval. Mean temperature (°C), salinity (PSU), dissolved oxygen (mg/L), and fluorescence (Relative Fluorescence Units), values were calculated for the depth range covered by each net at each station and included in the model to explain variability associated with the specific location of each station within the broader region.

For each family, GLMs were evaluated using a backwards elimination approach. Starting with the full model which included all possible predictor variables, Akaike information criterion (AIC) model selection was used to remove non-significant predictors until a model with the maximum significant predictors and lowest possible AIC was identified (Zuur *et al.* 2007; see Appendix B Table B1). Reduced models were only considered if they were significantly different from each other using Chi-square tests on residual sum of squares. Dissolved oxygen and fluorescence were highly correlated with each other ($r^2 = 0.73$), and therefore only one was included in any model at a time, but both were tested for significance separately (Table 3.1).

Abundance was standardised using the concentration (individuals per 1000 m^3) calculated from the filtered volume of water measured using a flow meter. The stage-abundance data were analysed using a negative binomial distribution to account for the over-dispersion of the data due to the high number of zeros. Despite the large number of zero observations, no models were considered to be zero-inflated after comparing the expected zeros of the data with a negative binomial model and a zero-inflated negative binomial model (Zuur *et al.* 2009). The larval fish length data was fitted with GLMs using a gamma distribution and log link function to account for the bounded non-normal distribution (possibly due to gear selection and high larval mortality), a common distribution used for fish length data (Pitcher 2002). Patterns of ontogenetic vertical migration were considered to be evident if in the stage-abundance models there was a depth and stage (DxS) interaction, and in the length models, there was an effect of depth (Table 3.1).

For conciseness, only the Wald chi-square analysis of deviance test results are presented. Post-hoc analysis of the GLMs was performed using pairwise tests on the least squares means with a Tukey adjustment. All analyses were conducted using the R programming language (R Core Team 2018). The following R packages were used in the analysis; *MASS* was used for negative binomial GLMs (Venables and Ripley 2002), *car* (Fox and Weisberg 2011) and *DHARMa* (Hartig 2017) were used for model validation, and *lsmeans* (Lenth 2016) and *multcomp* (Hothorn *et al.* 2008) were used for GLM post-hoc analysis.

Table 3.1: *The full Generalised Linear Models used to construct backwards parsimonious models for each fish family per response variable; C = concentration (individuals per 1000 m^3) or L = length; F = feature (eddy or coastal), D = depth (surface, middle, deep), S = ontogenetic stage (preflexion, flexion, postflexion), T = temperature (°C), Fl = fluorescence (Relative Fluorescence Unit), Do = dissolved oxygen (mg/L), and Sa = salinity (Practical Salinity Unit)).*

Response	Full model
Abundance	C = FxDxS + T + Sa + (Fl or Do)
Length	L = FxD + T + Sa + (Fl or Do)

3.4 Results

The seven reef-associated families comprised 2827 fish in total (a subset of 41346 identified ichthyoplankton), of which 44.3% came from the family Labridae (Table 3.2). One surface tow at station 8 was not included in the analysis because there were no flowmeter readings to determine concentration, and at station 16 the surface nets were not deployed due to rough conditions. Labridae were the most abundant of the seven families. There were differences in catches of ontogenetic stages, with some families such as Serranidae and Mullidae dominated by small preflexion larvae and Labridae was dominated by larger postflexion larvae (Table 3.2). Pomacentridae and Scaridae had low samples of postflexion and preflexion respectively. For Labridae, Mullidae, Scaridae, and Scorpaenidae, more than 65% of the larvae were sampled from water within an eddy (Table 3.2). Synodontidae were the longest larvae with a mean of 10.35 mm and Serranidae were the shortest overall at 3.22 mm.

Table 3.2: *The total catch numbers for the seven most abundant reef fish associated families caught during the cruise. The total number identified and the number at each ontogenetic stage (preflexion, flexion, and postflexion) is listed, as well as the mean standard length in mm (± standard deviation)*

Family	Preflexion	Flexion	Postflexion	Total	Coastal	Eddy	Standard length (mm)
Labridae	268	379	595	1242	412	830	5.93 (± 2.80)
Mullidae	123	61	60	244	81	163	7.44 (± 6.31)
Pomacentridae	102	84	8	194	107	87	3.88 (± 1.50)
Scaridae	9	126	94	229	58	170	5.90 (± 1.74)
Scorpaenidae	50	56	70	176	48	128	5.15 (± 2.16)
Serranidae	469	107	17	593	321	272	3.32 (± 1.47)
Synodontidae	63	39	38	140	64	76	10.35 (± 6.53)

3.4.1 Ontogenetic vertical migration patterns

For stage-abundance, the most parsimonious model for six of the seven families contained an interaction term between ontogenetic stage and depth; only the model for Scaridae did not have an interaction term (Table 3.3). The interaction between ontogenetic stage and depth, suggesting ontogenetic vertical migration, was significant for the families Labridae, Mullidae, Scorpaenidae, Serranidae and Synodontidae (Table 3.4).

Table 3.3*: The most parsimonious Generalised Linear Models constructed for each fish family per response variable; C = concentration (individuals per 1000 m*^{3}*) or L = length; F = feature (eddy or coastal), D = depth (surface, middle, deep), S = ontogenetic stage (preflexion, flexion, postflexion), T = temperature (°C), Fl = fluorescence (Relative Fluorescence Units), Do = dissolved oxygen (mg/L), and Sa = salinity (Practical Salinity Units)).*

Fish	Concentration model	Length model
Labridae	C = F + F(D) + F(S) + DxS + T	L = F + D + T + Fl
Mullidae	C = F + F(S) + DxS + Fl	L = F + D + T
Pomacentridae	C = FxSxD + T + Fl	L = F + D + T
Scaridae	C = F + FxD + D + S + T + Sa + Do	L = D + T + Sa
Scorpaenidae	C = F + F(S) + DxS + T	L = F + D + Sa
Serranidae	C = DxS + Do	L = F + D + T + Sa
Synodontidae	C = F + F(D) + F(S) + DxS + T + Do	L = F + D + Do

Table 3.4*: Wald chi-square analysis of deviance tests on the coefficients of the generalised linear models (Gamma distributed) for the larval fish stage abundance (measured as concentration m^3). The results are presented for the fish families; Labridae, Mullidae, Scorpaenidae, Serranidae, and Synodontidae. Statistical significance is denoted by asterisks: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. † denotes 1 degree of freedom and ‡ denotes 2 degrees of freedom.*

		Labridae	Mullidae	Pomacentridae	Scaridae	Scorpaenidae	Serranidae	Synodontidae
coefficient	*df*							
Depth	2	20.95***	35.14***	16.57***	2.11	1.73	1.15	2.98
Stage	2	1.64	0.15	1.68†	43.77***	15.60**	31.99***	16.20***
Feature	1	4.64*	27.29***	0.00	0.01	0.67		0.00
Depth x Stage	4	22.29***	15.51**	2.11‡		14.72**	16.84**	10.61*
Feature x Depth	2	14.78***		6.69*	5.2			5.52
Feature x Stage	2	24.58***	8.77*	0.75†		10.44**		5.21
Feature x Depth x Stage	4			3.81‡				
Temperature	1	8.93**		13.20***	45.37***	26.19***		22.09***
Salinity	1				13.05**			
D.Oxygen	1				3.38		5.70*	2.90
Fluorescence	1		16.75***	11.28***				
Observations		276	276	276	276	276	276	276

In general, most larvae across all ontogenetic stages were captured in the middle and surface layers of the water column (Figure 3.4). Preflexion larvae were almost exclusively found in the top 50 m. Larval fish were sampled across the predicted upper and lower length ranges — Serranidae and Scorpaenidae postflexion larvae were potentially under-sampled for postflexion larvae nearer transition to juveniles, although the range of species in these families naturally increases the upper range predicted for postflexion larvae (Moser 1996). The only larvae to occur in high proportions in the deep layer were Serranidae flexion and postflexion larvae, and Scorpaenidae postflexion larvae. Of the five families showing stage-abundance vertical migration, there were three patterns general patterns: migrate downwards with (1) flexion, migrate downward with flexion and then upwards with (2) postflexion, migrate downwards with flexion and further downwards with (3) postflexion (Figure 3.5). Pattern (1) was seen in Labridae and Synodontidae larvae, (2) in Mullidae, and (3) in Scorpaenidae and Serranidae. Similar migration was observed in Scaridae and Pomacentridae, patterns (2) and (3) respectively, though the changes in ontogenetic abundance were not significant.

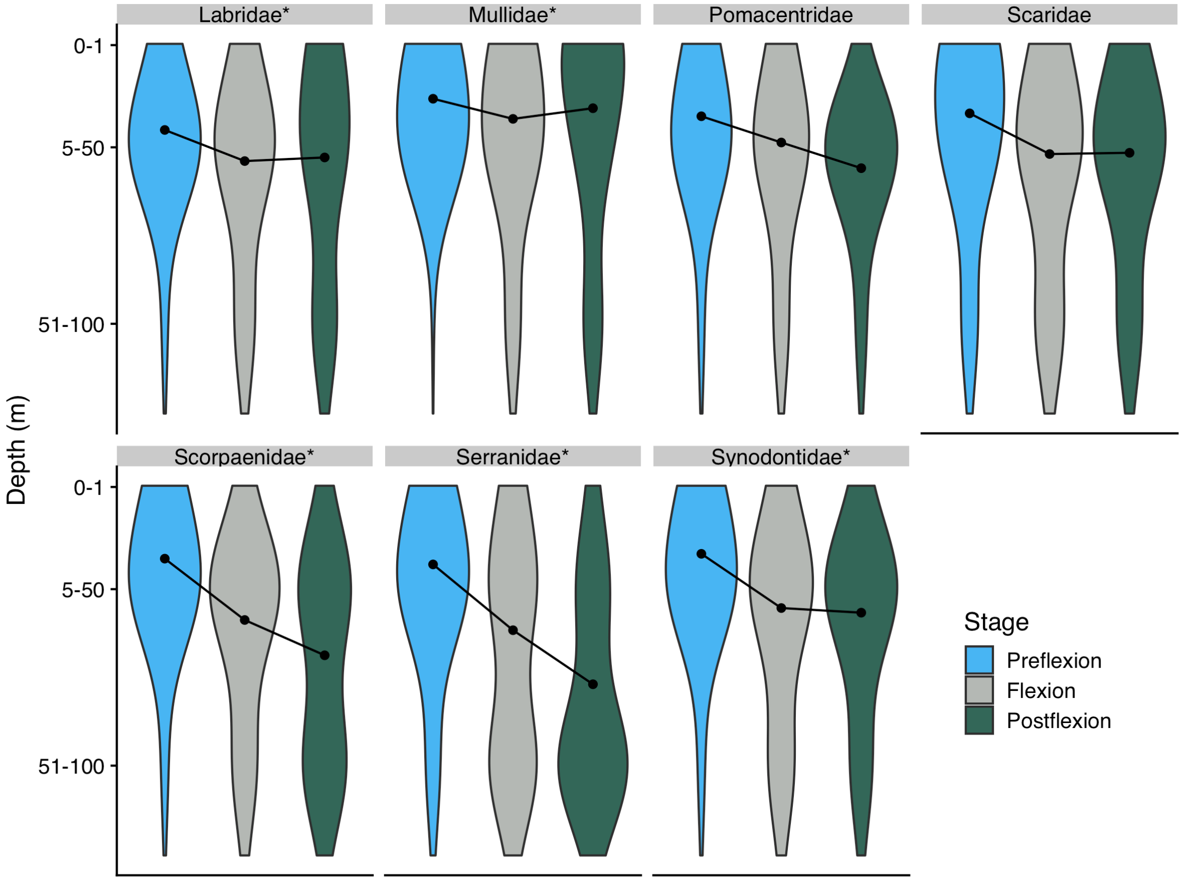

Figure 3.4: Violin plot of the proportion of larvae in each ontogenetic stage for the reef fish families at each depth range (0-1, 5-50, and 51-100 m). The width represents the proportion of each ontogenetic stage. A significant interaction between stage and depth is denoted by an asterisk (*). The weighted depth is indicated for each ontogenetic stage by the solid circle.

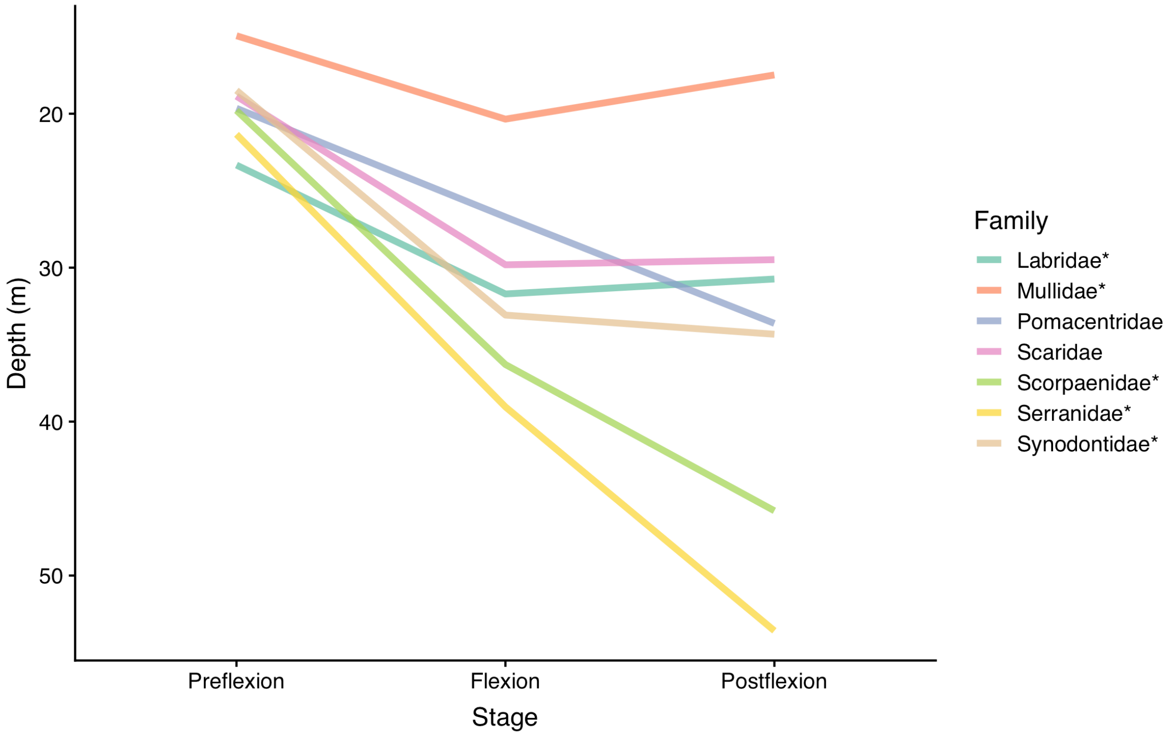

Figure 3.5: Proportion weighted average depth for each reef fish family by ontogenetic stage. A significant interaction between stage and depth is denoted by an asterisk (*). Note these are the same means presented in Figure 3.4, overlaid here for ease of comparison amongst different families.

Each reef fish family had depth as a predictor of length (Table 3.3), however, it was not a significant predictor for Synodontidae (Table 3.5). The effect of depth on length exhibited three general patterns; the larvae were shortest in the middle depth and longer at the surface and the deep (1), the larvae were longest in the deep layer (2), or the larvae were shortest at the surface (3; Figure 3.6). Pattern (1) was observed for Labridae and Mullidae larvae. Scaridae, Serranidae and Scorpaenidae larvae all displayed pattern (2). Pomacentridae was the only family to display pattern (3). Apart from Synodontidae, where length was not different across the three depths, the larvae were longer on average in the deep layer.

***Table 3.5**: Wald chi-square analysis of deviance tests on the coefficients of the generalised linear models (Gamma distributed) for the larval fish length. The results are presented for each of the fish taxonomic families Labridae, Mullidae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae, and Synodontidae. Statistical significance is denoted by asterisks: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.*

		Labridae	Mullidae	Pomacentridae	Scaridae	Scorpaenidae	Serranidae	Synodontidae
coefficient	*df*							
Feature	1	11.88***	69.05***	63.69***		9.54**	40.67***	12.84***
Depth	2	72.52***	31.45***	11.60**	6.68*	19.89***	145.00***	4.22
Temperature	1	10.81**	67.36***	19.39***	2.39		27.04***	
Salinity	1			8.51**	10.25**	4.42*		
D.Oxygen	1		2.53	7.22**				2.77
Fluorescence	1	53.37***						
Observations		1252	244	194	228	176	593	140

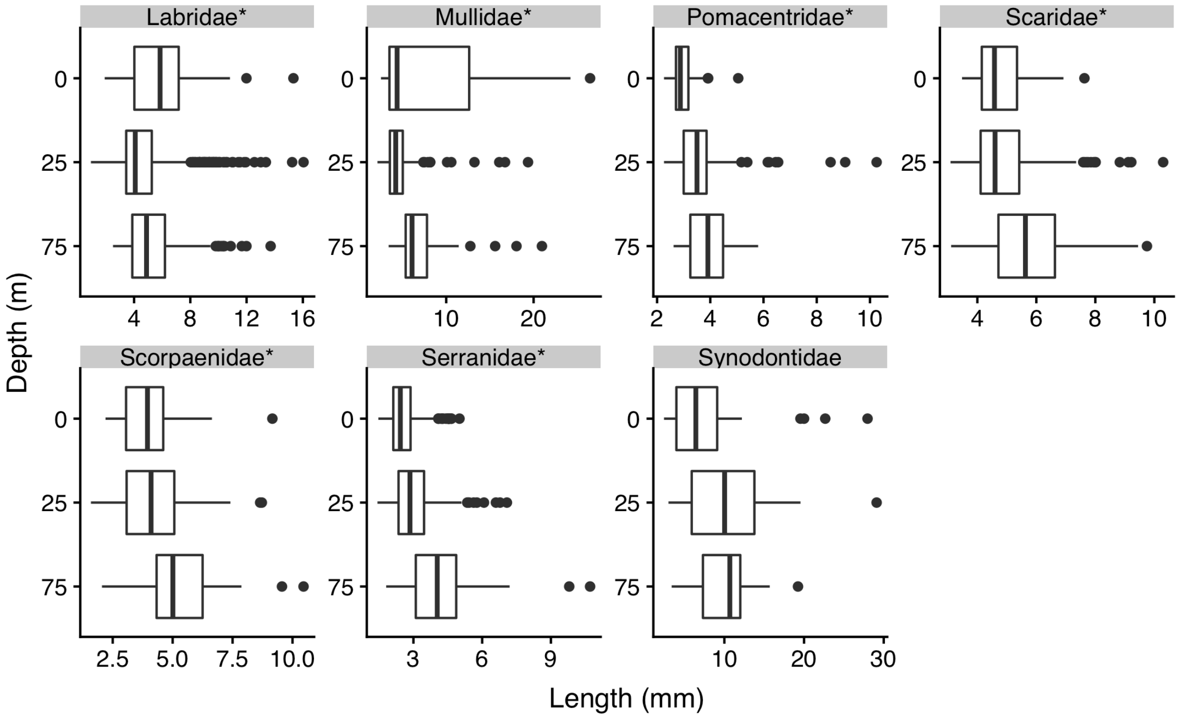

Figure 3.6: Boxplot of the length distribution (mm) of larval fish of seven temperate reef families (Labridae, Mullidae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae, and Synodontidae) at three depths (surface = 0-1 m, middle = 5-50 m, deep = 50-100 m), sampled from 16 different stations along the NSW coast. The vertical heavy line represents the median, the box hinges represent first and third quartiles, the horizontal line represents the largest and smallest observations less or greater than 1.5 times the inter-quartile range, and the points are outliers.

3.4.2 Effect of eddies on vertical migration distributions

Water feature type (whether eddy or coastal waters) was not found to change the patterns of vertical migration. For stage-abundance, the only parsimonious model that included the three-way interaction of Feature x Stage x Depth was Pomacentridae, but the interaction was not significant (Table 3.4). An interaction between Feature x Depth was not included in any of the parsimonious length models (Table 3.3). In three families, eddies had higher concentrations (Figure 3.7; Table 3.4) and in six families eddies had longer larvae (Figure 3.8; Table 3.5), but for several families no effect of water feature was seen. Eddies did have different makeups of ontogenetic stages for some families, either entraining older larvae (e.g. Labridae and Scorpaenidae) or in the case of Mullidae, younger larvae. The eddies also had depth effects on larval concentration, increasing the concentration at the surface waters for Labridae, and decreasing the concentration at the deep layer for Pomacentridae.

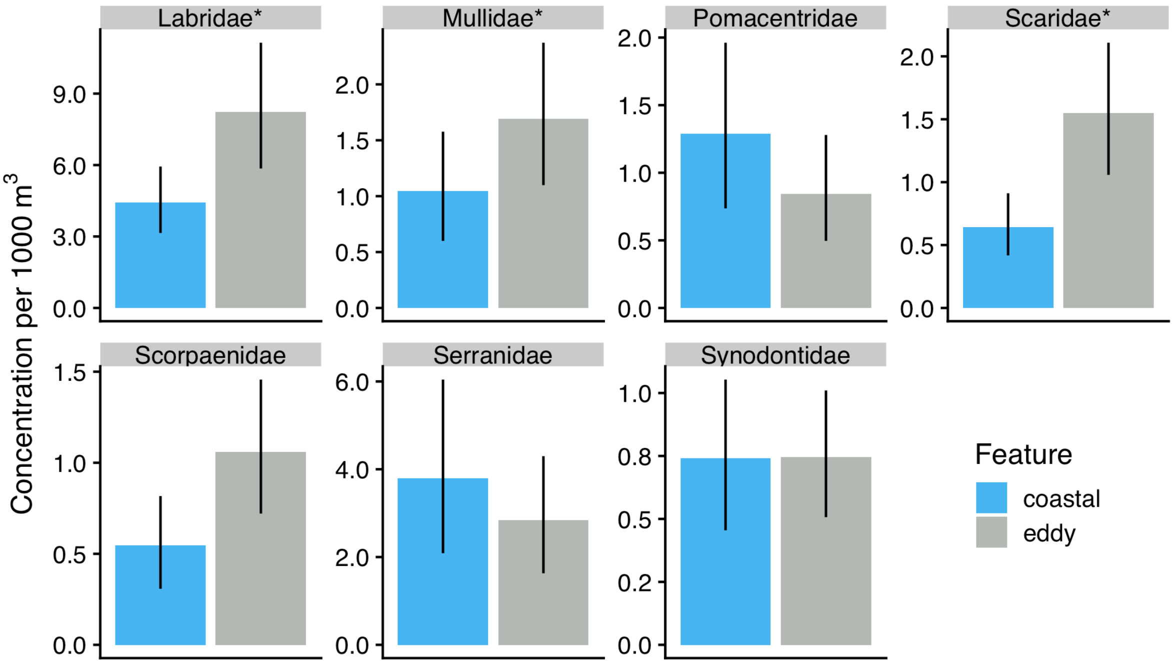

Figure 3.7: Average (± 95% CI) concentration of larval fish per 1000 m^3 for seven reef-associated families (Labridae, Mullidae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae, and Synodontidae) at two different water feature types (coastal water or eddy), sampled from 16 different stations (8 in an eddy and 8 in coastal water) along the NSW coast (* denotes statistical significance between features in the generalised linear model).

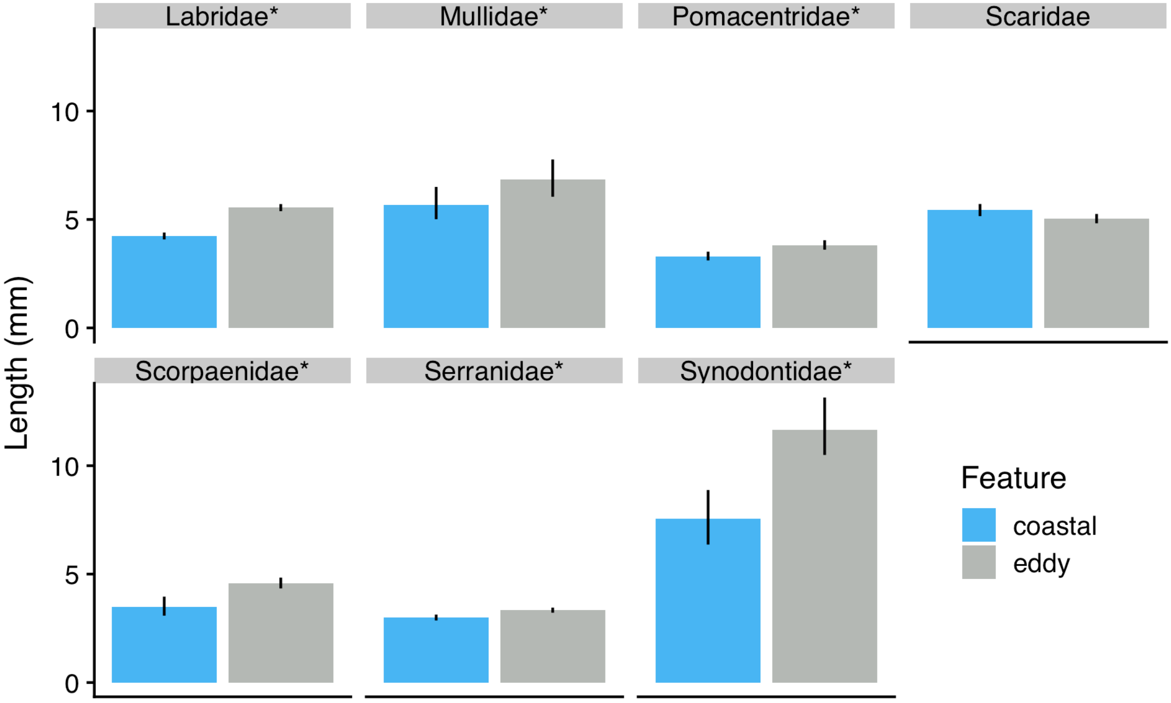

Figure 3.8: Average (± 95% CI) length (mm) of larval fish of seven reef-associated families (Labridae, Mullidae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae, and Synodontidae) at two different water feature types (coastal water or eddy), sampled from 16 different stations (8 in an eddy and 8 in coastal water) along the NSW coast (* denotes statistical significance between features in the generalised linear model).

3.4.3 Effect of water characteristics on abundance and length

The temperature of the water was on average one degree colder inside a cyclonic eddy (Figure 3.9 A). Temperature was the common predictor of both abundance (significant for five families) and length (significant for four families) of the sampled larval fish, although the direction of the effect was not consistent across families (Table 3.6). The halocline was most variable at the surface inside the eddy, and consistent for the middle and deep depths (Figure 3.9 B). Salinity predicted abundance in one family, Scaridae larvae, but predicted the length in three families (negative predictor for Pomacentridae and Scaridae, a positive predictor for Scorpaenidae; Table 3.6). Dissolved oxygen and fluorescence displayed similar patterns albeit with more variation, being consistent between the surface and the intermediate depths, but declining in the deep (Figure 3.9 C, D). Both were higher inside the eddy at the surface and middle depths, the effect of fluorescence being stronger, suggesting more production in the cyclonic eddies the than coastal waters. Dissolved oxygen predicted the abundance of Scaridae (negative) and Serranidae (positive), and only affected the length of Pomacentridae (positive; Table 3.6). In a similar trend, fluorescence was a negative predictor of abundance for Mullidae and Pomacentridae larvae, and a negative predictor for the length of Labridae.

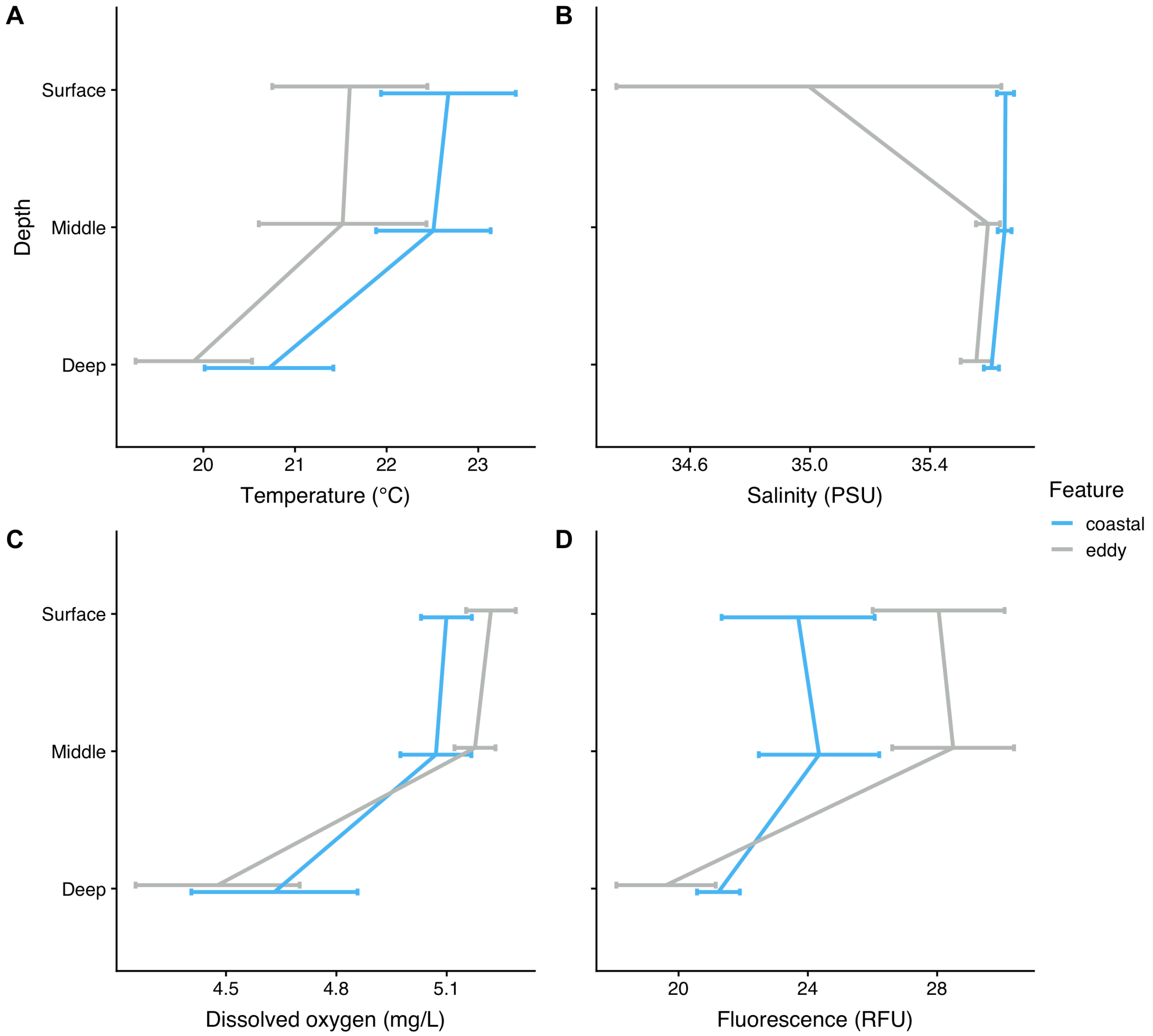

Figure 3.9: Average (± S.E.) environmental variables; temperature, salinity, dissolved oxygen, and fluorescence per depth across stations for both features (coastal and eddy).

***Table 3.6**: Summary of the effect of water characteristics; temperature (°C), salinity (Practical Salinity Units), dissolved oxygen (mg/L), and fluorescence (Relative Fluorescence Units) on the length and abundance of the larvae for seven temperate reef-associated families; Labridae, Mullidae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae, and Synodontidae collected at 16 stations off the coast of New South Wales, Australia. The arrows denote the direction of the significant predictor of the generalised linear model. No arrow indicates the water characteristic was not significant and therefore not included in the model.*

Measure	Family	Temperature	Salinity	Dissolved oxygen	Fluorescence
Abundance					
	Labridae	↑			
	Mullidae				↓
	Pomacentridae	↓			↓
	Scaridae	↑	↓	↓	
	Scorpaenidae	↑			
	Serranidae			↑	
	Synodontidae	↑			
Length					
	Labridae	↓			↓
	Mullidae	↓			
	Pomacentridae	↓	↓	↑	
	Scaridae		↓		
	Scorpaenidae		↑		
	Serranidae	↑			
	Synodontidae				

3.4.4 Family summaries

3.4.4.1 Labridae

Labridae larvae moved down the water column with flexion, with more flexion and postflexion larvae found below 50 m than preflexion ($p < 0.001$; Figure 3.4). The postflexion larvae were more abundant in the surface waters than flexion larvae. This pattern was reflected in the length model, which had the shortest larvae in the middle depth, and the longest at both the surface and deep depths (Figure 3.6). Labridae larvae were more abundant in eddies (Figure 3.7), and the entrained larvae were on average 1.14 times longer than found in coastal waters (Figure 3.8). Eddies had increased abundance of Labridae postflexion larvae, but also increased the concentration of larvae at the surface waters when compared to coastal waters (Table 3.4). Temperature was found to have a positive effect on the abundance, but a negative effect on the length of Labridae larvae (Table 3.6). Fluorescence also had a negative effect on Labridae length.

3.4.4.2 Mullidae

Mullidae larvae were most common at the surface and middle depths for all ontogenetic stages. The centre of mass moved downwards from preflexion to flexion (Figure 3.5), but upwards from flexion to postflexion (Figure 3.4). Postflexion larvae were also found to occur in the deep layer more often than preflexion larvae ($p = 0.045$). This pattern is supported in part by the length data, with the postflexion larvae in the surface and deep depths driving the patterns of longer lengths at these depths (Figure 3.6). Overall, Mullidae larvae were more abundant inside eddies (Figure 3.7), but this was driven by preflexion larvae that were 15.9 times more abundant (Table 3.4). Flexion and postflexion Mullidae larvae were found in lower numbers in eddies compared to the coastal waters. In contrast, the Mullidae larvae were on average longer in the eddies, an effect driven by the fewer but longer postflexion larvae as compared to the greater number of smaller preflexion larvae (Figure 3.8). Temperature had a small positive effect on the length of Mullidae larvae (Table 3.5).

3.4.4.3 Pomacentridae

No significant patterns of OVM were seen for Pomacentridae larvae, most likely due to the small sample size of postflexion larvae (Table 3.4, Table 3.2). Similar to most families, Pomacentridae larvae were rarely found in the deep depth (Figure 3.4). The length of Pomacentridae larvae significantly increased at each depth (Figure 3.6; Table 3.5). Eddies did not increase the overall concentration of Pomacentridae larvae (Figure 3.7), but within an eddy there were fewer Pomacentridae larvae in the deep layer. (Table 3.4). The larvae were slightly longer inside an eddy (Figure 3.8). Temperature was found to have a negative effect on both the length and concentration of larvae (Table 3.6). The length of Pomacentridae larvae was also negatively predicted by salinity, and positively predicted by dissolved oxygen.

3.4.4.4 Scaridae

Scaridae larvae did not show significant patterns of OVM, similar to Pomacentridae. One ontogenetic stage of scarids was uncommon, and that could have hindered detecting patterns due to low statistical power (Table 3.4, Table 3.2). Scaridae larvae were significantly longer at the deep depth than the other two depths (Figure 3.6). Scarids were more in high concentration within eddies than in coastal water (Figure 3.7), but not longer (Figure 3.8). Salinity was the strongest predictor of length, with increases in salinity associated with shorter larvae (Table 3.5; Table 3.6).

3.4.4.5 Scorpaenidae

Scorpaenidae larvae showed strong downwards OVM patterns with each ontogenetic stage (Figure 3.5; Table 3.4), driven by preflexion larvae that occurred in high abundances at the surface and middle depths, flexion larvae that occurred in high abundance at middle depth, and postflexion larvae that occurred in high abundance at middle and deep layers. The relationship of larvae length with depth showed the same downwards pattern, but it was not as defined, with a large increase in length occurring at the deep depth (Figure 3.6). Overall concentration did not increase within an eddy, but flexion and postflexion larvae were found at increased concentrations, 5.8 times and 10.4 respectively (Table 3.4; Figure 3.7), and the larvae were also more than 1 mm longer on average (Figure 3.8). Increasing water temperature was associated with an increasing abundance of Scorpaenidae while increasing salinity was associated with longer Scorpaenidae larvae (Table 3.6).

3.4.4.6 Serranidae

Serranidae were observed to show strong downwards OVM patterns, moving deeper with each ontogenetic stage (Figure 3.5; Table 3.4). The preflexion larvae were found at the surface and middle depths, the flexion larvae spread out across all three depths, and the postflexion larvae were found predominately at the deep depth range. This pattern was reflected by the increasing average larvae length with depth (Figure 3.6). Serranidae were shorter in eddies compared to coastal waters (Figure 3.8) and there was no effect on concentration. Increased concentration was significantly correlated with dissolved oxygen, and the increasing temperature was associated with longer Serranids.

3.4.4.7 Synodontidae

Synodontidae larvae ontogenetically migrated downwards from preflexion to flexion and then did not change their centre of mass (Figure 3.5; Table 3.4). No significant effect of depth on length was found, possibly due to the few but long postflexion larvae skewing the mean lengths (Table 3.2). Synodontidae larvae entrained in eddies were on average 30% longer compared to coastal waters (Figure 3.8), but they were not more abundant (Figure 3.7). The only environmental variable that positively predicted abundance was temperature (Table 3.6).

3.5 Discussion

This study provides evidence of ontogenetic vertical distribution patterns in many typical temperate fish families of south-eastern Australia. It also highlights that while the water mass and associated environmental characteristics had substantial effects on the abundance and length of the families considered, these mesoscale oceanographic features did not seem to affect the ontogenetic vertical distribution patterns.

3.5.1 Vertical distribution patterns

In all seven families, there were either ontogenetic shifts with depth or changes in the lengths of larvae at different depths. For stage-abundance, only the Pomacentridae and Scaridae families did not display significant patterns. All of the families with stage-abundance patterns showed ontogenetic shifts downwards, excepting Mullidae. Depth had an effect on length for all but one family, Synodontidae. Longer larvae were found at the deep layer, or in the surface and deep layers. The same pattern was not always seen in both stage-abundance and length. Length analysis does not show ontogenetic patterns as distributions as clearly as stage-abundance, as variations in the relative abundance of different stages, especially larger, post-flexion fish, can have large impacts on the length distribution at a particular depth.

Similar results to those presented here have been found in coral reef fish and other Perciformes, where an overall trend for a strong downward ontogenetic shift of the centre of mass of larval fish was seen (Boehlert *et al.* 1992; Cowen 2002; Irisson *et al.* 2010; Huebert *et al.* 2011). However, in contrast to my results, another study in south-eastern Australia found that larval fish did not show any changes in vertical distribution with ontogeny (comparing only two ontogenetic stages: preflexion and postflexion; Gray 1998). These patterns suggest that ontogenetic development in larval fish provides a greater ability to vertically migrate throughout the water column, and that they display a preference to move deeper. It is well understood that development through ontogeny provides larval fish with the ability to sense, swim and therefore regulate their depth (Leis 2010). One hypothesis is that smaller, less-developed larvae do not have the visual capabilities to see at depth (Job and Bellwood 2000). Alternative hypotheses to ontogenetic vertical migration being the mechanism for these patterns are that the vertical range of fish increases with ontogeny, allowing individuals to move more, rather than wholesale ontogenetic shifts (Irisson *et al.* 2010). Irisson *et al.* (2010) also suggested the observed patterns could be due to larval mortality, which tends to be selective in early-life (Johnson *et al.* 2014). If predation differed with depth and changed with ontogenetic stage or length, similar changes in patterns of vertical distribution might be seen.

The results of this study are consistent with previous work to varying degrees for the different fish families. Labridae larvae have been shown to not change their vertical position with ontogeny (Gray 1998; Cowen 2002), to migrate downwards with ontogeny (Irisson *et al.* 2010; Huebert *et al.* 2011), or to generally prefer the surface off the coast of NSW (Syahailatua *et al.* 2011). This study found Labridae larvae to also migrate deeper with ontogeny, with the distinction from previous studies that longer larvae were also found at the surface. Interestingly, the length distribution of Labridae predicted that longer larvae were in the surface rather than the middle depth, yet stage-abundance did not capture this relationship, instead suggesting Labridae larvae migrate downwards upon reaching flexion; an example of how length distributions alone do not always capture the patterns of ontogeny.

Serranidae larvae have been shown to vertically migrate deeper with ontogeny (Irisson *et al.* 2010; Huebert *et al.* 2011), a pattern I also observed here in both stage abundance and length data. Not all studies fully agreed with the findings from this study, suggesting strong species heterogeneity, among other factors (Olivar and Sabatés 1997; Rodríguez *et al.* 2006).

Mullidae larvae are considered surface dwelling (McCormick and Milicich 1993; Uiblein 2007), and these results partly support this, with all ontogenetic stages found in high proportions at the surface. A previous study off the NSW coastline found that Mullidae larvae were common at the surface and rare at 20 m (Gray 1993) yet found a high proportion of all stages within the middle depth. Other studies have also shown mullids to be in higher concentrations at the surface (Leis 1986; Syahailatua *et al.* 2011) or the top 10 m (Olivar and Sabatés 1997). One possible explanation for the increased vertical distribution seen in these results within the middle depth (range 5-50 m), could be that many larval fish were caught within the range 5-20 m. Giving some support to this was the rareness of Mullidae larvae in the deep layer.

Pomacentridae larvae have been shown to migrate vertically downwards (Paris and Cowen 2004) or upwards (Irisson *et al.* 2010) with ontogeny, or to prefer shallower depths across all ontogenetic stages (Leis 1991). While no significant stage-abundance vertical migration pattern was found in these results for Pomacentridae, it did suggest a downward shift and is supported by Pomacentridae larvae having increased length at the depths below the surface. The low sample size of postflexion Pomacentridae larvae most likely contributed to the statistical non-significance of the results in the stage-abundance results.

Scaridae larvae have been seen to prefer deeper depths (Leis 1991) and with increasing length (Huebert *et al.* 2011). However, these results found no change in vertical distribution for either length or stage-abundance. Similar to Pomacentridae, low sample sizes of preflexion Scaridae larvae could have contributed to the non-significant OVM findings.

Scorpaenidae showed strong structured patterns of ontogenetic downward shifts in vertical distribution. However, other studies on Scorpaenidae saw no changes in their vertical distribution (Huebert *et al.* 2011) or that larvae concentrated towards the surface and rarely found below 50 m (Kuwahara and Suzuki 1983). These contrasting results suggest Scorpaenidae have heterogenous vertical migration patterns. One explanation for these contrasting patterns could be the differences that are inherent with geographical location — this study took place in temperate waters off Australia whereas the other patterns seen were in temperate waters off Wakasa Bay, Japan (Kuwahara and Suzuki 1983) or in tropical waters in the Straits of Florida (Huebert *et al.* 2011).

While I could find no specific studies on the ontogenetic vertical distribution of Synodontidae larvae they are considered prefer depths below the surface (Leis 1991; Syahailatua *et al.* 2011). The findings of this study partly support this observation in that stage-abundance did show a downwards migration from preflexion to flexion. However, Synodontidae larvae were relatively common at the surface and included many that were well developed. The occurrence of these late-stage and large individuals at the surface is likely the reason I did not observe an increase in average length with depth which would match the stage abundance patterns.

