

Assuming stationarity compromises understanding of the dynamics and management of open marine populations

Carla C.M. Chen^{1,2*} and M. Julian Caley^{1,2,3+}

¹College of Science and Engineering, James Cook University, Douglas, QLD 4814, Australia

²ARC Centre of Excellence for Mathematical & Statistical Frontiers (ACEMS)

³School of Mathematical Sciences, Queensland University of Technology, Brisbane, QLD 4001, Australia

*Carla.ewels@jcu.edu.au

+julian.caley@gmail.com

Keywords: Reef Connectivity, Pelagic larval duration, Temporal variation, Crown of thorns starfish

Running title

Effect of assuming stationarity in connectivity

Type of article

Letters

Word counts

4961

Statement of authorship

C.C.C conceived of the study, programed and executed the simulations, carried out data analyses, and took the lead in writing the manuscript.

M.J.C. conceived of the study, contributed to the interpretation of the results ,and contributed equally in the writing of the manuscript

Statement of Data accessibility

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository and the link will be provided

Abstract

Understanding connectivity of marine species is crucial for their management. This connectivity, however, is difficult to quantify; propagules of marine species are typically small, numerous, and can travel large distances. Consequently, oceanographic models are often used to simulate larval dispersal. To avoid high computational costs, these models typically use, pooled or cross-sectional data and fixed biological parameters. Here we explore how temporal and spatial variation in current velocities, and pelagic larval duration and buoyancy can alter patterns of marine connectivity of Crown-of-Thorns starfish on Australia's Great Barrier Reef. Our results reveal highly variable reef connectivity in space and time mediated by all three factors. No individual reef acted consistently as a population source or sink. It is, therefore, important to consider many factors concurrently when estimating connectivity for understanding these population dynamics, especially where such estimates are relied on for evidence-based decision making.

Introduction

Populations of benthic marine species are typically studied and managed at spatial scales smaller than the regional scales on which their metapopulations operate. Consequently, the dynamics of these populations are most usefully understood as demographically open (Caley *et al.*, 1996) embedded in larger metapopulations (Bay *et al.*, 2008) whereby local replenishment is largely independent of reproduction at that location. By definition then, the replenishment of these populations must mostly rely on immigration from other populations. Because complex life cycles predominate in marine species, this replenishment is typically reliant on the movement of larvae. This reliance has resulted in a strong focus in marine research on understanding connectivity for advancing knowledge of both the demographic processes operating and the conservation and management options available for these species (Botsford *et al.*, 2001) including the design of networks of marine reserves (Botsford *et al.*, 2001, Stockhausen *et al.*, 2000) and the control of invasive species (Hock *et al.*, 2016, Mellin *et al.*, 2016a).

The importance of connectivity for marine populations is widely recognized; so too are the difficulties inherent in its study. These difficulties arise from myriad factors. Pelagic larval durations (PLDs) can vary inter-specifically from hours (e.g. corals and bryozoan (Shanks *et al.*, 2003)) to many months (e.g. reef fishes (Shanks, 2009)) and within species PLDs can be highly variable (Bay *et al.*, 2006b, Fabricius *et al.*, 2010, Uthicke *et al.*, 2015, Wolfe *et al.*, 2015) presumably because conditions experienced in the pelagic environment affect their growth and development (Bay *et al.*, 2006b, Uthicke *et al.*, 2015), as well as maternal conditions (Caballes *et al.*, 2016). The hydrodynamics that can drive connectivity can also be highly variable in space and time (Wolanski, 1994) and are, therefore, also likely to contribute to connectivity variability. Further complications that frustrate our understanding of connectivity in marine populations is the often extreme fecundity of marine species (Thorson, 1950), the small size and cryptic behaviour of their offspring following settlement (e.g CoTS), and vast volumes of ocean through which they travel making them impossible to track directly. Therefore, in understanding the causes and consequences of larval connectivity in these populations, due regard must be given to the uncertainty that is likely to surround such estimates.

Notwithstanding the difficulties of reliably observing and predicting larval recruitment patterns in space and time, the

importance of doing so is undiminished. Consequently, many approaches to estimating connectivity have been developed including direct marking of larvae (e.g. [Cuif et al., 2015](#), [Jones et al., 1999](#)), estimates of genetic differences among populations (e.g. [Bay et al., 2006a](#), [Hogan et al., 2012](#)) and tracing movements of genetic markers (e.g. [Miller et al., 2016](#)). More widely applied though are two-stage numerical approaches which simulate velocity data using a hydrodynamic model built using observed climatic and oceanic conditions as inputs, then applying particle tracking algorithms to estimate inter-population connectivity (e.g. [Frys et al., 2020](#), [Hock et al., 2014, 2016](#), [James et al., 2002](#)) (Figure S1). This approach is particularly useful and informative for predicting connectivity across large geographical areas such as Australia's Great Barrier Reef (GBR). Connectivity matrices derived from these methods are then used in subsequent analyses such as population dynamic or network models to predict the distribution of organisms, to identify key locations for marine protected areas (MPAs), or other management interventions.

In such meta-model approaches, and because they sequentially link multiple models, model outputs can be highly prone to the uncertainties that propagate through each stage of these models. Consequently, variation in any of these steps can alter the conclusions drawn, and therefore, affect the knowledge and the management recommendations and decisions drawn. Furthermore, because different levels of detail are required for different sub-models, temporal and/or spatial resolutions are often inconsistent among sub-models. In response to such inconsistency, common approaches include 1) making inferences based on cross-sectional data, e.g. a single year ([Frys et al., 2020](#), [Hock et al., 2014](#)) or 2) repeating later stage sub-model runs with values from a probability distribution assumed to be representative of the outputs derived from the preceding model ([Hock et al., 2017](#)). Such approaches can be sensible when temporal or spatial variation is small, or when probability distributions properly represent long-term temporal/spatial variation. Typically though, such assumptions are not tested, thereby potentially compromising the veracity of model outputs.

Beyond climatic and physical oceanographic conditions, PLDs and larval behaviour during the pelagic phase can strongly influence estimated connectivity ([Shanks, 2009](#), [Shanks et al., 2003](#)). Although species with longer PLDs are generally believed to have greater dispersal potential, the behaviour of larvae can affect dispersal distances ([Largier, 2003](#), [Shanks, 2009](#), [Shanks et al., 2003](#)). For example, larvae of some species can migrate vertically in and out of surface boundary layers, thereby increasing or decreasing their dispersal distances ([Largier, 2003](#)). Moreover, even within species, PLDs can vary greatly ([Bay et al., 2006b](#), [Uthicke et al., 2015](#)) likely depending on environmental conditions such as nutrient levels and water quality.

These potential effects of PLD and larval behaviour on the dispersal distances of propagules have been acknowledged for decades ([Brothers & Thresher, 1985](#), [Shanks, 2009](#), [Shanks et al., 2003](#)). However, little focus has been placed on how intraspecific variation in PLDs, in conjunction with reef connectivity, might influence their dispersal patterns. To date, for simplicity of simulation/computation, most connectivity network models have used a fixed PLD and static larval behaviour during the pelagic larval phase ([Hock et al., 2014](#), [James et al., 2002](#), [Kininmonth et al., 2010](#), [Thomas, 2015](#)). Logic suggests, these modelling decisions could cause both considerable overestimation/underestimation of dispersal distances.

Here we explore how simplifying assumptions can compromise our understanding of connectivity patterns and dynamics of

open marine populations and their management. To do so, we 1) explore how temporal variation in hydrodynamic connectivity could affect population connectivity of Crown-of-Thorns Starfish (CoTS, *Acanthaster spp.*) on Australia's GBR; and 2) explore how variation in CoTS PLD and behaviour could further compromise our current understanding of these connectivity patterns.

