Coral Reefs (2025) 44:1–13
https://doi.org/10.1007/s00338-024-02563-z

REPORT

Larval dispersal predictions are highly sensitive to hydrodynamic modelling choices

Severine Choukroun[1] · **Owen B. Stewart**[2] · **Luciano B. Mason**[3] · **Michael Bode**[2,4]

Received: 11 January 2024 / Accepted: 9 September 2024 / Published online: 2 December 2024

Abstract Larval dispersal is a critical ecological process in marine ecosystems, responsible for connecting and replenishing populations in patchy habitat. Because empirical measurements of larval dispersal are very challenging, coupled biological and oceanographic simulations ("biophysical models") of larval dispersal are commonly used to answer ecological questions and support conservation management decisions. In the process of creating biophysical models, a series of choices must be made that do not have a single correct answer—sometimes because the oceanographic or ecological processes are uncertain; sometimes because trade-offs are required between different goals (e.g. computational time versus spatial resolution). In this paper, we demonstrate that larval dispersal estimates at management scales are strongly affected by these choices. Using three different hydrodynamic models of the Great Barrier Reef, we estimated the dispersal of crown-of-thorns starfish larvae in the spawning seasons between 2018 and 2021. Despite sharing similar physical forcings and using similar models of larval behaviour, we find that the different hydrodynamic models produce divergent predictions of larval dispersal between the reefs. If used to support crown-of-thorns starfish control decisions, these different predictions would recommend different priority reefs. Our results caution against the use of single models of larval dispersal, and suggest that multi-model ensembles may offer a valuable new perspective on dispersal patterns in marine environments.

Keywords Crown-of-thorns starfish · Biological oceanography · Connectivity · Coral reefs

Introduction

The process of larval dispersal is critical to the dynamics, structure, and biodiversity of marine ecosystems (Leis and McCormick 2002; Cowen and Sponaugle 2009; Jones 2015). When suitable habitat is patchily distributed, larval dispersal is often the only process that connects spatially discrete populations, and therefore creates essential demographic and genetic links between patch populations. In ecosystems where habitat is ephemeral or frequently disturbed, larval dispersal enables the colonisation and re-colonisation of empty habitat, supporting the recovery and persistence of species in dynamic environments (Weersing and Toonen 2009; Almany et al. 2017).

To understand and manage marine ecosystems, we therefore need to understand the patterns and dynamics of larval dispersal (Botsford et al. 2001; Armsworth 2002; Pelc et al. 2010). However, it is extremely challenging to obtain empirical data on larval dispersal—the process takes place over large spatial and temporal scales, while the larvae

---

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-024-02563-z.

✉ Michael Bode
michael.bode@qut.edu.au

Severine Choukroun
severine.choukroun@jcu.edu.au

Owen B. Stewart
owen.stewart@connect.qut.edu.au

[1] Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Townsville, QLD 4810, Australia

[2] School of Mathematical Sciences, Queensland University of Technology, Brisbane 4000, Australia

[3] Rocky Point, Australia

[4] Securing Antarctica's Environmental Future, Queensland University of Technology, Brisbane 4000, Australia

are often too small and too numerous to track individually (Jones 2015). Despite considerable innovation and effort, it has proven difficult to conduct experiments or make observations that accurately capture the entire process (D'Aloia et al. 2015; Williamson et al. 2016; Bode et al. 2019).

To resolve this empirical data gap, biological oceanographers have created sophisticated "biophysical" simulation models (Dight et al. 1990; James et al. 2002; Mitarai et al. 2008). Biophysical models integrate biological and hydrodynamic sub-models to resolve the dynamics of larval dispersal. Advances in high-performance computing have allowed increasingly fine-scale hydrodynamic models, across thousands of kilometres of seascape. At the same time, the models' biological components have steadily improved, and can now simulate the complex behaviour of billions of dispersing larvae based on empirical measurements of their behaviour and capabilities. Biophysical models are now routinely incorporated into ecological research (Burgess et al. 2021), fishery management decisions (Whomersley et al. 2018; Criales et al. 2019; Nolasco et al. 2022), and marine spatial management tools (Beger et al. 2010; Kininmonth et al. 2011; Bode et al. 2012).

However, at each step in the process of creating a biophysical model of larval dispersal, the modeller is faced with a set of difficult choices, between options that are equally reasonable and defensible. Broadly speaking, there are three types of decisions that modellers must commonly make.