The process of entrainment of larval fish within eddies is a well understood phenomena (Syahailatua *et al.* 2011; Matis *et al.* 2014), but the effects are less understood, with the hypothesis that eddies limit dispersal and therefore allowing for local retention (Reiss *et al.* 2000). As envisaged, ontogenetic vertical migration patterns did not differ between coastal waters and eddies. The reef-associated larval fish of the studied taxa are known to be commonly found within the top 100 m of the water column, and the thermocline depth did not change between coastal water and the eddies sampled. Even though cyclonic eddies are predicted to have higher nutrient rich waters, increased food availability had no effect on the centre of mass for the ontogenetic stage. Larval fish were found to be longer within an eddy as predicted, with the exception of Scaridae, and that is most likely a result of the small sample size of postflexion larvae. There are two probably explanations for this: increased survivorship though growth rates and food availability (Meekan *et al.* 2003; Sponaugle and Pinkard 2004; Sponaugle *et al.* 2005; Mullaney and Suthers 2013; Sabatés *et al.* 2013; Shulzitski *et al.* 2015, 2016) and as the sampled eddies moved off the continental shelf (Roughan *et al.* 2017) no more recently spawned larvae are getting entrained, therefore, typically the entrained fish larvae are longer, older and more developed. Increased concentration of postflexion larvae was only seen in two families, even though longer larvae were found — suggesting that the water feature has more of an effect on the size of the larvae compared to the development. An alternative explanation for these patterns is that regular spawning of reef fish leads to continued entrainment of preflexion larvae into the eddies, reducing any noticeable effect of stage-abundance. The sampled eddies were also of different ages, the first eddy was ~26 days and the second eddy was ~7 days old at the time of sampling (Roughan *et al.* 2017), therefore, the effect of survivorship will be weakened for species with longer development times in the second eddy, however, growth rates are fastest (Bergenius *et al.* 2002) and predicted that mortality is highest (Houde 2008) in this early period when the fish larvae are preflexion and flexion which should still allow for a small effect to be seen.

Environmental factors were also important in explaining the differences in larval abundance. The environmental variables measured explained some of the patchiness in larval fish assemblages seen between stations. It has been shown that larval fish distributions are inherently patchy (Cowen *et al.* 1993; Gray 1993), with temperature, salinity, light, tide, and flow, all influencing assemblages (Leis 2006) and vertical distribution (Aceves-Medina *et al.* 2008). Complexity is further increased by these factors interacting, such that every single factor has been seen to explain only a small amount of the variability of assemblages (Cowen *et al.* 1993). Temperature, seen to regulate depth for some species of larval fish (Olla *et al.*

1996), had the strongest effect, seen to predict both abundance and length for several families. A strong positive effect of temperature was seen most strongly in Mullidae, evidenced by the preflexion and postflexion larvae commonly found in the warmer surface waters. In general, increasing temperature was a positive predictor of abundance, Pomacentridae being the exception with an inverse pattern observed. Salinity, known to regulate depth in some species (Lougee *et al.* 2002), was only a positive predictor of Scaridae abundance but was a significant predictor of length in four of the families. Dissolved oxygen positively predicted the abundance of Mullidae and Serranidae, suggesting that larval fish migrate to areas of increased phytoplankton for feeding. However, this relationship was not consistent, with lower Pomacentridae abundance negatively associated with dissolved oxygen. Other studies did not find general trends with temperature or salinity, but some species did choose depths in the water column based on temperature (Huebert *et al.* 2010; Irisson *et al.* 2010).

Pooling larvae into taxa at the family level potentially conceals divergent species-specific patterns and therefore confounded the results (Hendriks *et al.* 2001). The decision was made in order to increase the sample size and because of both the potential for mis-identification and time constraints of identifying larval fish down to species-level without using DNA barcoding (Ko *et al.* 2013). It also provides a relevant starting point for modellers requiring early-life history information on vertical distribution patterns of larval fish. Additionally, the sampling approach used cannot measure the larval behaviour and can only provide information on the distribution (Pearre 1979). Other methods to measure vertical migration distributions are to undertake repeated sampling at a station over a 24-hour period or through visual observations by divers (Leis 2010). Observational data does measure actual behaviour, but it is limited by the length of time divers can spend in the water and how deep they can safely go to make observations and cannot be done over the depths and spatial scales used in this study.

The traditional net sampling method most likely under-sampled postflexion larvae for several of the families due to the ability to evade the nets (Leis 2006). Gear avoidance contributes to this under sampling, but high larval mortality also causes an over representation of younger larval fish making a balanced sampling design difficult. Another limitation of the study was the coarseness of the depth ranges used. Only sampling the surface waters, 5-50 m, and 50-100 m depth bins do not allow for finer ontogenetic vertical migration distributional patterns to be captured. It has been argued that ontogenetic vertical migration is a moderate adjustment in the water column and not stratification (Huebert *et al.* 2010), which is more difficult to capture using coarser depth scales. It would also be useful to sample for vertical distributions patterns during different temporal scales, from day/night time scales to seasonal scales and to test the consistency of these ontogenetic vertical distributions. For many species of larval fish, they are known to have different vertical patterns between the day and night, often exhibiting a more homogenous distribution at night (Leis 1991). The difficulty is that the cost of sampling by tows is increased over spatial and temporal scales. As a general rule, oceanographic sampling studies suffer from issues of under sampling at both the spatial scale (only 16 stations), and the ability to measure all of the factors affecting assemblages in the water column. There are additional complications when comparing larval fish sampling studies using different gears (Heino *et al.* 2011), although calibration techniques are being developed to control for sampling gear (Kwong *et al.* 2018). Replication of eddy water masses in this study was limited (two eddy and two coastal sites), which also limits the inference of patterns. Future studies should involve more stratified sampling, sampling across different time frames to detect seasonal ontogenetic changes, and comparisons between day and night to understand patterns of diel vertical migration. High resolution stratified sampling also allows for investigating the interactions of environmental variables and depth on the vertical position of the larval fish.

3.6 Conclusion

Ontogenetic vertical distributions are not uniform for reef-associated fish families of NSW, but the general pattern for these seven families was to increase depth with age. When larval fish do exhibit patterns that could be associated with ontogenetic vertical migration, variables of length and stage-abundance can show contrasting patterns because of the large influence of the relative abundance of different stages. Nevertheless, much of this variability can be put down to the difficulty in sampling individual larvae across all ontogenetic stage groups. Even when vertical patterns are seen, it needs to be remembered that a complex number of variables can also affect this distributional pattern, e.g. light, temperature, and food. Larval fish entrainment in eddies does not change ontogenetic vertical distribution patterns, but there is an effect on the abundance of larval stages and length of larvae at depths within an eddy compared to coastal waters. The vertical migration shown for the sampled larval fish have the potential to influence their dispersal due to differences in current velocities across a stratified water column. The ontogenetic vertical patterns described by this study will be useful for parameterising biophysical dispersal models, with the aim of understanding connectivity patterns of NSW reef fish larvae from each of these seven families.

4 Comparing the influence of the implementation of different larval behavioural strategies on connectivity patterns in biophysical dispersal models

4.1 Abstract

Many species of marine teleost fish have a pelagic larval phase, and until recently it was assumed that any behaviour during this larval stage had little effect on dispersal. Biophysical dispersal models (BDM) allow us to infer the relative influence of different physical and biological processes on connectivity and dispersal patterns. This chapter aimed to investigate the impact on dispersal of a combination of behaviours: ontogenetic vertical migration, diel vertical migration, and orientated horizontal swimming. Also, to compare how changing the values and processes of ontogenetic vertical migration affects the dispersal patterns. A hydrodynamic model of the waters off the eastern coast of Australia was used for the study, which is characterised by a southward western boundary current. The results showed that while the largest driver of connectivity was the location and timing of spawning, larval behaviour also was a pivotal driver. Orientated horizontal swimming was found to influence connectivity patterns the most and ontogenetic vertical migration the least. Therefore, future modelling connectivity studies should strive to include orientated horizontal swimming, and more empirical research is required into understanding the cues of settlement. Different values of ontogenetic vertical migration also had little effect on connectivity. However, the processes (timing) of the migration had a stronger effect. For modellers this result suggests that decisions on how to encapsulate behaviour are more important than making behavioural assumptions when parameterising a BDM.

4.2 Introduction

Recent empirical studies have demonstrated how pelagic larval fish, far from being passive as previously thought, can exhibit a variety of behaviours to influence where they settle (Leis 2006). The swimming behaviours of larval fish known to change patterns of dispersal are vertical migration—ontogenetic (Paris and Cowen 2004; Paris *et al.* 2007) and diel (Huebert *et al.* 2011)—and orientated horizontal swimming (both pre-competent larvae; Leis 2006; and competent larvae towards preferred settlement habitat; Gerlach *et al.* 2007). Swimming behaviours can provide a mechanism for the larvae of reef associated fish retention close their spawning habitat, through both vertically migrating to avoid advection by strong wind driven surface currents and directed horizontal swimming towards preferred settlement reef by sensing cues (e.g. larvae could sense their natal reef; Cowen and Sponaugle 2009). Connectivity is a challenging problem to study empirically even with recent advancements in experimental techniques (Gillanders 2002; Jones *et al.* 2005; Hedgecock *et al.* 2007; Williamson *et al.* 2016). Understanding the effect of swimming behaviours on dispersal across a region is a significant challenge due to the size of larvae and the expansive nature of the marine environment, making *in situ* observations of swimming behaviour difficult. Therefore, biophysical dispersal models (BDMs; coupled hydrodynamic models with individual based models of larvae with biological and behavioural traits) becomes useful tool with which to predict dispersal patterns and to consider ecological questions on the processes behind marine larval dispersal (Treml *et al.* 2008; Staaterman and Paris 2014).

Advances in our understanding of the behavioural abilities of fish larvae has given rise to questions about how these behaviours influence dispersal for both specific populations and oceanographic regions (Werner *et al.* 2007). Modelling studies have implemented different migration behaviours; ontogenetic vertical migration (OVM; Paris *et al.* 2007; Staaterman *et al.* 2012), diel vertical migration (DVM; Aiken *et al.* 2011; Robins *et al.* 2013), and orientated horizontal swimming (OHS; Staaterman *et al.* 2012; Armsworth 2000; Wolanski and Kingsford 2014), and found that all the behaviours are predicted to influence larval dispersal, in general, by increasing local retention and reducing the overall dispersal. Modellers and empiricists need to collaborate to ensure that behaviours predicted to be influential for BDMs are also a focus data collection in empirical research, allowing for more realistic models. Often when there is consensus on the influence of a behaviour on dispersal, i.e. OVM, empirical data is only available for few species making parametrisation of BDMs difficult (Leis 2006). Scarcity of data had forced several modelling studies to include OVM behaviour due to its importance (Rochette *et al.* 2012; Holstein *et al.* 2014; Donahue *et al.* 2015) even when the specific values for a species or taxa of larval fish are unavailable. Data scarcity forces connectivity modellers to choose between either limiting the behaviour of marine larvae (Andrello *et al.* 2013), using generalisations or substitute species to parametrise a model (Young *et al.* 2012), or estimating universal larval traits across taxa (Corell *et al.* 2012).

Another important modelling decision when choosing behaviours to include in a BDM is how to realistically capture the processes that drive the behaviour, it is relatively simple to make a larva swim in a model but more difficult to ensure the larva swims in a biologically meaningful way. Due to the difficulty in obtaining ichthyoplankton early-life history data, this information is often unknown, which leads to assumptions, e.g. how do fish larvae vertically migrate with ontogeny - are these migrations gradual or sudden, or do offshore currents vertically advect the larvae; and do fish larvae swim at a speeds similar to those observed in flow chambers (Fisher *et al.* 2000), or is swimming speed better approximated by swimming speeds measured *in situ*, and what stage of development should be chosen to measure these speeds (Leis and Carson-Ewart 1997). The exact mechanisms behind movement with ontogeny are still unknown (Irisson *et al.* 2010), leading to different BDMs capturing the same behaviour but with differing approaches to modelling the underlying processes (Paris *et al.* 2007; Puckett *et al.* 2014; García-García *et al.* 2016).

BDM studies provide us with a mechanism to model the complex behaviour of larval fish and understand how different behavioural characteristics influence dispersal patterns, with the intention of increasing the accuracy and precision of the modelled patterns. Often this occurs within the framework of a sensitivity analysis, where the values of a parameter are tested over a range to determine how much effect it has on dispersal patterns (Treml *et al.* 2015; Monroy *et al.* 2017; Kvile *et al.* 2018) or similarly by comparing the effect of behavioural traits on dispersal within (Ayata *et al.* 2010; Herbert *et al.* 2011; Koeck *et al.* 2015) or across modelled taxa (Watson *et al.* 2010; Young *et al.* 2012). At the present stage there is no consensus on the relative importance of larval behaviours to include within the model - often due to contrasting results (Puckett *et al.* 2014; Treml *et al.* 2015), and the complexity of BDMs make comparisons between studies problematic (see Chapter 2). Most likely behaviours are chosen based on what empirical data is available, and the high amount of studies still implementing BDMs with only passive larvae suggests that modellers are taking a cautious approach to including behavioural assumptions even when these behaviours are seen to be influential (see Chapter 2).

The overarching aim of this chapter is to provide an integrated assessment of the relative importance of the inclusion of various larval behavioural processes on connectivity patterns in BDMs, specifically the use of OVM, DVM, and OHS. The relative importance will be measured using comparisons of the predicted connectivity patterns, and by using common metrics of connectivity (local retention, self-recruitment, settlement success, and dispersal distance). The study specifically investigates three scenarios to compare the influence of behaviours on dispersal patterns for regions with a poleward western boundary current: (1) comparing the dispersal patterns of modelled taxa with different behavioural traits to determine the influence of including combinations of behaviours, (2) comparing the effect of different OVM strategies using a sensitivity analysis based on observed values of taxa for the study region from Chapter 3, and (3) comparing how modellers choice in implementing the underlying process of a behaviour (OVM) has the potential to influence the dispersal patterns. I expect that all behaviours (and combinations of) will influence the modelled dispersal patterns and resulting metrics, compared to no swimming behaviour. I also predict that vertical migration (OVM and DVM) will have a stronger effect than OHS for this study, as minor they become competent to horizontally swim. For the second and third scenarios, I expect that the patterns of movement and not the underlying process should be the primary influence of connectivity patterns.

4.3 Methods

4.3.1 Model development

The biophysical dispersal model—Zooplankton Interconnections and Source-Sink Observation Utility (ZISSOU, v1.1.4; Hawes 2018)—is an individual-based model (IBM) developed following recommendations from the "Manual of recommended practices for modelling physical-biological interactions during fish early life" (North *et al.* 2009). The major processes captured by ZISSOU are described in the flow chart shown in Figure 4.1. Movement of particles within the model is forced by offline oceanographic current data but can be influenced by larval behavioural traits parameterised using probability distributions capturing observed biological variability. The driver for developing a bespoke model for this study instead of using other open-source BDMs (Lett *et al.* 2008; North *et al.* 2008; Paris *et al.* 2013) was to facilitate the development of customised (and multiple) implementations of the processes behind the behavioural traits of larvae with the vision of producing more complex larval behaviours as the model matures, while using modern coding paradigms with complete code test coverage for end-user confidence. The system was designed for high-performance, high customisation, and platform independence utilising the language Scala (v2.12.4; http://www.scala-lang.org) with parallel libraries for scalability.

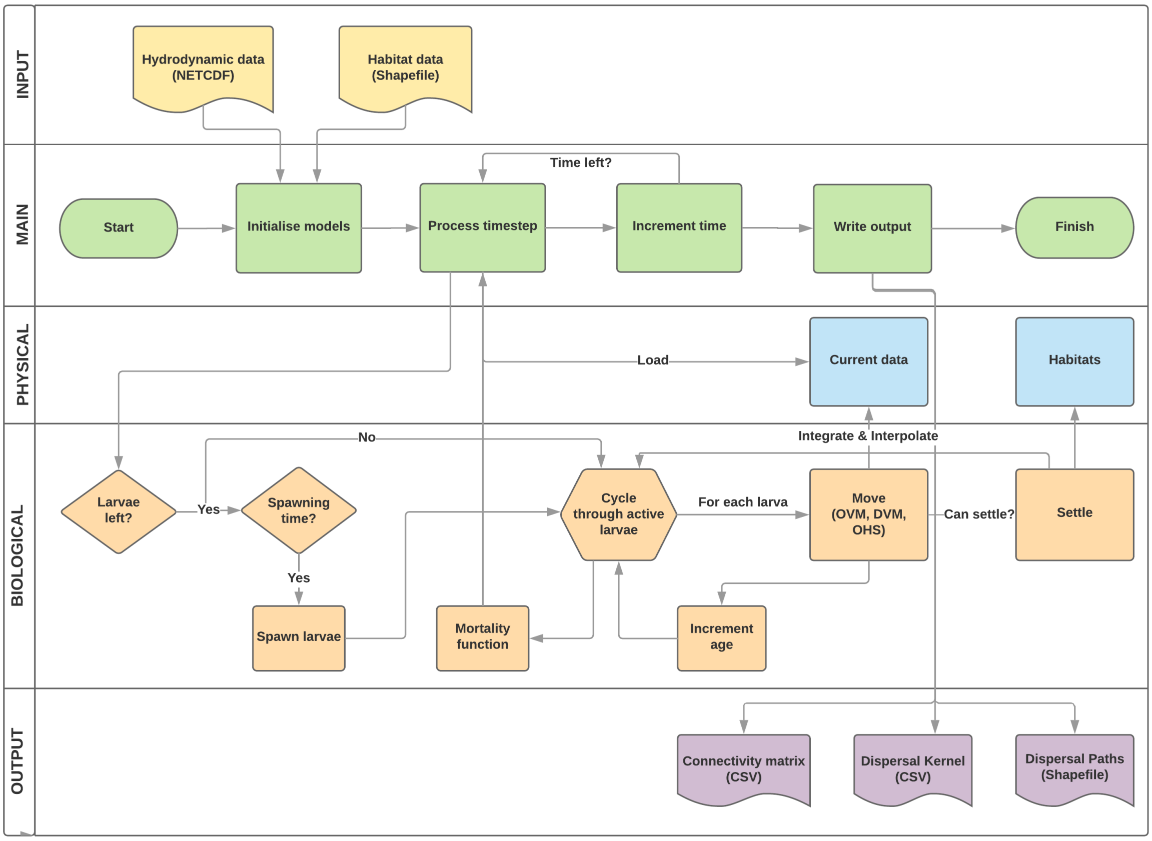

Figure 4.1: The flow chart of ZISSOU (Zooplankton Interconnections and Source-Sink Observation Utility), the biophysical dispersal model used in this study, highlighting the major processes used to disperse the larvae using both physical and biological processes. The move process encapsulates all migration: DVM = diel vertical migration, OHS = orientated horizontal swimming, OVM = ontogenetic vertical migration.

4.3.1.1 Physical sub-model

ZISSOU accesses ocean circulation or hydrodynamic data as network common data forms (NetCDF) — self-describing, machine-independent data formats. The data can be obtained either using locally stored files or using the Open-source Project for a Network Data Access Protocol (OPeNDAP; http://www.opendap.org). This project took advantage of Java NetCDF software libraries developed by UCAR/Unidata (http://doi.org/10.5065/D6H70CW6). The ocean data must be in an Arakawa-A or Arakawa-B grid structure (Arakawa 1997). Currently, ZISSOU utilises the 3-dimensional velocity fields of hydrodynamic models only, with environmental variables such as salinity or temperature to be incorporated into future versions.

Runge-Kutta fourth-order integration (RK4) is the ordinary differential equations solver used to move the particle through space and time (North *et al.* 2009), calculating a weighted average over four increments using the chosen model time step (Equation 4.2). The velocity at any given position in space is interpolated using a tri-cubic interpolation scheme on the hydrodynamic model grid, such that the velocity for a given particle in the oceanographic space is interpolated from neighbouring grids using 64 points (4^3; Equation 4.1). If this is not possible, for example, due to boundary conditions, trilinear interpolation using 8 points (2^3) is substituted.

$$f(x, y, z) = \sum_{i=0}^{3}\sum_{j=0}^{3}\sum_{k=0}^{3} v_{ijk}\, x^i y^j z^k \qquad (4.1)$$

where the velocity v at the point *(x,y,z)*; x is the longitude, y is the latitude, and z is the depth; is interpolated using the 64 nearest neighbours.

$$\overrightarrow{v_{t+h}} = \overrightarrow{v_t} + \frac{(k_1 + 2k_2 + 2k_3 + k_4)\Delta t}{6} \qquad (4.2)$$

$$k_1 = f(x_t, y_t, z_t)$$

$$k_2 = k_1 + f\left(x_{\left(t+\frac{\Delta t}{2}\right)}, y_{\left(t+\frac{\Delta t}{2}\right)}, z_{\left(t+\frac{\Delta t}{2}\right)}\right)$$

$$k_3 = k_2 + f\left(x_{\left(t+\frac{\Delta t}{2}\right)}, y_{\left(t+\frac{\Delta t}{2}\right)}, z_{\left(t+\frac{\Delta t}{2}\right)}\right)$$

$$k_4 = k_3 + f(x_{(t+\Delta t)}, y_{(t+\Delta t)}, z_{(t+\Delta t)})$$

where the integrated velocity vector ($v_{t+\Delta t}$), at time t and time step Δt is calculated using the weighted average of the four separate interpolations (k_1, k_2, k_3, k_4). The velocities are interpolated at the current time, two midpoint approximations of the time with half the time step added, and at the time incremented by the time step. The tri-cubic interpolation function $f(x,y,z)$ calculates the velocities as described above (Equation 4.1).

To model the natural turbulent effect of ocean systems in a 3D stochastic model, ZISSOU uses a random displacement mechanism Equation 4.3, (Brickman and Smith 2002; North *et al.* 2009).

$$D = \sqrt{\frac{2K}{\Delta t}\mathbb{Z}} \qquad (4.3)$$

where D is the displacement for a given direction, K is the eddy diffusivity parameter, the model time step Δt and a random number Z from a Gaussian distribution with a mean of zero. The displacement is added to the velocity for the specified direction (u, v or w) at each time step.

Pseudo-random numbers are generated in the model using a Mersenne Twister algorithm, WELL44497b (Panneton *et al.* 2006). The seed for the random number generator is an optional parameter of the model to allow for exact reproducibility of results if needed.

4.3.1.2 Biological sub-model

Biological traits are specified using a configurable XML file as input to the model. The biological model implements many biological processes that are considered to be important for marine larval dispersal (Table 4.1). The pelagic larval duration is specified by the length of the larval period in days. Larvae can be assigned a pre-competency period, whereby they cannot settle before a specified number of days, otherwise, larvae can attempt to settle until they reach their PLD. If no pre-competency period is assigned, then larvae attempt to settle when their age reaches their assigned PLD. Spawning sites are indicated using GPS locations (latitude and longitude in decimal degrees), with spawning time and frequency, the spawning depth in the water column, and the number of larvae to spawn as configurable options. The particles seeded in the model are referred to as larvae but can also simulate pelagic eggs (with egg buoyancy) through the inclusion of a specific age stage. The larval fish developmental stages (hatching, preflexion, flexion, postflexion) are described using the mean (± standard deviation) age (in days) of larvae at each ontogenetic stage. From this input, stage transition ages (day at which the larvae transitions from one developmental stage to another) are assigned to individual larvae at birth using a Gaussian distribution (if no standard deviation is specified, the mean is the value).

***Table 4.1**: Summary of the biological and behavioural traits that can be specified in the biological sub-model.*

Trait	Options	Description	Units
Pelagic larval duration	-	Larvae assigned a PLD sampled from a Gaussian distribution	days (Gaussian)
Non-settlement competency period	-	Larvae are only allowed to settle once competent, competency age sampled from a Gaussian distribution	days
Development age	Preflexion	Age of preflexion sampled from a Gaussian distribution. If this value is greater than 0, the larvae are considered to be pelagic eggs during the first period.	days
	Flexion	Age of flexion sampled from a Gaussian distribution	days
	Postflexion	Age of postflexion sampled from a Gaussian distribution	days
Spawning sites	Location	The latitude and longitude of larval release location	GPS Coordinates
	Depth	The depth the larvae are spawned	metres (m)
	Number	The number of larvae to spawn	Positive integer
	Period	The period to release the larvae over	Date range
	Interval	The number of days between releases	Days (e.g. 1 = daily, 7 = weekly)
Settlement sites	-	Polygons representing settlement sites	GIS Shapefile
Mortality	Linear	The percentage of larvae to be randomly killed each day	Rate (% per day)
Vertical migration	Diel	Vertically migrates the particles twice daily at sunset and sunrise	Probabilities of larvae day/night distributions at user specified depths
	Ontogenetic	Vertically migrates to another depth based on their ontogenetic stage	Probabilities of larvae ontogenetic distributions at user specified depths
Settlement buffer	-	The distance within which a larva can settle to a reef	Kilometres (km)
Sensory distance	-	The distance at which a larva can sense a reef and orientate towards it	Kilometres (km)

Horizontal swimming	Critical swimming speed (U_{crit})	The speed at which a fish can swim before it fatigues as measured in a laboratory setting	Metres per second (ms^{-1})
	In situ swimming speed	The swimming speed of the fish larvae recorded by divers *in situ* as a proportion of the U_{crit}	Proportion
	Swimming endurance	The proportion of time the fish can spend swimming as measured in a laboratory setting	Proportion

Settlement sites are represented as GIS polygons within the model, using point in polygon algorithms to determine if larvae are over settlement sites. The polygons are supplied as input in the Shapefile format, a standard geospatial vector data format specified by the Environmental Systems Research Institute (Esri; https://www.esri.com/). Larval mortality can be included in the model, specified as a percentage daily rate of mortality applied randomly across the population, a common approach in connectivity studies (Butler *et al.* 2011; Kool *et al.* 2011; Treml *et al.* 2015).

Vertical migration can be implemented as either diel or ontogenetic vertical migration. Both are based on the probability of being in a specific depth range based on either the time of day (i.e. night or day) or their ontogenetic stage (Figure 4.2). The vertical position of larvae was changed by applying a probability distribution function to determine to which depth the larvae moved. For diel vertical migration, this probability distribution function was applied one hour before sunset or sunrise using an approximation calculated using the current latitude/longitude of the larvae.

There are three choices for the timing of ontogenetic vertical migration using different methodologies: vertically migrating when the next developmental stage is reached, at the end of a 24-hour period (daily migration), or during each time step within chosen constraints of movement. Moving larvae vertically with the onset of an ontogenetic stage is the most straightforward method and has been used in many studies (García-García *et al.* 2016) but creates a wholly stratified larval distribution (all members of a stage class are at the same depth). Another approach, which doesn't lead to this strict, and perhaps biologically unrealistic stage distribution pattern is to allow some amount of vertical migration every day or time step but with movement restricted to certain depth ranges based on ontogeny. This strategy has been used in many studies (Paris *et al.* 2007; Puckett *et al.* 2014) and creates a more random process with a centre of mass at specific depths. In essence, these strategies allow for modelling vertical behaviour whereby different species of larval fish change vertical position restricted or unrestricted by depth.

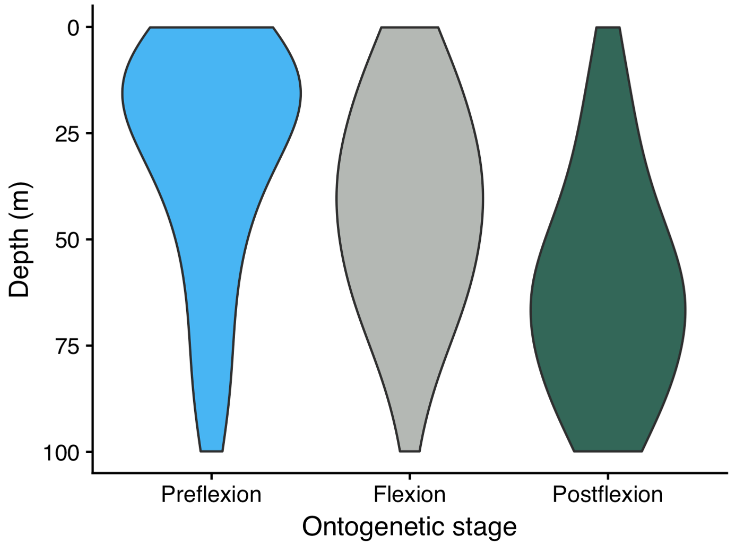

Figure 4.2: Example of ontogenetic vertical migration input for a fish that migrates downwards with ontogeny, where the proportions of larval occurrence at different depths are specified for each stage (preflexion, flexion, and postflexion), and must sum to one for each developmental stage

A settlement buffer can be specified that enables the larvae to discover settlement habitat if they pass within the prescribed distance. The distance is measured as the nearest point on the habitat polygon. If multiple polygons are detected within the distance, the closest habitat polygon to the larvae is settled. The settlement buffer simulates the ability of larvae to detect and orientate towards settlement habitat over distances seen for fish larvae (Leis 2006), compensation for factors not captured in the model such as unresolved habitats and behaviours that help propel larvae towards settlement habitat.

While there are numerous measures of larval swimming capacity developed in the literature—U_{crit}, maximum speed, endurance, *in-situ* speed—there is little consensus on which is most appropriate to use within a modelling context. The approach I take here assumes the larvae swim at a rate somewhere between *in-situ* speed and U_{crit} but not continuously. Specifically, the horizontal swimming speed in the model is calculated using U_{crit} as the maximum sustained swimming speed and using the *in-situ* speed as the minimum sustained swimming speed, with a random number generator determining a speed between the two for each time step (Equation 4.4). The critical swimming speed (U_{crit}, Brett 1964), is a standard measure of the swimming potential of larval fish and is commonly available for many reef fish species and easy to measure (Hogan *et al.* 2007). The *in situ* swimming speed is a measure of the swimming ability of larval fish in the ocean (as measured by divers) and correlates with U_{crit} (Leis and Fisher 2006). I also assume the fish cannot swim for the entire duration of the time step; the period the fish can swim is specified using a parameter of endurance potential (Equation 4.4). The direction of movement is calculated using the orientation of the sensed reef (Equation 4.5; Equation 4.6). Larvae only have the ability to swim once they reach flexion and have started to develop a caudal fin. The larvae swim in a random direction and only orientate when they swim close to settlement habitat (within the given sensory distance), the sensory distance acts as pseudo-behaviour for cues such as vision, hearing or olfaction (Kingsford *et al.* 2002; Leis 2006). Some species of larval fish can smell reefs from distances of several kilometres (Paris *et al.* 2013). Once within the sensory range of viable habitat, larvae can orientate towards it while they are swimming.

$$s_{fish} = U_{crit}\mathbb{Z}_{[s_p,1]}E_p \qquad (4.4)$$

$$u' = u + s_{fish}\cos\theta \qquad (4.5)$$

$$v' = v + s_{fish}\sin\theta \qquad (4.6)$$

where s_{fish} is the horizontal swimming speed, U_{crit} is the critical swimming speed, Z is a random number with a minimum value of the *in situ* swimming potential s_p and a maximum value of 1, and E_p is the endurance potential. u is the longitude vector, v is the latitude vector, and θ is the angle of orientation towards the sensed reef.

4.3.2 Model configuration

4.3.2.1 Study location

The New South Wales (NSW) coastline (2,137 km) was divided into 17 equally sized regions of approximately 125 km each (Figure 4.3; for ZISSOU configuration files see Appendix C). Rocky reef patches were identified using benthic data obtained from NSW Office of Environment and Heritage (OEH; http://data.environment.nsw.gov.au). Within each sub-region, four rocky reef patches (approximately 30 hectares in size) from across the sub-region were chosen as spawning sites. Larvae were released weekly from the centre of each spawning site in batches of 1000 over the period July 2007 to June 2008. In total, 3.5 million larvae were spawned. Larvae were allowed to settle to the identified rocky reef patches or benthic habitat patches which had been categorised as “unknown” unmapped patches could be potential rocky reef settlement sites.

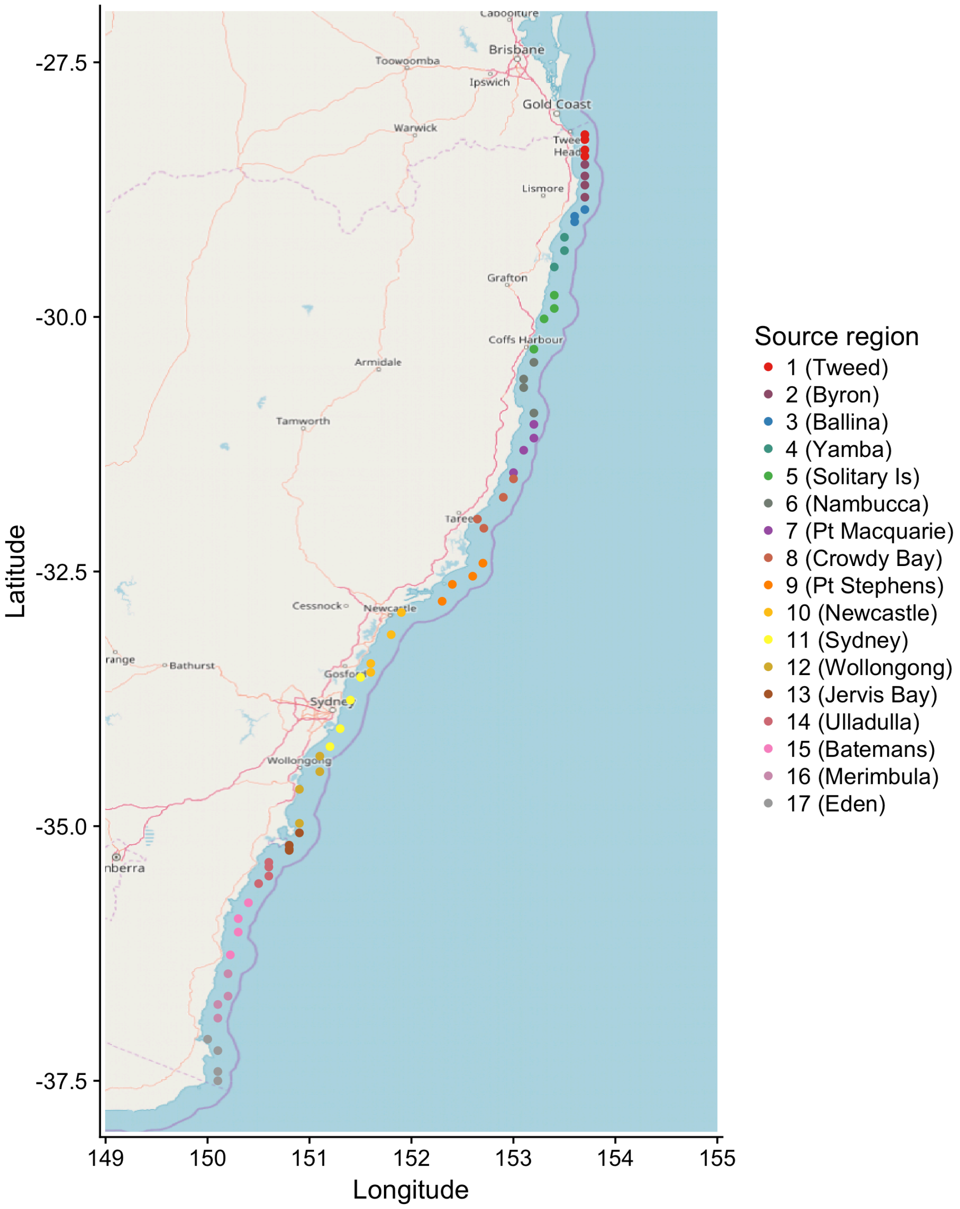

Figure 4.3: The 17 regions (each containing four rock reef patches) used to spawn the reef fish larvae along the coastline of New South Wales, Australia

4.3.2.2 Physical sub-model

The oceanographic circulation model used was BRAN3 (Bluelink reanalysis, version 3p5; Oke *et al.* 2013), a well validated (Chiswell and Rickard 2014; Vasile *et al.* 2018) hindcast model based on the Ocean Forecasting Australia Model (OFAM). BRAN is a data-assimilating model that aims to resolve mesoscale eddies in 3-dimensions, at the scale of 10 km in the horizontal (0.1° latitude and longitude) and 5-10 m vertically (15 depth bins between 0 and 105 m). The model output consists of mean daily current velocities, sea-level anomaly, sea-surface temperature, and salinity over the period January 1993 to September 2012. An eddy diffusivity value (*K*) of 300 ms^{-1} was used, as per similar studies in the region (Chiswell and Rickard 2011; Condie and Condie 2016). The time step of the model was two hours.

4.3.2.3 Biological sub-model

Model parameters are based on characteristics of a temperate rock reef fish from the family Pomacentridae (Damselfishes). This family was chosen as it is relatively well studied, thus providing reasonable estimates of the various parameters required for modelling. The literature on fish early-life histories is biased towards tropical and sub-tropical species, therefore where values for temperate Pomacentridae were not found, information of tropical larvae was utilised (Table 4.1). Individual larvae only settled at the end of their pelagic larval duration if it was within the settlement buffer distance of suitable settlement habitat. The larvae were spawned in the preflexion stage, assuming a species with benthic eggs which is common for Pomacentridae. The lack of velocity data near the coast is an inherent property of the grid structure of the flow model but one that can limit the ability of fish to settle on some reef patches. In order to compensate for the grid structure and the relative coarseness of the oceanographic model (e.g. 10 km resolution), larvae were given a settlement buffer of 10 km, which was slightly larger (but within one standard deviation) of the mean settlement buffer distance of 8.3 km (± 5.2) identified in the review of existing studies presented in Chapter 2 (Table 4.2). No mortality was applied for the simulations described in this chapter, due to the aim of comparing patterns of potential connectivity rather than realised connectivity.

***Table 4.2**: Biological features of the Pomacentridae larvae that were used in every model run of this study*

Biological feature	Value	Reference
PLD	18.3 (± 1.5) days	Wellington and Victor (1989)
Preflexion age	0 days	Murphy *et al.* (2007)
Flexion age	5 (± 0.5) days	Murphy *et al.* (2007)
Postflexion age	8 (± 0.5) days	Murphy *et al.* (2007)
Settlement buffer	10 km	Chapter 2

In order to address the first aim of evaluating the influence of different behaviours on connectivity patterns I ran a series of models with varying combinations of the behaviours to compare patterns resulting from the implementation of (1) vertical advection (VA), (2) diel vertical migration (DVM), (3) ontogenetic vertical migration (OVM), and (4) orientated horizontal swimming (OHS). Each behaviour (and a combination of congruent behaviours) was compared to a base case of passive, vertically-restricted (no movement in the horizontal direction, either passive or active) transport (scenario 1, Table 4.3).

Table 4.3: *Summary of the implementation of the four-movement mechanisms (one passive and three behaviours) in the ten different model scenarios run in the study. Mechanisms are abbreviated as: VA = vertical advection, DVM = diel vertical migration, OVM = ontogenetic vertical migration, and OHS = orientated horizontal swimming.*

Model	VA	DVM	OVM	OHS
1	—	—	—	—
2	Yes	—	—	—
3	—	Yes	—	—
4	—	—	Yes	—
5	—	—	—	Yes
6	Yes	—	—	Yes
7	—	Yes	Yes	—
8	—	Yes	—	Yes
9	—	—	Yes	Yes
10	—	Yes	Yes	Yes

The vertical advection scenarios were included because the implementation of this in existing models is varied and has the potential to impact connectivity like the behaviourally driven vertical movement. This mechanism only applies to models with no other vertical migration component, as DVM and OVM change the vertical position of the larvae after it has been advected by the *w* (vertical) vector (Table 4.3). Larvae were given the DVM probabilities for Pomacentridae derived from a larval fish study in the same oceanic region (Gray 1998). Larvae were migrated using a probability distribution function between 25 m depth bins within the top 100 m of the water column (Figure 4.4; see Appendix C, Table C1).

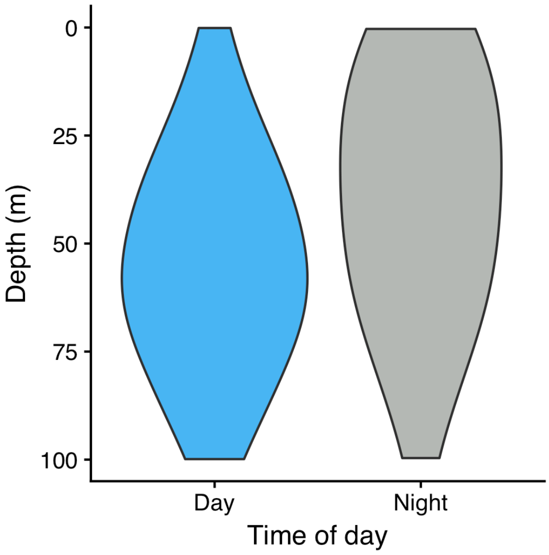

Figure 4.4: The diel vertical distribution patterns used in the model for the day and night time.

The OVM models used the values for OVM distribution values of Pomacentridae larvae observed in the empirical study described in Chapter 3 (see Appendix C, Table C2). This data indicated that the larvae centre of mass moves downwards from the surface during preflexion, commonly to the top 50 m during postflexion (Figure 4.5).

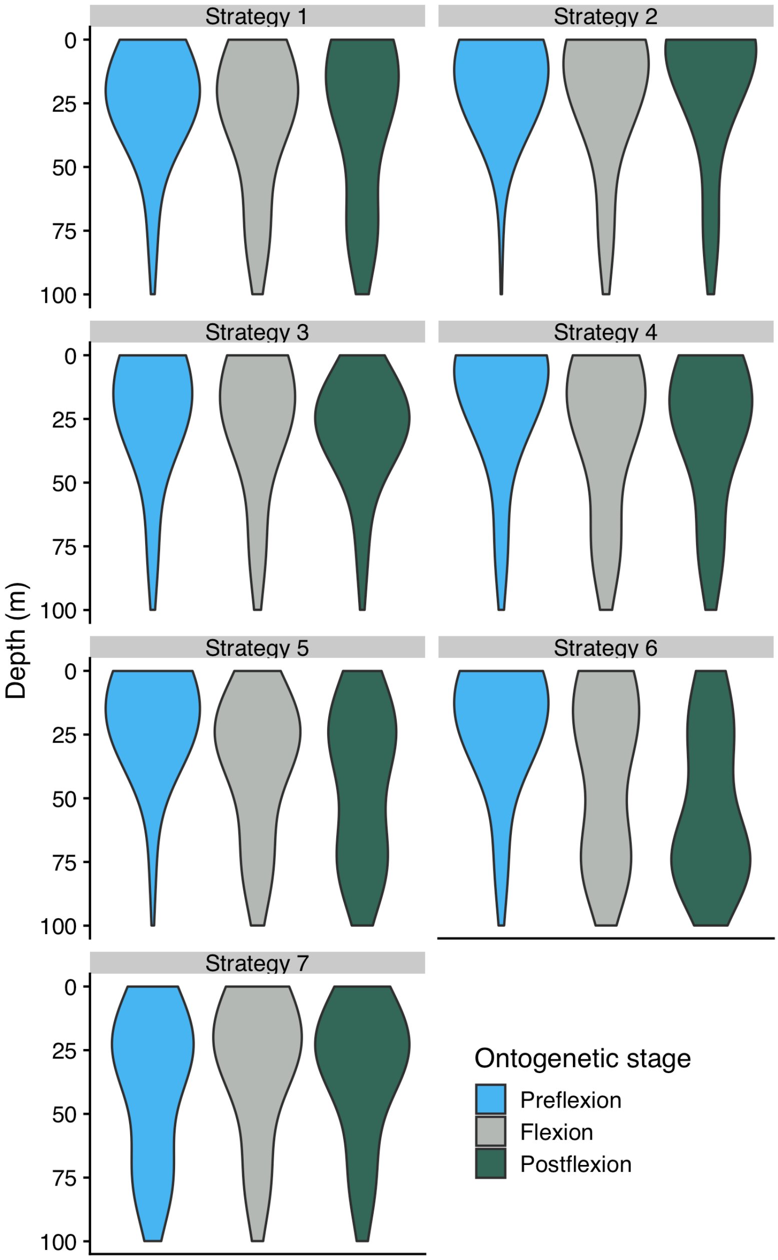

Figure 4.5: Proportional depth stage abundance profiles for each of the seven different ontogenetic vertical migration strategies evaluated in Chapter 3. Values represent the proportional (within a stage) abundance of each ontogenetic stage (preflexion, flexion, postflexion) within each of three depth ranges (surface: 0-1 m; middle: 5-50 m; deep layer: 50-100 m) and are used to parameterise models run to address Aim 2 of this study.