Material and methods

Connectivity model

One of the first connectivity models developed for the GBR was for CoTS larvae (Dight *et al.*, 1990, Dight, 1992). The hydrodynamic model used in these studies was based on SURGE (Sobey *et al.*, 1977) and TRACK, programs designed for tracking passive particles. In the early 2000s, James *et al.* (2002) further advanced the hydrodynamic model developed by Dight *et al.* (1990) to estimate the two-dimensional depth-integrated current field with a finer spatial resolution. This model added eddy formation and horizontal mixing around reefs and implemented a second-order Runge-Kutta algorithm for particle tracking allowing larval behaviour to be incorporated when predicting particle dispersal.

Increased computational power since the early 2000s has enabled the development of more complex hydrodynamic models that better predict reef connectivity. To date, the two most widely adopted approaches for modelling inter-reef connectivity of the GBR are ConnIe2¹ (Condie & Hepburn, 2012) and the model developed by Thomas (2015). In ConnIe2, inter-reef connectivity is simulated by applying Lagrangian particle tracking to velocity data simulated from the Sparse Hydrodynamic Ocean Code (SHOC) model with off-shore boundary conditions provided by Oceanmap. This latter model coupled an individual-based particle tracking method (IBM) with velocity data simulated from the second-generation Louvain-la-Neuve Ice-ocean Model (SLIM, Thomas (2015)).

At time of writing, ConnIe2 was the only GBR connectivity model capable of simulating particles beyond stationary vertical movements. Therefore, we used ConnIe2 to simulate GBR connectivity. We used six years of connectivity data. These years (2009-2016) were selected because data were available for the annual CoTS spawning period. From these data sets, annual patterns of connectivity were modelled during this spawning period (December-March) as this is when populations of CoTS are connected by dispersing larvae on the GBR (Babcock & Mundy, 1992).

Ecology of CoTS

Crown-of-thorns starfish (CoTS) are an important predator of corals on the GBR. They mostly occur at low densities. Every 15 to 20 years, however, CoTS emerge in plague numbers causing large declines in coral cover (Pratchett *et al.*, 2014). According to a recent longitudinal study, CoTS outbreaks have been a major cause of coral decline on the GBR since 1985, second only to cyclones (Deáth *et al.*, 2012, Vercelloni *et al.*, 2017). CoTS outbreaks also reduce the resilience of GBR coral communities to disturbances (Vercelloni *et al.*, 2017). On the GBR, CoTs outbreaks are believed to start in the northern section of the GBR between Lizard Island (14.6°S) and Cairns (17°S), and propagate southward (Pratchett *et al.*, 2014). This area between Lizard Island and Cairns is often referred to as the CoTS initiation box (IB).

¹In 2018, ConnIe2 was updated to ConnIe3 allowing for larger geographic areas but the underlying algorithm remains mostly unchanged

Simulation settings

We limited the geographic area considered in our simulations to the 378 reefs in the CoTS IB (14°30'S-17°20'S, 145°E-146°30'E). Within this area, 13 reefs for which long-term monitoring by the Australian Institute of Marine Science supports the repeated occurrences of CoTS outbreaks were selected as source reefs; those reefs that feed larvae into the IB metapopulation of 378 reefs. Conversely, all 378 IB reefs were modelled as sink reefs; reefs that receive larvae from the 13 source reefs (Figure S3 and Table S1 in *Supporting Information*). Although the exact spawning period of COTs can vary annually, we assumed a spawning season from 1 December to 28 February for all years studied.

To examine how connectivity might vary purely as a function of differences in hydrodynamics from year to year, we ran simulations for each year for which velocity data were available in ConnIe2 (i.e. 2009, 2011-2013, 2015 and 2016). We ran simulations with particles released independently from the 13 source reefs during each of the spawning seasons. Our objective here was to examine temporal variation in connectivity. PLD was fixed at 21 days with larvae suspended at 1m water depth (Table S2). We then investigated how variation in PLD could affect reef connectivity by releasing particles from 13 reefs with PLDs ranging from 5 to 40 days, in 5 day increments. We selected this range of PLDs based on Pratchett *et al.* (2014) who reported that CoTS PLDs range from 9 to 42 days. We simulated connectivity with variable PLDs using only 2009 and 2012 velocity data. This subset of years was selected to encompass the greatest variation in the hydrodynamic regimes for these reefs in the years examined. To control effects due to larval behaviour, we again assumed larvae were suspended at 1m depth throughout their pelagic phase (Table S2).

Lastly, we examined how larval behaviour could affect reef connectivity by exploring how vertical movement of CoTS larvae in the water column might modify reef connectivity. For simplicity, we set the PLD to 25 days (mid-range of CoTS PLDs) and tested two scenarios: 1) CoTS larvae maintained their position 1m from the surface for the entire PLD, and 2) larvae maintained a depth of 1m for the first half of their PLD and then moved to 5m on day 12 and remained at that depth for the remainder of the PLD (i.e. 5m Table S2). This is similar to the assumptions of Hock *et al.* (2014).

Spatial data processing

Following simulations using ConnIe2, connectivity estimates for all grid cells were downloaded. Because different grid alignments were used in the 2009 version of ConnIe2, connectivity estimates were re-aligned to a standard grid, where the IB was divided into 4 x 4 km grid cells, starting from the western and northern boundaries. Estimated connectivities were then assigned to the nearest grid box. Similar to Hock *et al.* (2014), we assumed a larva arrived at a reef when it was within 1km of that reef polygon at the end of its PLD.

Results

Due to the spatial resolution of ConnIe2 (4km), and the proximity of Linnet and Martin reefs, we were not able to treat Linnet and Martin reefs as two separate source reefs. Therefore even though all simulations were run with 13 source reefs, we only report results for 12 reefs as the results for Martin and Linnet reefs were identical.

Effects of temporal variation on reef connectivity

Reef connectivities were highly variable over time as were which source reefs provided the most recruits to other reefs (Figures S4 to Figures S14 in *Supporting Information*). There was strong inter-reef connectivity in 2009, particularly for source reefs in the northern end of the IB. For example, particles released from Lizard Island remained mostly in the IB after 21 days drifting (Figure 1); the same level of connectivity was not evident in 2011. Regardless of source reef location, particles released from all source reefs were washed into the Coral Sea in 2011.

For source reefs in the northern end of the IB (i.e. north of 15°), currents bifurcated around 15°S in 2013 and 2016. Consequently, a large proportion of particles had dispersed into the Coral Sea at the end of the 21 day PLD with only a small proportion of particles remaining within the GBR. In 2012, reefs in this northern section had strong connectivity to reefs north of the IB. In contrast, the same group of reefs had stronger connectivity to mid-shelf reefs (between 15°S and 16°S) in 2015.

For source reefs in the southern section of the IB (south of 16°S), connectivity showed some similarities among reefs between 2015 and 2016. During these periods, reefs in this section of the IB were strongly connected to most of the inshore reefs in the IB and mid-shelf reefs located in the southern-section of the IB. However, little connectivity was observed with the mid- and outer-shelves reefs in the mid- and northern part of the IB (north of 15°S).

For 6 years analysed, the majority of reefs in the IB were not connected to any of the source reefs and only a small proportion of IB reefs were consistent (i.e 4+ years) in their connection to them (< 5%, Figure 2). For example, around 73% of reefs in the IB were not connected to any of the four source reefs located in the northern end of IB during those six years; approximately 16% of reefs in the IB were connected to four source reefs located in the northern end of IB only once in the 6 spawning seasons, and no reefs in the IB were connected to four source reefs located in the northern end of the IB for 5+ years. Similar trends were observed for source reefs located in the mid and southern sections of the IB.