First, there are different defensible ways to computationally model ocean currents. For example, different numerical techniques can be used to solve the equations of fluid motion. These include finite element, finite volume, finite difference, boundary element, and Euler–Lagrangian methods (Durran 2010). Similarly, sub-grid scale processes like turbulence can be approximated using multiple defensible models (e.g. k-epsilon or Mellor-Yamada), whose performance will vary depending on the flow conditions being modelled (Burchard et al. 1998).

Second, choices need to be made about uncertain biological processes. For example, depth distribution is an important determinant of larval movement, and is believed to vary with time, space, and larval age (Treml et al. 2015). Unfortunately, this distribution is almost completely unknown for most important species. Two other larval processes are critical but uncertain: the rate of larval mortality, and the rate at which they achieve "competency"—essentially, when a larva becomes sufficiently developed to settle on a reef (Moneghetti et al. 2019).

Third, modellers need to choose how to allocate their computational resources. Larval dispersal simulations require models that are both very high resolution (since the processes of larval retention and settlement are often driven by small-scale eddy structure around reefs (Andutta et al. 2012; Black 1993)) and large scale (since larvae can travel hundreds of kilometres (Williamson et al. 2016; Almany et al. 2017)). These contrasting demands quickly produce computational constraints. The most important choice is whether to use a depth-integrated model with a high spatial resolution, or a 3D model with lower spatial resolution. Hydrodynamic models discretise the ocean along both the horizontal and vertical dimensions. Models that offer better horizontal resolution generally have lower vertical resolution, and may even be depth-averaged—that is, they may ignore depth variation entirely (Saint-Amand et al. 2023b). While the former assumption is clearly more accurate, it places substantial computational demands that are often met by reducing complexity elsewhere (e.g. by reducing the model's horizontal resolution). Particularly when using adaptive mesh sizes, depth-averaged hydrodynamic models are able to deliver far higher horizontal spatial resolution, which may be particularly important for modelling critical connectivity pathways like self-recruitment, or diffuse local dispersal patterns (Saint-Amand et al. 2023a; b).

Any one of these broad issues can force modellers to choose between equally defensible alternatives. Any larval dispersal modelling project could therefore produce many different predictions, none of which represents an unambiguously superior choice to the others (Bode et al. 2018). The fact that different modelling choices produce different predictions about larval dispersal is relatively well-known, but primarily for uncertain biological assumptions, where a number of sensitivity analyses have been undertaken (Simons et al. 2013; Treml et al. 2015; Burgess et al. 2021). The sensitivity of model predictions to choices made during the hydrodynamic modelling process has been studied before, generally with a focus on choices made within a single hydrodynamic modelling framework. For example, the effect of increasing the model resolution has been studied a number of times (Dauhajre et al. 2019; Saint-Amand et al. 2023a; b). Fewer analyses compare the predictions of different hydrodynamic models (Bode et al. 2018; Ross et al. 2020), because the hydrodynamic components of biophysical models are the most time-consuming to create, to parameterise, and to simulate. Essentially, it is difficult enough to create a single hydrodynamic model—researchers rarely create and compare multiple hydrodynamic models.

Consequently, there is a need for direct comparisons between competing hydrodynamic models to assess the sensitivity of predictions to defensible choices made during hydrodynamic modelling. In this paper, we undertake this challenge by comparing the larval dispersal predictions made by different hydrodynamic models. Using crown-of-thorns starfish (COTS) populations on Australia's Great Barrier Reef (GBR) as a case-study, we create parallel models of COTS larval dispersal, forced by flow fields generated by three different hydrodynamic models. We use these models to create parallel simulations of dispersal events during the

2019, 2020, and 2021 spawning seasons, across the whole GBR. Using these simulations, we compare the predicted patterns of larval dispersal, and consider how the divergence between the predictions will affect management decisions.

Material and methods

Study system and species

The Great Barrier Reef is a UNESCO World Heritage Area, recognised as one of the most biodiverse and complex ecosystems on the planet. It is an irreplaceable source of food, recreation, and cultural significance for indigenous and local communities. Furthermore, it plays an enormous role in the Australian economy, generating billions of dollars in tourism revenue and supporting tens of thousands of jobs (Deloitte 2013).