For the OHS scenario, to orientate and swim towards a reef, the larval fish were given a reef sensory distance of 10 km, which was the maximum extent used in other studies (Staaterman *et al.* 2012; Wolanski and Kingsford 2014), Table 4.4. The swimming ability of the larvae was based on the common tropical Pomacentridae species *Abudefduf vaigensis*. Tropical species are strongly represented in studies of larval fish swimming speeds, and therefore more data is available. They are predicted to swim faster than temperate species due to hydrodynamic differences in temperature (Herbing 2002) and viscosity (Fuiman and Batty 1997); however, this study only compared the effect of including swimming behaviour and not predicting realistic patterns of connectivity for the region. Each larval fish was given a critical swimming speed (U_{crit}) of 0.463 ms^{-1} and an *in situ* potential of 25%, values observed for *A. vaigensis* (Leis and Fisher 2006); therefore the actual swimming speed ranged between 0.116 to 0.463 ms^{-1}. Pomacentridae larval fish are competent swimmers, having been seen to sustain constant speeds on average for 50 hours and with a maximum effort of more than 230 hours in laboratory settings (Stobutzki and Bellwood 1997). In this study I used a conservative estimate of endurance, only allowing the larval fish to swim for 50% of each time step (one hour), similar to a metric of FV_{50} (50% fatigue velocity) used in other studies to measure the sustained speed over a 1-2 hour period (Jenkins and Welsford 2002). It is reasonable to believe this speed is less than U_{crit} (Leis 2006).

***Table 4.4**: Orientated horizontal swimming (OHS) parameterisation, used in the swimming equation described above*

OHS feature	Value	Reference
Sensory distance	10 km	Chapter 2
U_{crit}	0.463 ms^{-1}	Leis and Fisher (2006)
In situ swimming potential	25%	Leis and Fisher (2006)
Endurance	50%	Stobutzki and Bellwood (1997), Jenkins and Welsford (2002), Leis (2006)

The second aim, to assess the impact on connectivity of using different ontogenetic vertical migration parameters was addressed by conducting model runs using proportional depth stage abundance profiles which represented the seven strategies seen in Chapter 3 (Figure 4.5; see Appendix C, Table C2). Ontogenetic vertical migration was implemented such that the larvae moved when they reached their next ontogenetic stage (based on developmental time).

Lastly, to explore the impact of the OVM implementation strategy on connectivity patterns I compared three different methods of ontogenetic vertical migration; time step, daily and ontogenetic stage migration (Table 4.5). The vertical position of the larvae is changed using a probability distribution function at the different times in the model iterations (1) at each time step, (2) after 24 hours in the model, and (3) when the larvae developed into the next ontogenetic stage. Settlement stage Pomacentridae larvae of *Chromis atripectoralis* have been seen to change vertical position up to 15 m within six minutes (Leis 2004), but the behaviour of less developed larval fish is unknown. Therefore, for the migration method in (1), due to the higher frequency of positional change, larvae are restricted to moving only 25 m or less.

Table 4.5: *The three different scenarios for implementing larval fish ontogenetic vertical migration (OVM) in the biophysical dispersal model*

Model	OVM migration timing
1	Time step migration
2	Daily migration
3	Stage migration

4.3.3 Data analysis

Each model run produced as output a connectivity matrix, which represents the connectivity between the larval source (row *i*) and settlement (column *j*) regions where each element *i,j* is the proportion of all larvae spawned at *i* which settled at *j* over the release period. Two main questions arise in connectivity studies: firstly, when larvae are spawned at a region, where do they settle, and secondly, where did the larvae that recruited to a region arrive from? Therefore, the connectivity patterns from a source region and to a settlement region were both investigated (estimated from one year of spawning and ignoring intra-annual variability). Multivariate comparisons of the connectivity patterns from source regions were made using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities. Similar to comparisons of ecological communities using abundance data, it allows for the assessment of the relative similarity of regional patterns (replicates/species) across different model scenarios (variables/communities). A square root transform was applied to the Bray-Curtis dissimilarity distance matrices to down-weight the influence of highly abundant areas of settlement (a common transformation for abundance data due and considering the amount of settlement reef was only approximately equal per region; Quinn and Keough 2002). There were substantial differences in settlement patterns of the source regions due to variations in regional oceanography (see Results). These differences are interesting but can serve mask meaningful comparisons when considering implications of larval behaviour on dispersal. Therefore, the settlement patterns of the model with no behaviour model (model 1; Table 4.3), were used to normalise the settlement patterns derived for the other models and investigating the deviations from this null model. To quantitatively measure if the dispersal patterns of the behavioural models within each scenario (behavioural, OVM strategy, and OVM method) significantly differed to the null model, distance-based permutational multivariate analysis of variance (PERMANOVA) was used (Anderson 2017).

To compare how different dispersal patterns were to each other within a scenario to each other, Constrained Analysis of Principal Coordinates (CAP)—constrained coordinates analysis allowing for non-Euclidean distances that reducing all the source region settlement patterns to a single point for univariate comparison—was used to visually compare the dissimilarity between models to the null model within each scenario (Anderson and Willis 2003). For each CAP ordination, significance tests of the CAP ordination, the ordination axes, and variable addition and deletion (Type I and Type III tests respectively) were performed. The differences in dispersal patterns within scenarios were also compared using the total settlement at each region for each model within a scenario. Dissimilarities were compared using both hierarchal cluster analysis (using an average-link clustering method with a Bray-Curtis dissimilarity measure) and using constrained coordinates analysis (CCA; using Euclidean distance metrics).

Comparisons of dispersal patterns between models were also measured using common metrics of connectivity to describe dispersal: self-recruitment, local retention, settlement success, dispersal distance (refer to Chapter 2, Table 2.1 for definitions). Quantitative differences between these metrics for all models within each scenario were determined using a one-way repeated measure ANOVA (with regions as replicates; $n = 17$, and models in a scenario as the within-subjects effect). Tukey post-hoc pairwise tests were used to assess differences amongst regions where ANOVAs were significant ($\alpha = 0.05$). In addition, other metrics to compare the dispersal patterns were also utilised (see Appendix C for results): settlement site richness (the number of reefs receiving settlers), diversity of settlement using the Shannon-Weiner index (using the number of reefs and total larvae settled per reef), and the connectance of the dispersal pattern for a model (the proportion of the edges connecting natal and settlement sites in a graph compared to the theoretical maximum number of edges.

All data analysis was performed using the R statistical programming environment (v3.5.1; R Core Team 2018). Some additional packages were used for analysis: *ConnMattTools* (Kaplan *et al.* 2017) to obtain connectivity metrics, *igraph* (Csardi and Nepusz 2006) and *NetIndices* (Kones *et al.* 2009) to construct the graphs and to obtain measures of connectance, and *vegan* to calculate dissimilarity matrices, NMDS, PERMANOVA (using the *adonis* function), and CAP analysis (Oksanen *et al.* 2018).

4.4 Results

4.4.1 Behaviour scenario: comparison of the different behavioural models

4.4.1.1 Connectivity from source regions

There were strong differences in source region connectivity patterns which displayed a marked geographical gradient across all behaviours, creating a “horseshoe” shape on the NMDS where regions were most similar with geographically proximate regions (Figure 4.6). For 59% of the source regions (1-4, 9-10, 14-17), there were two distinct clusters of settlement patterns; driven by the inclusion of orientated horizontal swimming (OHS) behaviour in the model (Figure 4.6). Region 9 showed the most robust differences between settlement patterns with or without OHS. An intriguing result was that the settlement patterns of region 16 with OHS were more similar to the settlement patterns of region 17 without OHS than region 16 without OHS. For the other 41% of source regions, the settlement patterns were grouped on region and not behaviour.

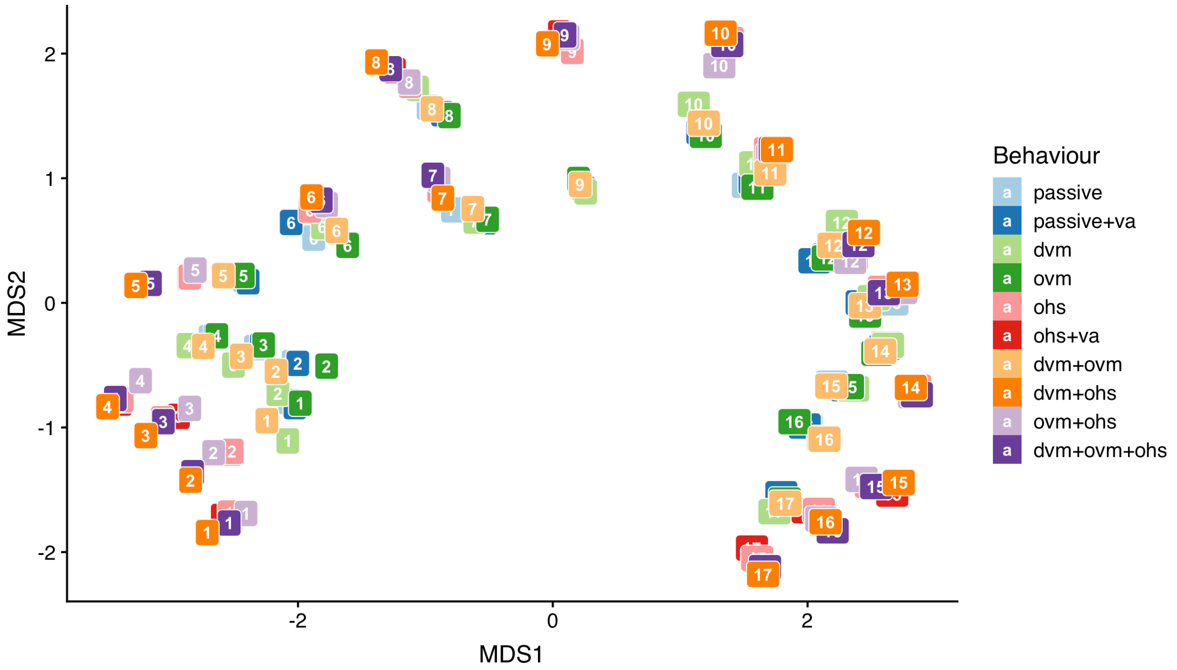

Figure 4.6: NMDS ordination plot (2D stress = 0.06) using Bray-Curtis dissimilarities between the different source-settlement patterns for each of the 17 source regions for the models within the behaviour scenario (Passive = no behaviour, VA = vertical advection, DVM = diel vertical migration, OVM = ontogenetic vertical migration; OHS = orientated horizontal swimming).

Standardising the settlement patterns by the passive model in multivariate space reduces the passive model to a single point (Figure 4.7) and therefore the size of the effect of behaviour is measured by the distance from this centremost point of passive connectivity. When standardised by the settlement patterns from the passive model, the strong clustering of OHS behaviours seen in Figure 4.6 becomes less distinct (Figure 4.7). The effect of models with OHS is considerably stronger than models without OHS, with the models OVM and OVM+DVM showing little differentiation for most regions (Figure 4.7). Interestingly for all the behavioural models, the settlement from source regions 11-13 was similar to the passive model. The effects of source region are strongest for the models with OHS included. For some source regions the models with OHS still clustered strongly (e.g. 3, 8, and 9), but for other regions, there were considerable dissimilarities between models with OHS (e.g. 1, 5, and 6). The model with diel vertical migration (DVM) showed unique settlement patterns, with little overlap from other models. PERMANOVA found no differences between the standardised settlement patterns from the source regions for the different behavioural models (R^2 = 0.03, p > 0.05), instead regional patterns explained most of the variation (R^2 = 0.60, p < 0.001).

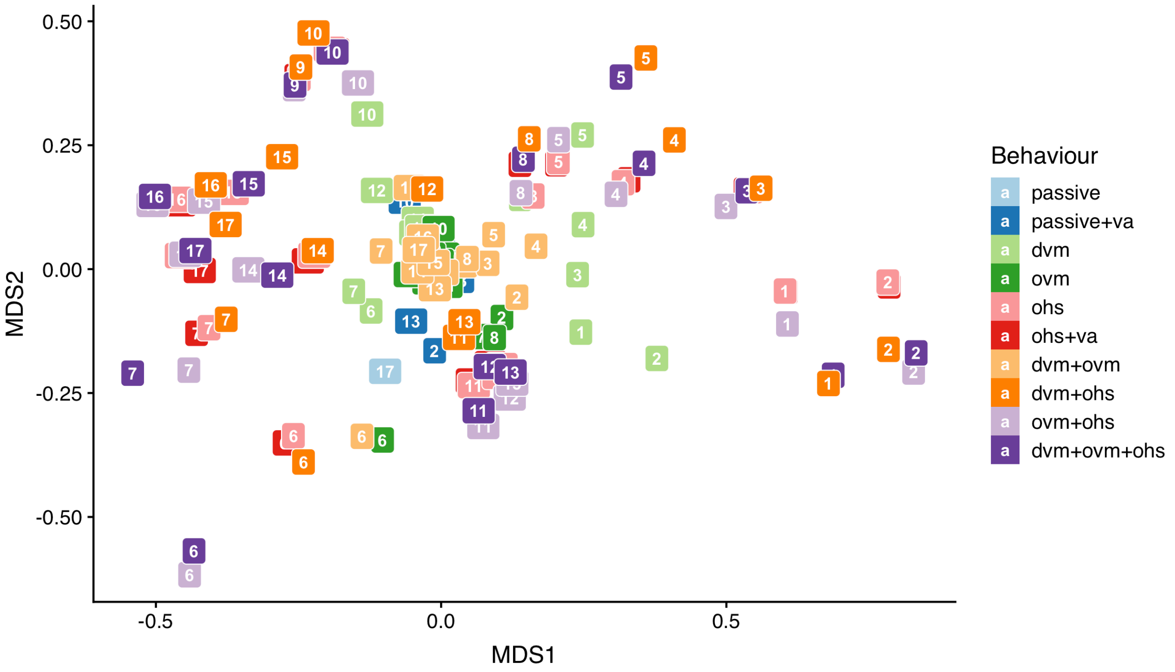

Figure 4.7: NMDS ordination plot (2D stress = 0.19) using Bray-Curtis dissimilarities between the different source-settlement patterns for each of the 17 source regions for the models within the behaviour scenario and normalised using the passive behaviour scenario (Passive = no behaviour, VA = with vertical advection, DVM = diel vertical migration, OVM = ontogenetic vertical migration; OHS = orientated horizontal swimming).

The CAP analysis indicated including behaviour in a model, and different combinations of behaviour changed the connectivity patterns of the larvae (Figure 4.8; $F_{(9,144)} = 1.35$; $p = 0.031$). The settlement patterns formed two clusters: models with or without OHS. Models with OHS were grouped in tighter clusters than models without OHS. Of the models without OHS, models with DVM migration were less similar than models with OVM to the passive model. The passive model with vertical advection was more similar to the model with OVM than the passive model alone. The most dissimilar models were the passive and the model with all three behaviours (DVM+OVM+OHS). Restricting the larvae to the surface (Passive) or allowing the particle to be advected vertically (Passive+VA) produced dissimilar connectivity patterns, but when combined with OHS the connectivity patterns were identical.

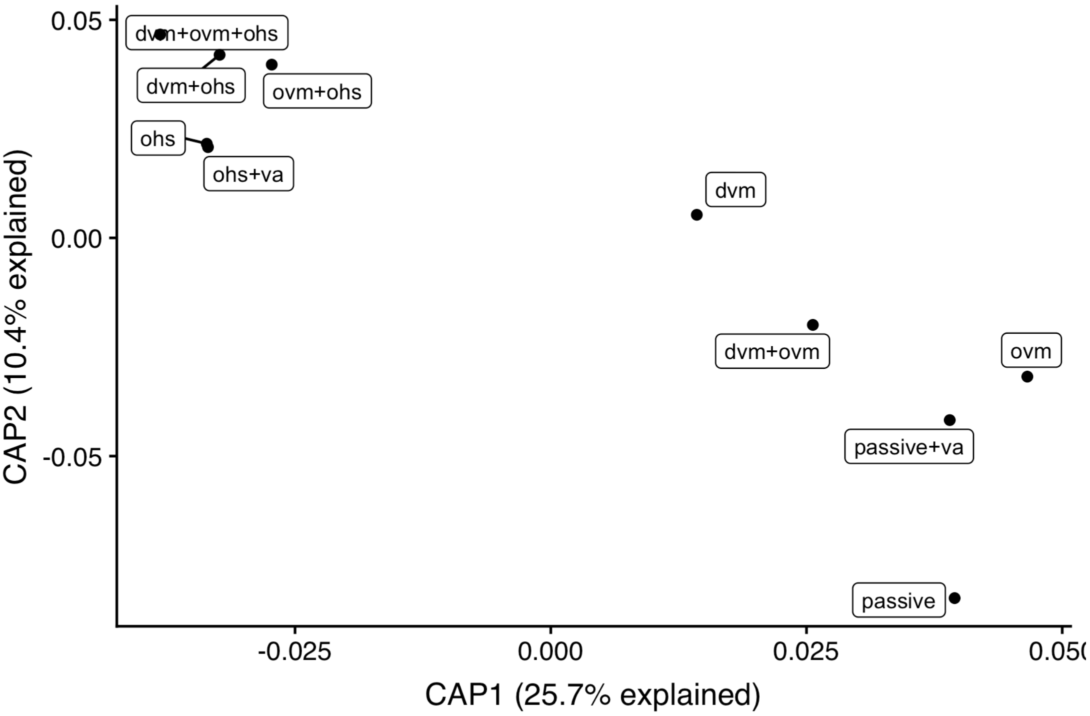

Figure 4.8: Constrained analysis of principal coordinates (CAP) for the models within the behaviour scenario using Bray-Curtis dissimilarities between the different source-settlement patterns for each of the 17 source regions. (Passive = no behaviour, VA = vertical advection, DVM = diel vertical migration, OVM = ontogenetic vertical migration; OHS = orientated horizontal swimming). The first two axes explain 39.4% of the inertia.

4.4.1.2 Connectivity metrics

Including behaviour in models increased self-recruitment to a region, compared to passive larvae ($F_{9,144} = 12.31$, $p < 0.05$; Figure 4.9 A; see Appendix C for connectivity matrices). The OVM model was an exception unless OVM behaviour was used in combination with another behaviour. The DVM and DVM+OHS models had the highest self-recruitment and the lowest variation across regions. The lowest self-recruitment occurred in the passive model with no VA. Similarly, local retention increased when including behaviours except OVM unless coupled with OHS ($F_{9,144} = 79.24$, $p < 0.05$; Figure 4.9 B). In particular, including OHS in a model approximately doubled the local retention to a region. Larvae that were passive with no vertical restriction or exhibited OVM behaviour had consistently lower local retention values. Including DVM gave rise to the most variation of local retention between regions. Considering the metric of settlement success, the effect of OHS was evident, increasing the chances of settlement success by ~30% ($F_{9,144} = 95.02$, $p < 0.05$; Figure 4.9 C). The models OVM, DVM, and DVM+OVM did not change the settlement success compared to passive larvae. Variation in settlement success between regions was greatest when passive larvae were only horizontally advected. OHS behaviour significantly reduced the dispersal distance by ~40% when compared to passive larvae, and also reducing the variation by ~75% ($F_{9,144} = 66.33$, $p < 0.05$; Figure 4.9 D; see Appendix C, Figure C1 for dispersal kernels). The OVM model did not significantly reduce the dispersal distance of larvae compared to the passive models.

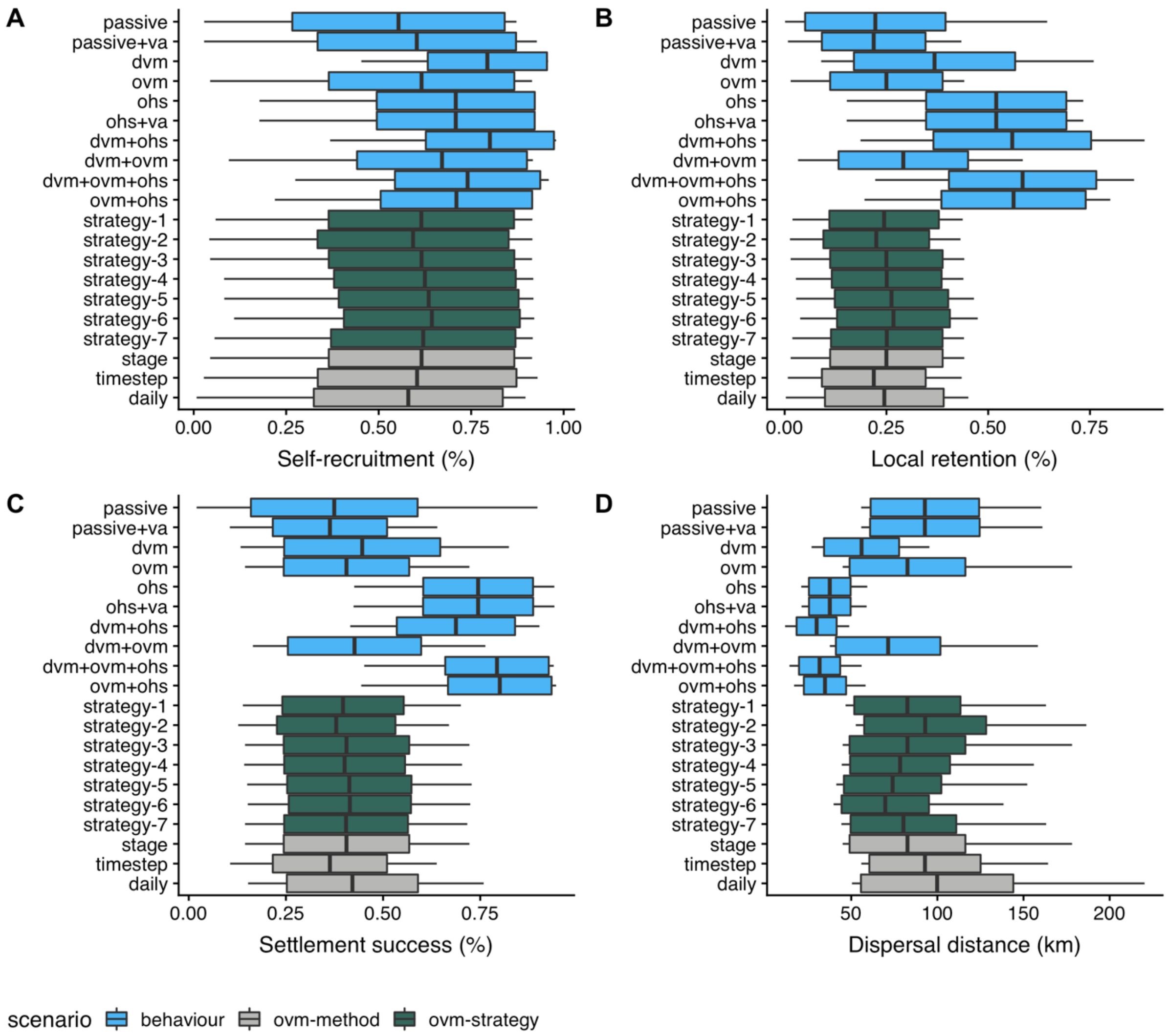

Figure 4.9: The connectivity metrics of mean self-recruitment (%; A), local-retention (%; B), settlement success (%; C) and dispersal distance (km; D) for each region, as measured for each modelling scenario grouped by the three aims; behaviour (Passive = no behaviour, DVM = diel vertical migration, OVM = ontogenetic vertical migration; OHS = orientated horizontal swimming), OVM strategy, and OVM method. The whisker plots denote the mean, one standard deviation either side of the mean and min/max values.

4.4.2 Comparison of ontogenetic vertical migration scenarios

4.4.2.1 Ontogenetic migration strategies

The effect (difference from base case) of different strategies was strongly regional, with the northern (1-5), central (6-10), and southern sites (11-17) clustering together (Figure 4.10; see Appendix C, Figure C2 for non-standardised nMDS). The variation described by OVM strategies using the standardised connectivity patterns from source regions was negligible ($R^2 < 0.01$, $p > 0.05$) compared to the variation between regions ($R^2 = 0.95$, $p = 0.005$). The differences between strategies also were not constant across regions, e.g. the OVM strategies 3 and 5 were more similar at region 6 than region 2.

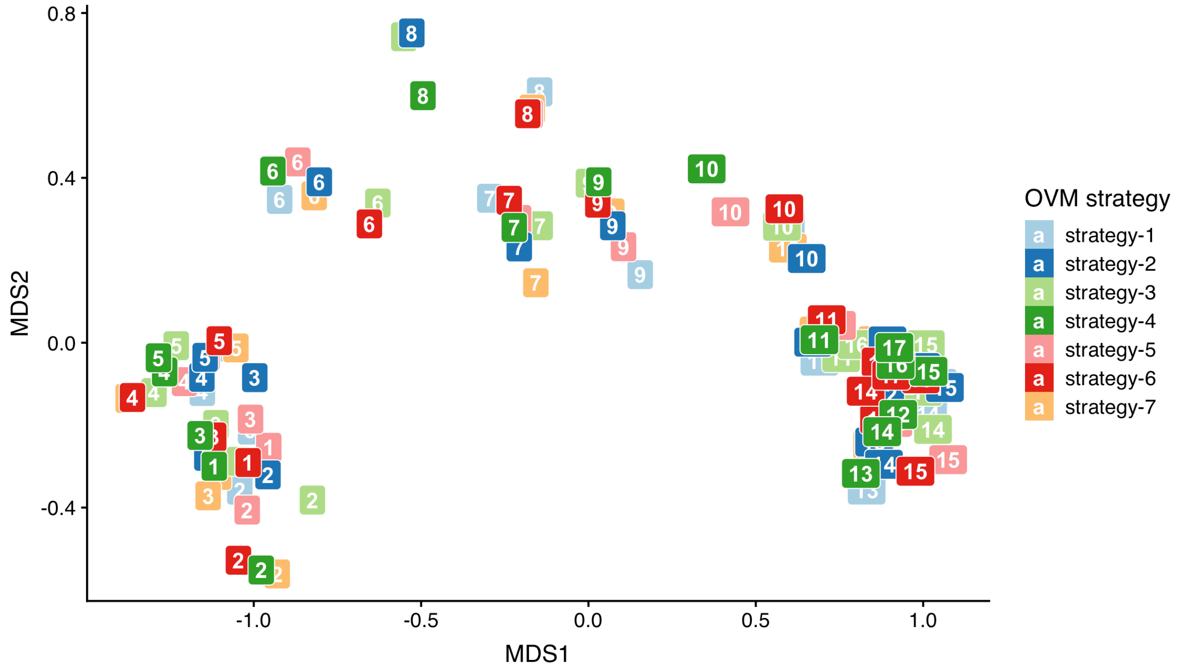

Figure 4.10: NMDS ordination plot (2D stress = 0.06) using the standardised Bray-Curtis dissimilarities between the different source-settlement patterns for each of the 17 source regions for the models within the behaviour scenario and normalised using the passive behaviour scenario (Passive = no behaviour, VA = vertical advection, DVM = diel vertical migration, OVM = ontogenetic vertical migration; OHS = orientated horizontal swimming).

The CAP analysis showed groupings between strategies of vertical migration upwards with ontogeny (strategy 2) and migrations downwards with ontogeny (the other six strategies; Figure 4.11). However, the groupings were not significantly different to each other ($F_{(6,96)}$ = 0.95, $p > 0.05$), likely due to the strong regional differences described above. Strategies 3 and 4 had the closest connectivity patterns between the OVM strategies.

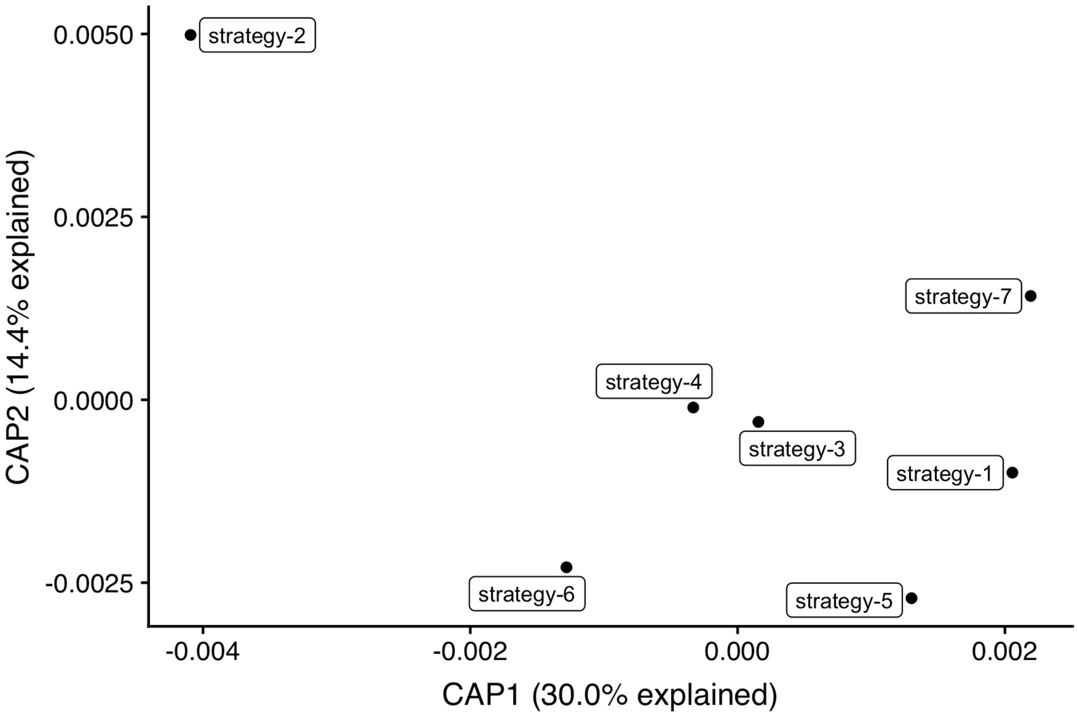

Figure 4.11: Constrained analysis of principal coordinates (CAP) for the models within the seven different ontogenetic vertical migration strategies using Bray-Curtis dissimilarities between the different source-settlement patterns for each of the 17 source regions. The first two axes explain 39.4% of the inertia.

Differences in OVM strategy affected each of the reported connectivity metrics; self-recruitment ($F_{(6,96)} = 31.88$, $p < 0.05$; Figure 4.9 A); local retention ($F_{(6,96)} = 40.90$, $p < 0.05$; Figure 4.9 B); settlement success ($F_{(6,96)} = 42.84$, $p < 0.05$; Figure 4.9 C); and dispersal distance ($F_{(6,96)} = 63.25$, $p < 0.05$; Figure 4.9 D; see Appendix C, Figure C3 for dispersal kernels). The strategy of remaining close to the surface during all stages of ontogeny, i.e. strategy 1, produced the lowest self-recruitment, local retention, settlement success, and the furthest dispersal distance. In contrast, the strategy of migrating downwards with ontogeny, most pronounced in the strategies 5 and 6, increased self-recruitment, local retention, settlement success, and lowered the dispersal distances.

4.4.2.2 Ontogenetic vertical migration methods

Daily migration of larvae as a function of ontogenetic stage produced different connectivity patterns to the OVM methods of stage and time step ($R^2 = 0.10$; $p = 0.005$). The stage and time step methods had a more consistent overlap of settlement patterns at most source regions (Figure 4.12; see Appendix C, Figure C4 for non-standardised nMDS). The effect of daily migration was diminished in the southern regions (13-17), where more overlap between all three methods was observed. The central regions (6-9) showed the strongest regional variation, both between and within for OVM methods. The CAP analysis showed all three methods as dissimilar to each other, with stage marginally more similar to time step than the daily method of OVM (Figure 4.13).

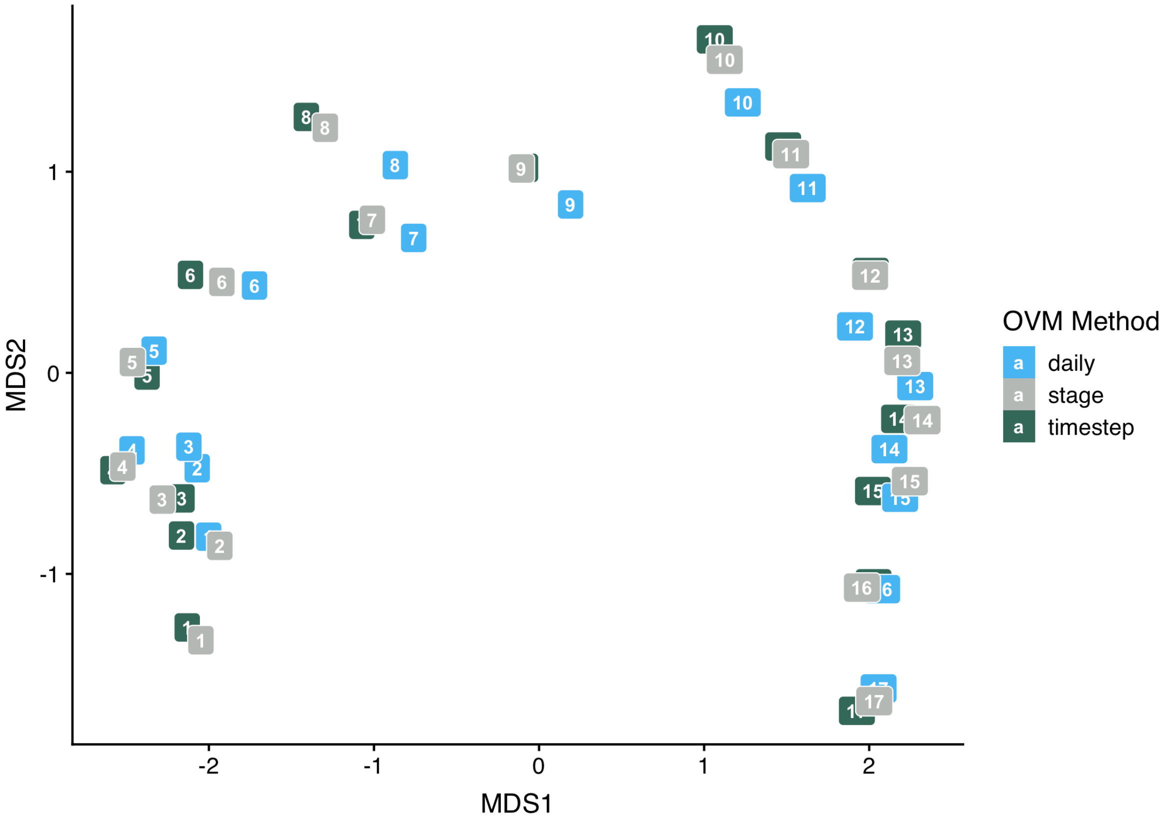

Figure 4.12: NMDS ordination plot using the standardised Bray-Curtis dissimilarities between the different source-settlement patterns of each NSW region for each model within the different ontogenetic vertical migration methods (time step, daily, and ontogenetic stage)

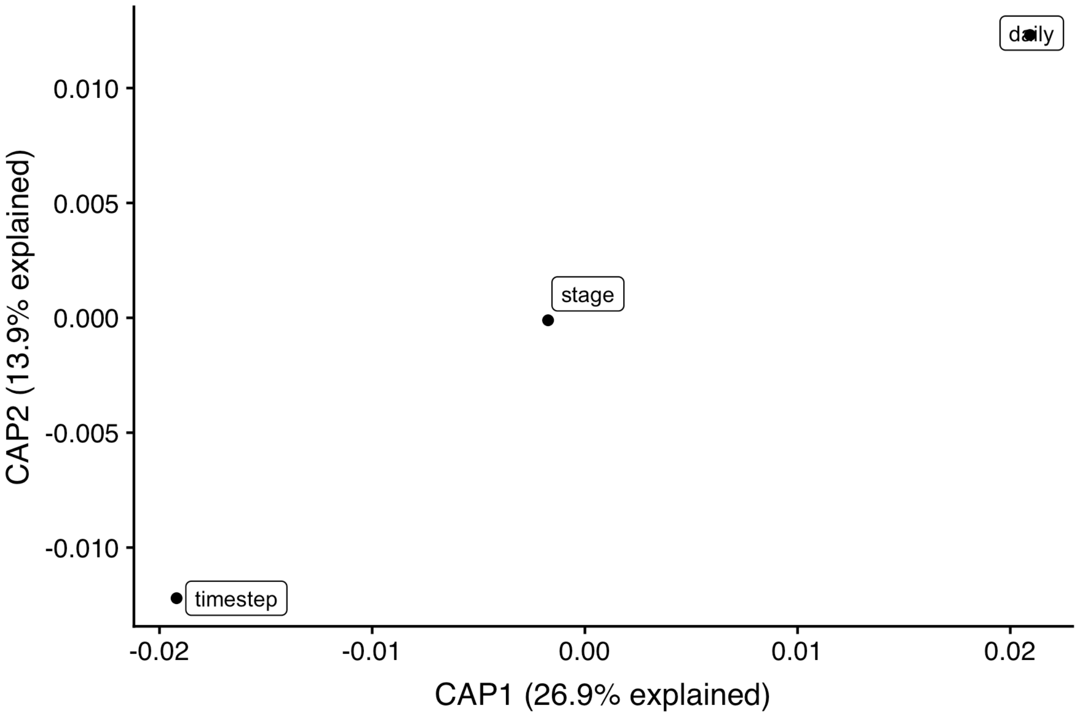

Figure 4.13: Constrained analysis of principal coordinates (CAP) for the models within the ontogenetic vertical migration methods (stage-based, daily, and time step) scenario using Bray-Curtis dissimilarities between the different source-settlement patterns for each of the 17 source regions. The first two axes explain 40.7% of the inertia.

There were significant differences between self-recruitment ($F_{(2,32)} = 5.68$, $p < 0.05$), with the daily method having lower self-recruitment than stage based migration (Figure 4.9 A). Time step migration had the lowest mean local retention ($F_{(2,32)} = 9.83$, $p < 0.05$; Figure 4.9 B) and settlement success ($F_{(2,32)} = 32.48$, $p < 0.05$; Figure 4.9 C) between the OVM methods. Larvae in the daily and time step methods dispersed significantly further than the stage OVM method ($F_{(2,32)} = 11.00$, $p < 0.05$; Figure 4.9 D; see Appendix C, Figure C5 for dispersal kernels). The variation of dispersal distance for the daily OVM method had a standard deviation estimated to be 30% greater than the other methods.

4.4.3 Overall context

The settlement patterns of the models in the behaviour scenario were the least similar of the three scenarios (Figure 4.14; for connectivity matrices see Appendix C), and the OVM methods scenario was less similar than the models within the OVM strategies scenario. The models within the OVM strategy scenario were tightly clustered, suggesting minimal differences in settlement patterns occur with OVM strategies. The difference in connectivity patterns between the OVM methods appeared to be equal or greater to the differences between the non-OHS models within the behavioural scenario. The OVM method of migrating at every time step had connectivity patterns most similar to the passive larvae advected vertically. Differences in behaviour were more influential on connectivity metrics, than changes within OVM strategy or OVM methodology (Figure 4.9). The one exception is dispersal distance, which also displayed high variation with for different models within the two OVM scenarios (Figure 4.9 D).

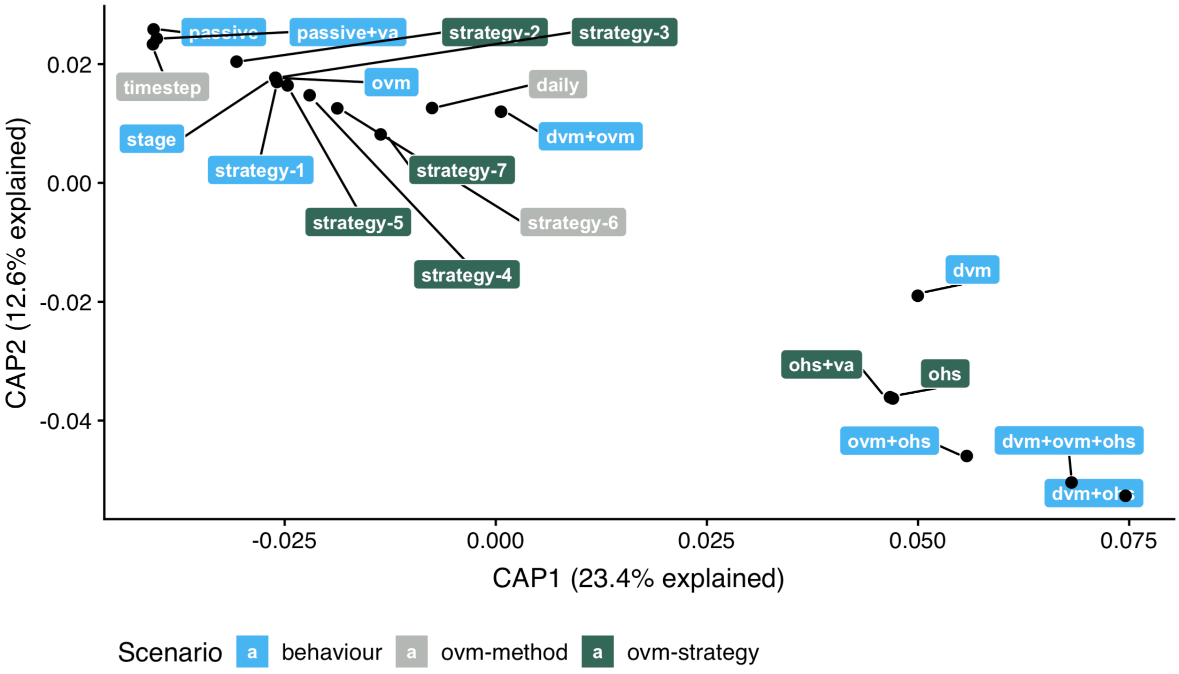

Figure 4.14: Constrained analysis of principal coordinates (CAP) of the connectivity matrices for each scenario within each of the treatments using Bray-Curtis dissimilarities; behaviour (Passive = no behaviour, VA = vertical advection, DVM = diel vertical migration, OVM = ontogenetic vertical migration; OHS = orientated horizontal swimming), ontogenetic vertical migration (OVM) strategy (seven different strategies), and OVM method (the larvae migrate at the time step (2 hours), daily, or ontogenetic stage based migration such that the larvae migrate vertically when the next stage of ontogeny is reached). The first two axes explain 36.0% of the inertia.

4.5 Discussion

4.5.1 Behavioural models

This study gives insight into the paradigm that larval fish can influence their dispersal patterns through horizontal and vertical swimming behaviours, by predicting how these patterns are affected using a biophysical dispersal model (BDM). Giving the larval fish the ability to move (vertical, horizontal, or both) drove changes in dispersal. The connectivity patterns of the different behavioural models grouped into models that included or did not include orientated horizontal swimming (OHS). Swimming behaviour, both horizontal and vertical, generally allowed larval fish to settle closer to their natal region (increasing local retention), reduced the distance of dispersal (restricting the connectivity pathways), and increased their chances of settlement success. The strength of this behavioural effect on connectivity patterns was noticeable with orientated horizontal swimming (OHS) and weakest with ontogenetic vertical migration (OVM). The compelling driver of the variation in connectivity patterns was the spawning location and presumably timing of spawning (not a factor in these permutations), which have been seen to be influential on predicted dispersal patterns in other modelling studies using similar approaches (Ayata *et al.* 2010; Treml *et al.* 2015; Kvile *et al.* 2018), and more influential than vertical migration behaviours (Puckett *et al.* 2014), although not in all systems (North *et al.* 2008). Driving these connectivity patterns are the hydrodynamics of the coast of New South Wales (NSW), dominated by a southward western boundary current (the East Australia Current) that separates off the coast approximately at the location of regions 7 and 8 that generates mesoscale eddies and entrains ichthyoplankton (Suthers *et al.* 2011).