Effects of Pelagic Larval Duration on Connectivity

The PLD of CoTS larvae also strongly influenced reef connectivity patterns (Figure S15 to Figures S25 in *Supporting Information*). Irrespective of source reef location, a small change in PLD (i.e. 5 days), substantially altered patterns of where larvae settled. For example, when PLD was 10 days, most larvae settled on middle and outer reefs north of 16°S when CoTS were spawned around Lizard Island in 2009 (Figure 3). However, during the same spawning season and from the same source reef, with an extra 5 days in the water column, there was an approximately 30 fold increase in the proportion of larvae that settled further south, between 16 and 17°S. The effect of PLD on reef connectivity was stronger when region-wide connectivity was lower (e.g. in 2012, bottom panel of Figure 3).

Changes in PLD also affected the number of larvae that settled in the IB, an important parameter in how outbreak initiation is thought to proceed. Although there was generally a negative correlation between PLD and the proportion of larvae settling in the IB (Figure 4), this rate of decline differed among source reefs. In 2009, when reef connectivities in the IB were greater in the northern section of the IB, the proportion of larvae that settled in the IB did not decline with PLD until PLD was greater than 25 days. The effect of PLD was consistent in 2012 when larvae originated from the mid- and southern sections of the IB.

However, due to low connectivities with source reefs, the proportion of larvae that settled in the IB declined linearly with PLD for source reefs in the mid- and southern sections of the IB. Conversely, during the same year, when released from the northern end of the IB, no effect of PLD was observed. PLD variation also affected the strength of source-sink connectivity. For the source reef Lizard Island, the predicted settlement locations were different for larvae with different PLDs (Table S3). Even with as little as 5 additional drifting days, locations of settlement differed greatly.

Effects of the Behaviour of Pelagic Larvae on Connectivity

Larval behaviour during the pelagic phase not only influenced the locations of sink reefs, it also affected the number of larvae that settled on reefs within the IB and the number of IB reefs propagated by the same source reef (Figure 5 and Figure 6, connectivity heat maps for other source reefs and different larval behaviours are in *Supporting Information*). Simulations showed that a greater proportion of larvae settled on the IB reefs, and more reefs in the IB were populated with larvae when assuming larvae become negatively buoyed in the second half of the PLD comparing with staying at 1m depth throughout the PLD.

The impact of larval behaviour on settlement patterns varied with the location of the source reef (Figure S29 in *Supporting Information*). For example, for source reefs located in the northern end of the IB, more larvae settled on IB reefs if they stayed at 1m depth throughout the entire PLD. In contrast, for source reefs located in the mid- and southern end of the IB, more larvae settled on IB reefs if they became negatively buoyed in the second half of the PLD (Figure 6 in *Supporting Information*).

The distribution of the larvae also varied with larval behaviour during the PLD and the location of the source reef. In general, more reefs acted as sink reefs in the IB if particles became negatively buoyed in the second half of the PLD, compared to particles remaining at 1m depth throughout the PLD (Figure 6 in *Supporting Information*).

Discussion

Despite inherent difficulties in quantifying connectivity, doing so is critically important for understanding the population dynamics of open marine populations and options for their management. For example, connectivity of populations between reefs on the GBR is important for maintaining genetic diversity, viable local populations, and the spatial distributions of the species it hosts, the vast majority of which have a dispersive larval phase. Understanding the patterns of connectivity of these species will assist many aspects of their management (e.g., CoTS (Mellin *et al.*, 2016b, Pratchett *et al.*, 2017)). Particularly in the case of CoTS, it is imperative to know with a high degree of confidence if particular reefs consistently provide a greater proportion of new recruits to CoTS populations on other reefs. If such reefs can be identified, such knowledge could underpin effective CoTS management. While direct observation of reef connectivity is difficult, velocity data simulated from hydrodynamic models and real-time climatic data coupled with particle tracking algorithms can provide valuable insight into reef connectivity. Relying on such indirect inference, however, demands a high degree of caution because model assumptions have the potential to substantially bias inferences derived in this way.

Due to the very large spatial extent of Australia's GBR, graph theory has been used to summarise the large volumes of

spatially explicit connectivity data that can be generated from such models to draw ecological conclusions (Frys *et al.*, 2020, Hock *et al.*, 2014, Kininmonth *et al.*, 2010, Thomas *et al.*, 2014) and potentially guide management. Here again, caution is required to ensure that additional uncertainty is not propagated through to the results when using these methods that could compromise management effectiveness. For example, Hock *et al.* (2014) coupled graph theory with ConnIe2 to identify CoTS hotspots that they named superspreader reefs. Similarly, Thomas (2015) used the combination of SLIM and individually based models (IBM) to simulate the dispersal of larvae of four coral species to identify sparsely connected reef populations and barriers affecting larval dispersal. Temporal variation in reef connectivity, however, is often overlooked in such studies. Because of the size and complexity of the task, biotic and abiotic variation is often removed from consideration through the application of simplifying assumptions. For example, Hock *et al.* (2014) only used a single year (2009) of connectivity modelling to identify super-spreader reefs. To be useful to management, it is important to understand the consequences of applying such simplifying assumptions. Our work here is focused on these consequences.

Temporal variation in reef connectivity has previously been suggested (Hogan *et al.*, 2012, Klein *et al.*, 2016). Hogan *et al.* (2012) used genetic assignment to track the dispersal of larval fishes in the western Caribbean for over three years. Dispersal distance, local retention, and patterns of connectivity all varied substantially among years. With a simpler hydrodynamic model, James *et al.* (2002) also identified considerable temporal and spatial variation in reef connectivity on the GBR. Temporal variation, however, was excluded from their subsequent consideration by modelling larval dispersal using mean connectivities. Given that connectivities can be highly variable, the use of mean statistics is unlikely to be justifiable. Furthermore, the large variability in the six year connectivity data used here were insufficient to infer stable distributions of connectivities.

Water circulation on the GBR results from the effects of tidal and wind driven currents which, in combination, lead to substantial water movements long shore with exchanges across the continental shelf with the Coral Sea. Given the directions and strengths of these flows vary in time and space, temporal variation of reef connectivity would be expected, especially from models that assume passive transport of larvae. Here, however, the level of variation was much greater than might be expected. Six substantially different reef connectivity patterns were derived for each of six years when the source reefs in the northern end of the IB were modeled. Therefore, it appears unlikely that reefs in the northern-end of the IB consistently act as source reefs for CoTS populations during outbreaks or non-outbreaking periods. Instead, the role of these reefs are likely to vary from year to year. This however does not diminish the possibility that reefs in the northern end of the IB might act as possible sources of the initiation of outbreaks in some cases. AIMS LTMP data indicated that CoTS first appeared around Lizard Island, and MacGillivray and Martin reefs in 2009; two years before CoTS were detected on the other reefs surveyed in the IB. Given there was strong reef connectivity in the IB sourced from Lizard Island, and MacGillivray and Martin Reefs in 2009, it is plausible that the most recent CoTS outbreak did begin in this area. These reefs, however, were not connected to other reefs in the IB in 2011 and 2012, and only minimally connected in 2013, 2015 and 2016. Therefore, while these northern reefs may initially act as spreaders, they are unlikely to continue to feed downstream outbreaks because of changes in connectivities through time. Consequently, management decisions, say to remove adult CoTS from these reefs, could waste

substantial precious resources if the objective is for large-scale CoTS control. Because patterns of connectivity between these reefs can not yet be predicted with sufficient accuracy far enough in advance, it is unlikely that this risk of wasting management resources can be adequately managed. For the other nine reefs located in the middle and southern end of the IB, there was no evidence of consistent patterns of inter-reef connectivity that could robustly support culling of CoTS from source reefs. Only two of six years modelled displayed much similarity in reef connectivities (e.g. 2015 and 2016), while in other years, connectivity patterns were vastly different.