In geomorphological terms, the GBR comprises thousands of coral reefs, shoals, and islands on the shallow, wide continental shelf of eastern Queensland, Australia. The GBR is the largest barrier reef system on the planet, stretching across 2300 kms of coastline, and extending from the mainland coast to the shelf break. Its hydrodynamics are driven by tidal, wind, thermohaline forcing, and its interface with the complex circulation of the Coral Sea, creating highly variable flow patterns as they move across and around the reefs. High-resolution data and modelling are required to accurately capture the flow dynamics in the highly variable bathymetry of the reef-shelf complex (Bode et al. 1997).

The crown of thorns starfish *Acanthaster planci* is a venomous invertebrate predator that feeds on coral polyps. Although it is native to the GBR, high densities of COTS can decimate the live coral cover on reefs, and periodic irruptive outbreaks of the species have been identified as one of the major contributors to wide-scale coral loss on the GBR in recent decades (De'Ath et al. 2012; Vercelloni et al. 2017). The Australian government spends millions of dollars each year attempting to control COTS outbreaks on the GBR. A large part of this investment is focused on the targeted physical removal of COTS adults from outbreak reefs (Westcott et al. 2020).

Larval dispersal plays a crucial role in the dynamics of regional-scale outbreaks. COTS larvae are planktonic, and can disperse for 2–4 weeks before they settle on a new reef. Larval dispersal from outbreak reefs likely produces settlement pulses on downstream reefs, potentially driving outbreaks in subsequent years (Matthews et al. 2020). Understanding COTS larval dispersal may be needed to predict how outbreaks evolve, and to prioritise decisions about where and when to control COTS populations.

Hydrodynamic modelling

Three competing numerical hydrodynamic models were used to hindcast coastal water currents in the GBR (Table 1). We label these models *GBR1*, *SLIM*, and *GBRL*. Each was used to compute flow fields for the entire GBR World Heritage Area, as well as a buffer of the surrounding Coral Sea. Dispersal simulations were run in 2018–2019, 2019–2020, and 2020–2021.

Each model incorporates as much physical information as possible. This includes: (i) regional circulation and tidal conditions at the boundary—GBR1 and SLIM are forced at the open boundary by a regional model, while GBRL has developed its own regional Coral Sea model that provides the open boundary forcing; (ii) bathymetry of the reef-shelf complex; and (iii) measurements of surface atmospheric conditions at a high spatiotemporal resolution, including wind, surface pressure, and heat fluxes (GBR1 only).

Resolving the circulation in the GBR requires the application of a suite of nested models, resolving in turns the Coral Sea, the continental shelf, and the reef-scale circulation. While the hydrodynamic models applied in the study do not assimilate data directly, GBR1 and SLIM are nested within GBR4 which is in turn forced by the Ocean Model, Analysis and Prediction (OceanMAPS) at 1/10° (Chamberlain et al. 2021), and by the Australian Community Climate and Earth System Simulator (ACCESS-R 12 km resolution). Both incorporate satellites and in situ observations using a data assimilation system. GBRL has developed its own regional Coral Sea model, forced by wind stress and sea levels signals synthetised from coastal and island tide gauges. Performing further data assimilation at the complex coastal and reef processes scale would require the application of

Table 1 Physical and biological characteristics of the three biophysical models used in this study

Model name	Horizontal resolution	Vertical resolution	Temporal resolution (LPT)	Baroclinic/barotropic	Numerical scheme	Depth of egg release	Period modelled
GBR1	1 km	48 z-layers,	60 min	Baroclinic	Finite difference	5 m	2018–2019
SLIM	250 m–4 km	Depth-averaged	60 min	No depth	Finite element	N/A	2019–2020,
GBRL	1.85 km	6 σ-layers, barotropic	60 min	barotropic	Finite difference	5 m	2020–2021

Gaussian nonlinear and fully Bayesian nonlinear techniques that are beyond the scope of this study.

Despite their similarities, the models differ in important ways that illustrate the types of trade-offs required when modelling larval dispersal at a fine spatial resolution, across a large geographic region. The *GBR1* model was developed and is maintained by the CSIRO Coastal Environment Modelling team. The 3D baroclinic model solves currents using a finite-difference numerical scheme (Herzfeld 2006). It has a 1 km horizontal grid and 48 vertical layers, with sub-grid scale parameterisations that have been tailored to account for the impact of the GBR's complex reef matrix on currents. The model's vertical structure allows for wetting and drying of surface cells. More details of the model are available in references (Herzfeld 2006; Steven et al. 2019).