Orientated horizontal swimming (OHS) was the behaviour that affected the modelled connectivity patterns the greatest, although the size of this effect presumably depends on the spatiotemporal scale of the modelled domain. Larvae with OHS behaviour increased local retention to the natal region, increased self-recruitment and reduced the dispersal distance. Giving larvae the ability to sense, orient, and swim towards a reef, also substantially increased their chances of settlement success. The reduced dispersal distance resulted in lower settlement richness, diversity, and connectance. These results are in agreement with modelling studies from other oceanographic locations that have seen OHS increase the local retention and self-recruitment of larval fish at similar levels (Wolanski and Kingsford 2014) and improve the settlement success and reduce the dispersal distance (Staaterman *et al.* 2012). It must be borne in mind that the implementation of OHS in the BDM used in this study was closer to the implementation used by Staaterman *et al.* (2012) than Wolanski and Kingsford (2014). Aligned with the results of the models, it is predicted that larval fish that can sense and orientate towards a reef benefit with an increased likelihood of settlement success and the ability to directly influence the trajectory of dispersal. The effect of OHS on the connectivity patterns was so pronounced, that advecting larvae with a vertical component in addition to

OHS produced homologous patterns of connectivity. Even subsequent models with additional vertical behavioural traits only marginally altered the connectivity patterns. This strong influence of OHS behaviour on connectivity patterns, relative to the other behaviours (i.e. DVM and OVM), is likely the result of the directed nature of the swimming (towards viable settlement habitat) as much as the swimming speed itself. The ability to alter dispersal comes from larvae being able to swim in the direction of a reef if they can swim faster than the prevailing current. While the other migration behaviours provide larvae with mechanisms that alter dispersal, without OHS they can only indirectly influence their dispersal outcome. Although, it must be put into context with the influence of other behavioural traits (Cowen and Sponaugle 2009), e.g. another study comparing a wider range of behavioural traits found OHS to only have an intermediate effect compared to other traits such as mortality, PLD, and size of the settlement competency window (Treml *et al.* 2015).

Surprisingly, compared to the other behaviours, OVM did not have patterns that differed strongly from passive larvae and had limited influence on the connectivity metrics. Local retention and settlement success were not affected when adding OVM to a passive model, only the self-recruitment of a region was increased. Larvae in the model exhibit vertical behaviour more during the pelagic larval stage than OHS (larvae orientate and swim when a reef is sensed), therefore it was hypothesised that vertical migration would have a greater influence on the dispersal. Vertical migration occurs early in ontogeny and changing position in the water column allows larvae to be advected by currents with different velocities. In contrast, for horizontal swimming to influence connectivity patterns, the larvae have to be competent to settle, and within a sensory distance of the reef to orientate and swim towards the settlement habitat. In general, observed distributions tend to be smaller than estimates of BDMs using passive drift (Shanks 2009). Previous studies have found OVM to increase modelled local retention (Paris *et al.* 2007; Kough *et al.* 2016) and transform the predicted dispersal patterns compared to non-swimming (passive) larvae (Butler *et al.* 2011; Drake *et al.* 2013; Kough and Paris 2015), however, this is not universal (Zhang *et al.* 2015). Vertically migrating with ontogeny is considered a strong retention mechanism as moving downwards in the water column exposes larvae to weaker and directionally divergent currents (Paris and Cowen 2004), yet in this study the evidence for increased retention was weak. The results suggest the effect size of OVM on larval retention is dependent on the regional hydrodynamics, perhaps a combination of the influence of the nearshore boundary current and a limitation of the hydrodynamic model resolution in capturing the coastal dynamics. Local retention was highest when the EAC was closest to the coast and reduced dramatically at the separation zone. Non-swimming larvae that were moved by a vertical component (Passive+VA) had connectivity patterns that were more similar to models with OVM than the non-swimming passive larvae, suggesting the vertical component advected larvae downwards at a slow rate that closely resembled the restricted movement of the stage based ontogenetic vertical migration used. Diel vertical migration (DVM) had a stronger effect on the connectivity patterns and connectivity metrics than OVM (where OVM used the stage-based method described above), suggesting the time the larvae spend at different depths in the water column influences local retention. Connectivity models with DVM, similar to OVM, have been seen to increase settlement success, local retention and decrease the dispersal distance (Aiken *et al.* 2011; Butler *et al.* 2011; Robins *et al.* 2013). The results of this study further confirm these previous findings.

4.5.2 Ontogenetic vertical migration scenarios

The hypothesis that the strategy of ontogenetic vertical migration (OVM) would influence the patterns and metrics of dispersal was not supported. The effect of OVM strategy on the connectivity and settlement patterns was minimal, with only nuanced differences between strategies observed, especially compared with variation seen from the use of different behaviours. Similar patterns have been seen when comparing OVM between taxa (Holstein *et al.* 2014; Kough *et al.* 2016), but the relative differences are highly predicted to be dependent on the oceanography. The largest differences were seen in taxa with upwards versus downwards OVM strategies. The direction of migration created a trade-off; upwards migration increased the dispersal distance, and downward migration increased local retention. This result partially correlates with similar observations, where ontogenetically migrating downwards has been shown to reduce transport (Werner *et al.* 1993; Huebert *et al.* 2011), however in this study no decreases in dispersal were seen for larvae migrating below 50 m. Migrating deeper with ontogeny reduces the overall dispersal distance, but it does increase the number of different areas settled, e.g. the genetic connectivity. These results suggest that the choice of vertical migration strategy only has an effect on dispersal and it may be quite appropriate to utilise general parameter values where taxon-specific ones are not available as long as the general direction of migration is known.

The choice of method used to vertically migrate the larvae with ontogeny can affect the connectivity patterns, contrary to the prediction. When constructing a BDM, a modeller has to make many choices about how to encapsulate real world processes, and these results show that there are potential ramifications for these choices. While the frequency of larval fish vertical migration is unknown, these results suggest that fish migrating at an intermediate frequency (daily) had the strongest influence on the resultant connectivity patterns, with fast migration (time step) and slow migration (stage) strategies closer to each other. These results are supported by other research that has observed the speed of vertical migration can alter the direction and distance of dispersal (Sundelöf and Jonsson 2012). Changing position quickly suggests the larval fish do not get the benefit of different velocities for sustained periods (in this model only two hours) and changing position with changes in ontogeny perhaps does not expose the larvae to enough variation in current velocities. The BDM gives all larvae the same migrating frequency, which may be unrealistic given the individual variation is seen in larval fish (Nanninga and Berumen 2014).

4.5.3 Context

When considering a biophysical dispersal model to estimate connectivity of larval fish, the results of this study suggest that the choice of which behaviours to include is more important than the parameterisation or implementation method for OVM behaviour. For connectivity modelling, greater emphasis should be placed on what behaviours are specific to a species. General values for a behaviour (specifically OVM) can be utilised when no specific values are available in the literature without potentially influencing the patterns as much as the choice of including the behaviour. For regions with nearshore boundary currents and species with limited empirical data on their ontogenetic vertical distribution, these results suggest that allowing passive larvae to migrate with a vertical component can produce similar patterns of connectivity. Interestingly, differences in the speed (method) of vertical migration were more of consequence than differences in distribution (strategy). This result highlights the importance of the modelled behavioural processes. The modelling choice, however rational or arbitrary, can influence the patterns of connectivity more than the parameterisation. More sound knowledge of the processes behind these behaviours is fundamental to producing a more accurate and precise connectivity pattern (e.g. speed of vertical migration, settlement detecting distance, and development of senses).

The strong effect of OHS raises the need models to incorporate the ability of different taxa to sense settlement habitat, the frequency at which they orientate towards sensed habitat and the sustained speeds at which the larvae swim towards the sensed habitat (Leis and Carson-Ewart 2003; Montgomery *et al.* 2006; Mouritsen *et al.* 2013; Leis *et al.* 2014). In this BDM study, each settlement reef was considered to be equally attractive to the larval fish, an unrealistic assumption, as it has been demonstrated that reef fish can sense natal reefs (Bottesch *et al.* 2016) and can most likely discriminate between other sensed reefs. The settlement sensory distance was also kept constant for all larvae, which again doesn't reflect the individual variation of sensory abilities for larvae (Leis *et al.* 2014), and does not capture how settlement cues could be affected by hydrodynamics (i.e. odour, Gerlach *et al.* 2007; Foretich *et al.* 2017), location of sun (i.e. sight, Berenshtein *et al.* 2014), or environmental variables such as temperature and salinity (i.e. sound, Sallarès *et al.* 2009). While out of scope for this study, further modelling studies should follow suggestions by Staaterman and Paris (2014) and investigate the effect of different sensory abilities and their environmental cues on connectivity patterns.

Of course, it must be caveated that these results occur in a poleward western boundary current oceanic system and that it does not necessarily the interpretation of behavioural influence applicable to other regions. Different oceanographic dynamics could lead to certain behaviours having stronger or weaker effects of dispersal and connectivity metrics. Another limitation in this study was the coarseness of the hydrodynamic model, which does not effectively capture nearshore processes along this region (e.g. it does not capture dynamics such as near-shore tides, wind-forcing, and currents influenced by topography; Vasile *et al.* 2018), and therefore, small-scale effects on dispersal and the interaction with larval behaviour is not modelled in this study. However, this shortfall in nearshore resolution is consistent across each model within a scenario. Another limitation might arise from only using hydrodynamic data over a spawning period of 12 months, the variability inherent in ocean circulation might enhance or moderate the effect of a particular behaviour in the system over the given period. In addition, these results are only estimates and without model validation using empirical data, there is no way to determine if these behaviours have a similar effect on the actual dispersal patterns of reef fish larvae. Instead these results are designed to clarify model input and what behaviours are important to choose when approaching a BDM study of fish larvae.

4.6 Conclusion

This study emphasises the importance of giving larval fish in biophysical dispersal models the ability to horizontally or vertically migrate, and not only passively advecting them by currents with neutral buoyancy, principally for model domains off eastern Australia or with a western boundary current. Orientated horizontal swimming appears to be considerably influential on the potential connectivity patterns. The caveat to including more behaviour in a biophysical dispersal model is that parameterisation requires empirical knowledge that is often unavailable or limited for many species or taxa of larval fish. However, this study shows that for ontogenetic vertical migration (OVM), in a region influenced by a western boundary current, general taxa-specific data might not give patterns much different to species-specific data. Further research should be considered on both the depth distributional trends and the underlying processes of OVM (e.g. sudden or gradual frequency of migration), as changes in implementation method were seen to be influential on the estimated dispersal of larval fish.

5 Estimating the larval dispersal of black cod *Epinephelus daemelii* across is distribution along the eastern coast of Australia and potential implications for its conservation management

5.1 Abstract

The black cod (*Epinephelus daemelii*) is a large, long-lived reef fish of the family Serranidae, and found mostly along the New South Wales (NSW) coastline. Population declines from fishing pressure throughout the 20th century warranted the listing *E. daemelii* as a threatened species in 1983. Within the distribution of *E. daemelii*, there is a network of marine protected areas (MPAs; both NSW and Commonwealth) established since 2007 (with no-take zones of varying sizes). Despite most known *E. daemelii* populations occurring inside these MPAs, this protection has not resulted in population recovery. One explanation is that the MPA network does not meet its objectives for *E. daemelii*. This chapter aimed to investigate the connectivity of *E. daemelii* along its known distribution using a biophysical dispersal model, identifying potential strong spawning regions and regions of strong settlement, and comparing this possible connectivity with the MPA network. *E. daemelii* larvae were released during April-May (2004-2011) from 19 known regions across its distribution and tracked until settlement (both reefs and rocky intertidal shores). The results predicted high local retention and self-recruitment for Solitary Islands, Nambucca and Port Stephens, suggesting sustaining these populations is critical to the persistence of populations in these regions. *E. daemelii* connectivity was predicted to occur between the offshore populations (Elizabeth and Middleton reefs) and the NSW coast, suggesting genetic, if not demographic, connectivity exists. The model identified four strongly connected communities of *E. daemelii* across the distribution. While each community contained marine protected areas (and no-take areas), regions within a community that were predicted to have strong settlement success, high local retention and strong settlement could benefit from additional protection. Further research is required to determine if *E. daemelii* dispersal can be predicted by the model, noting that post-settlement processes were not considered. This study provides predictions of dispersal for *E. daemelii* across the NSW coast and offshore regions, which can be used as part of a suite of tools for conservation managers to aid in its recovery.

5.2 Introduction

In marine systems, spatially discrete populations can be connected to each other through larval exchange. This connectivity (exchange of individuals between populations) provides both demographic and genetic functionality and is fundamental to the viability of marine populations. Metapopulation dynamics can arise from spatially connected independent populations and the volatility of the dispersal connecting these populations can have important ecological and evolutionary repercussions (Hanski 1998; Sale *et al.* 2006). Connectivity variation drives metapopulation dynamics, i.e. the number of individuals exchanged, the direction of the exchange, and the distance of dispersal (Figueira 2009).

For marine species, including many reef fish species, this connectivity often occurs primarily during a pelagic larval stage (Sale 1991). Reef fish often have sedentary adult phases, and therefore any connectivity between populations occurs only during this period when the larvae are pelagic (Cowen *et al.* 2007). Recent empirical understanding has identified that larval dispersal is not merely passive advection by ocean currents and turbulent systems, instead it is complex, driven by a combination of physical and biological processes (Leis *et al.* 2007; Paris *et al.* 2007; Cowen and Sponaugle 2009). Larval development allows for larvae to influence their dispersal through behaviours such as vertical migration (Paris and Cowen 2004; Irisson *et al.* 2010) and sensory abilities which larvae can use to orientate and swim, including towards settlement sites (Berenshtein *et al.* 2014; Faillettaz *et al.* 2015). Measuring this connectivity is difficult using empirical methods, which have spatial and temporal limitations. Instead, biophysical dispersal modelling is a useful tool to estimate connectivity using oceanographical models coupled with biological models, which enable prediction of connectivity over large spatial and temporal scales (Roberts *et al.* 2010; Paris *et al.* 2013; Kool and Nichol 2015).

Connectivity is often overlooked when designing marine protected areas (MPAs) in favour of protecting habitat (Crowder and Figueira 2006). Global change in the time of the Anthropocene makes designing well connected MPAs an important problem for ensuring the resilience of marine metapopulations from threats such climate change, overfishing and diseases (Almany *et al.* 2009; Botsford *et al.* 2009). Well-connected MPA networks can satisfy the objectives of both conservation and fisheries management (Christie *et al.* 2010; Gaines *et al.* 2010). Understanding and measuring connectivity within a marine metapopulation is necessary to design effective networks MPAs, with optimal locations, size, and spacing (Anadón *et al.* 2013).

Black cod, *Epinephelus daemelii* (Gunther, 1876), also known commonly as the black rockcod, the saddled rockcod, and the potted black grouper, are large groupers of the teleost family Serranidae. *E. daemelii* is native to Australia and New Zealand in the south-western Pacific Ocean. Its known distribution ranges from eastern Australia (southern Queensland down to Bass Strait) to Northern New Zealand and the Kermadec Islands, with populations on Lord Howe Island, Norfolk Island, and Elizabeth and Middleton Reefs (Froese and Pauly 2017; Atlas of Living Australia 2018). Along eastern Australia, *E. daemelii* is primarily distributed along the temperate waters of the New South Wales (NSW) coastline. *E. daemelii* can reach the age of 65 years, grow to 170 cm total length (TL) and weigh 80 kg (Francis *et al.* 2016). Like many large groupers, it is a protogynous hermaphrodite, with protogyny not occurring until the adult fish reaches lengths of over 100 cm (TL), which occurs at ~25 years (Francis *et al.* 2016). Anecdotally, black cod are thought to breed April-May, as this is when aggregations have been seen on the north coast of NSW (D. Harasti, personal communication, 9 March 2017). *E. daemelii* spawn pelagic eggs with the pelagic larval stage estimated to last 60 days as they transition to the juvenile ontogenetic stage for settlement (Francis *et al.* 2016). The post-settlement juveniles of black cod are found in rock pools and shallow reef intertidal habitats, migrating to estuaries as they grow older and as adults they live in the caves and crevices found on rocky reefs at depths of up to 50 m (Harasti *et al.* 2014; Francis *et al.* 2016).

E. daemelii has traditionally been under fishing pressure in Australia, it is considered a trophy fish for spearfishers and as targeted species for its palatable taste by commercial and recreational fishers (it was commonly sold at the Sydney fish markets; Francis *et al.* 2016). *E. daemelii* is a *K* strategist with a long life-span, large body size, low mortality rate and late sexual maturity (Adams 1980) and combined with other traits such as aggregate spawning (anecdotally), specific habitat requirements, and a sedentary/curious nature, all increase the vulnerability of *E. daemelii* to fishing. Population declines for the black cod have been recorded since 1916 and in 1983, due to dwindling numbers, it was eventually listed for protection in NSW (Francis *et al.* 2016). The protection listing was driven by notable population declines coinciding with the rise in popularity of spearfishing in the late 1960s and

1970s (Pogonoski *et al.* 2002; Young *et al.* 2015). Black cod is currently listed as "Near Threatened" on the ICUN red list (Pollard and Sadovy 2018) and listed as "Vulnerable" under the Australian Commonwealth *Environment Protection and Biodiversity Conservation Act* since 2006 (Department of the Environment 2018).

The predominant threat to the *E. daemelii* population comes from hook and line fishing, other substantial threats come from climate change and water pollution (NSW DPI 2012). The total ban on fishing *E. daemelii* since 1983 results in by-catch (or unintended catch) and illegal fishing being the primary threats to population recovery. Protecting *E. daemelii* involves both safeguarding known (and potential) areas of aggregation of mature sexually active *E. daemelii* adults from fishing pressure to maximise the reproductive output of spawning populations and habitat protection for the intertidal rocky reef and estuarine habitats it uses throughout its lifecycle (Harasti and Malcolm 2013). Marine protected areas (MPAs) are a management tool that can assist in the population recovery of *E. daemelii* by achieving both of these priorities of protection with no-take (sanctuary) zones. However, no-take zones are not a panacea for *K* strategists such as the black cod, population recovery is a slow process and these populations are sensitive to low levels of fishing mortality even within no-take reserves (Friedlander and DeMartini 2002; Abesamis *et al.* 2016). Therefore, the current NSW recovery plan for *E. daemelii* has established a long-term goal (20 years) to de-list it as a vulnerable species (NSW DPI 2012).

E. daemelii exist in populations of various sizes within the NSW marine parks (i.e. MPAs) and a few of the aquatic reserves, along with two of the Commonwealth marine reserves (Cod Grounds and Lord Howe Island Marine Reserve; Pogonoski *et al.* 2002), potentially providing adequate protection. For MPAs to be effective for a species, there must be connectivity between the protected areas and/or strong local retention within the protected areas (Botsford *et al.* 2001, 2009), and adequate protection of high-quality habitat, e.g. carrying capacity (Cabral *et al.* 2016). MPAs have been seen to be effective in increasing Serranidae populations (Chiappone *et al.* 2000; Hackradt *et al.* 2014). Protecting high-quality habitat is also important for maintaining reef soundscapes used by ichthyoplankton to orientate and settle (Gordon *et al.* 2018). The current network of marine parks in NSW, while spatially distributed, has been shown to provide strong connectivity for some species, but not others (Coleman *et al.* 2011). Therefore, even though many of these parks have been in place since

2002 and it has been protected since 1983 from recreational and commercial fisheries (Georgeson *et al.* 2014), no noticeable signs of population recovery have been seen for *E. daemelii* (Francis *et al.* 2016) and it is still not found to reside in many habitats where it was known to occur in prolific numbers (Harasti and Malcolm 2013). However, marine protected areas, specifically no-take zones, are not a panacea to population recovery. *E. daemelii* population densities within the protected offshore reef regions have been seen to decrease (Pratchett *et al.* 2011). One potential explanation for this lack of improvement is that the current MPA network is not optimal for *E. daemelii*. Unfortunately, there is currently little information on the connectivity and recruitment dynamics of *E. daemelii* (Francis *et al.* 2016) against which to assess the adequacy of protection measures.

The first aim of this chapter is to investigate the spatiotemporal differences in predicted dispersal patterns of *E. daemelii* using a biophysical dispersal model. To investigate temporal variation and increasing the predictive power (Wiens 1989), the biophysical dispersal model was run using eight years (2004-2011) of hydrodynamic data. The aim was broken down into three parts (1) to identify differences in potential dispersal considering the two different spatial contexts, (2) identifying potential sub-populations defined by strong and stable dispersal between regions, and (3) comparing predicted dispersal patterns from releasing larvae across its known distribution and releasing larvae from only regions known spawning aggregations. The second aim is to understand how the current network of MPAs, both Commonwealth and NSW, align with areas of high settlement, local retention and spawning success from the estimated dispersal patterns. Modelled dispersal patterns, derived from both known aggregations as well as the entire known distribution, can assist conservation management decisions in aiding the recovery of the *E. daemelii* population.

5.3 Methods

5.3.1 Study location

The model domain covered the known distribution of *E. daemelii* (Francis *et al.* 2016); the eastern coast of Australia and the offshore reefs: Lord Howe Island, Elizabeth and Middleton Reefs (Figure 5.1). The coastal region of New South Wales (NSW) consists of a narrow continental shelf, with a boundary current, the East Australian Current (EAC), which strongly influences dispersal in the region with its poleward direction and by the mesoscales eddies it generates (Suthers *et al.* 2011). The study area was divided into 19 spawning regions (see Chapter 4 methods for more detail), 17 approximately equally sized regions (~125 km of coastline) along the NSW coast, and two off-shore regions, Lord Howe Island and Elizabeth and Middleton (EM) reefs. Within each region, areas of approximately equally sized sections of contiguous reef were demarcated as specific reef patches. In total there were 560 reef patches in the model domain with about ~25 reef patches per region, except the offshore areas which were considered one continuous reef (as per Chapter 3). Elizabeth and Middleton reefs were considered one region due to local proximity and strong local demographic connectivity and are thought to be a single stock (Van Herwerden *et al.* 2009). *E. daemelii* were allowed to settle to other areas within their known distribution that were not used as spawning sites due to their distance from the eastern coast of Australia, the small size of their populations, or where they are considered to be non-breeding, i.e. Queensland, Victoria, Norfolk Island, and New Zealand (Francis *et al.* 2016). While all specific areas of spawning are not known, the most abundant known populations within the model domain occur at the regions Solitary Islands, Nambucca (Fish Rock), Port Stephens, Lord Howe Island, and Elizabeth and Middleton reefs (Harasti and Malcolm 2013).

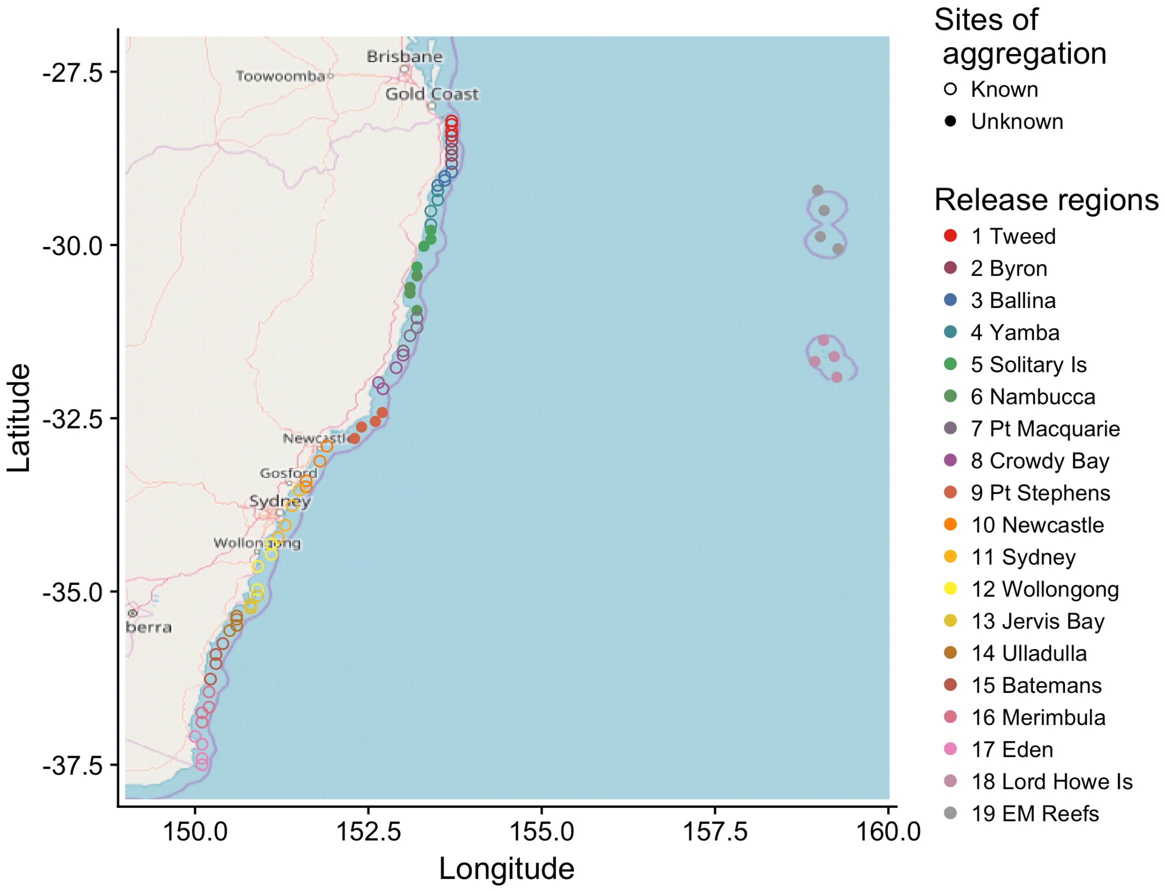

Figure 5.1: Location of rocky reef patches used for spawning *Epinephelus daemelii* larvae in each of the 19 regions along the coastline of New South Wales, Australia and the offshore areas of Lord Howe Island, Elizabeth reef and Middleton reef (EM Reefs)

Within the model domain, I identified 20 marine protected areas that were relevant to *E. daemelii* habitat (ignoring most protected areas in Commonwealth waters more than three nautical miles from the coast of Australia as they do not contain adult or juvenile habitat for *E. daemelii* and fishing pressure on larval fish is considered to be negligible). The MPAs fall under two jurisdictions: the NSW Government (18 MPAs) and the Commonwealth Government of Australia (2 MPAs). The 18 NSW MPAs consist of six marine parks known to occur within the modelled domain (Cape Byron Marine Park, Solitary Islands Marine Park, Lord Howe Island Marine Park, Port Stephens-Great Lakes Marine Park, Jervis Bay Marine Park, and Batemans Marine Park) and 12 aquatic reserves (Figure 5.2). In addition, two Commonwealth MPAs which are located within the model domain were considered: Lord Howe Commonwealth Marine Reserve (which contains Elizabeth and Middleton reefs), and Cod Grounds Commonwealth Marine Reserve (Figure 5.3). Information on the size of the MPA and no-take zone areas of current marine parks was sourced from the NSW

Government (http://www.marine.nsw.gov.au), and the Commonwealth Government of Australia (http://www.environment.gov.au/marine). The NSW MPAs have four levels of protection: no-take zones (no-take areas), habitat protection zones (recreational fishing and some commercial fishing allowed), general use zones (recreational and commercial fishing permitted), and special protection zones (reserved for traditional Aboriginal use). For the two Commonwealth MPAs of interest, recreational and commercial fishing is only authorised by permit, and commercial fishing permits do not extend within two nautical miles of Elizabeth Reef. While protecting both spawning aggregations through reduced fishing pressure and maintaining critical habitats for adults and juvenile populations are key management priorities, in this analysis, I have not assessed MPAs for the amount of critical *E. daemelii* habitat that falls within the protection zones.

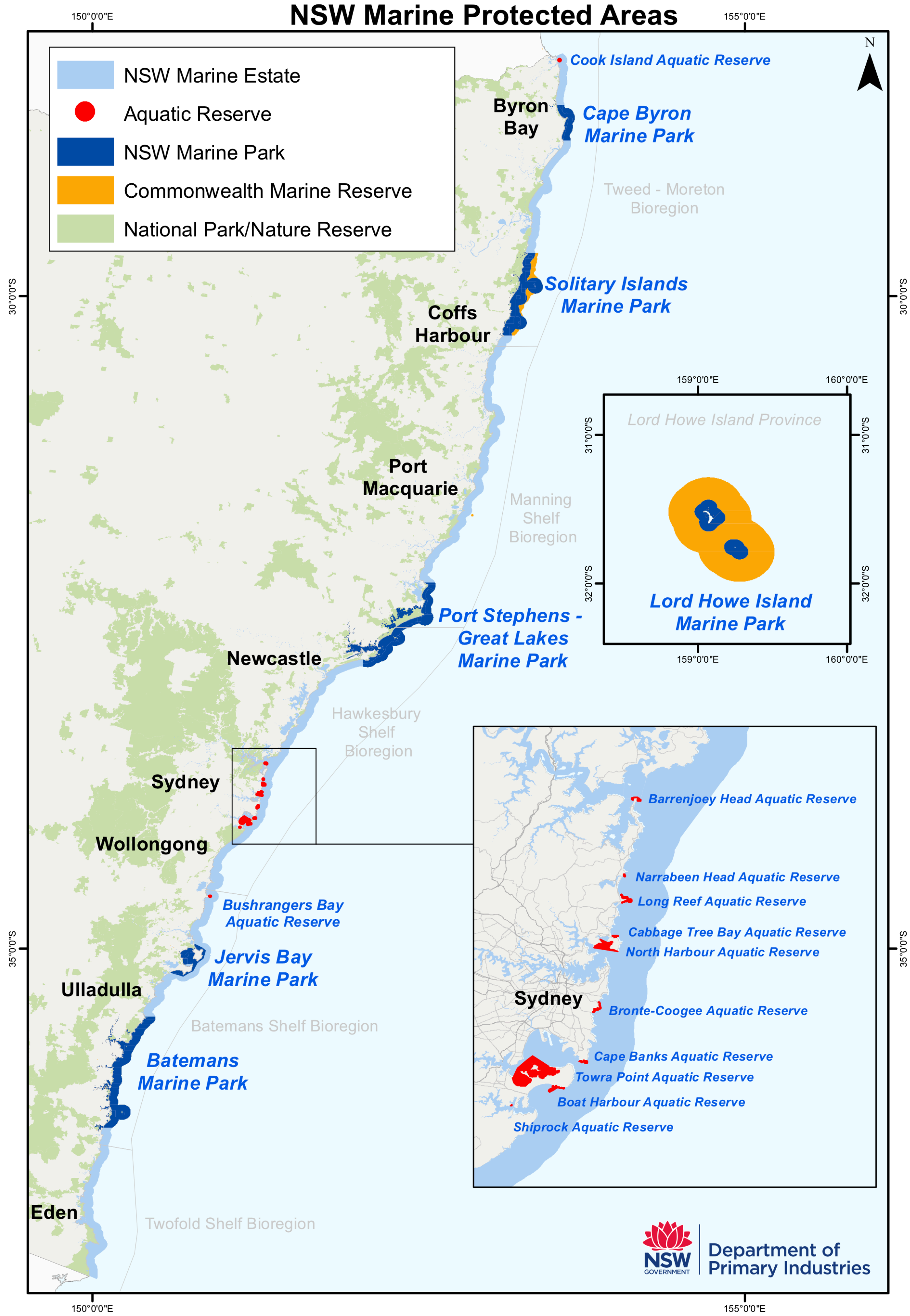

Figure 5.2: Map of the New South Wales (NSW) system of marine protected areas. Image downloaded from https://www.dpi.nsw.gov.au/fishing/habitat/protecting-habitats/mpa in March 2018.

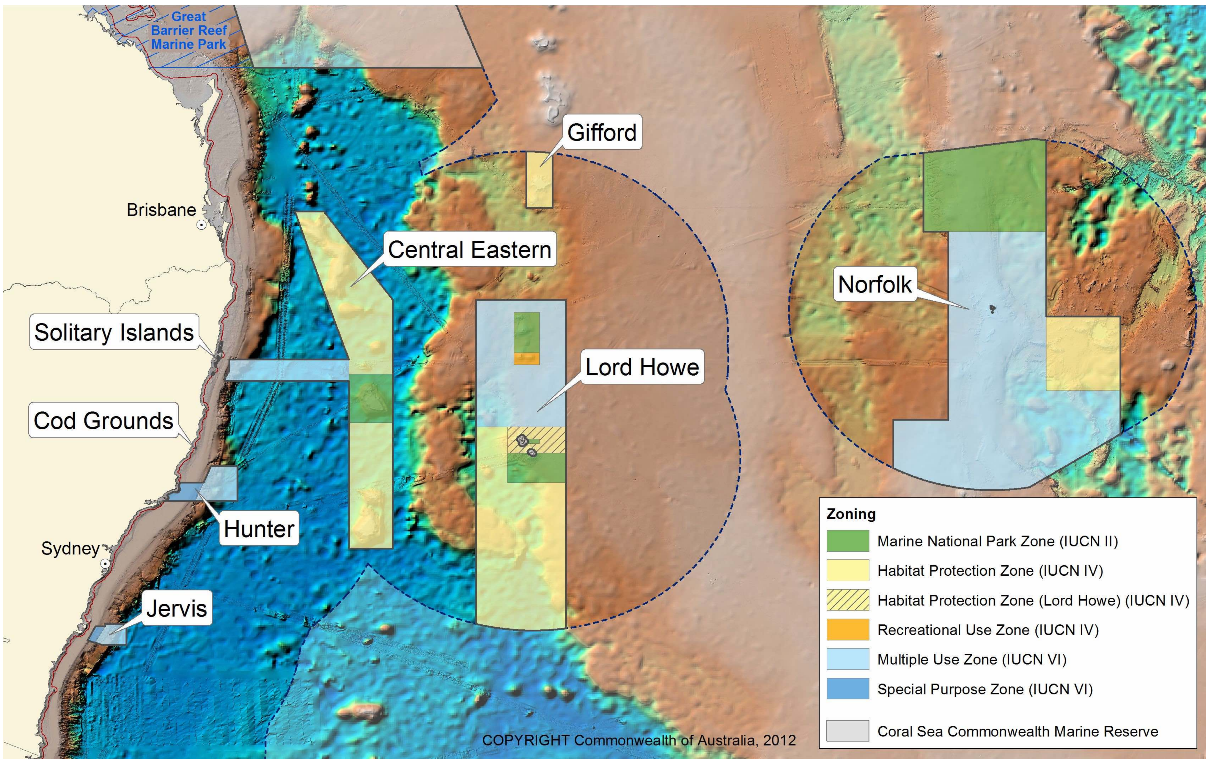

Figure 5.3: Map of the Temperate East Commonwealth Marine Reserves Network. Image downloaded from http://www.environment.gov.au/topics/marine/marine-reserves/temperate-east in March 2018.

5.3.2 The biophysical model

Connectivity patterns of *E. daemelii* were estimated using the ZISSOU biophysical dispersal model (BDM; v1.1.3; Hawes 2018); see the methods in Chapter 4 for a complete description (see Appendix D for configuration files). ZISSOU is an individual-based model, moving larvae within the system using a coupled biological-physical model. Larvae are advected within the model domain using the output from a hydrodynamic model and turbulent processes. The biological model applies traits (i.e. pelagic larval duration, developmental rates) and behaviours (i.e. ontogenetic vertical migration, orientated horizontal swimming) that influence the dispersal. If an individual larva reaches suitable habitat before the end of the pelagic larval duration it settles, and no post-settlement processes are considered.

The physical model was forced with hydrodynamic flow data from BRAN3 (Bluelink reanalysis, version 3p5; Oke *et al.* 2013), a data-assimilating hindcast model which resolves mesoscale eddies with mean daily velocities. BRAN3 has a resolution of 0.1° latitude and longitude and resolves depth velocities at bins of 5-10 m. As with similar studies (Chiswell and Rickard 2011; Condie and Condie 2016), an eddy diffusivity value (K) of 300 ms^{-1} was implemented in the model. Larvae positions in the BDM were updated based on a time step of two hours.

The biological model was parametrised with values obtained from the literature for the species *E. daemelii* where possible. In the cases where values could not be sourced for a particular parameter, values for similar species or averages across species within the genus were used instead. If this was not possible, then general values from the review in Chapter 2 were utilised (Table 5.1). Noting that some of the values were taken from studies on *Epinephelus* larvae reared in mesocosms (Cunha *et al.* 2013), which can have longer developmental times than wild fish (Miller and Kendall 2009).

***Table 5.1**: Biological parametrisation for the larvae of Epinephelus daemelii in the biophysical dispersal model. For sourcing parameters, if no specific values were found, general values used across ichthyoplankton connectivity studies seen in chapter 2 were used.*

Parameter	Value (± s.d.)	Species	Reference
Spawning time	April-May	*Epinephelus daemelii*	D. Harasti, personal communication, 9 March 2017
Pelagic larval duration	60 (± 10) days	*E. daemelii*	Francis *et al.* (2016)
Settlement competency window	40 days	General	Values taken from the meta-analysis in Chapter 2
Hatching	0-3 (± 1) days	*Epinephelus marginatus*	Cunha *et al.* (2013)
Preflexion	4-12 (± 1) days	*E. marginatus*	Cunha *et al.* (2013)
Flexion	12-16 (± 1) days	*E. marginatus*	Cunha *et al.* (2013)
Postflexion	16-60 (± 1) days	*E. marginatus*	Cunha *et al.* (2013)
Settlement buffer	7 km	General	Values taken from the meta-analysis in Chapter 2
Sensory zone	10 km	General	Values taken from the meta-analysis in Chapter 2
U_{crit}	0.3 ms^{-1}	*Epinephelus spp.*	Leis and Fisher (2006)
In situ swim speed	0.16	*Epinephelus spp.*	Leis and Fisher (2006)
Endurance	0.5	*Epinephelus spp.*	Leis and Fisher (2006)
Mortality	10% day^{-1}	General	Values taken from the meta-analysis in Chapter 2

Larvae were released from four reef patches per region daily (chosen ad hoc, unless specific reef patches were known to contain sightings of *E. daemelii*), during the hypothesised spawning months April-May, over eight years (2004-2011). For each reef patch, 4000 pelagic eggs were spawned per day (16,000 per region) over the 61-day period. In total, 18.5 million eggs were released each breeding season and 148 million over the course of the experiment. Larvae were allowed to settle at rocky reef & rocky intertidal patches if they came within the settlement buffer distance of 7 km, after the settlement competency window and before the pelagic larval duration (Table 5.1). A settlement buffer (settlement sensory zone; Andutta *et al.* 2012) is a common concept used in many BDM studies (refer to Chapter 2) and helps overcome the coarseness of the hydrodynamic model (~10 km), whereby some reefs will fall outside the physical model domain as the grid structure is mapped to the contours of the coastline.

The pelagic larval duration (PLD) assigned for individual larvae was sampled from a Gaussian distribution with a mean value of 60 days and a standard deviation of 10 days (Table 5.1) to account for the empirical uncertainty in PLD values and considering PLDs recorded for other *Epinephelus* species (Wilson and McCormick 1999; Lara *et al.* 2009; Jackson *et al.* 2014). Larvae were given a non-settlement period of 40 days, during which they were considered not developed enough to settle. A daily larval mortality rate of 10% was applied randomly to all swimming larvae, similar to that used for reef fish in other connectivity studies (seen in the meta-analysis from Chapter 2).

The larvae undergo four defined stages of ontogeny; hatching, preflexion, flexion, and postflexion Table 5.1, (Adams 1980). During the hatching stage, the larvae are considered passive as they remain within the egg. Once hatched, preflexion begins and the larvae start developing behavioural traits. The age of ontogeny is specified using days, and the specific value was sampled from a Gaussian distribution with a standard deviation of one day to account for natural variation in developmental times.

While it is unknown if *E. daemelii* larvae exhibit ontogenetic vertical migration, at a family level Serranidae (including subfamily Epinephelinae), have been seen to show patterns of downwards vertical migration with ontogeny (Irisson *et al.* 2010; Huebert *et al.* 2011). Ontogenetic vertical migration (OVM) is known to influence dispersal patterns by allowing larvae to be advected by currents of different directions and magnitudes (refer to Chapter 4), and this behaviour is therefore included in this model. The values of OVM were taken for the Serranidae larvae sampled within the study region in Chapter 3 (Figure 5.4).

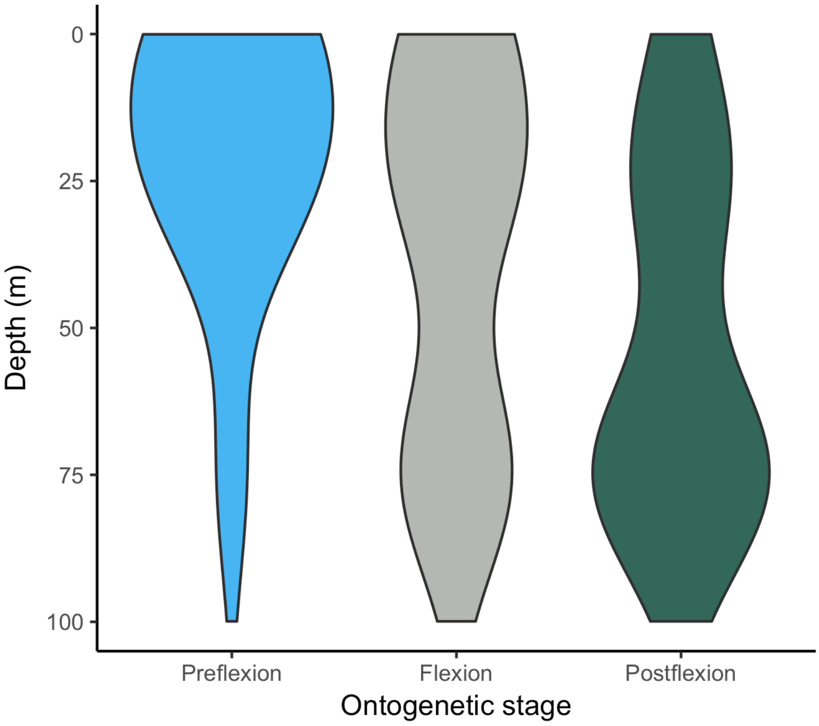

Figure 5.4: Proportional depth stage abundance profile for Serranidae from Chapter 3. The width represents the proportional (within a stage) abundance of each ontogenetic stage (preflexion, flexion, postflexion) within each of three depth ranges (surface: 0-1 m; middle: 5-50 m; deep: 50-100 m) and are used to parameterise the ontogenetic vertical migration behaviour of *Epinephelus daemelii* in the connectivity model.

Orientated horizontal swimming (OHS) is known also to influence dispersal patterns (see Chapter 4), and we know that the larvae of most species do not swim aimlessly, instead orientating themselves using sensory cues that are onset with ontogenetic development (Leis 2010). While the orientation of *E. daemelii* has not been studied, the ability of *Epinephelus* to orient towards cues has been documented (Arreguín-Sanchez *et al.* 1996; Leis *et al.* 2009). In the model, larvae were given OHS behaviour once postflexion (the development of the caudal fin) was reached. Black cod larvae were given a post-flexion age of 16 days (Table 5.1). The sensory distance, from within which it was assumed a fish could sense settlement habitat through olfactory, auditory cues etc., was 10 km (Table 5.1). A larva would only be able to orient and swim towards the "sensed" habitat if it was within this distance and in the postflexion stage, otherwise the larvae swim in a random direction upon reaching flexion. Olfactory lamellae, the lateral line and inner ears fully develop during the period post-flexion to PLD period in a similar species, *Epinephelus fuscoguttatus* (Lim and Mukai 2014). Using the modelled OHS behaviour described in the Chapter 4 methods, *E. daemelii* larvae were given a U_{crit} speed of 0.3 ms^{-1} (Table 5.1). The U_{crit} speed was tempered by an *in situ* swimming potential of 16%, using swimming abilities observed in other *Epinephelus* species (Leis and Fisher 2006). Larvae were assigned a swimming endurance of 50%, the proportion of each time step they would be able to swim, or one out of every two hours in the model.