The potential effects of differences in PLDs and larval behaviour during the pelagic phase on dispersal distances has been previously acknowledged in the literature ([Brothers & Thresher, 1985](#), [Shanks, 2009](#), [Shanks *et al.*, 2003](#)). However, comparatively little research has focused on how intraspecific variation in PLDs can influence connectivity patterns. By incorporating intraspecific variation in PLDs and larval behaviour into our connectivity model, we demonstrate that even a small increase in PLD (i.e. 5 extra days) can reduce the proportion of larvae settling within the IB. Given that the PLD of CoTS varies from 9 to 42 days ([Pratchett *et al.*, 2014](#)), and factors such as maternal condition ([Caballes *et al.*, 2016](#)), nutrients in the water column, and water temperature ([Fabricius *et al.*, 2010](#), [Uthicke *et al.*, 2015](#), [Wolfe *et al.*, 2015](#)) all affect the development of CoTS larvae, it is likely that PLDs of CoTS vary substantially in nature. Therefore, environmental conditions which affect larval development should also be considered when trying to model the dispersal of CoTS, and likely, other marine species with biphasic life cycles. In contrast, assuming CoTS larvae are neutrally buoyant (e.g. [Hock *et al.* \(2014\)](#)) substantially underestimates the likely proportion of larvae produced in the IB that remain in the IB. In our results, up to twice as many larvae remained in the IB when we assumed larvae sank to 5m in the second half of their PLD. If more CoTS larvae do remain in the IB, and if the conditions there favour the development of the larvae, any outbreak observed initiating from the IB could potentially be sourced from a small number of upstream reefs. While these two processes, intraspecific variation in PLD and larval behavior, can have opposite effects on reef connectivity, it is not sufficient to assume that they simply cancel each other. Without further understanding of how these processes vary and interact at relevant ecological scales, our ability to understand and manage these species will be compromised.

Further complicating our understanding of these systems are some of the details of the hydrodynamic models that are coupled with particle tracking algorithms to provide insights into connectivity patterns. For instance, the velocity data used here was simulated using the 4km SHOCK model. This spatial resolution is too coarse for the prediction of flows at the reef scale ([Thomas, 2015](#)). Although GBR velocity data is now available at 1km resolution, this resolution is still too coarse for predictions of small scale movements such as self-recruitment, and simulations using these data become very computationally expensive, very quickly. Therefore, greater spatial resolution of velocity data may not provide a solution to these problems. A solution may lie in the use of other velocity modelling approaches. For example, the hydrodynamic model SLIM, uses an unstructured mesh to simulate flows on the GBR instead of the fixed grid approach of SHOCK. This unstructured mesh approach is computationally less intensive and capable of modelling circulations simultaneously at both large and small scales. For example, [Frys *et al.* \(2020\)](#) developed a bio-physical dispersal model with a resolution of around 100m. It is still unclear,

however, how the performances of these two models, namely large- and fine-scale dispersal models compare with respect to understanding reef connectivity patterns. Furthermore, even with the same resolution and similar biological settings, two functionally equivalent hydrodynamic models produced vastly different results (Bode *et al.*, 2018). Validations with *in-situ* empirical data are required for all connectivity models. In addition, greater clarity around the effects of reef bathymetry on reef connectivity mediated by larval behaviour at settlement may provide greater insight into reef connectivity patterns.

Our purpose here was to explore how differences in hydrodynamics through time, the lengths of PLDs and larval behaviour during the pelagic phase might affect modelled connectivities, not to provide definitive estimates of them. Accordingly, we made choices about how we modeled the scenarios presented here that differ from previous studies of connectivity of CoTS populations on the GBR. For example, unlike Hock *et al.* (2014) who used all reefs in the IB as potential sources of CoTS larvae, we limited our source reefs to the twelve reefs that were monitored by the AIMS Long-term Monitoring Program; this program provided direct evidence of large numbers of CoTS on the reefs in the years we modeled. Due to the size of the GBR and the limited number of sites monitored, we can not know if any other reefs in the IB had CoTS populations that seeded other reefs during those years. Furthermore, our assumption that CoTS larvae remain at either 1m through their pelagic phase or moved to 5m of depth in the second part is potentially a gross over simplification of how CoTS larvae are distributed in the water column at various times during their development. Irrespective of the validity of these assumptions, the effects of these factors on connectivity patterns appear to be profound and should motivate greater caution when interpreting their effects, and on-going research to improve these models. Moreover, here we explored only a small number of factors that could alter modelled connectivities.

Understanding connectivity between populations of reef-based and other marine populations is a fundamental goal of modern ecology. Such knowledge can contribute to understanding patterns of genetic diversity of these species, what drives their metapopulation dynamics (Hedgecock, 1994, Hogan *et al.*, 2012, Holland & Hastings, 2008), their capacity to evolve, and underpin management decisions regarding a range of options from planning networks of protected areas to, in the case of CoTS, direct intervention by culling individuals. Our work here indicates that connectivity between reefs of the GBR are likely to be highly dynamic, is the result of many interacting factors, and results in highly variable patterns of connectivity. To advance our understanding of connectivity through modelling studies, it will be necessary to find an appropriate balance between model complexity and reliability of results. Over simplification of these models whether for convenience, or in response to data and/or computational constraints without appropriate validation, risks wasting valuable research and management resources.

Acknowledgements

We thank the Long-Term Monitoring Team of the Australian Marine Science Institute whose efforts over decades has made data available which make modelling studies of reef dynamics such as this possible. Our work here has also benefited greatly from the many conversations and collaborations with many CoTS researchers all focused on a very complex problem.