5.3.3 Data analysis

5.3.3.1 Spatiotemporal differences in dispersal patterns

The data analysis was performed on the output files of the BDM, which for each modelled year, generates a connectivity matrix, a dispersal kernel and a GIS Shapefile of larval trajectories. The connectivity matrix summarises connectivity between larval source region (row_i) and settlement region ($column_j$), where each $element_{i,j}$ is the proportion of all larvae spawned at *i* which settled at *j* over the release period. The dispersal kernel summarises the distribution of larval path distances over the modelled period from source region to settlement region. The GIS Shapefile records the movements using the GPS position of individual larvae for each time-step, it was restricted to a subset of all larvae (5%), chosen randomly due to minimise storage requirements. Patterns of connectivity described by univariate metrics of self-recruitment, local retention, settlement success, and dispersal distance were also compared amongst regions and years. Settlement richness (the number of regions settled from a source region) and diversity (Shannon-Weiner diversity measure using the richness and number of larvae settled using the R package *vegan* — see results in Appendix D; Oksanen *et al.* 2018) were also measured to describe settlement patterns. One-way ANOVAs with the factor source region (using years as the unit of replication) or year (using source regions as the unit of replication) were used to test for significant differences between metrics. Student-Newman-Keuls (SNK) post-hoc tests were used to make comparisons between groups if the ANOVA was significant using the R package *agricolae* (de Mendiburu 2017).

To address the first aim, evaluating the spatial and temporal variation in dispersal patterns, I compared the connectivity matrices using multivariate non-metric multidimensional scaling (NMDS) ordination. The connectivity matrix from each year of the model was considered a sampling unit for each of the 19 source regions (source to settlement linkages), with each point on the ordination representing the settlement from a source region to all settlement regions for a modelled year. The NMDS used a Bray-Curtis dissimilarity measure with a square root transformation commonly used for abundance data to down-weight areas of high settlement (Quinn and Keough 2002), and the analysis used the function *metaMDS* within the R package *vegan*. To quantitatively compare for spatial and temporal variation between the connectivity matrices, I used the multivariate analysis PERMANOVA via the *adonis* function within the R package *vegan*, using source regions as replicates. To further investigate differences in spatiotemporal settlement patterns, Constrained Analysis of Principal Coordinates (CAP) was performed using the function *capscale* in the R package *vegan*, which allows the use of Bray-Curtis dissimilarity measures, using the same dissimilarity matrices as above.

5.3.3.2 Strong and stable dispersal

To compare the strength of connectivity between regions heat maps were generated from the connectivity matrices displaying proportional settlement from a source region to settlement region, to highlight all connections (not only strong connections) a 4th-root transformation was applied to each element of the matrix. Regions of strong settlement were identified using the coefficient of variation % (CV) for settlement to a region, across the modelled years, for the entire distribution and known areas of aggregation. Strongly interconnected (bi-direction larval exchange) subregions were identified using modularity optimisation (Walktrap method) on a directed graph. Source regions were used as nodes, and the edges connecting nodes were weighted by the mean annual settlement between region, using the R package *igraph* (Csardi and Nepusz 2006). Communities are defined by vertexes (regions) having strongly weighted bi-directional edges (settlement) with each other. The Walktrap method uses random walks along the network to identify communities (Pons and Latapy 2006) and is considered accurate for graphs with a small number of vertices (Yang *et al.* 2016). Strong connections were defined as having a larval exchange greater than the mean, and stable connections were those with a CV for that exchange that was less than the mean CV across the modelled years. Edges that were not strong and stable, as defined here, were deleted from the graph for clarity. Communities were visualised using dendrograms for clustering and as connected graphs.

5.3.3.3 Comparisons with known regions of aggregation

The final analysis for the first aim was to compare dispersal patterns predicted by releasing larvae from known areas of aggregation with the dispersal patterns predicted by releasing *E. daemelii* larvae from across its known distribution, using measures of strongly connected areas (heat map and CV) and the univariate metrics (self-recruitment, local retention, settlement success, dispersal distance, settlement richness and diversity).

5.3.3.4 Marine protected areas

To investigate the second aim, assessing the effectiveness of the MPAs for *E. daemelii* using the modelled connectivity patterns, I compared both strong stable regions of settlement (using the CV of settlement described above) and important spawning regions (high settlement success and local retention) to regions with MPAs. Gaps in protection for protection of important potential spawning or settlement regions were identified using the connectivity matrices from the known regions of aggregation and the entire distribution.

All data analysis was performed using R version 3.4.3 (Kite-Eating Tree) and the specified packages above.

5.4 Results

Releasing *E. daemelii* larvae from across the known distribution produced potential settlement at each region within the distribution (Figure 5.5). Larvae that were released along the New South Wales (NSW) coastline tended to disperse close to the coast in the north (apart from the top of NSW), until the middle section of NSW where larvae separated from the coast, and the southern region where larvae appeared to be entrained in mesoscale eddies (identified as particles moving off the coast into swirls; Figure 5.5 A). Connectivity was seen between the New South Wales (NSW) coastline and the offshore reefs; Lord Howe Island, Elizabeth and Middleton Reefs (EM Reefs; Figure 5.5 B). Larvae that settled between the offshore islands and NSW coast were observed to disperse long distances via currents before reaching an appropriate settlement habitat.

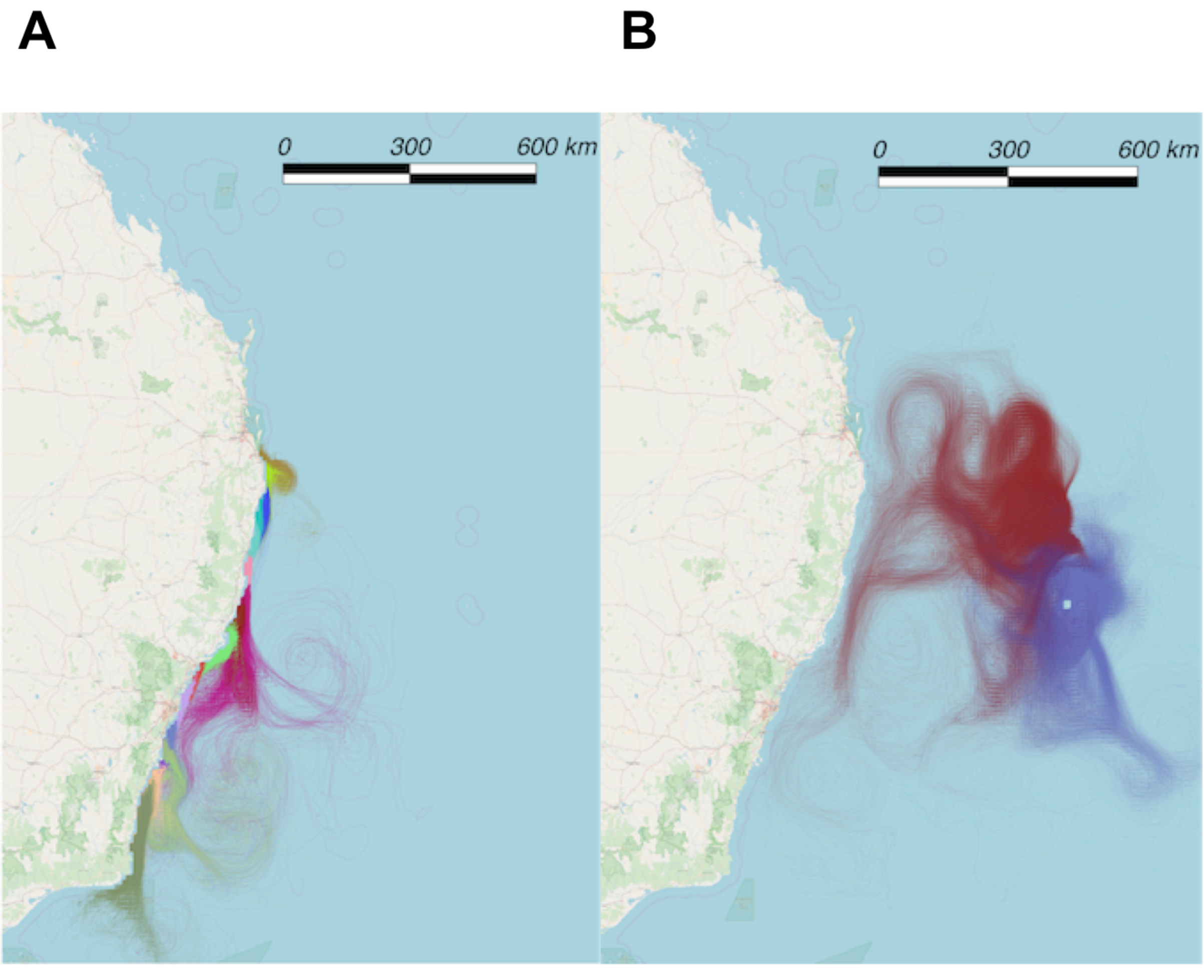

Figure 5.5: Larval trajectories for a random subset (5%) of settled *Epinephelus daemelii* larvae from all source regions released from the coastline of NSW (A) and released from the offshore reefs of Lord Howe Island and Elizabeth and Middleton Reefs (B; colours represent different source regions)

5.4.1 Spatial and temporal variation of settlement patterns

There was a strong latitudinal gradient of settlement from source regions (Figure 5.6), depicted by a horseshoe pattern (Podani and Miklós 2002) over the modelled period. The northern regions from the Tweed to the Solitary Islands, exhibit extensive overlap in settlement patterns (Figure 5.6). There is a suggestion of two separate clusters of settlement patterns, for the regions to the north (1-6) and south (8-17) of Port Macquarie. The southern regions along the NSW coast showed lower variation between years than the northern regions, but more dissimilar settlement patterns between regions. Using PERMANOVA, the settlement pattern between years was significantly different ($R^2 = 0.009$; $p = 0.005$; Figure 5.6), although most of the variation seen was driven by the different source regions ($R^2 = 0.92$; $p = 0.005$). The annual variation in settlement patterns was not consistent between regions. Regions that displayed the highest annual variation in descending order were Lord Howe

Island, Port Macquarie, and the Tweed. Eden, Crowdy Bay, and Nambucca appeared to have the lowest annual variability between settlement patterns.

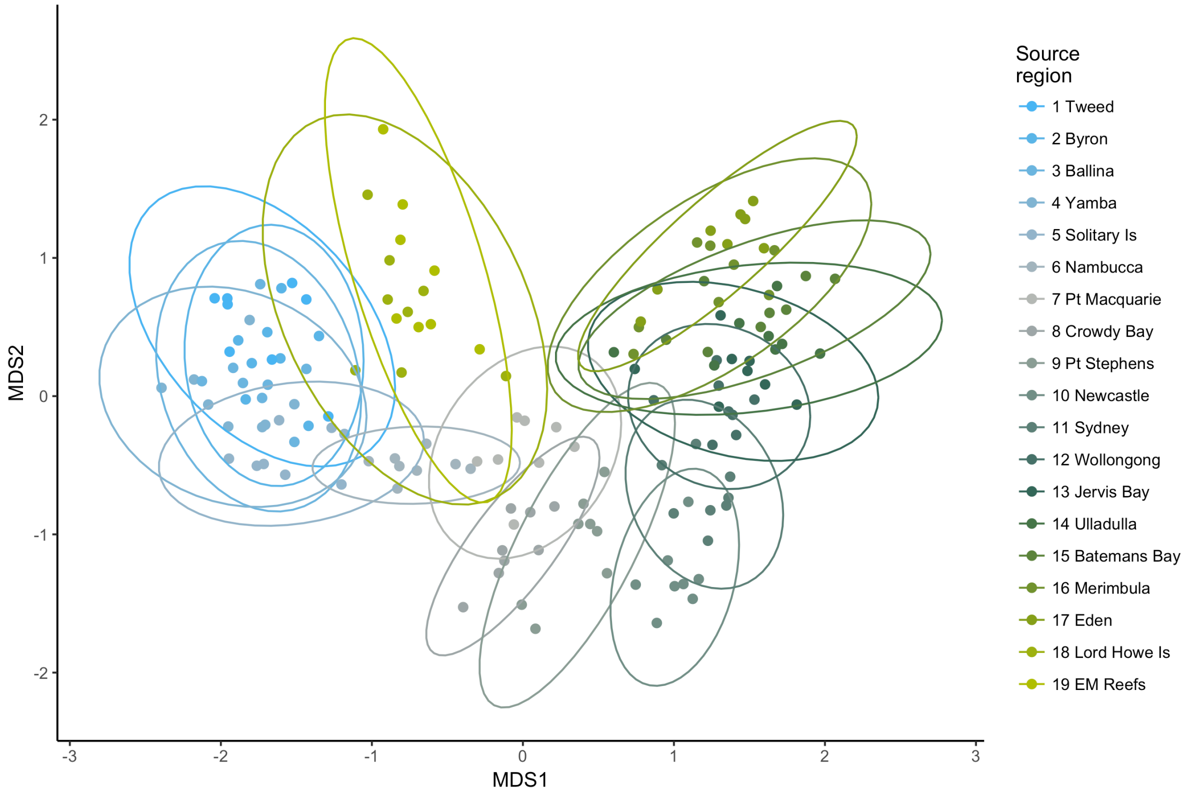

Figure 5.6: NMDS of the connectivity patterns from each source region (colour coded and grouped by ellipses) in each year (2004-2011; each year is a point within an ellipse) to all possible settlement regions (in descending latitudinal order 1-17 and 18-19 for the offshore regions). Bray-Curtis dissimilarities were used with a square-root transformation (2D stress = 0.12)

The CAP analysis showed distinct groupings between the settlement patterns of source regions (Figure 5.7 A). The northern regions (1-5), the central regions (7-11), and the southern regions (12-17) strongly group together. Nambucca is grouped with the offshore reefs—Lord Howe Islands and Elizabeth and Middleton Reefs—which has settlement patterns between the northern and central clusters. Comparing the connectivity matrices between years two broad clusters can be observed, with a grouping of 2005, 2009, and 2010 (Figure 5.7 B). The years 2004 and 2011 were the most similar to each other out of all the connectivity matrices.

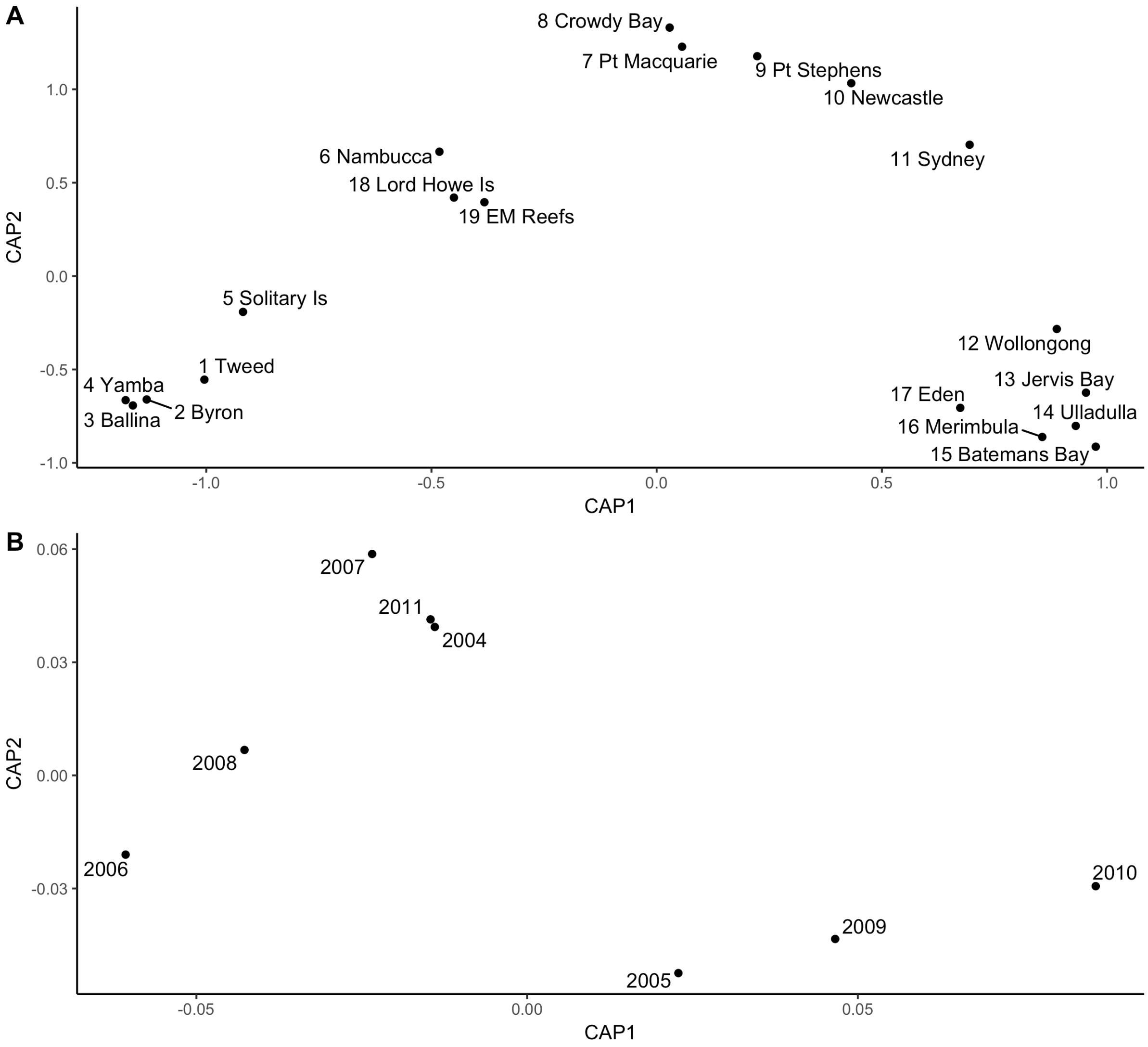

Figure 5.7: Constrained analysis of principal coordinates (CAP) on the *Epinephelus daemelii* connectivity matrices comparing source regions across their known distribution (A), and the annual variation between connectivity matrices (B; 2004-2011). Bray-Curtis dissimilarities were used with a square-root transformation.

There were significant differences in the self-recruitment values between source regions ($F_{(18,126)} = 52.60$, $p < 0.001$). Post-hoc tests determined there were seven source regions with the highest values of self-recruitment, with means above 75% (Nambucca, Crowdy Bay, Port Stephens, Wollongong, Ulladulla, Batemans Bay, and Eden; Figure 5.8 A). The lowest self-recruitment occurred in the Tweed region with 21%. Self-recruitment tended to either be above 65% or below 40%, with one or two exceptions. Local retention was more variable than self-recruitment across most source regions (Figure 5.8 B), and was different between regions ($F_{(18,126)} = 36.03$, $p < 0.001$). Local retention was highest in Yamba, Solitary Islands, and Crowdy Bay, and lowest at Lord Howe Island and EM Reefs. The settlement success of larvae also varied significantly between source regions ($F_{(18,126)} = 77.97$, $p < 0.001$). Settlement success exhibited latitudinal patterns, strongly increasing with latitude from the Tweed until Yamba and then reversing and strongly decreasing with latitude until Port Macquarie (Figure 5.8 C). Settlement success increased again until the Newcastle and Sydney regions, after which it decreased gradually with latitude. Settlement success was lowest at Lord Howe Island and EM Reefs (Figure 5.8 C), with the Tweed, Byron and Port Macquarie regions produced the largest variation of settlement success. Most regions had similar dispersal distances, yet several had significantly longer dispersal distances ($F_{(18,126)} = 175.71$, $p < 0.001$). Dispersal distance showed an inverse latitudinal pattern to settlement success, i.e. where settlement success is high, dispersal distance is low (Figure 5.8 D). Lord Howe Island EM Reefs larvae dispersed the longest, with mean distances over 1000km. Of the coastal regions, Eden, Merimbula, and Port Macquarie dispersed the longest. Latitudinal patterns in the settlement richness and diversity were also seen across regions, with increases in variation amongst the southern regions (see Appendix D, Figure D2).

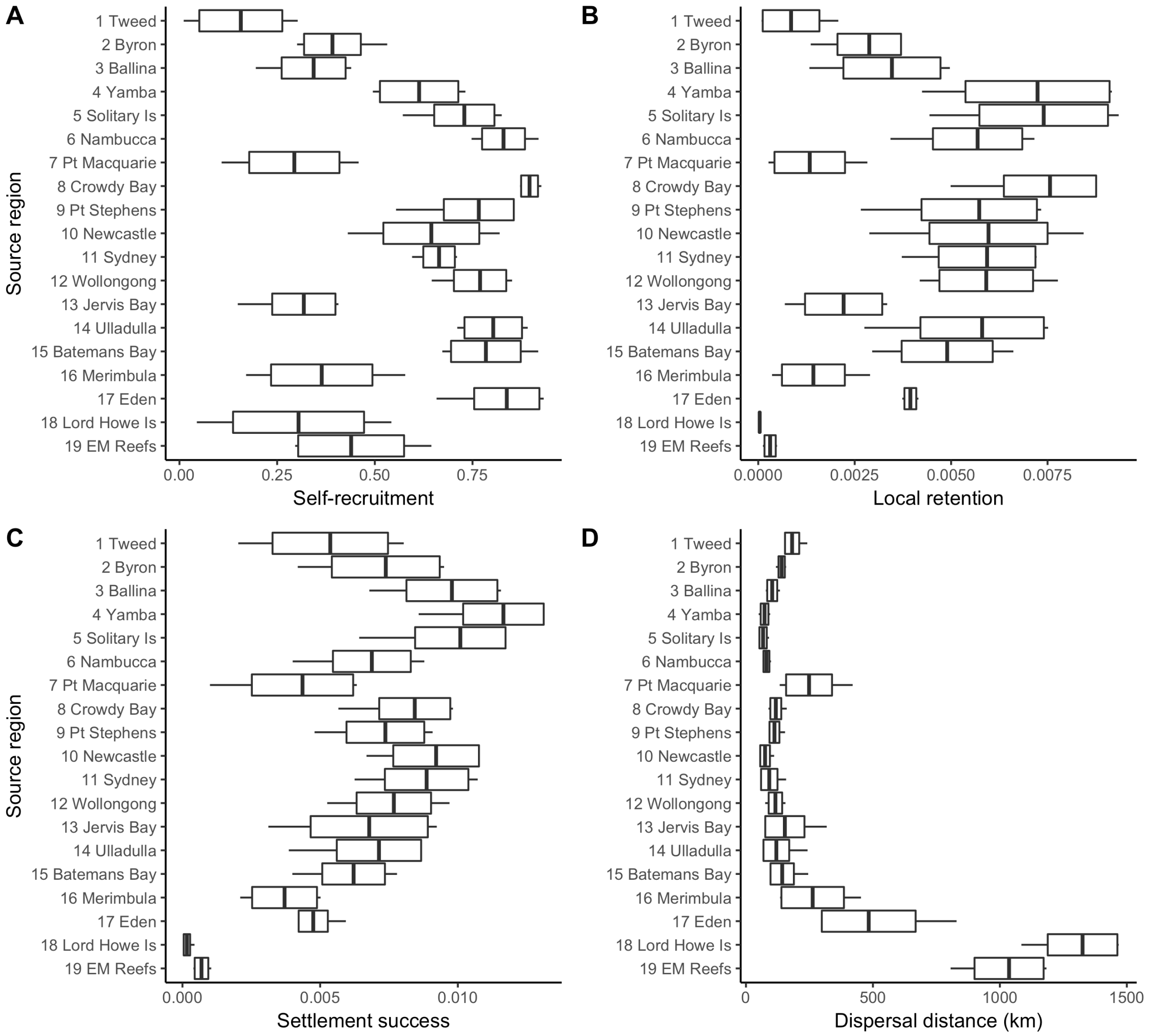

Figure 5.8: Average (vertical bar) connectivity metric values for all modelled years for self-recruitment (A), local retention (B), settlement success (C), and dispersal distance (D; km) for each of the 19 source regions from which *Epinephelus daemelii* larvae were released in the dispersal model. Boxes enclose ± 1 S.D., and whiskers indicate min/max values of the distribution.

Crowdy Bay and Sydney had the least variation in self-recruitment between the years 2004-2011, while the source regions of Lord Howe Island, Elizabeth and Middleton Reefs (EM Reefs), and Newcastle produced the greatest annual variation. There were also significant differences to the self-recruitment between years, averaged across all source regions ($F_{(7,126)}$ = 3.03, p = 0.006; Figure 5.9 A). Post-hoc tests indicated that in 2011 and 2008 self-recruitment was 10% higher than in 2010. The mean annual self-recruitment values were always above 50%. These two source regions, along with Eden, had the least annual variation in local retention. Yamba, Solitary Islands, and Newcastle had the largest annual variation in the larvae that were locally retained. The mean annual local retention across all regions varied significantly ($F_{(7,126)} = 22.214$, $p < 0.001$). The lowest annual local retention values occurred in 2007, which was 53% lower than 2008, the year when the highest local retention transpired (Figure 5.9 B). In 2007 there was also the least variation in local retention between source regions, while 2008 had the largest variation. There were annual differences in settlement success ($F_{(7,126)} = 27.068$, $p < 0.001$), which followed a similar pattern to local retention (Figure 5.9 B, C). The lowest annual settlement success again occurred in 2007, and the years with most successful settlement were 2006, 2008, 2010, and 2011 (approximately 1.6 times more likely to settle than 2007 Figure 5.9 C). There were only slight differences between the yearly mean dispersal differences ($F_{(7,126)} = 2.70$, $p = 0.01$), however, post-hoc tests were unable to identify years that were significantly different to each other (Figure 5.9 D). The mean dispersal distance per year was about 250 km (Figure 5.9 D; see Appendix D, Figure D1 for the dispersal kernels). Annual variation was also seen across the settlement richness and diversity (see Appendix D, Figure D4).

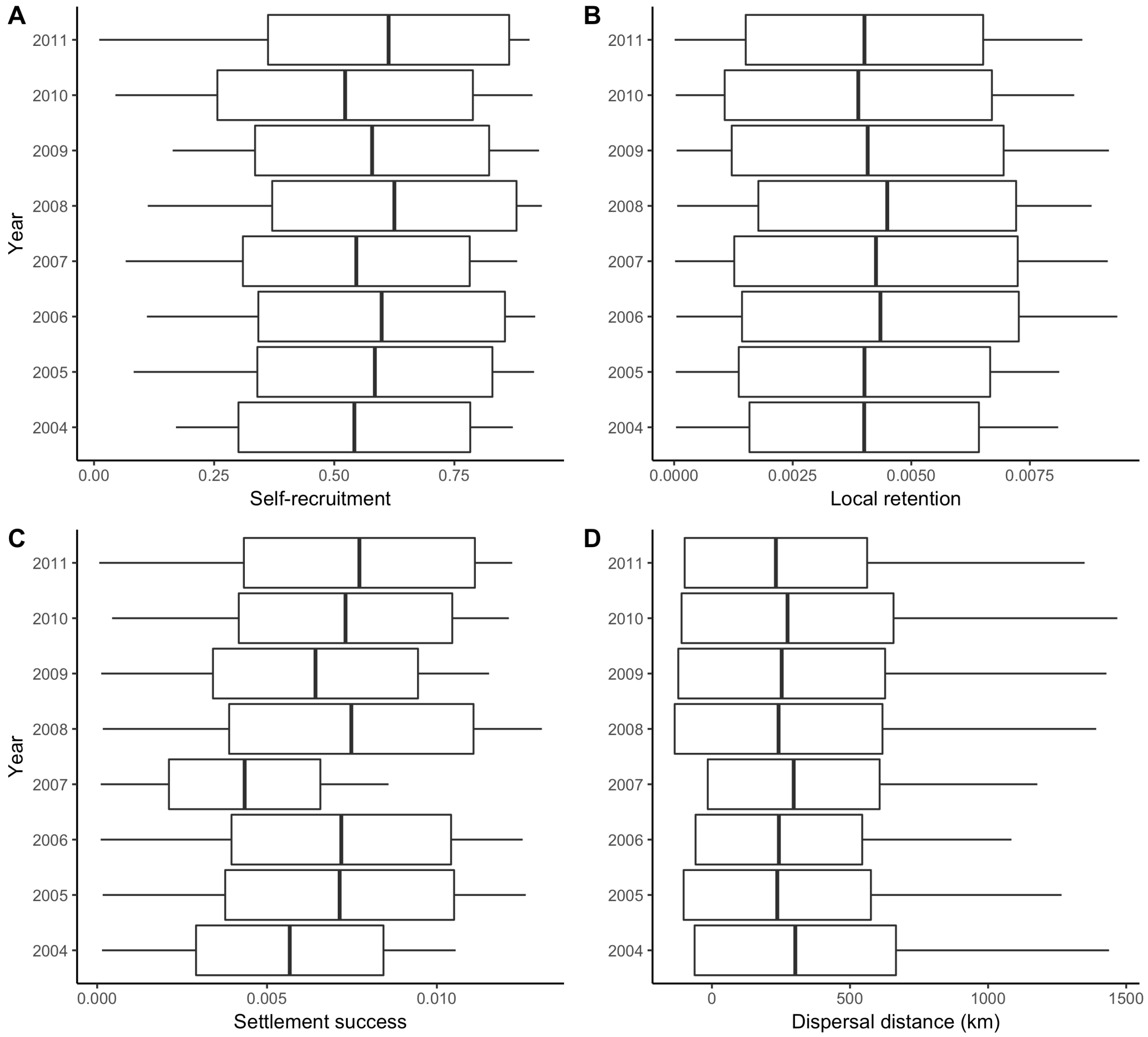

Figure 5.9: Average (vertical bar) connectivity metric values for all modelled regions for self-recruitment (A), local retention (B), settlement success (C), and dispersal distance (D; km) for each year (2004-2011) from which *Epinephelus daemelii* larvae were released in the dispersal model. Boxes enclose ± 1 S.D. and whiskers indicate min/max values of the distribution.

5.4.2 Identifying areas of strong connectivity

The strongest connectivity for all source regions occurred with geographically close settlement regions, although each source region along the NSW coast showed long tails of connectivity to the south (Figure 5.10; for connectivity matrix see Appendix D). In general, the larvae settled in highest numbers to their natal region, the exceptions being the regions Tweed, Port Macquarie, and Jervis Bay, whereas strong connectivity occurred with the regions directly to the north or south of the source region. Below Newcastle (Sydney to Eden), source regions had a more northward settlement, Ulladulla and Merimbula have limited connectivity to Tweed or Queensland, but this connectivity was weak and variable. The offshore areas of Lord Howe Island, and Elizabeth and Middleton (EM) reefs also mostly recruited from the natal regions and from each other, but both also connected to all regions along the NSW coastline and to Queensland, with the strongest connectivity to regions above Jervis Bay. The connectivity between Lord Howe, EM Reefs, and the NSW coastline, while weak, was bi-directional (Figure 5.10). No connectivity was seen to occur to either Norfolk Island or New Zealand from any of the chosen source regions.

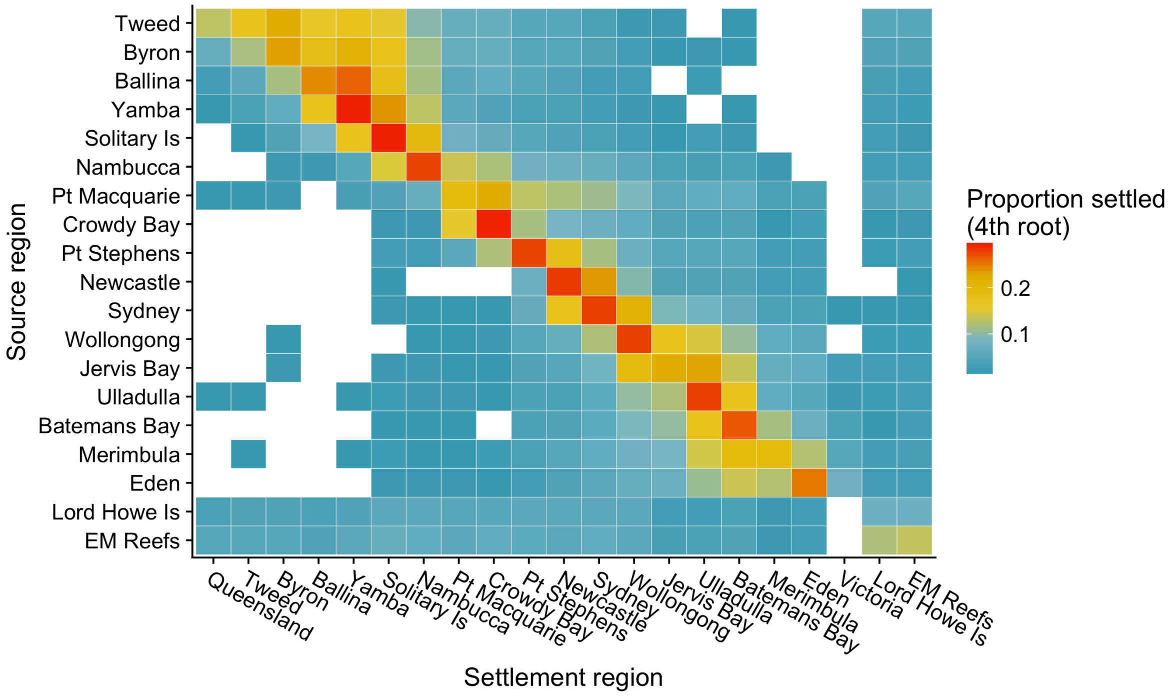

Figure 5.10: The connectivity matrix of the mean proportional settlement (4th root) between source regions and settlement regions over the years (2004-2011). Regions are organised latitudinal from north to south with the exception of Lord Howe Island and Elizabeth and Middleton Reefs (EM Reefs) which are listed last.

The strongest regions of settlement across the time series were Yamba and Solitary Islands, both of which were also the most consistent in having the lowest coefficients of variation across the modelled years of any regions in the domain (Figure 5.11 A). *E. daemelii* settlement was highest in the northern-central region of NSW when considering all source regions. The offshore islands of Lord Howe and EM Reefs, along with settlement regions in Queensland and Victoria had the lowest settlement numbers. Queensland and the most northern NSW region of the Tweed had the highest variation, but for the rest of the regions, the annual variation was consistent.

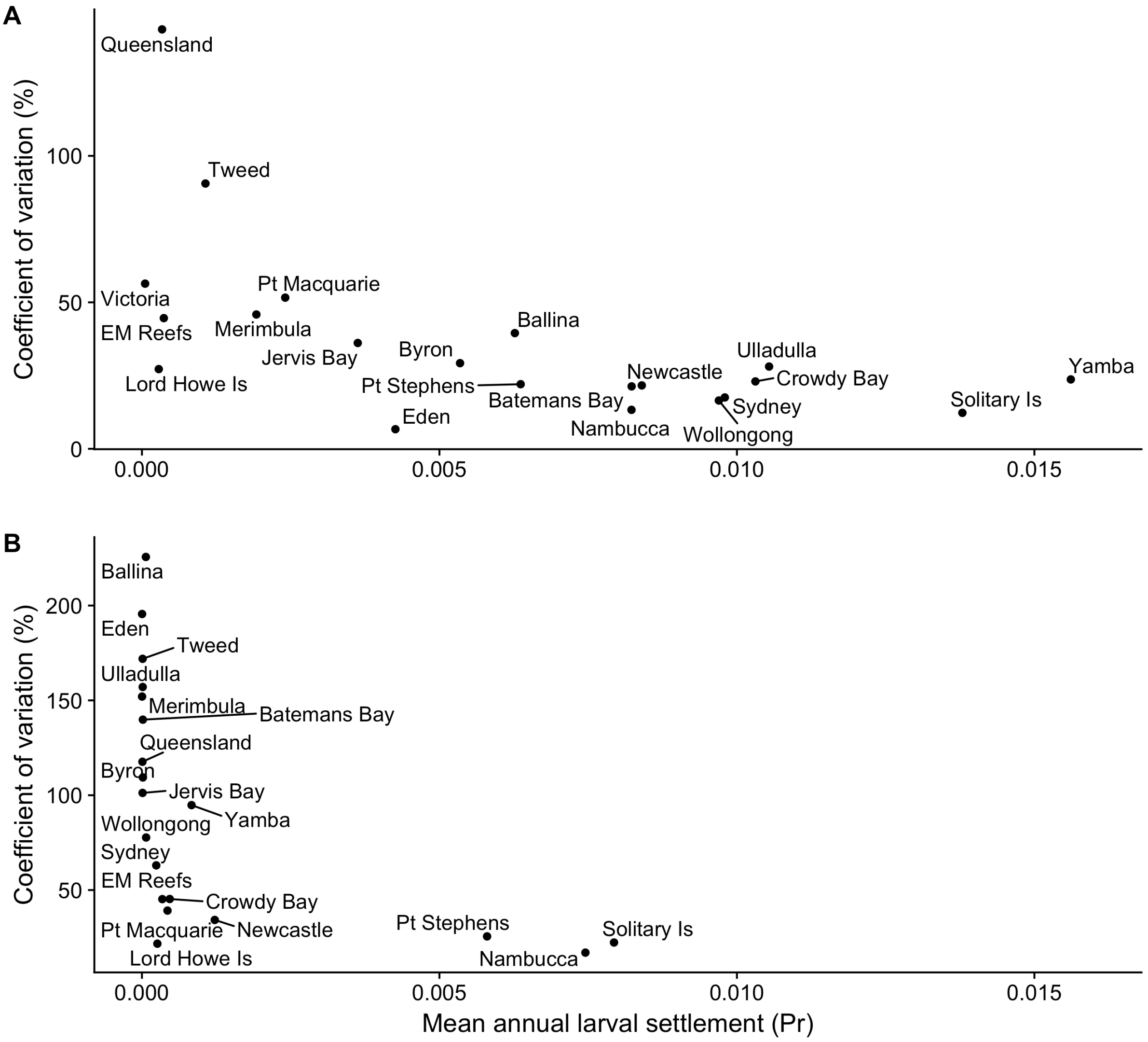

Figure 5.11: Mean versus coefficient of variation of annual settlement to regions based on larval releases from all regions across the known distribution (A) and based on larval releases from only the known aggregation regions (B).

Four identified sub-communities form the network of demographically connected regions from all possible spawning regions when considering the mean annual settlement (Figure 5.12 A). Latitude and geographic location group the communities. The most dissimilar group is the offshore areas Lord Howe Island and EM Reefs. The next grouping is the south coast, from Ulladulla to Eden. Within this community, Batemans Bay and Merimbula have the most similar settlement patterns. The central community (Port Macquarie to Sydney) and the northern community (Tweed to Nambucca) were more similar to each other than the southern community. Inside the northern community, Tweed and Byron, and Ballina and Yamba were the two grouping of regions that were most similar when comparing the settlement patterns of all regions. Within the central community, Port Macquarie and Crowdy Bay had the most similar settlement patterns.

The only strong link between these sub-communities occurred between central and southern communities, at the Sydney and Wollongong regions (Figure 5.12 B). In the northern community each region had strong connectivity with the region latitudinally above or below, except between Byron and Ballina. The northern community was also the only region to have strong connectivity to regions further than this, with strong links between Tweed-Yamba, Byron-Solitary Islands, and Ballina-Solitary Islands. In the central community, the strongest linkages were between Pt Macquarie-Crowdy Bay and Newcastle-Sydney. Crowdy Bay and Port Stephens were not strongly linked, despite the spatial proximity. In the southern community, each region was connected strongly by latitude, the strongest linkage occurring between Jervis Bay and Ulladulla. Finally, in the offshore community there were neither strong linkages between each other or between other communities.

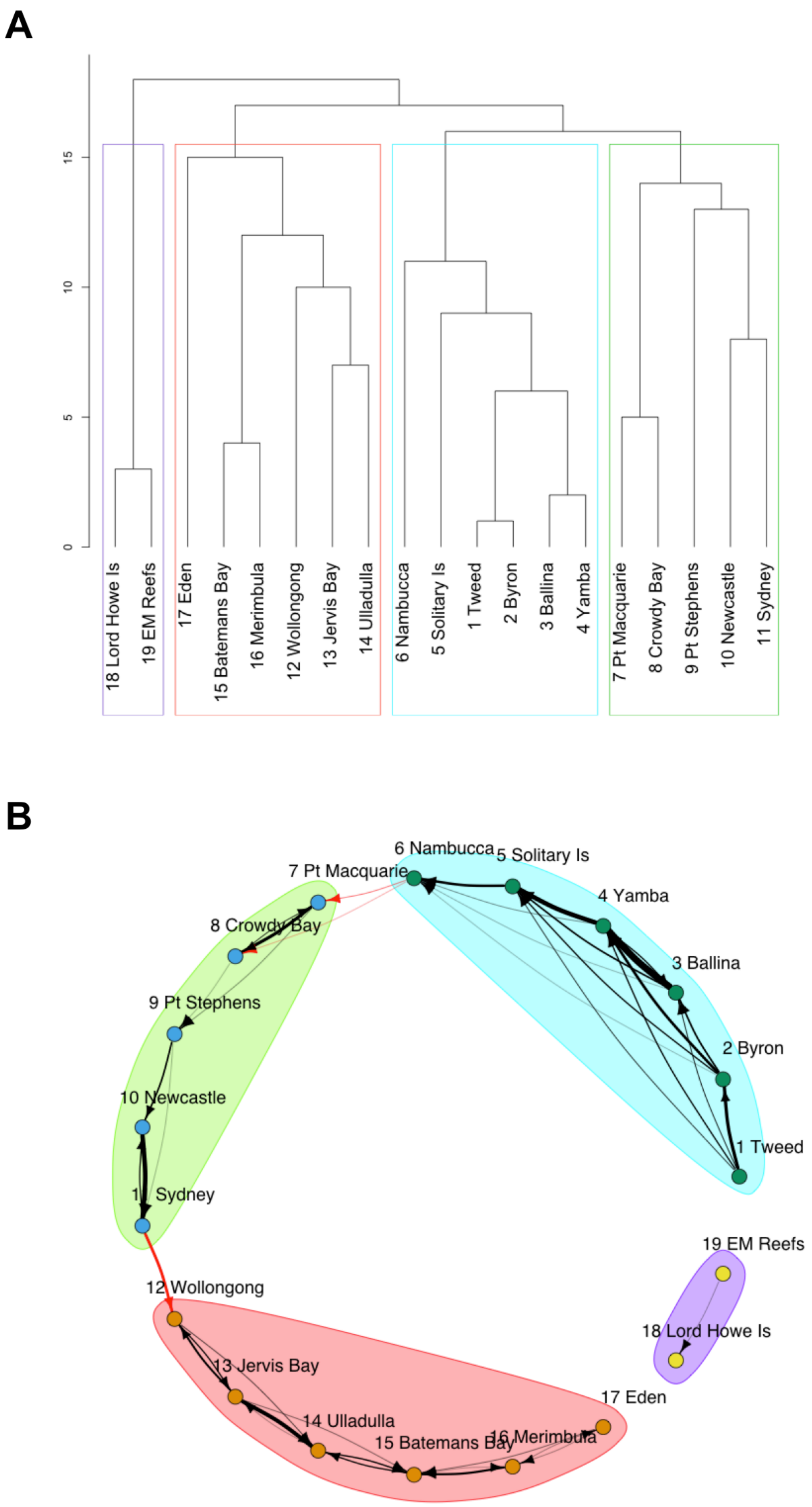

Figure 5.12: Dendrogram of communities detected using the Walktrap modularity method with edges weighted by the mean yearly settlement between the 19 source regions in NSW (A) and the graph of the communities (blue = northern; green = central, red = southern; purple = offshore) and showing edges within communities (black) and edges between communities (red), edge thickness is proportional to number of settlers. Only strong connections (edges) with a settlement greater than the mean and coefficient of variation less than the mean were shown.

5.4.3 Connectivity amongst known areas of aggregation

The settlement from the known aggregation regions (Nambucca, Solitary Islands, Pt Stephens, Lord Howe Island, and EM Reefs) was more restricted, with *E. daemelii* larvae not making it up towards Queensland or down into Victoria (Figure 5.13). Three of the source regions, Nambucca, Solitary Islands, and Pt Stephens, being the areas of highest settlement and with strong consistency, significantly different from the rest with settlement at Port Stephens was 4.8 times higher than the fourth most settled area ($F_{(19,133)} = 140.51$, $p < 0.001$; Figure 5.11 B). Yamba and Newcastle were the other regions receiving the highest numbers of recruits (connectivity was more variable to Yamba), and the south coast had seemingly negligible connectivity (high annual variation). From the five known areas of aggregation, larvae were successfully exported to every region within the domain, suggesting high connectedness.

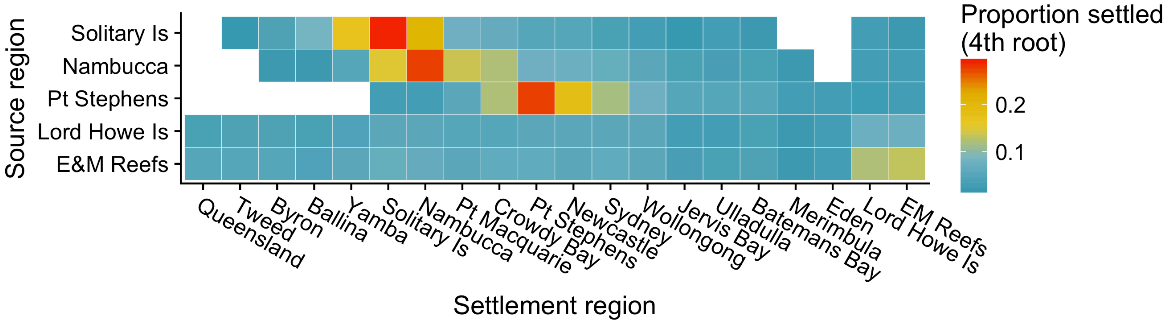

Figure 5.13: The connectivity matrix of the mean proportion of total settlement (4th root) from all source regions to settlement regions for the years (2004-2011), using a log scale on the settlement proportions.

Using only the known aggregating areas for larval release two clusters were identified; the coastal regions and the off-shore reefs (Figure 5.14 A). The off-shore regions, Lord Howe Island and EM Reefs were tightly clustered, suggesting equal flow of larvae between each region. For the coastal regions, Pt Stephens was the out-group to the geographic neighbours, Solitary Islands and Nambucca. Within the coastal population, the strong linkage occurred from Solitary Islands to Nambucca, and the off-shore population had a strong connection from EM Reef region to Lord Howe Island (Figure 5.14 B).

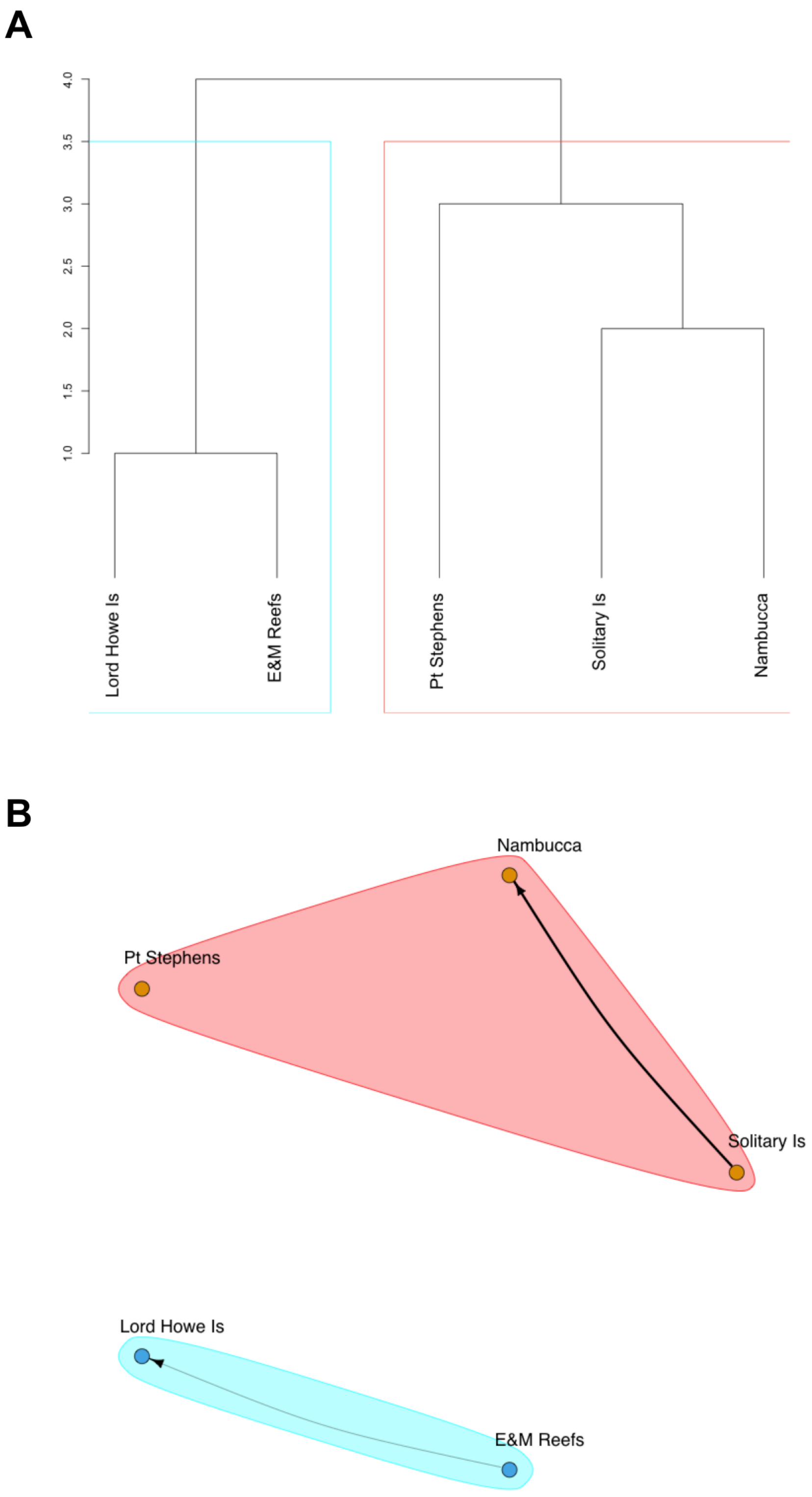

Figure 5.14: Dendrogram of communities detected using the Walktrap modularity method with edges weighted by the mean yearly settlement between the five known regions of aggregation (A) and the graph of the communities (blue = off-shore; red = coastal). Edge thickness is proportional to the number of settlers and only strong connections were considered to be edges with a settlement greater than the mean and coefficient of variation less than the mean.

Considering only the known areas of aggregation, Solitary Islands produced the most successfully settling larva, mostly through local retention (Figure 5.8 B), but also to Nambucca, the region below (Figure 5.13). This high local-retention was reflected by the low dispersal distance for larvae from the Solitary Islands (Figure 5.8 D). However, it is also the most important source region for itself, with annual self-recruitment values of 72.9 ± 7.7% (Figure 5.8 A). The other known aggregation regions on the NSW coast of Port Stephens and Nambucca also both have high self-recruitment at about 80% (Figure 5.8 A). The settlement at Nambucca showed slightly less annual variability than either the Solitary Islands or Pt Stephens (Figure 5.11 B), but the differences were small. Pt Stephens showed the strongest connectivity to the Sydney and Wollongong regions but had among the lowest overall settlement success (and most highly variable) for the NSW regions (Figure 5.8 C). Compared to Solitary Islands and Nambucca, larvae spawned from Port Stephens showed the strongest connections to the southern areas of NSW, dispersing with a mean distance of 112.2 km before settlement (Figure 5.8 D).

Even though Lord Howe Island and EM Reefs both support populations of *E. daemelii*, these regions had the lowest settlement success in the model (Figure 5.8 C). Both had little local retention and highly variable self-recruitment above 25% (Figure 5.8 A; Figure 5.8 B). Larvae spawned at Lord Howe Island settled consistently to all regions in NSW, apart from Yamba to Nambucca. EM Reefs showed similar settlement patterns to Lord Howe, except the larvae spawned at EM Reefs had limited connectivity to the most northern regions Tweed, Byron, and Ballina (Figure 5.13). The larvae from these regions were also the most dispersed, travelling on average more than 1000 km before successfully settling (Figure 5.8 D).

5.4.4 Marine Park Connectivity

The total marine protected area (MPA) within the modelled domain is 3297.5 km^2 (the entire NSW marine estate is in excess of 10,000 km^2; http://www.marine.nsw.gov.au), of which 702 km^2 (21.6%) are designated as no-take zones (providing protection from all fishing activity, i.e. commercial and recreational; Table 5.2). However, permits can be obtained to fish in a few of these zones, specifically, MPAs managed by the Commonwealth of Australia. Several of the no-take zones have policing amnesties while the policy on MPAs is currently under consideration. Eleven of the 19 source regions (58%) contained a marine protected area of some kind. The most coverage by area occurred in the Port Stephens region, with 980 km^2

and the least coverage was 0.78 km^2 within the Tweed region (Table 5.2). The EM Reefs had the most comprehensive coverage, as the entire region falls within a MPA. The Sydney region has the most MPAs within its boundaries (10), but the total extent of the protected area coverage is only 19 km^2, of which only 6 km^2 (32%) classifies as no-take zones. It must also be noted that not all of the no-take zones contain suitable habitat for *E. daemelii*, i.e. sandy beaches with no rocky reef.

***Table 5.2**: The legislated marine protected areas (MPAs) that are relevant to the Epinephelus daemelii, in both New South Wales (NSW) and Commonwealth of Australia jurisdictions, indicating the region they are located in the model domain, the size of the MPA (km^2), the percentage and size of the no-take zones (management areas where fishing, either recreational or commercial fishing is prohibited) within the MPA. All information sourced from the NSW Government (http://www.marine.nsw.gov.au) and the Commonwealth Government of Australia (http://www.environment.gov.au/marine/).*

Reserve	Region	Management	Established	Current rules	Size (km^2)	No-take zone (%)	No-take zone (km^2)
Cape Byron Marine Park	Byron	NSW	2002	2006	220	28%	61
Solitary Islands Marine Park	Solitary Islands	NSW	1998	2002	720	12%	86
Port Stephens - Great Lakes Marine Park	Pt Stephens	NSW	2005	2007	980	20%	196
Lord Howe Island Marine Park	Lord Howe	NSW	1999	2010	460	27%	124
Jervis Bay Marine Park	Jervis Bay	NSW	1998	2002	215	20%	43
Batemans Marine Park	Batemans Bay	NSW	2006	2007	850	19%	162
Cook Island Aquatic Reserve	Tweed	NSW	1998	1998	0.78	100%	0.78
Barrenjoey Head Aquatic Reserve	Sydney	NSW	2002	2002	0.29	0%	n/a
Narrabeen Head Aquatic Reserve	Sydney	NSW	2002	2002	0.06	0%	n/a
Long Reef Aquatic Reserve	Sydney	NSW	1980	1980	0.76	0%	n/a
Cabbage Tree Bay Aquatic Reserve	Sydney	NSW	2002	2002	0.2	100%	0.2
North Harbour Aquatic Reserve	Sydney	NSW	1982	1982	2.6	0%	n/a
Bronte - Coogee Aquatic Reserve	Sydney	NSW	2002	2002	0.43	0%	n/a
Cape Banks Aquatic Reserve	Sydney	NSW	2002	2002	0.22	0%	n/a
Boat Harbour Aquatic Reserve	Sydney	NSW	2002	2002	0.72	0%	n/a
Towra Point Aquatic Reserve	Sydney	NSW	1987	1987	14	40%	6
Shiprock Aquatic Reserve	Sydney	NSW	1982	1982	0.02	100%	n/a
Bushranger's Bay Aquatic Reserve	Wollongong	NSW	1982	1982	0.4	100%	0.4
Cod Grounds Commonwealth Marine Reserve	Pt Macquarie	Commonwealth	2007	2007	4	100%	4

Lord Howe Commonwealth Marine Reserve[1]	EM Reefs	Commonwealth	1987	2012	88	58%	51.04

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[1] For the Lord Howe Islands Marine Reserve, only the reef extent of the two offshore reefs, Elizabeth and Middleton reefs (88 km^2) was considered, instead of the total reserve size covering the region including the open ocean (1880 km^2). EM Reefs were part of the Elizabeth and Middleton Reefs Marine National Nature Reserve, which was included in the larger Lord Howe Commonwealth Marine Reserve in December 2012.

Of the four sub-communities identified, each community had at least one source region that contained some areas designated as no-take zone (Figure 5.12 A; Table 5.2). The offshore community of Lord Howe Island and EM Reefs had the most protection afforded to any of the communities per region, with both regions encompassed by MPAs (EM Reefs has 100% coverage) and containing 58% no-take zones at EM Reefs (Middleton Reef) and 27.0% no-take zones at Lord Howe Island covering 175 km^2 (Table 5.2). In the northern community, three of the six regions contained MPAs (Tweed, Byron, and Solitary Islands), although the aquatic reserve in Tweed is one of the smallest MPAs in size. The total MPA coverage within this northern community is 941 km^2, of which 148 km^2 (15.7%) is no-take zones. The central community also contained three regions with MPAs (Port Macquarie, Port Stephens, and Sydney), with a total coverage of 1003 km^2 (20.5% or 206 km^2 falls within no-take zones). In the southern community, half the regions contained MPAs (Wollongong, Jervis Bay, and Batemans Bay), with 1065 km^2 coverage, 19.2% (205 km^2) of the MPAs classified as no-take zones.

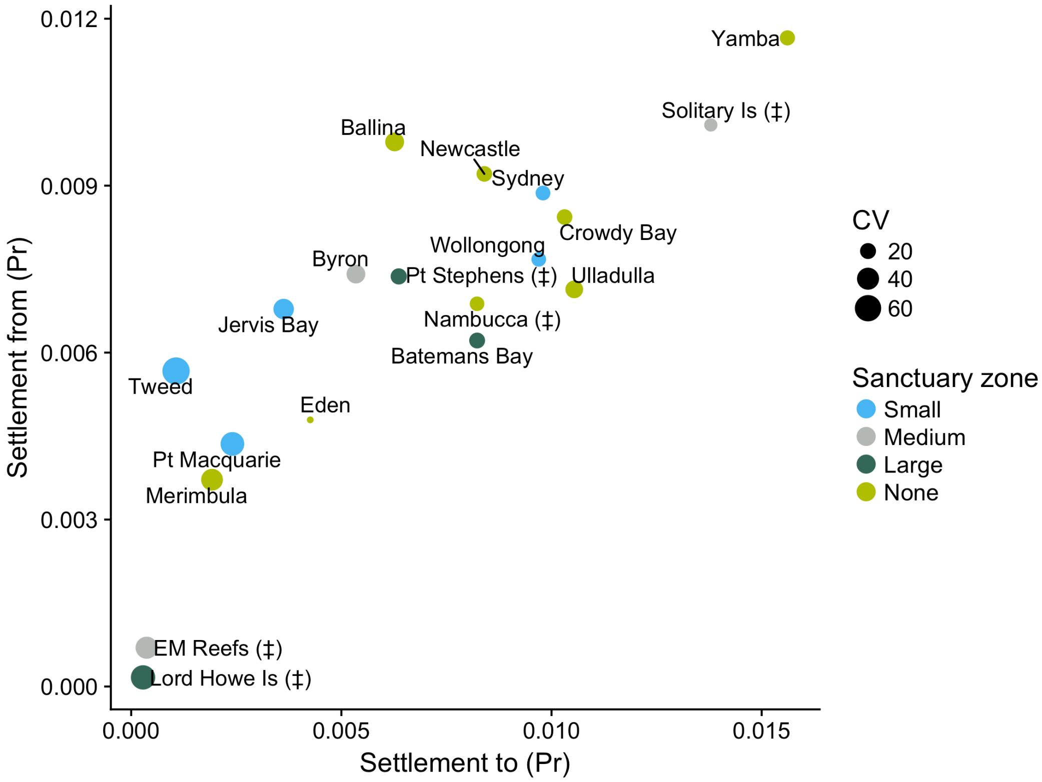

Figure 5.15: Summary of *Epinephelus daemelii* connectivity (strength of proportional settlement to and from) for each modelled region in this study, along with information about the consistency of settlement patterns (the average coefficient of variation, CV, of settlement to and from a region), the amount of no-take zones present in the region (none, small < 50 km2, medium < 100 km2, large > 100 km2) and the occurrence of known adult black cod aggregation sites in the region (‡).

Yamba is the region with the highest successful settlement for *E. daemelii* larvae moving both from and to it, but it does not contain any no-take zones within its region (Figure 5.15). The next highest region of bidirectional settlement is the Solitary Islands that has a medium level of no-take zone protection. Many regions of strong bidirectional settlement had small (e.g. Sydney) or no (e.g. Ballina, Newcastle, and Crowdy Bay) no-take zones, the exception being the Solitary Islands (Figure 5.15). Only 15.8% of the regions have greater than 100 km^2 of no-take zone protection, and of these regions only Port Stephens and Batemans Bay have median strength connectivity. The region with the most consistent settlement was Eden, although the settlement to and from it was the lowest 40% of regions (Figure 5.15) and it did not have any area classified as no-take zone protection. Tweed, EM Reefs, and Lord Howe Island had the highest variability of settlement patterns, and each had some level of no-take zones. For the known source regions, four of the five regions contained no-take zones (Figure 5.15). Nambucca was the one region that did not have any no-take zone coverage. Port Stephens and Lord Howe Island have greater than 100 km^2 of their area designated as no-take zones, and Solitary Islands and EM Reefs both have greater than 50 km^2 and less than 100 km^2.

Of the source regions with the highest self-recruitment (>75%), only 37.5% contained MPAs: Solitary Islands, Pt Stephens, and Batemans Bay (Figure 5.8 A). The MPAs within these three regions have no-take zone coverage greater than 80 km^2 (Table 5.2). For regions with MPAs, several had significantly lower local retention (Lord Howe Island, EM Reefs, Tweed, Pt Macquarie, Byron, and Jervis Bay), and for the highest local retention five of the ten regions have MPAs (Solitary Islands, Batemans Bay, Port Stephens, Sydney, and Wollongong; Figure 5.8 B).

Habitat protection was available in 40% of the strongest predicted settlement regions for the dispersal patterns of the known aggregations (Figure 5.15, Table 5.2). Pt Macquarie and Nambucca were particularly strong predicted regions that did not have protection (Figure 5.15). Across the known distribution, Crowdy Bay, Ulladulla, and Yamba were regions of high predicted settlement that contained no habitat protection. Sydney was a region of predicted high settlement and includes habitat protection, but the total protected area of 19.3 km^2 is minuscule compared to regions containing marine parks (Table 5.2).

5.5 Discussion

5.5.1 Spatiotemporal variation in patterns of dispersal

A biophysical dispersal model was used to investigate potential connectivity patterns of the *E. daemelii* larvae along the eastern coast of Australia. There was strong spatiotemporal variation amongst the forecasted connectivity patterns released from 19 source regions across eight years. The spatial variation exhibited a strong latitudinal gradient with consistently predicted dispersal connections between geographically close regions. This latitudinal gradient is driven by the ocean circulation off the New South Wales (NSW) coast. It is a heterogeneous system, driven by a weak flow poleward western boundary current with highly energetic eddies, the East Australia Current (EAC; Mata *et al.* 2006; Godfrey *et al.* 1980). The narrow continental shelf off NSW increases the opportunity for marine larvae to be advected by the EAC, a 30 km wide and 200 m deep current and travelling at 4 knots (Ridgway and Dunn 2003). The EAC brings water from the Coral Sea and moves along the northern NSW coast until it separates about 30.7°S - 32.4°S (Suthers *et al.* 2011). In this model domain, the separation zone occurs within the regions Nambucca (the southern end), Port Macquarie, and Crowdy Bay (the northern end) Figure 5.1, (Cetina-Heredia *et al.* 2014). At this separation zone the water mass is moved in two directions, westwards (where some water also recirculates northward) and southerly, further dispersing pelagic marine larvae along the coast of NSW (Ridgway 2007). Counter currents also allow for the northwards transport seen between regions (Coleman *et al.* 2011), seen in the *E. daemelii* dispersal patterns Figure 5.5. The northern regions (1-5) have similar predicted dispersal patterns, with restricted dispersal in a southerly direction most likely due to the close proximity of the EAC. Port Macquarie, which sits within the separation zone, had lower settlement success, local retention, and self-recruitment, with increased dispersal distance as larvae are dispersed away from the coast by the EAC. The separation of the EAC also markedly increases the settlement richness and diversity from a source region (see Appendix D).

High self-recruitment was predicted to occur across the source regions, often higher than 50%, an unexpected result for larval fish with a relatively long PLD (30-50 days). The self-recruitment and local retention values seen in our model were higher than observed for a similar modelled species (*Epinephelus marginatus*) in the Mediterranean (Andrello *et al.* 2013), with the qualification that the settlement regions for the Mediterranean study were of varying sizes (107 ± 259 km^2) and on average smaller than source regions in this study. While high self-recruitment of reef fish has been seen in regions with low levels of dispersion (Swearer *et al.* 1999; Almany *et al.* 2007; Berumen *et al.* 2012), the EAC was predicted to advect the *E. daemelii* larvae to more southerly regions. The estimated high self-recruitment (and local retention) can be partially explained by the size of the source regions (~125 km).

Local retention was estimated to be considerably higher for the source regions located on the coast of NSW compared to the off-shore reefs, explained by the larvae from the off-shore reefs having the ability to disperse in more directions. Considerable variation was seen in the estimated local retention, considered to be caused by the heterogeneous currents along the coast. Regional hydrodynamics along a coastline has been seen in other regions to strongly influence the dispersal causing high local retention of larval fish (Galindo *et al.* 2010; Watson *et al.* 2010) and veliger larvae (Teske *et al.* 2016). The local hydrodynamics of source regions with the nearshore western boundary current in northern NSW had the highest predicted local retention, however, high local retention was similarly forecast for source regions in southern NSW with mesoscale eddies predicted to entrain the larvae (Olson 1991; Everett *et al.* 2012). Estimated high self-recruitment for a region generally correlated with high local retention, this suggests larval immigration along coastal regions was quite consistent — high local retention regions had lower percentages of immigrant larvae that in turn increased self-recruitment. Only the estimated dispersal from the Eden source region did not display this pattern. However, Eden is the southern-most region on the coastline and therefore immigrants can only come from the north.

The predicted settlement success displayed a strong gradient, suggesting regional hydrodynamics had a strong effect on the ability of the *E. daemelii* larvae to settle. Dispersal distance of the modelled larvae had an almost inverse relationship to settlement success, suggesting that the less *E. daemelii* larvae disperse the better their chance of settling.

There was considerable temporal variation across the eight years of modelled *E. daemelii* dispersal patterns, underscoring the heterogeneity of the currents both spatially and temporally. However, the effect of the temporal variation on the predicted dispersal was not as strong as the spatial variation. In addition, annual variation in settlement patterns are thought to not affect the demographics of *K* strategists as strongly (Largier 2003; Cowen *et al.* 2006). Interestingly, while the connectivity patterns seen in 2011 were considered to be most similar to 2004, this was not reflected in the connectivity metrics. The annual variation is thought to be the result of the combination of both the changes in the EAC that has decadal cycles and is shifting southwards (Ridgway 2007; Suthers *et al.* 2011) and the natural variation in currents e.g. localised wind patterns that drive the surface currents and in the timing of formation, size, and rotation speed of mesoscale eddies off the south-east Australian coast, particularly in the region known as *'Eddy Avenue'* between 32°S and 39°S (Mata *et al.* 2006; Everett *et al.* 2012).

The annual variation could also not be explained by El Nino Southern Oscillation (ENSO) events La Nina and El Nino. The temporal extent of the model included El Nino conditions in 2006 (weak) and 2009 (moderate), and La Nina conditions in 2007 (moderate) and 2010 (strong) during the April-July modelling period (Bureau of Meteorology 2018). These conditions, one El Nino and one La Nina, only occurred in two of the three most dissimilar patterns (2005, 2009, and 2010), suggesting the variation was not highly correlated with ENSO events. The timing of release (only exposing the larvae to ENSO conditions during the winter months) and including larval behaviour in the model could explain not seeing an effect of ENSO conditions. Other studies have seen strong ENSO effects on modelled dispersal patterns, however, the larvae in these models were given neither vertical migration or swimming behaviours (Treml *et al.* 2008; Roughan *et al.* 2011), which potentially could allow the larval to directly or indirectly overcome changes in vertical stratification.

5.5.2 Strength of connections

E. daemelii larvae were strongly dispersed to the natal region and regions within direct geographical proximity (latitudinally above or below). Several coastal source regions had long poleward tails in their predicted dispersal patterns, with stronger settlement to regions of decreasing latitude. Similar poleward pattern of dispersal along the NSW coast has been predicted for modelled fish larvae with similar PLDs but with no explicit vertical or horizontal movement behaviour (Roughan *et al.* 2011). The proximity of settlement to the natal region is consistent with the knowledge that probability of survival for reef fish larvae decreases with dispersal distance (Buston *et al.* 2012). This local settlement phenomenon is emphasised by the regions with the strongest and most consistent settlement (Yamba, Solitary Islands, Crowdy Bay, Ulladulla, Sydney, and Wollongong) were also predicted to have relatively high local retention and self-recruitment of *E. daemelii* larvae.

Four potential sub-communities (an offshore reefs community, and northern, central, and southern coastal communities) were identified when *E. daemelii* were released across their known distribution. The source regions within the northern community had strong predicted dispersal connections to regions that were not the nearest neighbours. The potential sub-populations along the NSW coast were disconnected at the separation zone of the EAC and between Sydney and Wollongong. The coastal sub-populations identified from the predicted dispersal were closed systems with high local retention and self-recruitment, that has predicted can happen for species with long PLDs (Byers and Pringle 2006). In contrast, the potential sub-population consisting off the off-shore islands were open systems. Potential connections between all of the sub-communities were predicted by the model, including as has previously been hypothesised (Appleyard and Ward 2007) between the offshore islands and the NSW coast.

The difference between predicted patterns of dispersal between the entire distribution of *E. daemelii*, and the regions of aggregation was the low connectivity to the southern region of the NSW coast. For the regions with known aggregations, the two most southern regions (Merimbula and Eden) had the lowest connectivity, seemingly the limit of the dispersal range of *E. daemelii*, with no connectivity as far south as Victoria. Although settlement from the three known coastal regions did demonstrate connectivity across the model domain, only the offshore reefs were connected to the most northern regions. Even predicted low connectivity amongst most regions provides for genetic connectivity, seen in other reef fish along the NSW coast (Curley and Gillings 2009). The life history of *E. daemelii*, suggests that factors other than dispersal, i.e. coastal northward migration (Francis *et al.* 2016), also contribute to genetic diversity.

When considering the predicted dispersal from known distribution, the two regions with the strongest settlement were the northern regions of Solitary Islands and Nambucca — in contrast to surveys of juvenile *E. daemelii* that have rarely been recorded above Port Stephens (Harasti *et al.* 2014). Most likely these discrepancies arise when comparing only larval dispersal to population connectivity, connectivity involves many other post-settlement processes not captured in this model (see the limitations listed below). Juveniles in these regions could also be using habitats not considered in the survey, e.g. sub-tidal habitats. These surveys also identified juvenile *E. daemelii* in the regions of Sydney, Ulladulla, and Jervis Bay, all of which were not predicted to be strong settlement sites from the known aggregations. If the biophysical model used in this study is a reasonable predictor of *E. daemelii* dispersal despite the assumptions, the incongruence of these survey results suggests potential unknown aggregations along the NSW coast.

5.5.3 Comparisons with known spawning areas

The Solitary Islands was the only strong spawning and strong settlement region in common when comparing the predicted dispersal of the distribution and aggregating regions for *E. daemelii* larvae. When spawning *E. daemelii* larvae from across the distribution, several strong potential spawning sites with no known aggregating populations were identified in the northern (Ballina and Yamba) and central communities (Newcastle and Sydney). While these areas are not thought to have current populations (Francis *et al.* 2016), a century ago *E. daemelii* were generally more common throughout NSW waters (McCulloch 1922), including the Sydney region with an observed population at Port Jackson (Roughley 1916). The predicted dispersal across the distribution identified the southern region of Ulladulla as a region of strong settlement compared to Newcastle being the southernmost settled region estimated from the aggregation sites. Modelled spawning from the distribution identified Yamba as the area of strongest settlement, not identified as a strong area in the patterns of dispersal from estimated aggregating sites.

5.5.4 Overlap of predicted dispersal with current marine protected areas

Of the regions containing known aggregations of *E. daemelii* only two have area designated no-take zones over 100 km^2 and the Nambucca region has zero protection. The offshore community is the most protected, with seemingly all the available adult *E. daemelii* habitat, excluding Elizabeth Reef, falling within no-take zones. The Solitary Islands region is the best protected coastal region with known aggregations (across all protection levels) and predicted to have high functionality for *E. daemelii* with high local retention, high self-recruitment and strong settlement. Although while the extent of overall protection for the Solitary Islands Marine Park is high, only 12% of the park is designated as no-take zones, the lowest of the established marine parks, and the no-take zones are thought to be essential for the recovery of large Serranidae species (Chiappone *et al.* 2000; Friedlander and DeMartini 2002; Hackradt *et al.* 2014). Although, the current level of no-take protection does not seem to have had an effect on the population of *E. daemelii*, protected since 1983 (Francis *et al.* 2016). The area of no-take zones is variable between regions, however, if each no-take zone contains suitable adult *E. daemelii* habitat then reasonable protection for spawning aggregations should be provided. In the Solitary Islands, Nambucca and EM Reefs, there is there potential to increase the amount of no-take zone protection to similar levels seen in Port Stephens and Lord Howe Island. Each of four connected sub-population—identified from the predicted dispersal patterns across the known distribution—have sizeable MPA coverage within the regions collectively, but only the offshore community had protection in more than half of the regions. Protection in a sub-population was often skewed by one or two regions containing a large marine protected area.

Metrics for identification of regions for additional protection include high local retention (population persistence), high self-recruitment (the population relies heavily on itself), and strong stable settlement (Botsford *et al.* 2001). From the predicted dispersal patterns of the known aggregations, Nambucca was strongly identified as a region where *E. daemelii* would benefit from being protected due to the potential of high self-recruitment and local retention. The estimations of strong settlement to the Nambucca, Newcastle and Sydney regions suggest *E. daemelii* could benefit from increased protection of suitable settlement habitat in these areas.

There are several regions within the northern community (Ballina and Yamba) identified using the estimated dispersal from the entire distribution that have no current protection and *E. daemelii* could potentially benefit due to predicted strong connectivity. *E. daemelii* is observed to be most abundant within the extent of the northern community (Francis *et al.* 2016) and therefore should produce the largest spawning events and the most settlement stage larvae (ignoring post-settlement processes; Harasti and Malcolm 2013). The central community has the small coverage of protected areas, however, several regions within this community (Newcastle, Sydney, and Wollongong) were all predicted to have high settlement success of *E. daemelii* larvae and could benefit from settlement habitat protection. The most obvious candidate from the southern region—when considering the estimated dispersal—to benefit *E. daemelii* by increasing protection is Ulladulla due to high estimated local retention, settlement success, and strong connectivity. Warming oceans and a southward moving EAC are pushing temperate marine species further south down the eastern Australian coastline

(Figueira and Booth 2010; Suthers *et al.* 2011; Vergés *et al.* 2014; Wernberg *et al.* 2016), which can cause extinction at the uppermost edges of coastal populations (Shanks and Eckert 2005). Over time these changes might increase the importance of MPAs in the central and southern communities if the adult *E. daemelii* population migrates south — multiple areas of protection are more effective (Gaines *et al.* 2003).

5.5.5 Limitations of the biophysical dispersal model

These results must be qualified by the fact the biophysical dispersal model has not been validated with any empirical data and it limits the dispersal patterns to predictions and therefore caution must be applied when interpreting the results. Model validation is an important future direction for this study — to investigate if the genetic connectivity supports the estimated dispersal. The potential connectivity described in this study is in fact only larval dispersal, true connectivity between populations involves post-settlement processes not included in this model, e.g. larval condition at settlement drives survival and predation susceptibility (Caley *et al.* 1996; Vigliola and Meekan 2002; Almany and Webster 2006) or interspecific competition (McCormick and Weaver 2012). Therefore, there is potential some of these strong connections could be weaker due to poor larval conditioning driven by the path of dispersal. Future BDM studies should attempt to capture larval conditioning into their models when the empirical data is available. Assumptions were also made when parameterising the biological model for the *E. daemelii* larvae, e.g. using developmental ages from reared species and pooling taxa to get mean swimming speeds, therefore the dispersal might be slightly different than actual dispersal patterns of wild *E. daemelii* larvae. Another major limitation is the coarseness of the hydrodynamic model used, nearshore processes will not be captured in the BRAN model with its level of horizontal resolution (Largier 2003; Putman and He 2013). Nearshore dynamics are crucial to settlement dynamics and therefore the estimates of settlement might not reflect the real-world processes (Robertson *et al.* 1999; Swearer *et al.* 1999; Harlan *et al.* 2002). Many counter-currents will not be adequately capture by the hydrodynamics, potentially over-emphasising the strength of the southward dispersal and underestimating the strength of northward dispersal of *E. daemelii* larvae.

5.6 Conclusion

In summary, for the predicted dispersal patterns of *E. daemelii* larvae spawned from regions across their known distribution there are strong spatial differences in settlement patterns driven by a latitudinal gradient. The nearshore EAC in the north and the eddies in the south have a strong influence on dispersal patterns, moving larvae southwards with moderate northwards connectivity. The northern regions had long poleward tails in the estimated dispersal and the southern regions had the most northwards dispersal. The annual temporal variation in dispersal (also driven by variation in hydrodynamics) was smaller than the spatial variation. Four communities were identified from the potential connectivity patterns: a northern, central, and southern coastal community and a fourth community at the offshore reefs. The strongest settlement from each region along the coast was most commonly to the source region, i.e. local retention, or the regions geographically above and below. Weak connectivity was predicted to occur between all coastal regions and the offshore reefs. No connectivity was seen from the Australian coast or offshore islands to the known populations of Norfolk Island or New Zealand. Connectivity from the areas with known populations produced two communities, a coastal community and an offshore community, and the highest settlement was to the regions with the known populations. Solitary Islands was the only region with a known population predicted to be a strong source and settlement site when compared to the known distribution. Each of these identified communities, from the known distribution or populations, contained MPAs (and no-take zones within). After 35 years of protection, *E. daemelii* remains vulnerable with no apparent signs of population recovery, suggesting more management options should be considered. This work serves to identify regions where additional protection could aid in the recovery of *E. daemelii* using estimated dispersal patterns of *E. daemelii* larvae. From the estimated dispersal patterns (provided post-settlement processes do not greatly effect survivorship), two objectives can be identified: (1) to increase the number and area of no-take zones in the regions predicted to have strong connectivity with known aggregations, e.g. Solitary Islands and Nambucca, and (2) protect likely candidates for *E. daemelii* habitats even though there are no known populations, e.g. in the north the regions Ballina and Yamba and the central regions of Newcastle and Sydney. Further research should be conducted on finding aggregating adult populations through regular surveys of *E. daemelii* and protecting areas of suitable habitat, principally in locations where it has previously been found.

6 General discussion

The overarching aim of this thesis was to contribute to the understanding of the biological traits and behaviours that influence the dispersal and connectivity patterns of larval fish. Assuming that the models developed here provide realistic reproductions of larval dispersal, I have been able to give new insights into the connectivity of larval fish using a combination of meta-analysis of recent biophysical dispersal model (BDM) studies, an empirical study on the ontogenetic vertical distribution of larval fish, a theoretical modelling study investigating the influence of larval fish behaviours on connectivity, and finally predicting the connectivity of the reef fish *Epinephelus daemelii* and evaluating the potential effectiveness of marine reserves. The results of this thesis have implications for both the considerations of future BDM studies and the conservation and management of *E. daemelii*. This discussion chapter integrates the key findings of this thesis, providing summations of each data chapter and addresses similarities, differences, and implications for the field. In addition, the limitations of BDM studies are addressed, and directions and recommendations for future research are explored.

6.1 Summary of key findings

Biophysical dispersal models are a useful tool to estimate larval fish connectivity in the absence of readily obtained empirical results, however, these models are necessarily complex because so many variables contribute to dispersal outcomes. BDMs are becoming more prevalent and sophisticated as computing power increases and at the same time becomes more economical (Mumby 2017). The complexity of BDMs arises from coupling physical and biological models together, creating an influx of modelling parameters and choices — each with consequences for the degree of uncertainty in BDMs. To minimise this uncertainty, one approach is to use applicable model choices (i.e. generalities) from prior BDM studies in the literature. Therefore, to understand the trends of parameter choices (and their influence on predicted connectivity), I undertook a meta-analysis of BDM connectivity studies in Chapter 2. The meta-analysis used studies published from 2009 onwards, the publication year of the ICES manual detailing a standard approach for BDMs studies (North *et al.* 2009). The first aim of the chapter was to identify the trends of parameters included in BDMs for both the physical and biological models. The physical models are becoming more complex, using hydrodynamic models with increasing spatial resolution and nesting regional hydrodynamic models to capture spatial oceanography accurately, e.g. different hydrodynamic models capturing either near-shore or off-shore processes. Similar to the physical models, biological models are increasing in complexity with researchers encapsulating more behaviour in models over time, most likely correlated with increased knowledge of larval fish life history. However, there was still a strong tendency to use passive transport models — a surprising result given that it has been known for over a decade that reef fish larvae can influence their dispersal through vertical migration (Werner *et al.* 1993; Paris and Cowen 2004), or through sensory abilities (Gerlach *et al.* 2007), and it is generally accepted that reef fish become nektonic before they settle (Leis 2006). Of the three step progression for connectivity models in the ICES manual (North *et al.* 2009), Step 1: the minimum model (passive particles with spawning movement) was implemented the most (37.9%); Step 2: biological features (e.g. vertical movement behaviour and mortality) was implemented in 56.7% of models, and the final phase Step 3: small-scale features was only implemented in 5.4% of the studies. While it appears encouraging that a large percentage of the models were Step 2 using biological traits, it must be noted that 55.7% of those models were passive larvae with only a mortality function applied, and there are few empirical estimates of mortality rates for marine larvae.

The second aim of the meta-analysis was to examine the influence of these parameters on commonly identified metrics (self-recruitment, local retention, settlement success, and dispersal distance) of connectivity amongst the studies. Considerable variation was seen amongst the reported values for each of the metrics. This result highlights the differences in connectivity patterns both across regions and the effect parameter choice has on input parameters. The extensive suite of input parameters reduced the ability to perform analysis across all combinations. Moreover, transparent reporting of all included parameters and subsequent values did not always occur and there was no consensus on connectivity metrics. Comparisons between studies are inherently difficult because of the differences in each model's choices, based on principles such as study regions, species, or available knowledge. Despite these difficulties, I was able to derive several patterns regarding the influence of model choices on connectivity metrics. Firstly, in an open oceanic system the dispersal distance of larval fish was longer and there was a decrease in local retention. The hydrodynamic model resolution did not affect the metrics of predicted connectivity but using nested hydrodynamic models did result in less self-recruitment. Of the biological parameters investigated, the length of both the pelagic larval duration (PLD) and settlement competency window had no influence on the metrics. Including larval mortality in a BDM did not impact the settlement success to the extent expected. Settlement success was increased by the inclusion of any behaviour, while orientated horizontal swimming (OHS) specifically decreased self-recruitment, which was an unexpected result. To progress this field further, there is a need to decide upon common metrics that allow meaningful comparisons between models, which is addressed below. There is also a need for researchers to include more complex small-scale behaviour that can influence dispersal in their models. In North *et al.* (2009), three phases of model development were identified, the first phase has no behaviour (37.7% of models), the second phase has some behavioural traits (56.8% of models), and the third phase of models with behaviour affecting small scale processes only 3.4% of models. This review provides researchers with more context on what parameters are important to include in future BDM studies.

As mentioned within this thesis, a major challenge of using BDMs to predict connectivity is the scarcity of species-specific information on fish early-life history and on post-settlement but pre-recruitment effects. Modellers are often compelled to introduce assumptions in parameter choice for larval behaviours, i.e. by using values of congeners or confamilials (see methods in Chapter 5; Young *et al.* 2012), or general values (see methods in Chapter 5; Corell *et al.* 2012). If there is no information for a particular parameter choice, another option for modellers to limit uncertainty is to exclude specific behaviours from the BDM, even if the behaviour is known to strongly influence connectivity (Andrello *et al.* 2013). Although this approach arguably ignores the reality of processes involved in dispersal and therefore produces predictions that could be tenuous. Therefore, connectivity modelling requires the modeller to consider the inclusion of realistic biological processes against limiting the assumptions needed to parameterise these processes, noting that not modelling certain processes is also an assumption of realism. Another important modelling requisite is to understand the sensitivity of dispersal patterns to biological parameters within a complex model, allowing researchers to understand what values are ecologically relevant. Reducing these modelling assumptions is primarily addressed by collecting more data on larval fish.

Ontogenetic vertical migration (OVM) is a behaviour of larval fish known to influence dispersal by exposing larvae to currents with variable strengths and directions across the water column (Cowen and Sponaugle 2009). To date, OVM has not been explicitly studied for reef-associated larval fish of NSW. To address this knowledge gap and with the goal of using the data to parameterise a BDM, Chapter 3 measured the OVM distribution of seven reef-associated taxonomic families of fish off the coast of NSW. The ontogenetic stage (preflexion, flexion, and postflexion) and standard length of the larval fish were measured at three different depth bins; 0-1 m, 5-50 m, and 50-100 m. In addition, I also investigated any differences in these patterns between water masses, i.e. coastal or eddy waters. The experimental methodology, a common technique (Barnett *et al.* 1984; Paris and Cowen 2004; Irisson *et al.* 2010), does not explicitly capture OVM behaviour, but it does give a robust estimate of where the centre of mass is for each larval fish ontogenetic stage. Visual observation of OVM behaviour of larval fish in nature is limited to small spatial (e.g. upper 20m of water column) and temporal scales (e.g. minutes to hours), requiring other methods to assess vertical distribution (Leis 2010).

In general, the larval fish were found to migrate deeper with ontogeny and length, expected due to the high correlation between these traits. This pattern has been seen in other studies looking at the vertical distribution of reef fish (Irisson *et al.* 2010; Huebert *et al.* 2011). Mullidae was the exception to this pattern, migrating upwards towards the surface waters with ontogeny, corresponding to where postflexion Mullidae larvae have been found off NSW (Gray 1993). The type of water mass did not affect the vertical distribution of the larval fish, suggesting that other factors such as biological traits (e.g. metabolic constraints), predator-prey and resource allocation processes, or environmental conditions determine vertical migration behaviour (Wurtsbaugh and Neverman 1988; Lampert 1989; Fouzai *et al.* 2015). Older and longer larvae were found within eddies as expected, principally due to eddies entraining and entrapping larval fish near spawning areas and then moving off the shelf, and also the potential of eddy enrichment providing for growth (Lobel and Robinson 1986; Mullaney and Suthers 2013; Shulzitski *et al.* 2016).