Figures and Tables

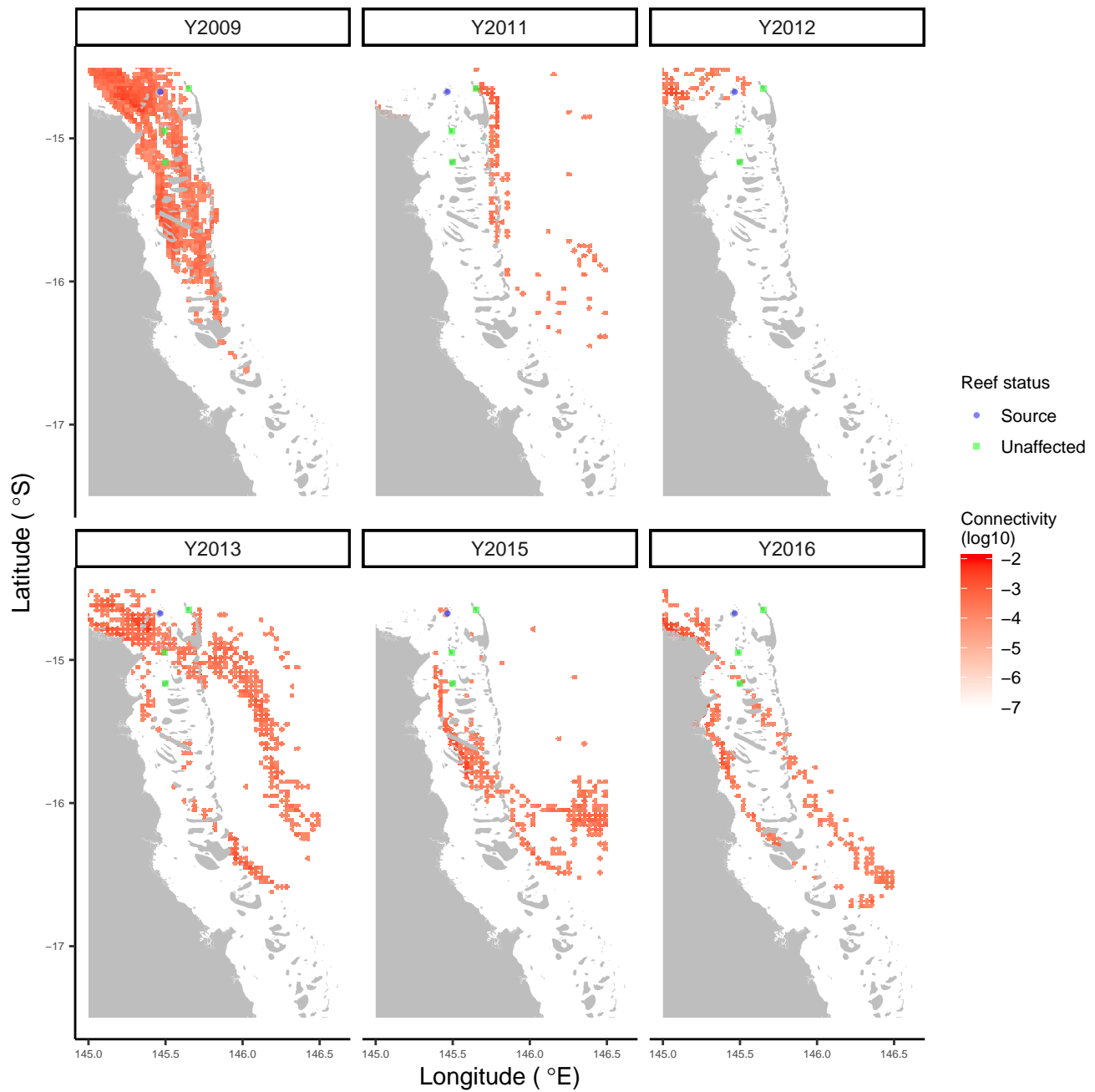


Figure 1. Reef connectivity for selected years from 2009 to 2016 when larvae were released from around Lizard Island during the spawning months (14°40'30"S, 145°28'1"E). Each panel represents a different year. Lizard Island (Blue dot) was selected for illustration of a source reef in the northern section of the IB, and the green squares indicate the reefs where CoTs were not observed by the AIMS Long-term Monitoring Program during the years studied here.

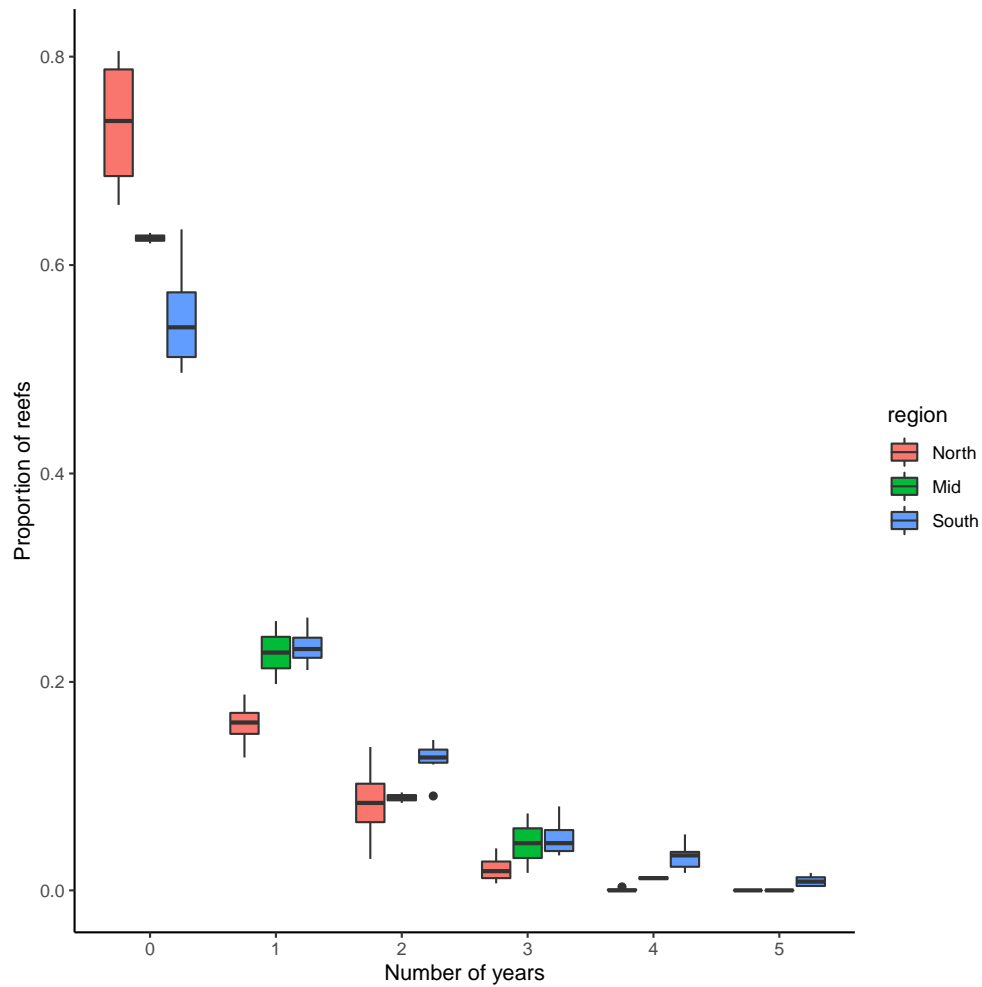


Figure 2. Proportion of reefs, in the IB, connected to one of the twelve source reefs located in the northern, mid and southern sections of the IB over the six spawning seasons modelled. The X-axis is the number of years that a sink reef was connected to a source reef over the six spawning periods. The Y-axis is the proportion of IB reefs with such a connection. Each colour represents a different sub-region.

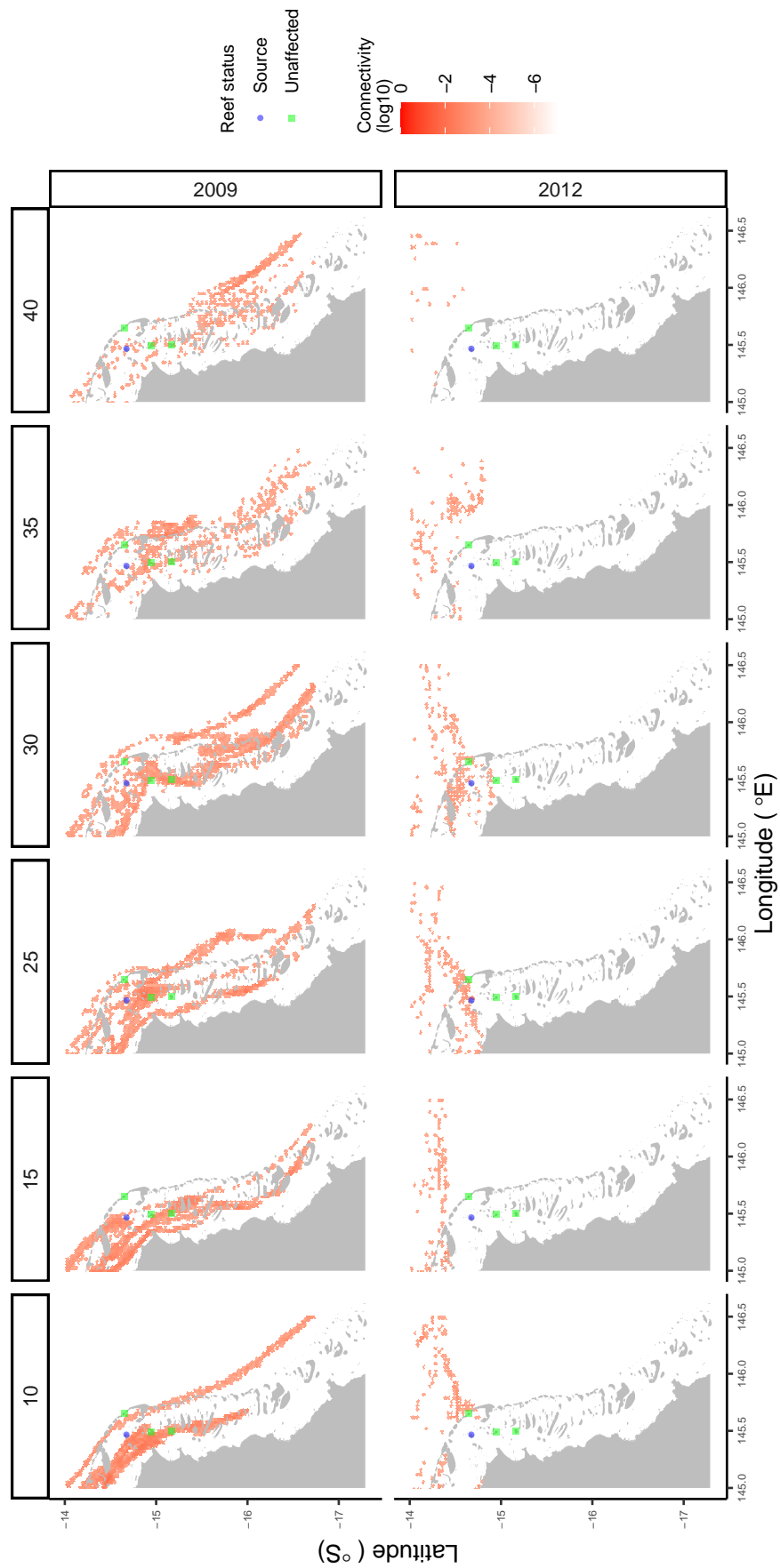


Figure 3. Changes in reef connectivity for CoTS with different pelagic larval durations when larvae originated from around Lizard Island in 2009 and 2012. Vertical panels depict different PLD durations while the horizontal panels depict different years

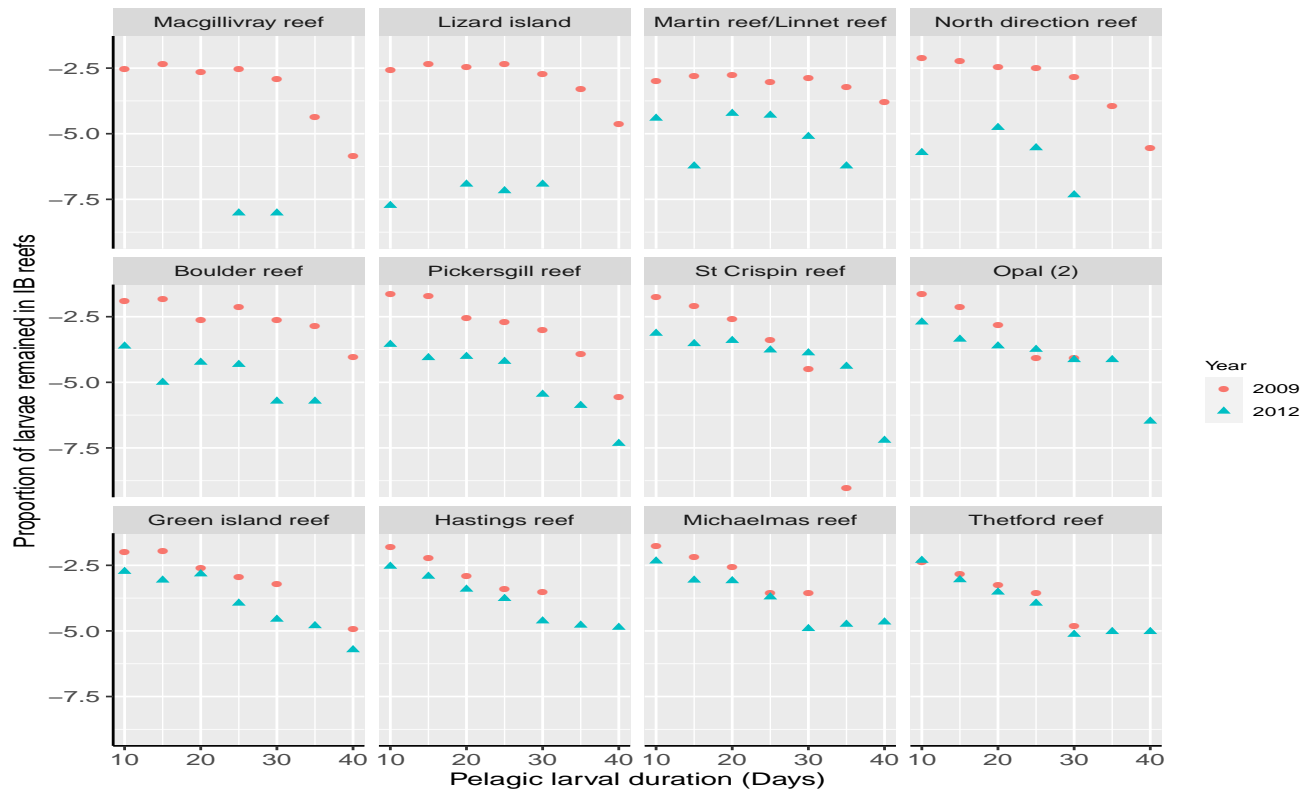


Figure 4. Proportion of larvae that settled on reefs within the initiation box (IB) at different pelagic larval durations simulated using 2009 (circle) and 2012 (triangle) velocity data. Each panel represents a different source reef. Missing values are times when the model indicated no larvae settlement on any of the IB reefs.