Vertical distribution patterns of larval fish are known to be highly variable both within and between species. Therefore, the results are often contrasting, e.g. in Chapter 3 I found a strong ontogenetic shift downwards for Scorpaenidae, yet other studies have found Scorpaenidae had either no ontogenetic movement (Huebert *et al.* 2011) or found postflexion larvae at the surface (Kuwahara and Suzuki 1983). One explanation could be the interactions between the different behaviours affect vertical position (OVM, DVM, and OHS) hide the underlying patterns of each behaviour. The discrepancies seen could be differences between species within a taxonomic grouping, as studies often group larval fish into taxonomic families (as seen in Chapter 3) due to the expert level knowledge required to use morphological diagnostics to identify larval fish to species. Species identification of larval fish is predicted to become less of an issue as genetic techniques such as DNA barcoding for larval fish mature and become cheaper for researchers to access (Hubert *et al.* 2015). Differences in species at geographic locations or can also drive the variation in results as larval fish are known to behave differently in tropical or temperate environments, i.e. latitudinal differences (Figueira *et al.* 2009; Leis *et al.* 2013). The date of sampling could also be another driver of the observed variation in vertical distribution, as it could be influenced by the structure and temperature of the water column, which undergoes seasonal changes (Malcolm *et al.* 2011). Inherent differences between species across spatial and temporal scales are one concern, but there is also the difficulty of ensuring equal sampling efforts across ontogenetic stages and depths due to net avoidance of postflexion fish (Leis 2006), high mortality rates (Houde 1989a, 1989b; White *et al.* 2014; Johnson *et al.* 2015), and general patchiness in distributions (Cowen *et al.* 1993; Gray 1993). Deriving general patterns for OVM for larval fish might therefore be impossible, with comparisons focused on studies with similar latitudes.

With the knowledge that behaviours of larval fish affect dispersal and connectivity patterns (Leis *et al.* 2007), Chapter 4 endeavoured to investigate the relative influence of behaviours on connectivity using a BDM. The aim was achieved twofold, through examining the effect of combinations of different larval fish behaviours, and by changing both the parameter values and implementation methodology of a specific behaviour. The larval fish behaviours were parameterised using a combination of values derived from the literature and the OVM results obtained in Chapter 3. The behaviours used in this chapter chosen were: OVM (Paris and Cowen 2004), DVM (diel vertical migration; Aiken *et al.* 2011) and OHS (Staaterman *et al.* 2012). Including behaviour in this model increased local retention and reduced the dispersal distance, confirming similar results in other studies (Paris *et al.* 2007; Shanks 2009). However, this pattern is not universal amongst studies as sometimes the opposite effect is seen, e.g. including behaviour can increase dispersal (Ospina-Alvarez *et al.* 2012). It was found that movement behaviour strongly influenced connectivity patterns, however, the choice of location and timing of larval release had an even stronger effect, due to the geographical differences in oceanography.

Amongst the different behaviours considered, the one most influential on connectivity was OHS, with the least influential being OVM. Other studies have found similar results for the strong effect of OHS, with the behaviour reducing dispersal distance and increasing local retention (Staaterman *et al.* 2012; Wolanski and Kingsford 2014). However, this result will be sensitive to the modelled implementation of OHS due to the ability of larval fish to swim at speeds greater than the prevailing current (Fisher 2005). So far there is no consensus on how to model the process of swimming for larval fish in a BDM (Willis 2011). Some approaches have periods where the fish cannot swim until a period of time passes (often the mid-point of the PLD; Smith *et al.* 2009; Abesamis *et al.* 2016), while other implementations such as ours, incrementally increase the fishes' swimming ability with age (Wolanski and Kingsford 2014). Unlike the approach taken in our model, many studies also do not provide a random component to the swimming ability and therefore all larvae in the model swim at the same parameterised speed. Once the larval fish have developed swimming abilities, it is often assumed that they swim constantly, except for one study using a similar approach to ours, which allowed the fish larvae to swim for a portion of each time step (Huebert and Sponaugle 2009). One considerable limitation of our modelled OHS (and an area for future research) is that we did not include the Reynolds number when estimating the swimming speed (i.e. turbulent processes; Armsworth 2001; Fisher *et al.* 2000) that could limit the swimming ability of larval fish when combined with temperature effects (Fuiman and Batty 1997; Herbing 2002) and the considered energetic choice between swimming and drifting for late stage larval fish (Derek Hogan and Mora 2005). A wide range of swimming speeds were implemented across the BDMs, ranging from 0.001 ms^{-1} (Porch 1998) to upper values at 0.45 ms^{-1} (Wolanski and Kingsford 2014), although similarly wide ranges have also been reported amongst observed swimming speeds for larval fish (Leis and Carson-Ewart 1997).

Despite this observed influence of OHS, only a small number of the reviewed studies in Chapter 2 included it in their models, either perhaps because OHS was not thought to be as influential as it was seen to be in Chapter 4, or due to insufficient data on the particular study species. Orientation behaviour of larval fish is a relatively recent field of interest, yet these results suggest that including OHS behaviour in future connectivity studies should be a priority. The influence of OHS on connectivity patterns emphasise the importance of future research into the sensory abilities of larval fish (e.g. hearing, vision, and chemosensation) and understanding how they discern habitat and settlement cues (Berenshtein *et al.* 2014; Leis *et al.* 2014; Faillettaz *et al.* 2015). The swimming abilities of larval fish, however, are one of the more well-studied facets of their early-life history (Leis and Carson-Ewart 1997; Stobutzki and Bellwood 1997; Fisher *et al.* 2000; Hogan *et al.* 2007), therefore fewer assumptions are required in model parameterisation — introducing a behaviour into a model will require more assumptions, hopefully with less impact on the modelled output. Although swimming behaviours are used for other well-established processes other than dispersal, i.e. escaping predators and capturing prey (Paradis *et al.* 1996; Job and Bellwood 2000; Houde 2008) and omitting these other processes from a model limits the achievable realism of the directed swimming.

Differences in connectivity patterns derived from the seven different ontogenetic vertical distribution patterns found in Chapter 3 were minimal. The sensitivity of the dispersal patterns increased when the ontogenetic vertical distribution remained constant but the timing of vertical movement for individual larva between depths was varied (i.e. difference implementations of the process). This result, acknowledging it is region specific or at most can be broadly applied to other western boundary currents, leads to the conclusion that accurately modelling the processes of a specific behaviour is more important than precision about the parameterisation of the behaviour. From these results, it can also be inferred that for OVM behaviour in a BDM, using assumptions to parametrise the behaviour could be a better modelling choice than not including the behaviour at all. Chapter 4 accentuates the importance of sensitivity analyses in BDM studies and how researchers should aspire to publish or make the results of sensitivity analyses available (Simons *et al.* 2013).

The final chapter of this thesis, Chapter 5, took an applied BDM direction, building upon the results of each of the previous data chapters. The central aim was to predict the larval connectivity patterns of the black cod (*E. daemelii*; Francis *et al.* 2016), a protected species of New South Wales (NSW). The BDM used for the study included the larval fish behaviours of OHS and OVM, based on the influence on connectivity patterns in the region seen in Chapter 4. Parameterisation of the OVM behaviour used the Serranidae vertical distribution results obtained in Chapter 3. *E. daemelii* larvae were released over the period 2004-2011 across its entire known distribution along the NSW coastline and the offshore islands, Elizabeth and Middleton Reefs and Lord Howe Island. The larval dispersal of *E. daemelii* was assessed to determine the connectivity of 19 regions within the distribution, specifically identifying regions of strong source and settlement, i.e. both consistent and relatively high settlement over the entire release period. Despite being protected since 1983 (enacted due to sharp population decline in the 20th century Francis *et al.* 2016), *E. daemelii* abundance has not increased. One potential explanation for this population stasis is that the protection framework, i.e. the marine reserve network of NSW, is not designed for *E. daemelii* connectivity. Therefore, the second aim of the chapter was to compare these modelled connectivity patterns, using both the entire distribution and considering only known regions of aggregation, to ascertain if there are gaps within the existing marine protected network and if so, what regions should be prioritised for protection.

Despite the near-shore boundary current along the NSW coastline, e.g. the Eastern Australian Current (EAC), the strongest predicted connectivity of *E. daemelii* larvae occurred either at the natal region or to the proximate regions. Some level of dispersal occurred between the majority of regions across the known distribution, providing predicted potential genetic connectivity, with dispersal tailing in a poleward direction (i.e. the direction of the EAC). Connectivity had been hypothesised to occur between the NSW coastline and the off-shore islands (Appleyard and Ward 2007) and weak connectivity was seen between the northern and southern regions of NSW. Four connected subpopulations were identified using graph theory: a northern, central, southern population along the NSW coastline, and an off-shore reef population. Within these subpopulations, robust demographic connectivity was predicted to occur, but importantly there was connectivity between the four subpopulations. Comparisons of the potential connectivity with the current marine protected area network of NSW found that regions strongly connected to other regions with known aggregations either had moderate sanctuary zone coverage (i.e. no-take areas) or none at all. Considering the entire distribution, many of the strongest sites of connectivity had no marine protection within the region. Therefore, these results suggest that while the current marine protected areas do contain the patches of known aggregation, there are regions with strong predicted settlement where increased protection could yield conservation benefits, e.g. Yamba. There was also strong predicted settlement to the regions of Newcastle and Sydney, two regions that have limited protection for both settlement and spawning sites (a marine reserve in the Hawkesbury Shelf bioregion, encompassing the regions Newcastle, Sydney, and Wollongong, is under active consideration; NSW Government 2018).

The results from Chapter 5 reveal the intricacies of designing marine protected areas and how the desire to protect the maximum amount of species (e.g. increasing biodiversity) does not necessarily benefit all targeted species. Marine reserves need to be constantly evaluated to ensure their protection goals are being met (Agardy *et al.* 2016; Watson *et al.* 2016). There are several factors that drive marine network design, e.g. the amount of fishing pressure a species is under (both recreational and commercial; Botsford *et al.* 2009), how contiguous the network of reserves needs to be using species connectivity patterns (Botsford *et al.* 2001) and deciding the size of the protected area relative to the migration of adults (Green *et al.* 2015). Ideally, marine reserves should be areas of high local retention (Botsford *et al.* 2009) and contain enough quality habitat for species to maximise carrying capacity (Cabral *et al.* 2016). Connectivity itself is a dynamic process, with changes in oceanography and biology affecting larval dispersal as demonstrated by the inter-annual variability seen in Chapter 5. Some adult populations are highly mobile (Welsh and Bellwood 2014), which could produce variation between spawning locations. Therefore, designing MPAs using patterns of larval connectivity is not a trivial task (Cudney-Bueno *et al.* 2009) as dispersal profiles seen in one year might not occur the following year. For example, the effects of a southward moving EAC (Ridgway 2007) on the modelled black cod connectivity patterns in Chapter 5 is unknown. The phenomenon of changing currents is not limited to Australia either, with other major oceanic systems showing a weakening of boundary currents (Thornalley *et al.* 2018). However, management complexity can be reduced by managing for larval connectivity, especially if the self-recruitment and local retention of a species are high (Bode *et al.* 2016).

The difficulty in designing marine protected areas arises due to species having variable traits, e.g. connectivity patterns, movement of adult populations, and habitat requirements. To deal with this issue, a triage approach can be taken, either prioritising the protection of certain assets (e.g. species or habitat; Bottrill *et al.* 2008) or ecosystem services (Pendleton *et al.* 2015). This approach to conservation is not without controversy as it raises many ethical questions about deciding which species will go extinct (Wilson and Law 2016). However, the threat of climate change is creating an atmosphere where researchers are more willing to take interventionist approaches (Hagerman and Satterfield 2014). Other approaches are to identify the critical subpopulations and linkages within a metapopulation to target for protection (Artzy-Randrup and Stone 2010; Watson *et al.* 2011) or connectivity surrogates when connectivity is unknown (Bode *et al.* 2012). A recent proposed solution to address the variability of connectivity is to use dynamic protected areas or a whole-ecosystem approach (Soria *et al.* 2014). Dynamic protection attempts to deal with the fundamental variability and openness of marine systems, an environment that is distinct to terrestrial systems and therefore requires different approaches (Carr *et al.* 2003). Dynamic protected areas provide benefits to species undergoing range-shifts and produce an even distribution of biomass to improve the resilience of species to a changing environment (Game *et al.* 2009). This dynamic approach has been implemented to some degree in Australia in oceanic areas to reduce fishing pressure on pelagic species (Smith *et al.* 2007; Melbourne-Thomas *et al.* 2017). Designing MPAs with a metacommunity approach (Leibold *et al.* 2004) can overcome this variability by using the connectivity patterns modelled from general larval traits or using multiple species across taxonomic groups (e.g. coral, crabs, and fish; Treml and Halpin 2012; Melià *et al.* 2016). Managing metacommunity dynamics is a complex system, e.g. changes in primary productivity can drive variation in community dynamics (Fernández *et al.* 2016), and novel techniques are still being developed to measure these dynamics to benefit marine spatial planning (Grainger and Gilbert 2016; Melià *et al.* 2016). This complexity suggests a community-wide range-shift due to changing conditions is unlikely; most likely, species within a community will exhibit different responses, complicating future conservation management (Yletyinen *et al.* 2016).

Before these approaches can be fully utilised in NSW, more knowledge of the population biology and connectivity of vulnerable and commercially important species (including *E. daemelii*) is required (Curley *et al.* 2013). Australia is in an enviable position to enact meaningful conservation because of the ability to legislate for marine protection over the entire distribution ranges of many temperate species. The primary impediment is the different jurisdictions between states and the Commonwealth. In this study, I only looked at source regions within NSW and the offshore islands, but the edges of the distribution range of *E. daemelii* occur in Queensland and Victoria. Therefore, multilateral mechanisms between governments must exist (e.g. ANZECC Task Force on Marine Protected Areas 1999), providing both a framework and tools for enacting conservation strategies that act over species distributions and potential range-shifts, instead of being dictated by arbitrary state and federal boundaries.

6.2 Limitations to biophysical dispersal modelling for measuring connectivity

Hydrodynamic models will always contain a degree of error and uncertainty in their predictions (Fossette *et al.* 2012) and the size of this uncertainty is not consistent between models (Nolasco *et al.* 2018), therefore this error is structural in BDM studies. Off-line hydrodynamic models were used in Chapter 4 and 5 as they allow for faster computation than in-line models (running physical and biological models simultaneously). However, using off-line hydrodynamic models can decrease the model precision depending on the size of the time step of resolution (increased time steps reduce data storage), therefore requiring interpolation to estimate current velocities at intermediate times. The hydrodynamic model used in this thesis had a 24-hour time step and therefore short-lived dynamic processes (e.g. tidal movements) are not captured in the model. Chapter 2 suggested that model resolution did not affect connectivity metrics, however, it is likely this depends on the regional coastal dynamics, e.g. the strong settlement effects of small-scale sticky reef dynamics are not captured on the scale of many large-scale hydrodynamic models (Golbuu *et al.* 2012), which are often required to ask ecologically relevant questions.

As mentioned above, assumptions of modelling choices made during the design of BDM studies can be a significant limitation to interpretation of the results. Decisions on assumptions are required about which biological traits and behaviours to include, and the subsequent values with which to parameterise them. Mortality rates of larval fish are a prime example of an almost universal assumption included in BDM studies, as for many species the exact rate of larval mortality is estimated from indirect sources (Johnson *et al.* 2015). In Chapter 5, specific data on the timing of development for *E. daemelii* was unavailable, therefore I assumed a similar species within the subfamily Epinephelinae would be representative. This approach is not unreasonable, but it must be acknowledged it is an assumption nonetheless, amplified due to the empirical experiments using laboratory reared larvae (Cunha *et al.* 2013) that may not mimic the timings of development seen in the wild. Another assumption in Chapter 5 was the size of the settlement sensory distance used, giving the larvae the ability to sense, orientate, and swim towards suitable habitat within a 7 km boundary based on studies seen in Chapter 2. The likelihood of *E. daemelii* larvae being able to sense habitat over considerable distance is the reason these assumptions were made (Leis 2010; Paris *et al.* 2013), however, the exact distance and ability are not explicitly known. Future research needs to concentrate on understanding OHS for larval fish, and many novel techniques are being designed to achieve this goal (Mouritsen *et al.* 2013; Paris *et al.* 2013; Berenshtein *et al.* 2014). In the short-term, accepting more assumptions will be required (with the goal of reducing the number and scope of assumptions over time), and understanding the consequences of these assumptions is an important research topic. In Chapter 4, I addressed this by testing for both the effects of parameter choice (different distributions throughout ontogeny for vertical migration) and the effects of different implementations of modelling behaviour (changing the distribution with ontogeny, daily, or with the time step).

6.3 Model validation

The predominant question for BDM studies concerns the veracity of the model and therefore the level of confidence in interpreting the results. It is a limitation of this thesis that the BDM used in Chapters 4 and 5 has not been validated against empirical data. Partial confidence in the dispersal patterns arises from validation of the hydrodynamic model used (Oke *et al.* 2013), which has been shown to provide accurate current velocities for the model domain when compared to other geographically relevant hydrodynamic models (Chiswell and Rickard 2014; Vasile *et al.* 2018). However, the absence of realistic coastal dynamics modelling is still a cause for concern. Validating the results of BDMs is increasingly achievable using empirical methods (if the scale of the ecological study and the physical model correlate) and an essential next step of the research (Burgess *et al.* 2014). Model validation for BDM studies commonly use a multi-methodological approach with genetic (Galindo *et al.* 2010; Coscia *et al.* 2012; Crandall *et al.* 2012; Feutry *et al.* 2013; Munguia-Vega *et al.* 2014; Sunday *et al.* 2014) or elemental markers (i.e. otolith chemistry; Crochelet *et al.* 2013) to compare the derived connectivity patterns against observed distributions. These multi-methodological approaches provide increased confidence in the predicted larval dispersal but do not (and for practical reasons, cannot) capture temporal and spatial variability. Empirical studies contain their own levels of uncertainty and therefore the power of a direct comparison is reduced unless this uncertainty is accounted for, e.g. by using confidence intervals (Nolasco *et al.* 2018). Model validation using known recruitment data has been performed in a handful of BDM studies, i.e. measuring recruitment with light traps explained 70% of the temporal variation predicted by a BDM (Domingues *et al.* 2012; Sponaugle *et al.* 2012). For rare species, such as *E. daemelii* modelled in Chapter 5, validation using recruitment data is difficult, and so utilising a priori model validation with known recruitment data for another species is an alternative approach.

6.4 Reproducibility and transparency

A trait common to nearly all biophysical connectivity studies is that they are attempting to estimate at least one of two fundamental and general patterns: the levels of connectivity between natal and settlement sites and the dispersal of larvae in the system. The former is mostly a measure of larval source-sink dynamics, looking at patterns of production and settlement in marine species with a pelagic larval phase that inherently links one patch in the system to another. The latter is a measure of the total dispersal area, looking at issues such as how far larvae disperse and where they occur in highest densities in the system. Both traits are useful in describing system connectivity and dispersal and are a product of the system and modelling environment. In undertaking the review in Chapter 2, I came across two impediments to a meta-analysis of these estimated metrics. Firstly, many studies utilised unique metrics to measure either of these patterns. In fact, I found over 25 different measures used to describe the patterns of connectivity & dispersal. Secondly, for a given metric, often only a single summary statistic was reported, e.g. mean, median, or upper quartile. Summary statistics are useful however, they were frequently reported without information on the underlying dispersal distribution, making rigorous qualitative comparisons difficult.

Reproducibility, a term often synonymous with open science, is an important facet in assessing the scientific merit of a published paper (Open Science Collaboration 2015; Allison *et al.* 2016). It can be difficult to achieve in ecological studies due to the inherent variability in nature (Schnitzer and Carson 2016). However, the same challenges do not exist in computational modelling (Peng 2011). Ideally, for reproducibility the model configurations, source code, and the output data are made available along with the publication. Transparency provides confidence to the reader and importantly the peer reviewer in the outcomes and interpretations of the study (Südhof 2016). Utilising common frameworks for designing, coding, and testing BDMs (e.g. TRACE; Grimm *et al.* 2014) and automating workflows (Wilson *et al.* 2014) are important steps to produce realistic and reliable models.

Sandve *et al.* (2013) produced ten rules of reproducibility for computational research, which all apply to studies involving a biophysical model. Most are intuitive, for example, tracking precisely how results were obtained, automating as many steps as possible, and using version control for scripts, code, and software. Others are not thought about as often, such as documenting the seed used for random number generators, which was not seen amongst the connectivity studies in Chapter 2. The most visible facet to a researcher reading a published study is Rule 10 of Sandve *et al.* (2013): "all input data, scripts, versions, parameters, and intermediate results should be made publicly and easily accessible". Ignoring the reporting of the random number seed and providing access to source code, only 34% of the studies in our review could be considered reproducible from the information made public.

Transparency is difficult to obtain for complex modelling studies, due to a large number of parameters and modelling choices involved. In my review, many common and rectifiable omissions prevented reproducibility, deduced while inspecting the methods and the supporting information (if available). 12% of the studies did not indicate the years used for their oceanographic model in their simulation. 34% did not mention the time step used when advecting the larvae in their model. 69% cited using diffusion in their model, but only 51% of these published the diffusion coefficient used. When mortality was implemented into the biophysical model, 25% of these studies did not include the mortality curve or rate used. It is advised, where possible, to use oceanographic models that are freely available to the public (although preference should be towards the most accurate model). This is fortunately becoming more common, whether it is government funded ocean models becoming available through legislative requirements or studies using open hydrodynamics models such as the Regional Ocean Modelling System (ROMS) or the Princeton Ocean Model (POM), which can be coupled with higher resolution models for specific site locations. Transparency amongst models (providing source code) allows other researchers without the necessary coding skills to utilise the system. There are several examples of BDMs already following an open source paradigm (e.g. Ichthyop; Lett *et al.* 2008; CMS; Paris *et al.* 2013; MGET; Roberts *et al.* 2010), suggesting widespread support for the reuse of models in the community.

Complexity in biophysical models derives from coupling two distinct models, biological and physical, creating an additive effect on the number of input parameters. However, it is impossible to reproduce a biophysical connectivity study without all of these parameters, hence the importance of publishing these parameters along with the results. The strong trend towards supplementary information (Kenyon and Sprague 2014; Pop and Salzberg 2015) in journals allow for publication of these parameters without obscuring the primary scientific message. The cost of reproducible research for biophysical studies is minimal as many free online repositories exist for both source code and data, two popular examples being GitHub (http://github.com - used for this thesis) and Dryad (http://datadryad.org). Only two studies in the review uploaded their data using such a portal, both choosing to use Dryad. Several journals are also making reproducibility a requirement and providing mechanisms for online storage of data (e.g. PLOS Biology).

6.4.1 A common approach

To provide transparency and allow for useful comparisons between connectivity studies using biophysical models, a common approach to publishing both methods and results is required. Two main problems with connectivity studies were identified that prevented meaningful comparisons. The first is a lack of commonality to the metrics used to describe the connectivity amongst studies. The second issue is the lack of reproducibility and clarity of the model parameters used in studies.

The suggested approach to achieve consistency between metrics is to utilise the two most common metrics currently reported. These provide useful measures and also, they should be readily accepted amongst the research community (Table 6.1). The first metric, a connectivity matrix (also referred to as a transition matrix), is the most useful for connectivity studies. The connectivity measures of self-recruitment, local retention and settlement success can all be calculated from the underlying matrix data (means of these values are also useful in publication for easy reference). Therefore, in addition to presenting the data in a heat map visualisation, the full connectivity matrix should be published. It is suggested these are published in an online data-repository or attached as supplementary information, rather than in the body of the paper. Publishing this data is especially important where studies may have simulated many connectivity matrices for different situations (e.g. time periods, parameter combinations). The supplied matrices can be data summaries, e.g. providing the mean connectivity matrix (with estimates of variation) for a study conducted over a five year period.

It is understood that the reporting of connectivity matrices can become non-trivial depending on the number of sites used in the model and the number of days larvae are spawned. There is no one solution, but instead a range of options from providing complete data dumps to summarising results into more manageable segments (e.g. years), or only providing data relating to the important findings of the paper. However, where a parameter such as PLD is varied, different matrices should be supplied for each value used for such results to be more broadly useful to the field in the future. Graph theory is also a useful technique to assess the connectivity of a system (Treml *et al.* 2008). There are easily derived and comparable metrics, however, it can be hard to calculate the underlying values of the connectivity matrix, which makes it hard to compare against studies that do not also use a graph theory approach. So even where graph theory has been utilised, publishing the fundamental connectivity matrix is still essential.

Table 6.1: *The two metrics that are required to make a comparative analysis of studies using biophysical connectivity models. From each of these metrics, four important measures can be derived for further analysis*

Published metric	Derivable measure parameters
Connectivity matrix	Site-site connectivity values
	Self-recruitment
	Local retention
	Dispersal success
Dispersal kernel	Mean distance travelled
	Median distance travelled
	Maximum distance travelled
	Measure of spread

The second most important metric used to describe the output of these models is the dispersal kernel. The dispersal kernel—a probability density function—gives information about the spread and distance of dispersed larvae in the system. For the dispersal kernel, publishing the density plot and a heat map is the recommendation. From a density plot, the mean, median and maximum distance travelled can be derived to allow for comparisons between studies, along with the distribution of the dispersal kernel. Note that distance refers to the actual distance travelled, therefore when other distances such as straight-line or alongshore distances are used it is important that they are specified. There is no consensus for a measure used of spread. A few studies in our review used a measure called positive or seeded area, which counted all the cells in the system that had greater than one particle to get a measure of the spread. Another two studies tried to calculate the centre of the mass of larvae to see how it changed over time. The positive area measure holds potential though it would need to be standardised to the size of the cells used in the model.

To provide transparency between studies on how the biophysical model is implemented, a non-exhaustive list of the sort of parameters required to reproduce these studies is provided (Table 6.2). The list covers parameters used for both the physical and biological models. This list is not definitive as models will increasingly become more complex and there will be more parameters added to the initialisation of the models. For reproducibility purposes, an individual set of parameter values should be supplied for every model run used in the study. Again, these can be supplied in the supporting information or online in a data repository.

***Table 6.2**: List of input parameters to a biophysical model that should be published as part of every connectivity study using a biophysical model. All values should be published in the appropriate SI units where applicable.*

Model	Name	Description
Particle	Particle model	Link to the source code of the particle model used and specifications with information on the type, movement and integration methods e.g. Individual based model, with Lagrangian model and using Runge-Kutta fourth order method for integration
	Random number seed	If random numbers are used, it is important to publish the seed used to generate the random number so the study can be replicated (Sandve *et al.* 2013)
Physical	Oceanographic model	Link to the specifications of the model, including all sub-models, bathymetry & tidal models used
	Spatial scale	The area the larvae can move
	Time step	The time step used to move the larvae using the oceanographic model (preferably in seconds)
	Diffusion / turbulence	Diffusion strategy (random walk, horizontal and/or vertical) and the turbulence values used
Biological	Release times	Release times of the larvae
	Release strategy	How the larvae were released (e.g. daily, lunar, temperature cues, depths)
	Release sites	The GPS locations and sizes of the release sites
	Settlement sites	The GPS locations and sizes of the settlement sites (if different from the release sites)
	Larvae released	The number of larvae released
	Pelagic larval duration	The pelagic larval duration of the taxa and whether you used a variable or fixed duration
	Pre-competency period	The pre-competency period given before settlement can occur
	Movement strategies	What movement strategies the larvae were given, and the values associated with these strategies (e.g. passive, diel, horizontal)
	Mortality strategies	The mortality strategy used (if any)
	Settlement strategies	How did the larvae choose a settlement site (e.g. passively, sites were buffered 10 km sensory cues)

To advance our understanding of connectivity in marine systems, biophysical modelling studies need to start publishing consistent quantitative metrics of dispersal and connectivity so that comparisons can be made. Studies must also be more transparent about the parameters used. The template provides the basic information seen to be necessary based on the review in Chapter 2. This template should be used as the basis for discussion amongst scientists in the field, but I actively encourage all researchers publishing the results of biophysical connectivity studies to adopt at least the principles of cohesion, consistency and transparency which are at its core. Such an approach will greatly speed advancements in our understanding of the drivers and outcomes of connectivity more generally. Ultimately, it is confidence in the generality of the results of these models, along with more empirical validation of the modelled output, which will allow for their more widespread use within management and conservation initiatives.

6.5 Future research

There are unanswered questions about the ontogenetic vertical distributions seen in Chapter 3 – do these distributions reflect actual behaviour of larvae, and if they do vertically migrate, why are different patterns seen between families? It has been argued that the patterns observed do not relate to individual behaviour at all and could be a result of differing mortality both between ontogenetic stages and between species (Irisson *et al.* 2010). As mentioned in Chapter 3, other drivers of vertical distribution could be due to environmental factors (Job and Bellwood 2000; Lougee *et al.* 2002; Aceves-Medina *et al.* 2008), metabolic factors (Wurtsbaugh and Neverman 1988), feeding strategies (Pearre 2003; Llopiz and Cowen 2009), or predator avoidance. These patterns could also be explained as be snapshots in time of diel vertical migration patterns, and not specifically ontogenetic. Our understanding of ontogenetic vertical migration behaviour is still cursory at best; it is known that these patterns exist. and they influence dispersal, but why these patterns occur is still up for debate. Due to the influence of vertical migration on connectivity, it is important to understand the processes behind these patterns, and how warming oceans and ocean acidification might affect vertical migration and thus dispersal patterns.

Currently BDMs are the most effective tool to measure connectivity over large-scale spatial and temporal scales, and advances in computing are only making connectivity modelling more realistic of natural processes and more accessible to researchers. The ability to manipulate parameters allows for understanding the influential processes of connectivity, as seen in Chapter 4. The results showed that OHS was the most influential behaviour for regional connectivity, and similar to vertical migration, the exact processes underlying the ability for reef fish to sense settlement habitat is unknown for many species. Suggested processes include sight (Berenshtein *et al.* 2014), sound (Sallarès *et al.* 2009), smell (Gerlach *et al.* 2007), magnetic compass (Bottesch *et al.* 2016), or hydrostatic pressure (Huebert *et al.* 2010). Further research in understanding which processes contribute the most to the ability of larval fish to orient will provide more accurate BDMs with a realistic implementation of OHS behaviour. Other factors that influence swimming should be explored in BDM connectivity studies, such as the effects of temperature and viscosity (Fuiman and Batty 1997; Herbing 2002) on connectivity patterns.

A caveat to some of the conclusions of this thesis is the potential impact of global climate change on the dispersal of marine larvae, specifically warming and acidification (Chan *et al.* 2018). There is a strong likelihood that ocean acidification will adversely impact the sensory ability of larval fish (Ashur *et al.* 2017), potentially reducing larval dispersal to a passive process and making OHS behaviour redundant for predicting connectivity patterns (Leis 2018). Research has shown that a common neurotransmitter, present in larval fish, is adversely affected at the high CO_2 levels predicted to occur at the end of the century (Nilsson *et al.* 2012; Nagelkerken and Munday 2016). Preliminary research into several species of larval fish has shown ocean acidification interferes with senses such as hearing (Rossi *et al.* 2016), vision (Allan *et al.* 2014), and chemosensation (Ferrari *et al.* 2011; Sundin *et al.* 2017), impairing the ability of fish to orientate towards settlement cues. Therefore, even if swimming ability is not affected by the predicted increased of CO_2 in the ocean, undirected horizontal swimming is essentially passive transport with increased randomness, i.e. stronger turbulence, and has limited influence on connectivity. As stated in Leis (2018), ocean acidification could jettison the biophysical dispersal paradigm, resulting in increased dispersal distance, lower local retention, lower self-recruitment, and lower settlement success.

6.6 Conclusion

This thesis provides guidance on important biological processes for future connectivity studies, particularly for the larval fish dispersal of south-eastern Australia. Future connectivity studies will hopefully utilise this research and include important dispersal influencing behaviours in BDMs, i.e. OHS and vertical migration — I described the ontogenetic vertical distribution patterns for seven families of larval fish that can be used for parameterisation. This outcome, which along with improved reproducibility of BDM studies, should strengthen the accuracy of modelled connectivity patterns. Using this thesis, conservation managers can feasibly use the modelled connectivity patterns of *E. daemelii* to produce more informed decisions for the population recovery of this threatened species, which has been elusive to date.

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Appendix A

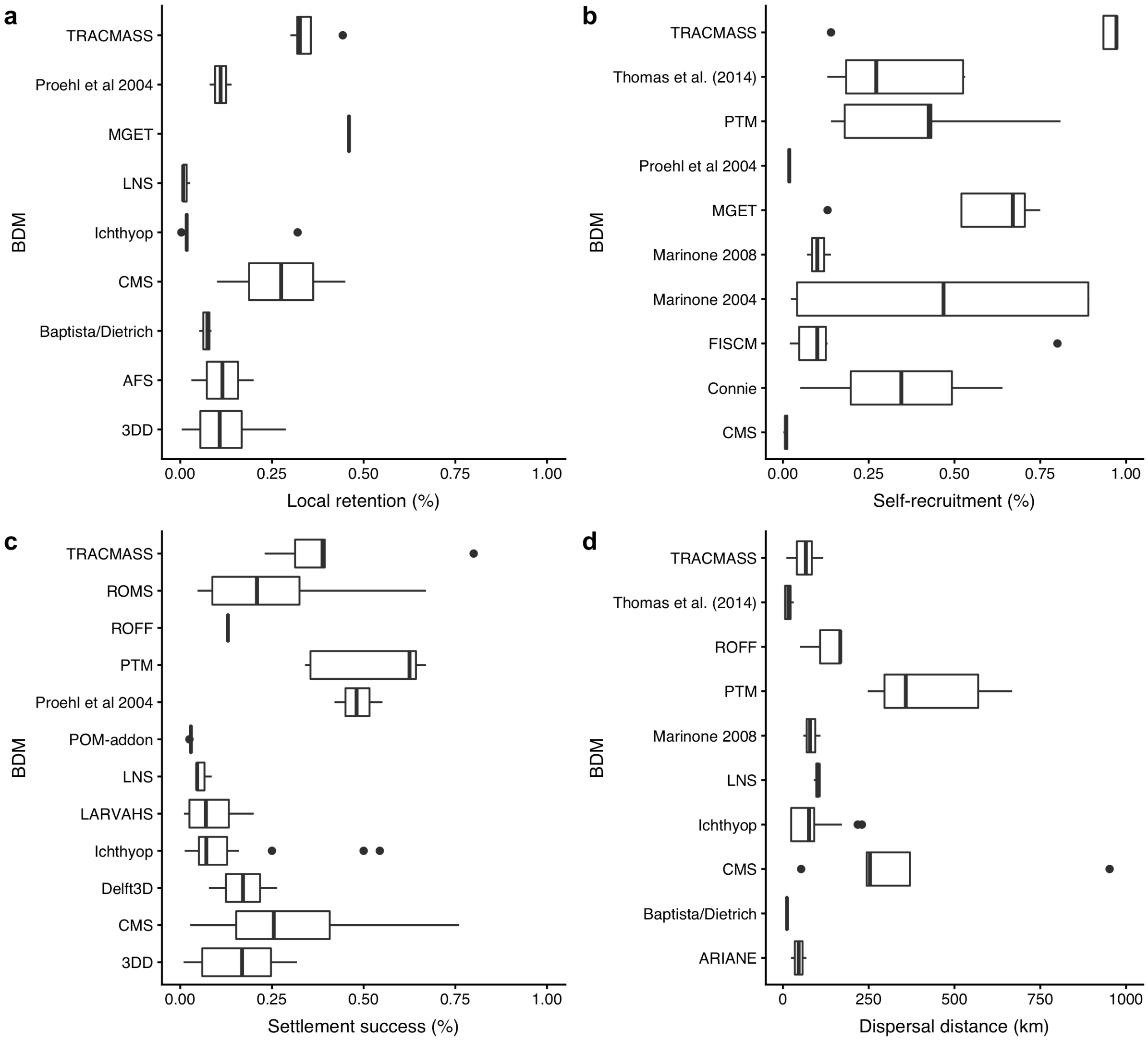
Supplementary materials for Chapter 2

A1. Methods

List of references used in the meta-analysis can be found at doi:

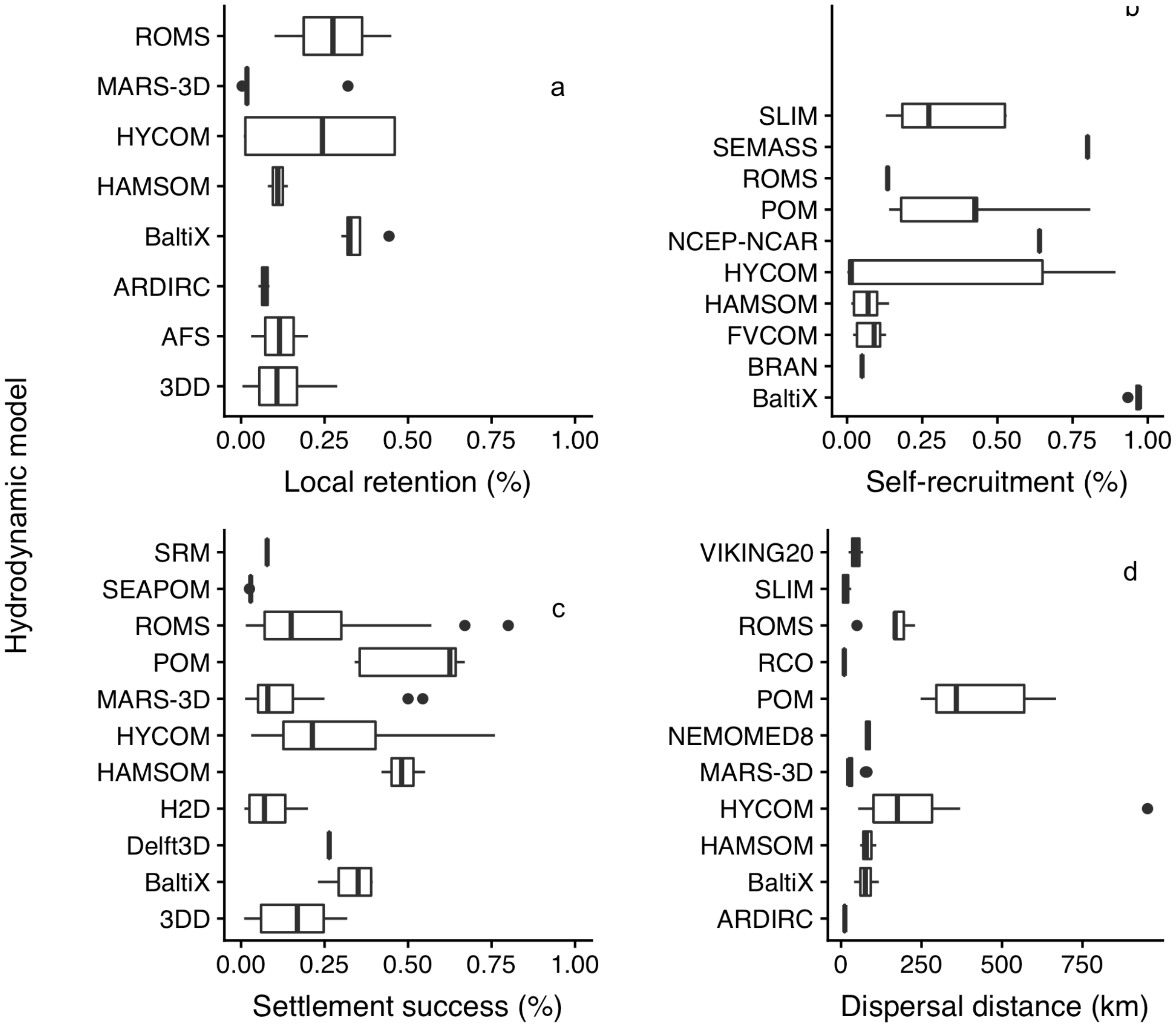
http://doi.org/10.25910/5c0ddb78bd9a1 File: chapter-2-meta-analysis-refs.pdf

Figure A1.



Comparing choice of particle tracking models with the metrics of local retention (%; a), self-recruitment (%; b), settlement success (%; c) and dispersal distance (km; d). Only models with more than two reported values of a metric were included.

Figure A2.



Comparing choice of hydrodynamic models with the metrics of local retention (%; a), self-recruitment (%; b), settlement success (%; c) and dispersal distance (km; d). Only models with more than two reported values of a metric were included.

Appendix B

Supplementary materials for Chapter 3

Table B1.

Model selection for the abundance and length models using AIC.

Fish	Measure	Model	AIC
Labridae	abundance	C = FxDxS + T	1280.13
		C = F + FxD + FxS + DxS + T	1276.7
	length	L = FxD + T + Cl	4845.2
Mullidae	abundance	C = FxDxS +Cl	602.52
		C = F + FxD + FxS + DxS +Cl	601.11
	length	L = FxD + T + Do	1150.55
		L = F + D + T + Do	1147.4
Pomacentridae	abundance	C = FxDxS + T + Cl	517.4
	length	L = FxD + T + S + Do	441.94
		L = F + D + T + S + Do	441.78
Scaridae	abundance	C = FxDxS + T + S + Do	477.5
		C = F + FxD + FxS + DxS + T + S + Do	477.3
		C = F + FxD + DxS + T + S + Do	475.4
		C = F + FxD + T + S + Do	471.4
	length	L = FxD + T + S	741.28
		L = F + D + T + S	738.35
		L = D + T + S	737.4
Scorpaenidae	abundance	C = FxDxS + T	478.3
		C = F + FxD + FxS + DxS + T	477.1
		C = F + FxS + DxS + T	476.14
	length	L = FxD + S	603.82
		L = F + D + S	602.21
Serranidae	abundance	C = FxDxS + Do	795.45
		C = F + D + S + FxD + FxS + DxS + Do	791.62

		C = F + D + S + FxD + DxS + Do	787.99
		C = F + D + S + DxS + Do	787.28
		C = D + S + DxS + Do	786.86
	length	L = FxD + T	1494.3
		L = F + D + T	1492.6
Synodontidae	abundance	C= FxDxS + T + Do	467.68
		C = F + FxD + FxS + DxS + T + Do	467.39
	length	L = FxD + T	823.75
		F + D + T	820.34

Appendix C

Supplementary materials for Chapter 4

C1. Methods

ZISSOU configuration files can be found at doi: http://doi.org/10.25910/5c0ddb78bd9a1 File: chapter-4-zissou.zip

C2. Results

All connectivity matrices can be found at doi: http://doi.org/10.25910/5c0ddb78bd9a1 File: chapter-4-connectivity-matrices.zip

Table C1.

Diel vertical migration (DVM) values used, providing more stratified depth positions during the day and more even distribution at night as seen in temperate fish off NSW [@gray1998].