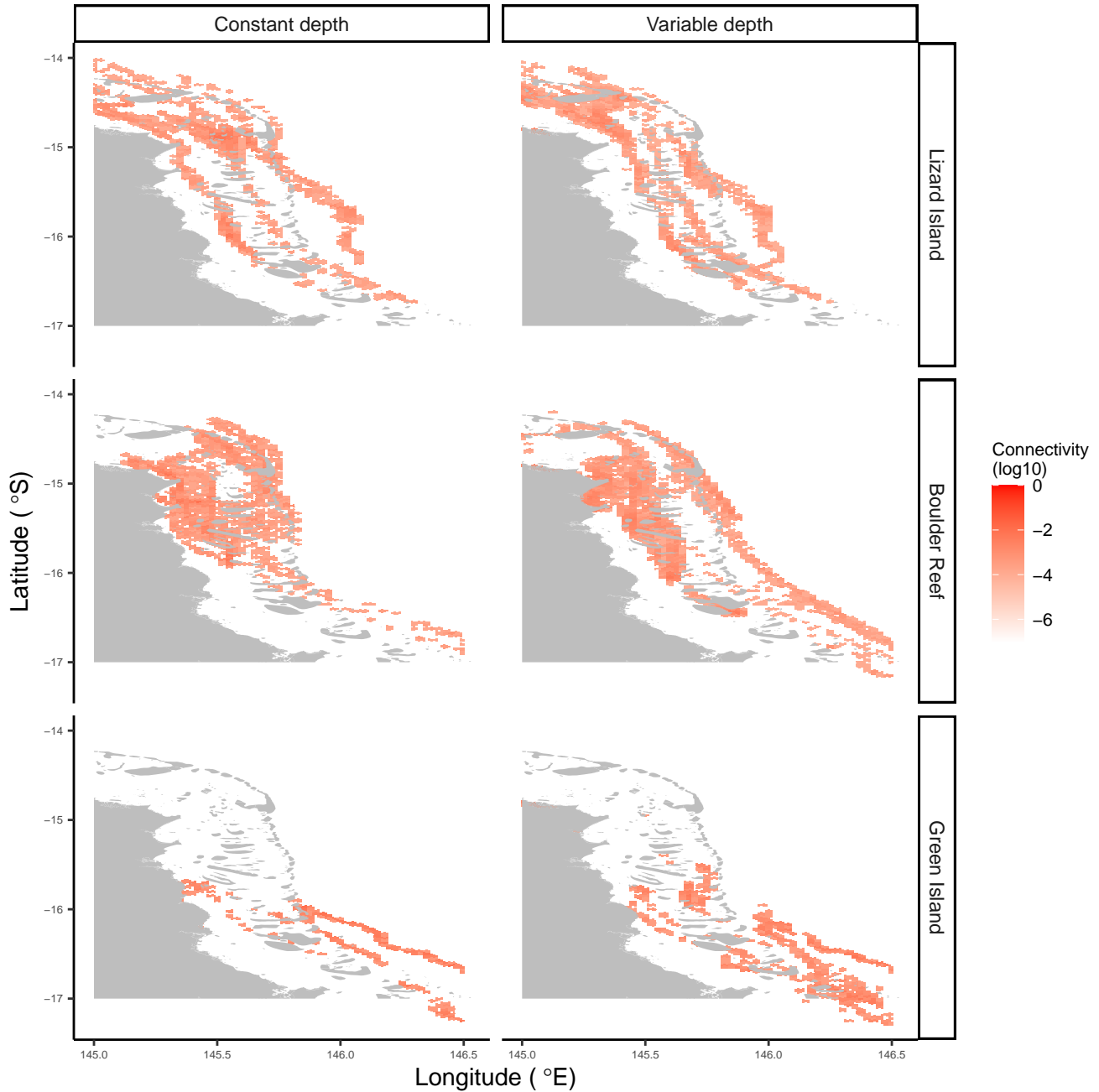


Figure 5. Changes in reef connectivity for reefs in the initiation box for different behaviour of CoTS larvae during the pelagic larval phase. Figures on the left shows reef connectivity assuming larvae remained positively buoyed (~1m) during a 25 day PLD, while figures on the right are reef connectivity assuming larvae were positively buoyed during the first half of the PLD and became negatively buoyed ~5m for the second half. Each row represents a different spawning location: Lizard Island, Boulder reef and Green Island.

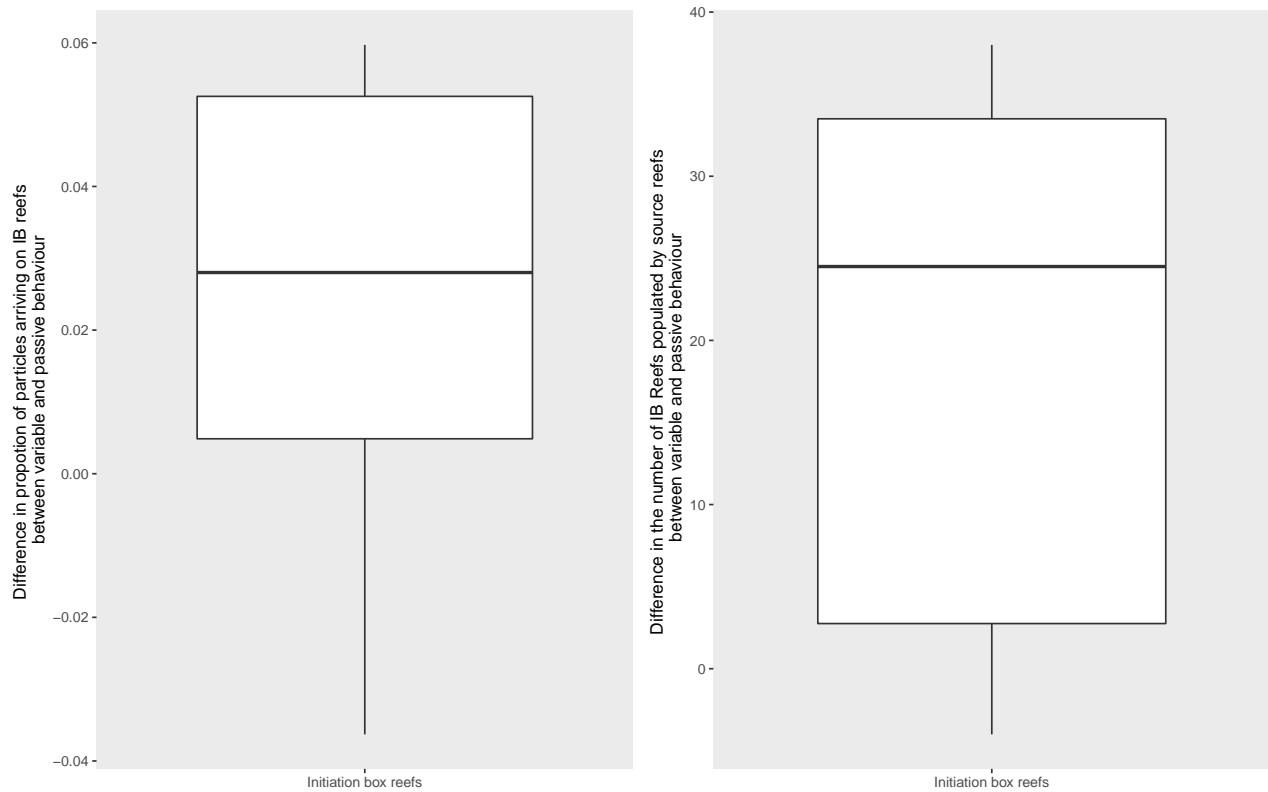


Figure 6. Difference in proportions of particles arriving at reefs in the initiation box (left, median=0.03, min=-0.04, max=0.06) and difference in the number of reefs in the IB receiving larvae from source reefs (right, median=24, min= -4, max=38) simulated assuming varying versus constant depths of pelagic larvae during a pelagic larval duration (PLD) of 25 days for different source reefs. Passive pelagic larval behaviour assumed larvae remained at 1m during the entire PLD: varying pelagic larval behaviour assumed that larvae remained at 1m during the first half of the PLD then sank to 5m for the remainder. Except for MacGillvray reef, North Direction reef and Lizard Island, more particles remained in the IB when simulated with variable depth.