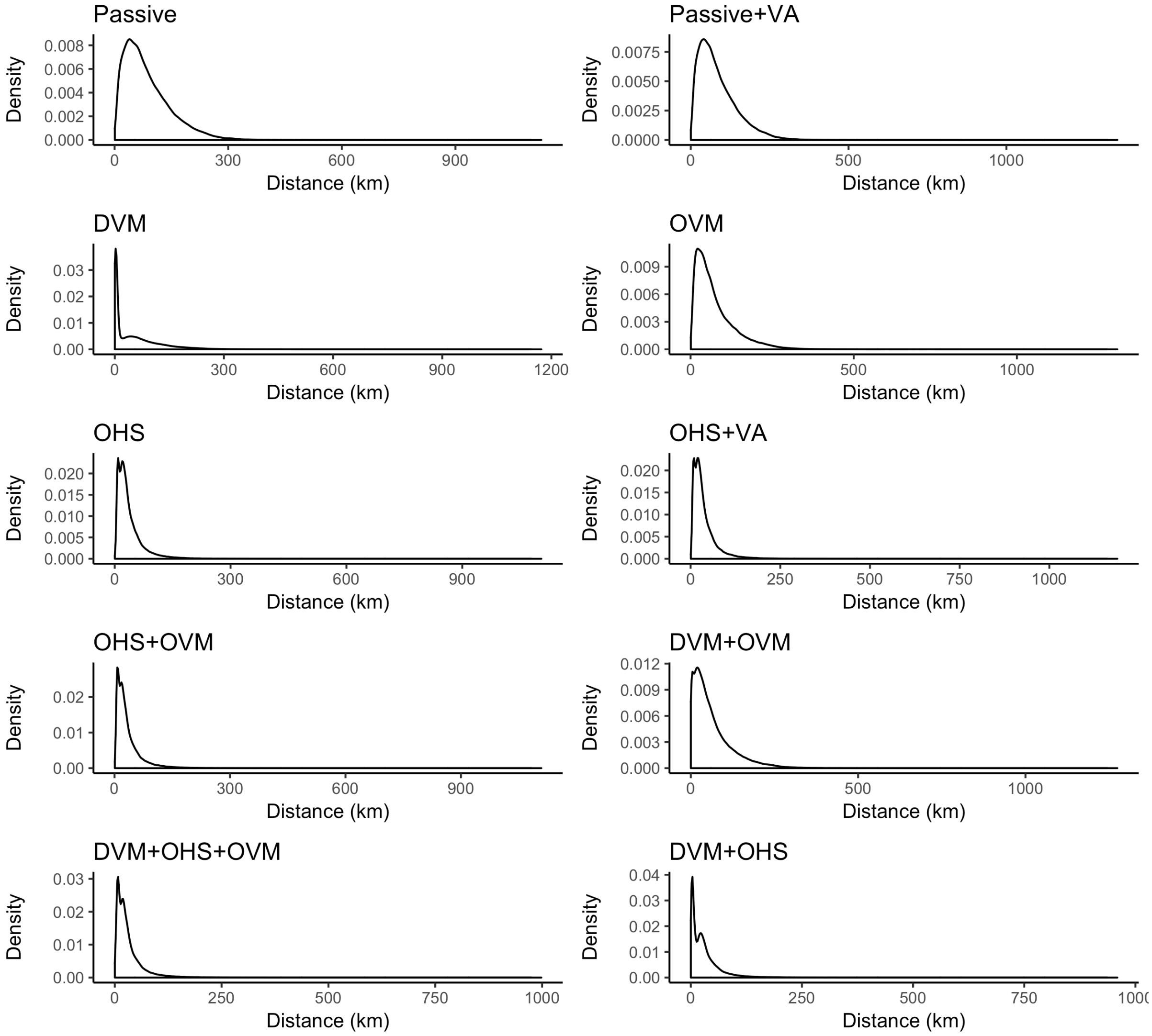
Time of day	Depth range (m)	Probability
Day	0-25	0.1
	26-50	0.3
	51-75	0.4
	76-100	0.2
Night	0-25	0.3
	26-50	0.3
	51-75	0.3
	76-100	0.1

Table C2.

Proportional depth stage abundance profiles for each of the seven fish families evaluated in Chapter 3. Values represent the proportional (within a stage) abundance of each stage within each of three depth ranges (surface: 0-1 m; mixed layer: 5-50 m; deep layer: 50-100 m) and are used to parameterise models run to address Aim 2 of this study.

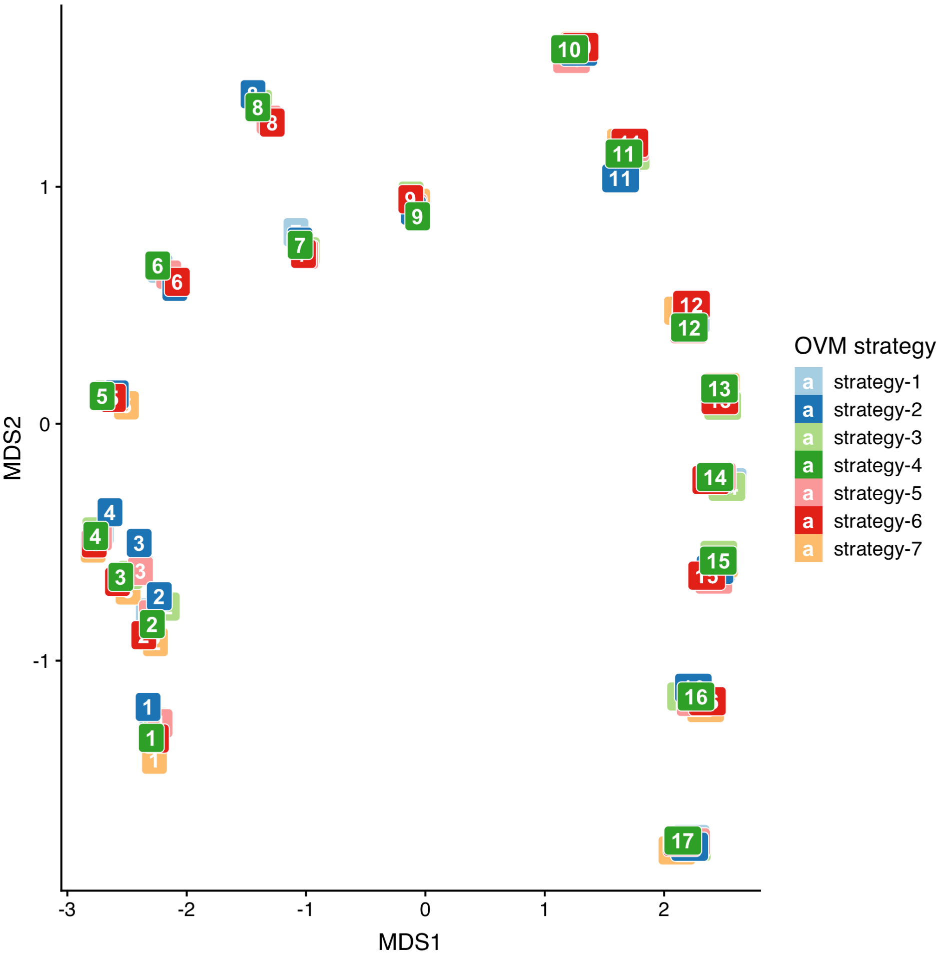
Model	Depth (m)	Preflexion	Flexion	Postflexion
Labridae	0-1	.275	.250	.350
	5-50	.650	.550	.400
	50-100	.075	.200	.250
Mullidae	0-1	.500	.500	.650
	5-50	.475	.375	.225
	50-100	.025	.125	.125
Pomacentridae	0-1	.400	.350	.050
	5-50	.500	.500	.850
	50-100	.100	.150	.100
Scaridae	0-1	.600	.350	.300
	5-50	.300	.425	.500
	50-100	.100	.225	.200
Scorpaenidae	0-1	.425	.100	.100
	5-50	.525	.650	.500
	50-100	.050	.250	.400
Serranidae	0-1	.450	.275	.100
	5-50	.450	.350	.300
	50-100	.100	.375	.600
Synodontidae	0-1	.150	.250	.150
	5-50	.550	.550	.650
	50-100	.300	.200	.200

Figure C1.



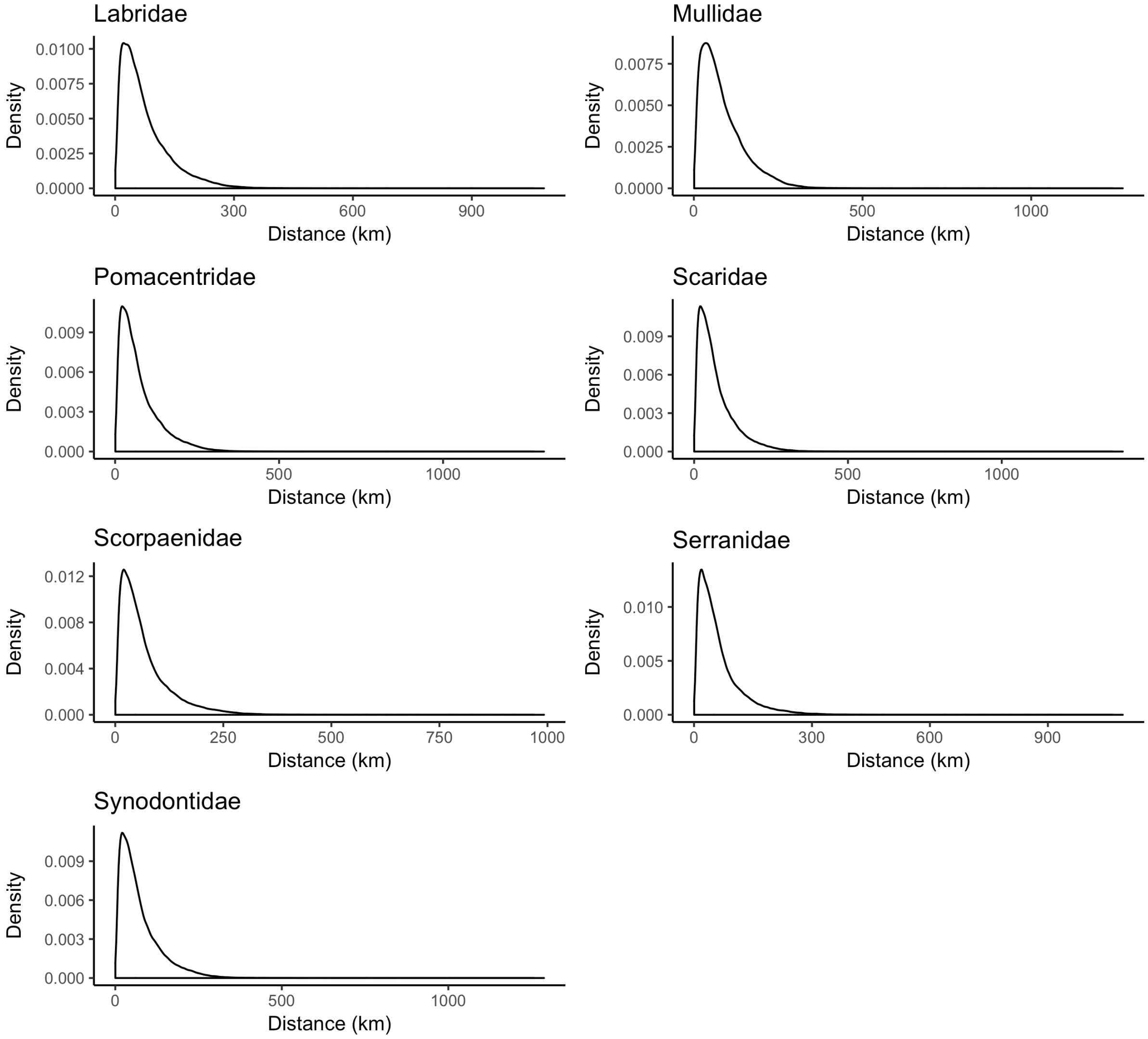
Dispersal kernels of distance (km) for the settled larvae for model runs considering different behaviours (VA = vertical advection, DVM = diel vertical migration, OHS = orientated horizontal swimming, and OVM = ontogenetic vertical migration).

Figure C2.



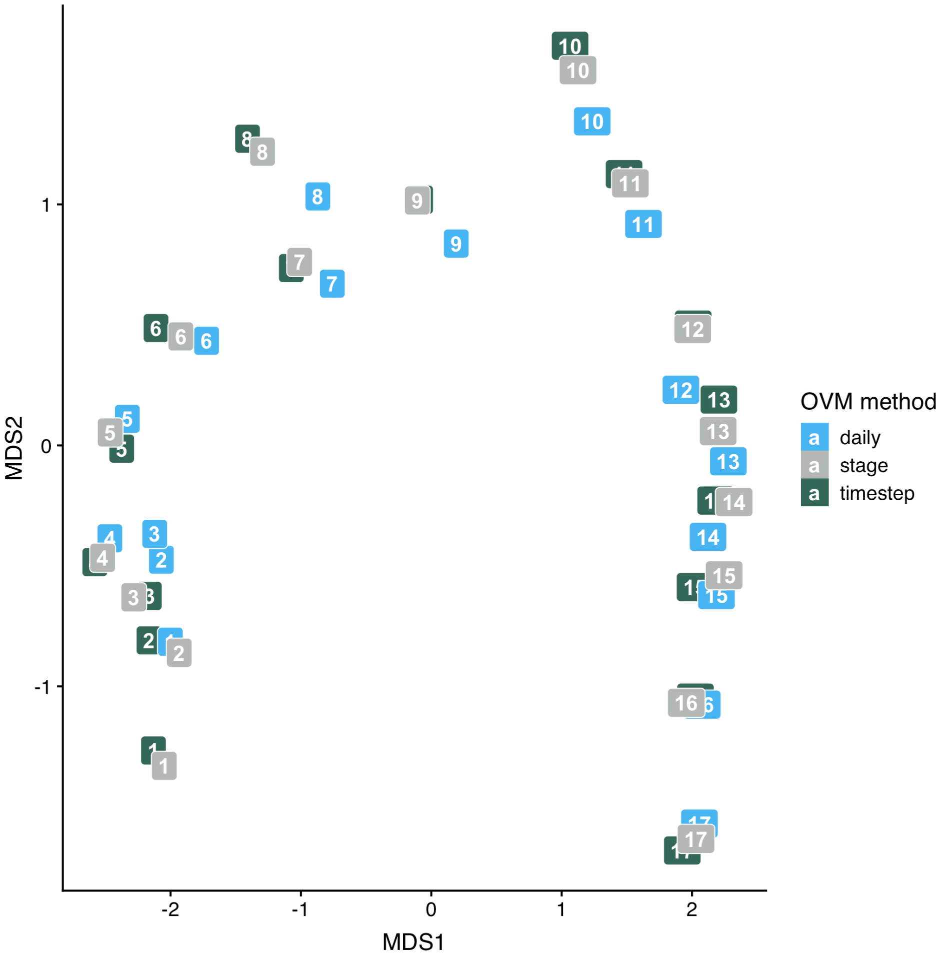
NMDS ordination plot using Bray-Curtis dissimilarities between the different source-settlement patterns of each NSW region for each model within the different ontogenetic vertical migration strategies for reef fish (2D stress = 0.06)

Figure C3.



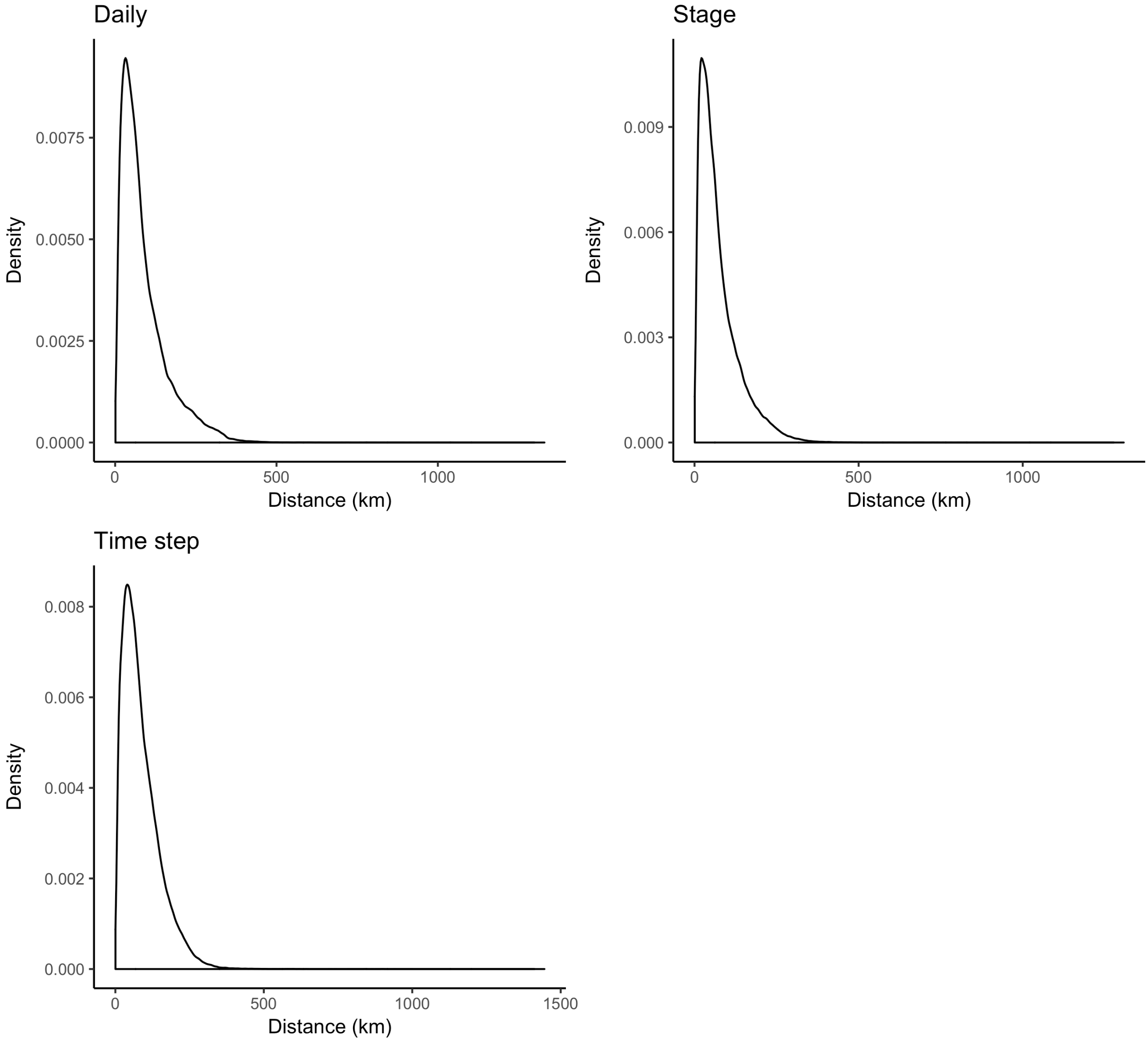
Dispersal kernels of distance (km) for the settled larvae for model runs considering different vertical migration strategies for seven reef fish families.

Figure C4.



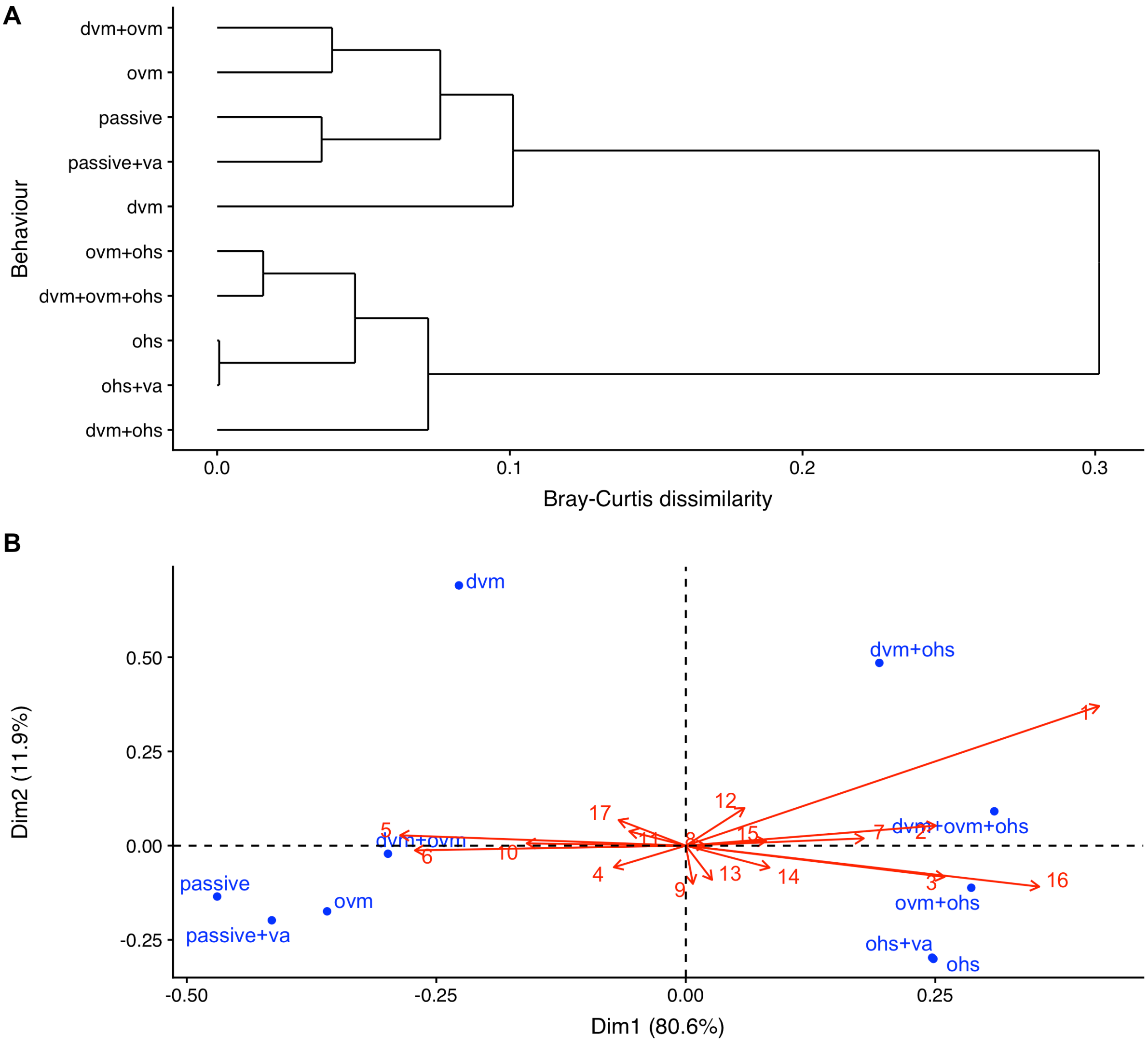
NMDS ordination plot using Bray-Curtis dissimilarities between the different source-settlement patterns of each NSW region for each model within the different ontogenetic vertical migration methods (2D stress = 0.08)

Figure C5.



Dispersal kernels of distance (km) for the settled larvae for model runs considering different implementations of ontogenetic vertical migration. The larvae fish changed position: daily, at each time step (2 hours), or when reaching the next ontogenetic stage.

Figure C6.



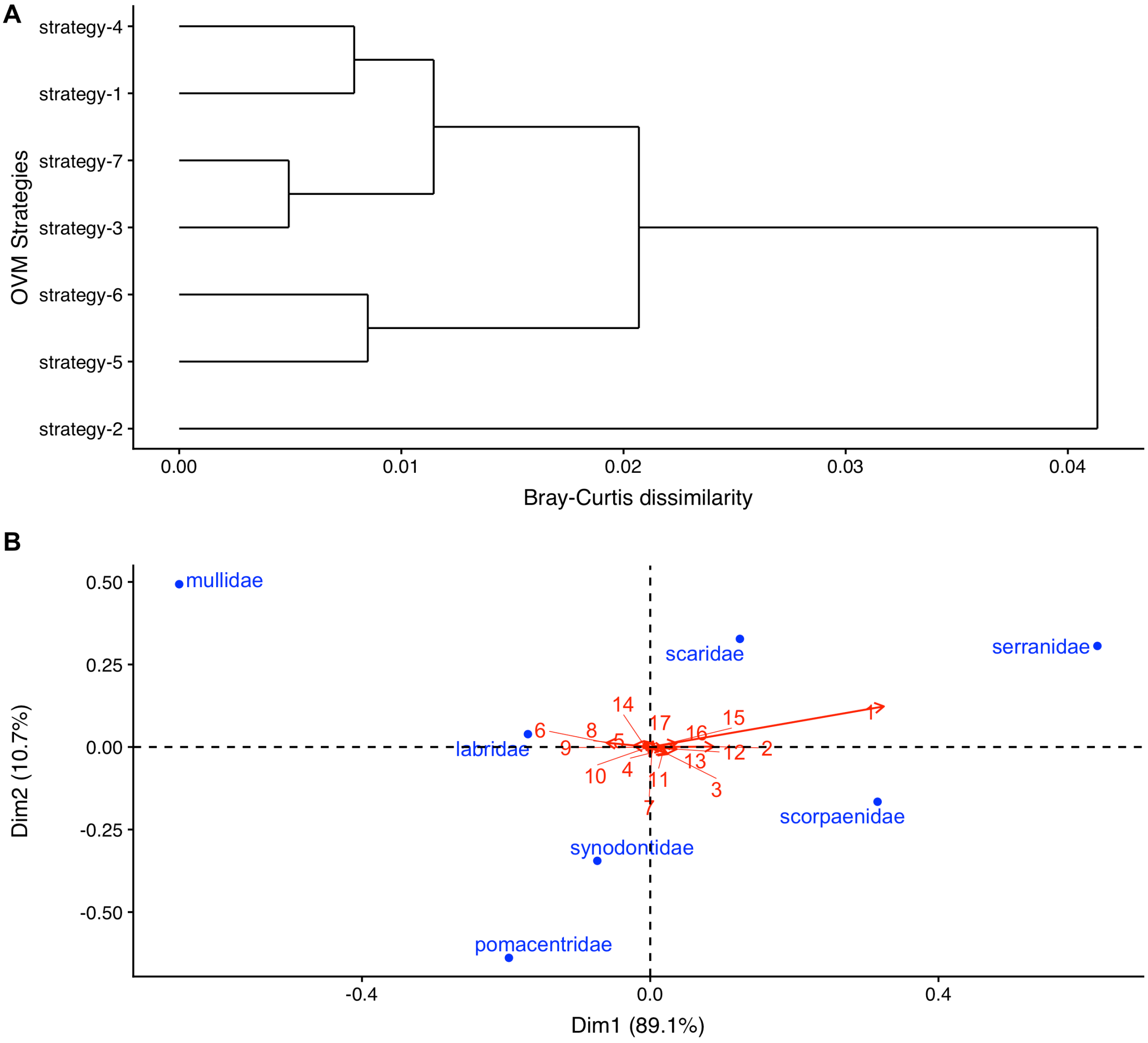
Comparison of the total settlement to source regions for the different models within the behaviour scenario (Passive = no behaviour, VA = vertical advection, DVM = diel vertical migration, OVM = ontogenetic vertical migration; OHS = orientated horizontal swimming). Cluster analysis (A) using a Bray-Curtis dissimilarity measure and clustered using the average-link method and constrained correspondence analysis (B) using Euclidean distance metrics.

Comparing the connectivity of the behavioural models to settlement region, cluster analysis of the settlement regions by behavioural models produced two distinct clusters; models with and without OHS (Figure C6 A). Within the OHS cluster, models without vertical migration behaviour (regardless of the use of vertical advection) were highly similar. In the non-OHS cluster, the most dissimilar model was DVM. Across both clusters, models with OVM were more similar than models with DVM. In the non-OHS cluster, the passive models and the OVM models were grouped (Figure C6 A). The settlement patterns of the models OHS and

OHS with VA were homologous, in contrast to the dissimilarity of the settlement patterns from the passive and passive with VA models.

Comparisons of the connectivity to settlement regions using CCA analysis also produced two clusters, similar to the CAP analysis on the entire connectivity matrix (Figure C6 B; Figure C6 C). However, the dissimilarity between models within a cluster displayed opposite patterns, whereby using the total settlement OHS models were less similar than the non-OHS models (excluding DVM). The models with OHS are more dissimilar to each other using total settlement as compared to the analysis using regional settlement patterns. The variation between behaviour scenario models was explained by a combination of settlement regions (Figure C6 B). OHS models had increased settlement at regions 1, 2, 3, and 16 and decreased settlement at the regions 5, 6, and 10.

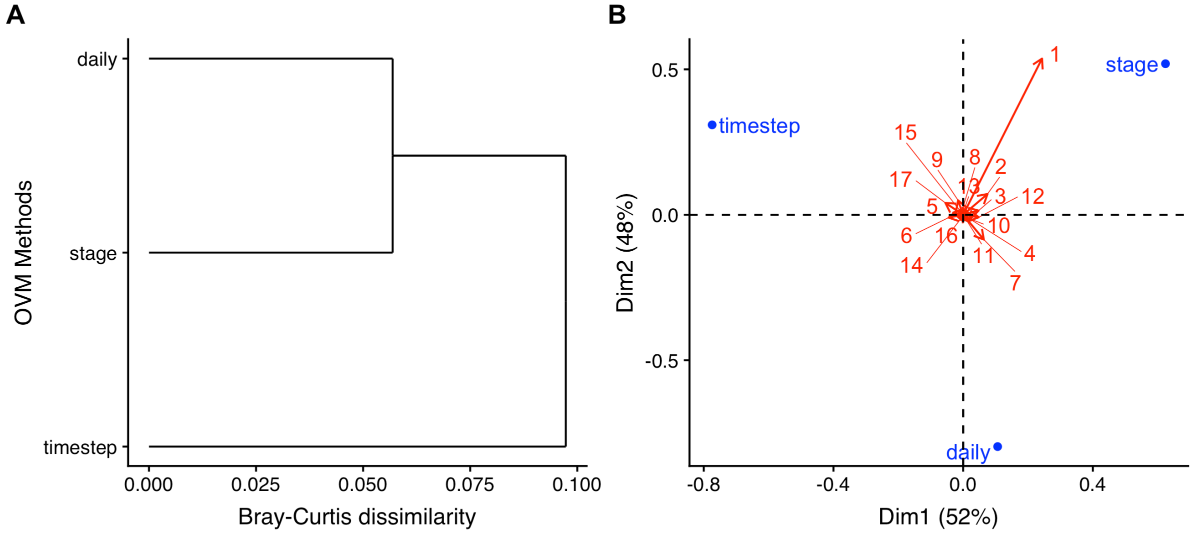
Figure C7.



Comparison of the total settlement to source regions for the different OVM strategies. Cluster analysis (A) using a Bray-Curtis dissimilarity measure and clustered using the average-link method and constrained correspondence analysis (B) using Euclidean distance metrics.

Two clusters were identified when comparing the total settlement of the different migration strategies. The first cluster contained only strategy 2, and the second comprised all the other OVM strategies (Figure C7 A). Within the latter group the sub-groupings were based on strategy, with one sub-group consisting of a strategy that migrated deepest with increasing ontogeny (strategies 5 and 6), and the other group using the OVM strategy whereby the centre of mass is in the 5-50 m depth layer at postflexion (strategies 1, 3, 4, and 7). The differences in the total settlement were driven by small regional changes, with the most notable effect of increased settlement at region 1 for the OVM strategies that migrated deeper with ontogeny (Figure C7 B).

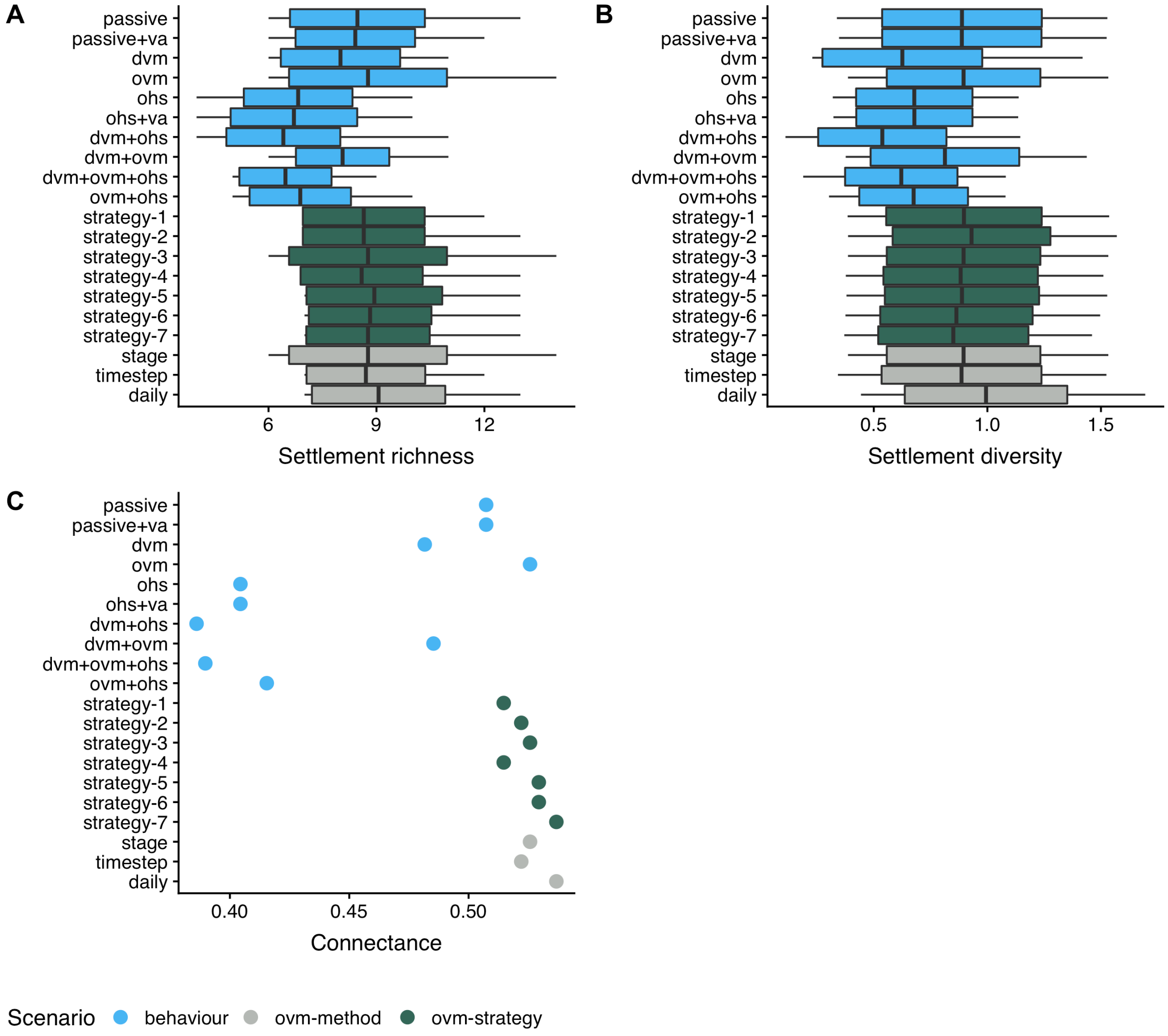
Figure C8



Comparison of the total settlement to source regions for the different OVM methods. Cluster analysis (A) using a Bray-Curtis dissimilarity measure and clustered using the average-link method and constrained correspondence analysis (B) using Euclidean distance metrics.

Comparisons of total settlement to regions found time step to have the most dissimilar settlement patterns (Figure C8 A). The differences were again driven by small regional differences, most notably an increased settlement at region 1 for stage and time step compared to the daily migration model (Figure C8 B).

Figure C9



The metrics of mean settlement richness (A; a measure of the number of regions settled), settlement diversity (B; a measure of richness and abundance using the Shannon-Weiner index), and connectance (C; a measure of describing the proportion of all links between the natal and settlement sites that are realised) for each region, as measured for each modelling scenario grouped by the three aims; behaviour (Passive = no behaviour, VA = vertical advection, DVM = diel vertical migration, OVM = ontogenetic vertical migration; OHS = orientated horizontal swimming), OVM strategy, and OVM method. The whisker plots denote the mean, one standard deviation either side of the mean and min/max values.

Settlement richness was decreased when OHS or DVM behaviour was in a model, but increased with OVM behaviour ($F_{7,144} = 17.50$, $p < 0.05$; Figure C9 A). The settlement diversity showed a similar effect as behaviour on richness, with OHS and DVM reducing diversity ($F_{7,144} = 18.79$, $p < 0.05$; Figure C9 B). The variation of settlement diversity between regions was increased with OHS and DVM. Connectance was highest for the models with only OVM behaviour or the passive models, and lowest for models with OHS behaviours

(Figure C9 C). DVM behaviour was observed to reduce the connectance between regions. Different OVM strategies did not produce any differences in richness ($F_{(6,96)} = 1.11$, $p > 0.05$; Figure C9 A) or diversity ($F_{(6,96)} = 0.79$, $p > 0.05$; Figure C9 B). The strategies with the lowest connectance occurred with strategies 1 and 4, while strategy 7 had the highest connectance values (Figure C9 C). OVM methods did not have an effect on settlement site richness ($F_{(2,32)} = 1.04$, $p > 0.05$; Figure C9 A) though there was an effect on diversity ($F_{(2,32)} = 11.02$, $p < 0.05$; Figure C9 B). This effect was caused by the OVM method of daily migration, which had lower settlement site diversity than the other OVM methods. However, the daily method of migration had the highest value of connectance (Figure C9 C). Differences in behaviour were more influential in determining the settlement richness, diversity, and connectance between regions (Figure C9). Diversity was impacted more by changes in OVM method than the strategy choice (Figure C9 B).

Appendix D

Supplementary materials for Chapter 5

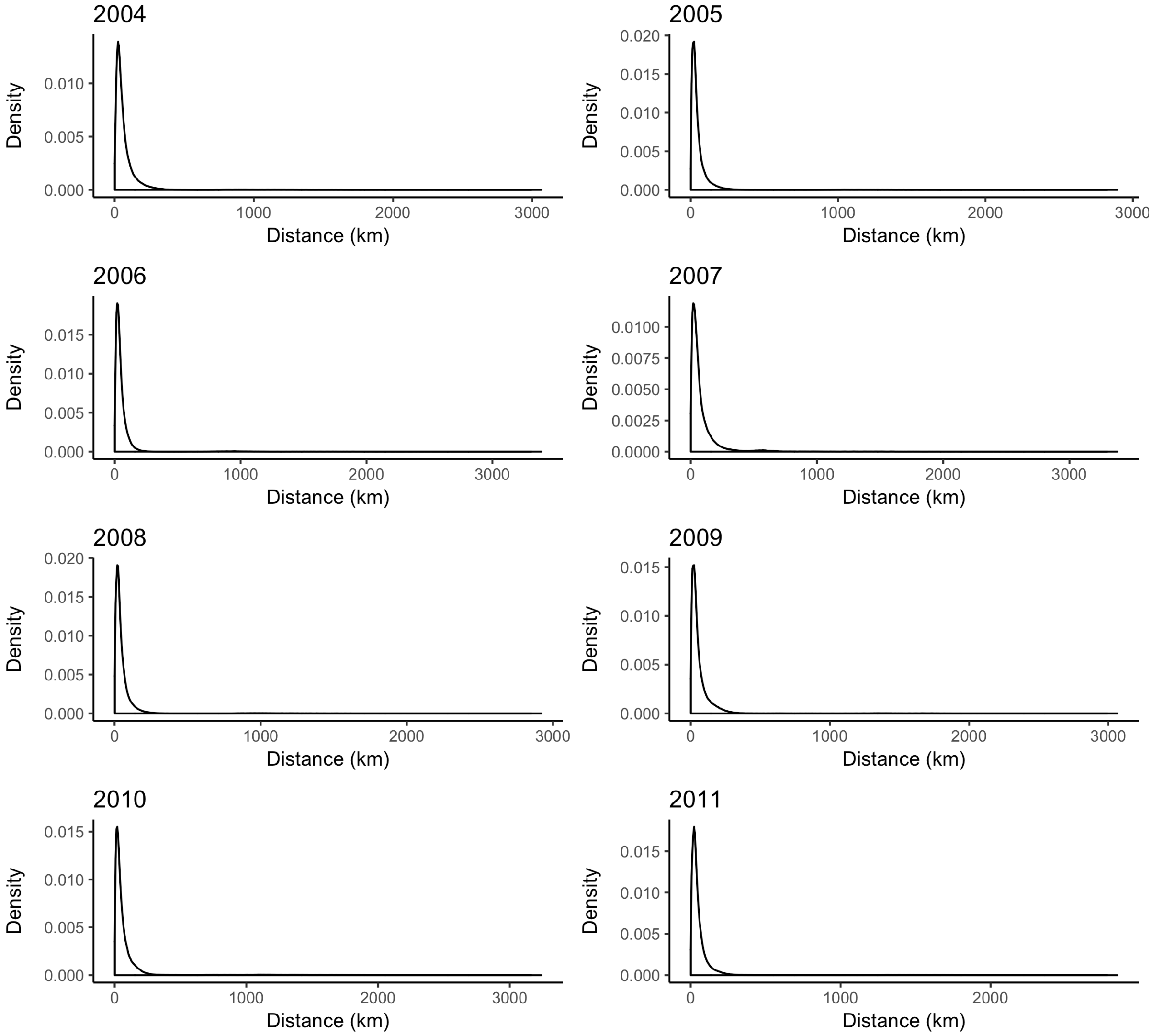
D1. Methods

ZISSOU configuration files can be found at doi: http://doi.org/10.25910/5c0ddb78bd9a1 chapter-5-zissou.zip

D2. Results

The connectivity matrix can be found at doi: http://doi.org/10.25910/5c0ddb78bd9a1 chapter-5-connectivity-matrix-all.csv

Figure D1.



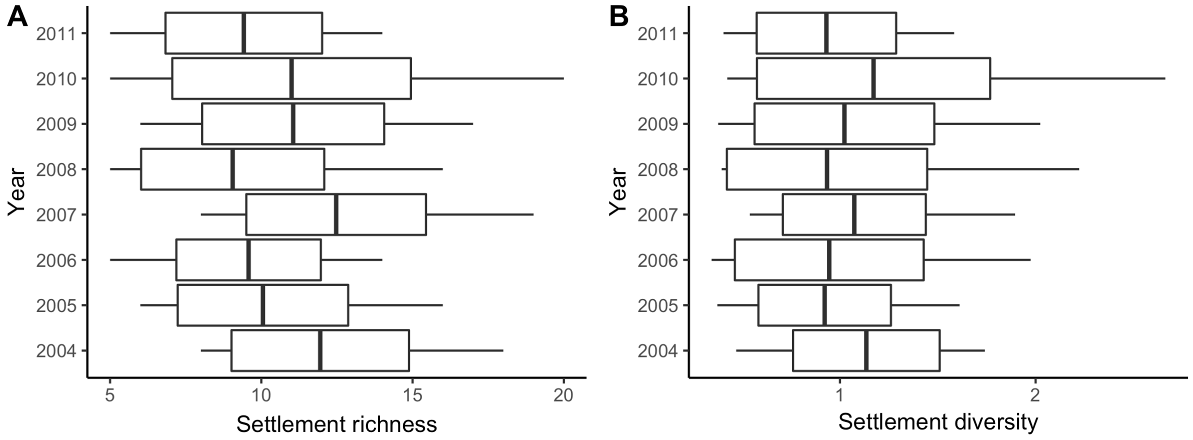
Dispersal kernels of distance (km) for the settled *Epinephelus daemelii* larvae over the years 2004-2011 along their known distribution.

Figure D2.

Average (vertical bar) values for all modelled years for settlement richness (A) and settlement diversity (B) for each of the 19 source regions from which *Epinephelus daemelii* larvae were released in the dispersal model. Boxes enclose ± 1 S.D., and whiskers indicate min/max values of the distribution.

Settlement richness differed between regions, showing similar patterns to the other connectivity metrics ($F_{(18,126)} = 7.12$, $p < 0.05$; Figure D2 A). The mean number of regions settled each year over the time series ranged from 6.75 at Newcastle, up to 15.25 for EM Reefs. The central source regions of NSW had the lowest richness values. Port Macquarie had the highest richness of the source regions along the coast. Annual variation of settlement richness occurred in all regions but was larger for the southern and offshore source regions. The diversity also differed between regions; however, it showed a different pattern than richness ($F_{(18,126)} = 24.85$, $p < 0.05$; Figure D2 B), declining from regions Tweed to Nambucca, and a more random pattern from Port Macquarie to Eden. Diversity was highest at Lord Howe Island, with the next group identified by post-hoc tests being EM Reefs, Tweed, and Byron. The offshore reefs had the largest variation of diversity, suggesting a strong effect of year in these regions, and Port Macquarie had the highest variation amongst the coastal regions. The diversity of settlement patterns from Sydney and Crowdy Bay exhibited the least annual variation.

Figure D3



Average (vertical bar) values for all modelled years for settlement richness (A) and settlement diversity (B) for each year (2004-2011) from which *Epinephelus daemelii* larvae were released in the dispersal model. Boxes enclose ± 1 S.D. and whiskers indicate min/max values of the distribution.

Annual variation of settlement richness was found amongst the connectivity patterns ($F_{(7,126)} = 5.79$, $p < 0.05$; Figure D3 A). Settlement richness was lowest in the years 2008, 2011, and 2006, and peaked in 2007; however, the variation between years was minimal. The settlement diversity was also different between years, but with less variation than the richness ($F_{(7,126)} = 3.81$, $p < 0.05$; Figure D3 B). The years of highest diversity were 2010 and 2004, and the lowest was 2005, 2011, 2008 and 2006