References

- Babcock, RC, & Mundy, CN. (1992). Reproductive biology, spawning and field fertilization rates of *Acanthaster planci*. *Mar Freshwater Res*, **43**(3), 525–533.
- Bay, L. K., Crozier, R. H., & Caley, M. J. (2006a). The relationship between population genetic structure and pelagic larval duration in coral reef fishes on the Great Barrier Reef. *Mar Biol*, **149**(5), 1247–1256.
- Bay, L. K., Caley, M. J., & Crozier, R. H. (2008). Meta-population structure in a coral reef fish demonstrated by genetic data on patterns of migration, extinction and re-colonisation. *BMC Evol. Biol.*, **8**(1), 248.
- Bay, Line K., Buechler, K., Gagliano, M., & Caley, M. J. (2006b). Intraspecific variation in the pelagic larval duration of tropical reef fishes. *J. Fish Biol.*, **68**(4), 1206–1214.
- Bode, Michael, Bode, Lance, Choukroun, Severine, James, Maurice K, & Mason, Luciano B. (2018). Resilient reefs may exist, but can larval dispersal models find them? *PLoS biology*, **16**(8), e2005964.
- Botsford, Louis W, Hastings, Alan, & Gaines, Steven D. (2001). Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.*, **4**(2).
- Brothers, E. B., & Thresher, R. E. (1985). Pelagic duration, dispersal, and the distribution of Indo-Pacific coral reef fishes. *Chap. 2, pages 53–69 of: Reaka, M (ed), The Ecology of Deep and Shallow Coral Reefs. NOAA Symposia Series for Undersea Research.*, vol. 3. NOAA, Washington.
- Caballes, C. F., Pratchett, M. S, Kerr, A. M., & Rivera-Posada, J. A. (2016). The Role of Maternal Nutrition on Oocyte Size and Quality, with Respect to Early Larval Development in The Coral-Eating Starfish, *Acanthaster planci*. *PLOS ONE*, **11**(6), e0158007.
- Caley, M J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., & Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Annu Rev Ecol Evol Syst*, **27**(1), 477–500.
- Condie, S. A., & Hepburn, M. and Mansbridge, J. (2012). Modelling and visualisation of connectivity of the Great Barrier Reef. *Pages 9–13 of: Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia.*
- Cuif, M. and Kaplan, D. M., Fauvelot, C, Lett, C, & Vigliola, L. (2015). Monthly variability of self-recruitment for a coral reef damselfish. *Coral Reefs*, **34**(3), 759–770.
- Deáth, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27–year decline of coral cover on the Great Barrier Reef and its causes. *PNAS*, **109**(44), 17995–17999.
- Dight, I. J., Bode, L., & James, M. K. (1990). Modelling the larval dispersal of *Acanthaster planci*. I. Large-scale hydrodynamics, Cairns Section, Great Barrier Reef. *Coral Reefs*, **9**(3), 115–123.
- Dight, I.J. (1992). *Numerical simulation of larval dispersal and recruitment within the Great Barrier Reef and its application to the Acanthaster phenomenon and coral reef resource management*. Ph.D. thesis, James Cook University, Australia.
- Fabricius, K. E., Okaji, K., & Deáth, G. (2010). Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. *Coral Reefs*, **29**(3), 593–605.

- Frys, C., Saint-Amand, A., Le Hénaff, M., Figueiredo, J., Kuba, A., Walker, B., Lambrechts, J., Vallaey, V., Vincent, D., & Hanert, E. (2020). Fine-scale coral connectivity pathways in the Florida Reef Tract: Implications for conservation and restoration. *Front. Mar. Sci.*
- Hedgecock, D. (1994). Does variance in reproductive success limit effective population sizes of marine organisms. *Genetics and evolution of aquatic organisms*, 122–134.
- Hock, K., Wolff, N. H., Condie, S. A., Anthony, K., & Mumby, P. J. (2014). Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. *J. Appl. Ecol.*, **51**(5), 1188–1196.
- Hock, K., Wolff, N. H., Beeden, R., Hoey, J., Condie, S. A., Anthony, K., Possingham, H. P., & Mumby, P. J. (2016). Controlling range expansion in habitat networks by adaptively targeting source populations. *Conserv. Biol.*, **30**(4), 856–866.
- Hock, K., Wolff, N. H., Ortiz, J. C., Condie, S. A., Anthony, K. R. N., Blackwell, P. G., & Mumby, P. J. (2017). Connectivity and systemic resilience of the Great Barrier Reef. *PLoS Biol.*, **15**(11), e2003355.
- Hogan, J. D., Thiessen, R. J., Sale, P. F., & Heath, D. D. (2012). Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia*, **168**(1), 61–71.
- Holland, M. D., & Hastings, A. (2008). Strong effect of dispersal network structure on ecological dynamics. *Nature*, **456**(7223), 792.
- James, M. K., Armsworth, P. R., Mason, L. B., & Bode, L. (2002). The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proc. Royal Soc. B*, **269**(1505), 2079–2086.
- Jones, G. P., Milicich, M. J., Emslie, M. J., & Lunow, C. (1999). Self-recruitment in a coral reef fish population. *Nature*, **402**(6763), 802–804.
- Kininmonth, S. J., DeÁth, G., & Possingham, H. P. (2010). Graph theoretic topology of the Great but small Barrier Reef world. *Theor. Ecol.*, **3**(2), 75–88.
- Klein, M., Teixeira, S., Assis, J., Serrão, E. A., Gonçalves, E. J., & Borges, R. (2016). High interannual variability in connectivity and genetic pool of a temperate clingfish matches oceanographic transport predictions. *PLOS ONE*, **11**(12), e0165881.
- Largier, J. L. (2003). Considerations in estimating larval dispersal distances from oceanographic data. *Ecol. Appl.*, **13**(sp1), 71–89.
- Mellin, C., Lurgi, M., Matthews, S., MacNeil, M. A., Caley, M. J., Bax, N., Przeslawski, R., & Fordham, D. A. (2016a). Forecasting marine invasions under climate change: Biotic interactions and demographic processes matter. *Biol. Conserv.*, **204**, 459–467.
- Mellin, C., MacNeil, M. A., Cheal, A. J., Emslie, M., & Caley, M. (2016b). Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.*, **19**(6), 629–637.
- Miller, A. D., van Rooyen, A., Rašić, G., Ierodiaconou, D. A., Gorfine, H. K., Day, R., Wong, C., Hoffmann, A. A., & Weeks, A. R. (2016). Contrasting patterns of population connectivity between regions in a commercially important mollusc *Haliotis*

- rubra: integrating population genetics, genomics and marine LiDAR data. *Mol. Ecol.*, **25**(16), 3845–3864.
- Pratchett, M. S., Caballes, C. F., River a Posada, J. A., & Sweatman, H. P. (2014). Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). *Oceanogr Mar Biol: An Annual Review*, **52**, 133–200.
- Pratchett, M. S., Caballes, C. F., Wilmes, J. C., Matthews, S., Mellin, C., Sweatman, H., Nadler, L. E., Brodie, J., Thompson, C. A., Hoey, J., *et al.* (2017). Thirty years of research on crown-of-thorns starfish (1986–2016): scientific advances and emerging opportunities. *Diversity*, **9**(4), 41.
- Shanks, A. L. (2009). Pelagic larval duration and dispersal distance revisited. *Biol Bull*, **216**(3), 373–385.
- Shanks, A. L., Grantham, B. A., & Carr, M. H. (2003). Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.*, **13**(sp1), 159–169.
- Sobey, Rodney John, Harper, BA, & Stark, KP. (1977). *Numerical simulation of tropical cyclone storm surge*. James Cook University of North Queensland, Department of Civil & Systems Engineering.
- Stockhausen, W. T., Lipcius, R. N., & Hickey, B. M. (2000). Joint effects of larval dispersal, population regulation, marine reserve design, and exploitation on production and recruitment in the Caribbean spiny lobster. *Bull. Mar. Sci.*, **66**(3), 957–990.
- Thomas, C. (2015). *Modelling marine connectivity in the Great Barrier Reef and exploring its ecological implications*. Ph.D. thesis, Ecole Polytechnique de Louvain.
- Thomas, C. J., Lambrechts, J., Wolanski, E., Traag, V. A., Blondel, V. D., Deleersnijder, E., & Hanert, E. (2014). Numerical modelling and graph theory tools to study ecological connectivity in the Great Barrier Reef. *Ecol. Modell.*, **272**, 160 – 174.
- Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, **25**(1), 1–45.
- Uthicke, S, Logan, M, Liddy, M, Francis, D, Hardy, N, & Lamare, M. (2015). Climate change as an unexpected co-factor promoting coral eating seastar (*Acanthaster planci*) outbreaks. *Sci. Rep.*, **5**.
- Vercelloni, J., Caley, M. J., & Mengersen, K. (2017). Crown-of-thorns starfish undermine the resilience of coral populations on the Great Barrier Reef. *Global Ecol. Biogeogr.*, **26**(7), 846–853.
- Wolanski, E. (1994). *Physical oceanographic processes of the Great Barrier Reef*. CRC Press.
- Wolfe, K., Graba-Landry, A., Dworjanyn, S. A., & Byrne, M. (2015). Larval starvation to satiation: Influence of nutrient regime on the success of *Acanthaster planci*. *PLOS ONE*, **10**(3), e0122010.