SLIM is a depth-averaged barotropic model, simulated on an unstructured mesh and solved using a finite-element numerical scheme (Lambrechts et al. 2008). Its 2D horizontal scheme and variable grid size allow for a very high-resolution description of the most variable and important flow-fields, particularly the narrow channel transport between reefs. For the GBR, our set-up of *SLIM* uses 880,768 triangles varying in size between 250 m and 4 km, with the smaller grids being applied close to the reef and the coast. For our application of SLIM, wetting and drying is not modelled. More details about the model are available in references (Lambrechts et al. 2008).

The *GBRL* model is a 3D barotropic model, solved using a finite-difference numerical scheme. Like *GBR1*, it incorporates a (different) sub-grid scale parameterisation scheme (Bode et al. 1997) developed particularly for flows in the GBR shelf. The model is solved on a 1.85 km grid, with 6 vertical σ-layers, with the surface cell allowing for wetting and drying. More details about the model are available in references (James et al. 2002; Luick et al. 2007).

Larval dispersal simulations

Larval dispersal was simulated using individual-based models, forced by the flow fields from each respective hydrodynamic model. We modelled the release of COTS eggs from 3861 individual patch reefs, whose outlines were based on digital shape files provided by the Great Barrier Reef Marine Park Authority. To estimate the probability of larval exchange between reefs, eggs were released randomly over the reef area. For the two 3D models (*GBR1* and *GBRL*) the eggs were released at a depth of 5 m; release depth could not be chosen for the depth-averaged *SLIM* model. In GBRL and SLIM, the releases were timed over a 24 h period between 4 and 4 pm the next day on the 1st, 7th, 14th, 21st, 28th of December and January 2018–19, 2019–20, 2020–21. For GBR1, the release was timed between 10 am and 3 pm, releasing 10 particles randomly in the vicinity of each reef area every 30 min and repeated daily for 10 days, starting on the 1st and 15th of December and January. Particles which were randomly allocated outside the 20 m depth isobath were randomly relocated.

For all models, eggs were positively buoyant for the first 24 h after release, after which they became neutrally buoyant for the remainder of dispersal. The larval trajectories are outputted hourly over 45 days with their instantaneous location, between December and March inclusive, the most likely COTS spawning period (Caballes et al. 2021).

To settle on a reef, these COTS larvae must survive, become competent (i.e. develop the ability to settle), and be carried into the near vicinity of a reef. The dynamics of COTS survival and competency were based on observational data for COTS. Following Moneghetti and colleagues (Moneghetti et al. 2019), we model the probability of a larvae being alive and competent using piecewise models: a Weibull-Weibull for the survival and a Weibull-exponential for competency, fitted to observations (Pratchett et al. 2017). This model assumes a rapid and almost complete onset of competency at 14 days post-release (Fig. 1), which follows the available evidence, but likely underestimates variation in the process. The settlement behaviour of late-stage COTS larvae is not understood, but we follow previous models (e.g. Hock et al. 2017) which assume that they settle if they are carried within 1 km of a reef during a competent period.

We applied this probability function to produce a settlement window for each particle, which allowed us to predict the destination of every COTS larvae released on a given spawning date. We then combined the results into annual probability matrices, called *connectivity matrices*. The elements c_{ijt}^{m} of these matrices represent the proportion of larvae that are released from reef i that survive, become competent, and settle on reef j, in release event t, as predicted by each of the biophysical models (m).

Efforts were made to keep the biological components of the models as similar as possible, to focus attention on the impacts of the different hydrodynamic models. However, some differences could not be avoided. In particular, the egg release times of the GBRL and SLIM models were slightly different to those of GBR1—a consequence of the hydrodynamic models being maintained by different research groups.

Comparing the three biophysical models

We measure the differences between the predictions of the three different biophysical dispersal models with three sets of comparisons. The first set focuses on the connections between the reefs: the c_{ijt}^{m} values. Comparison 1 visualises the entirety of the connectivity matrices, and comparison 2 produces graphs of reefs linked by connectivity. The GBR connectivity matrices contain millions of edges, and

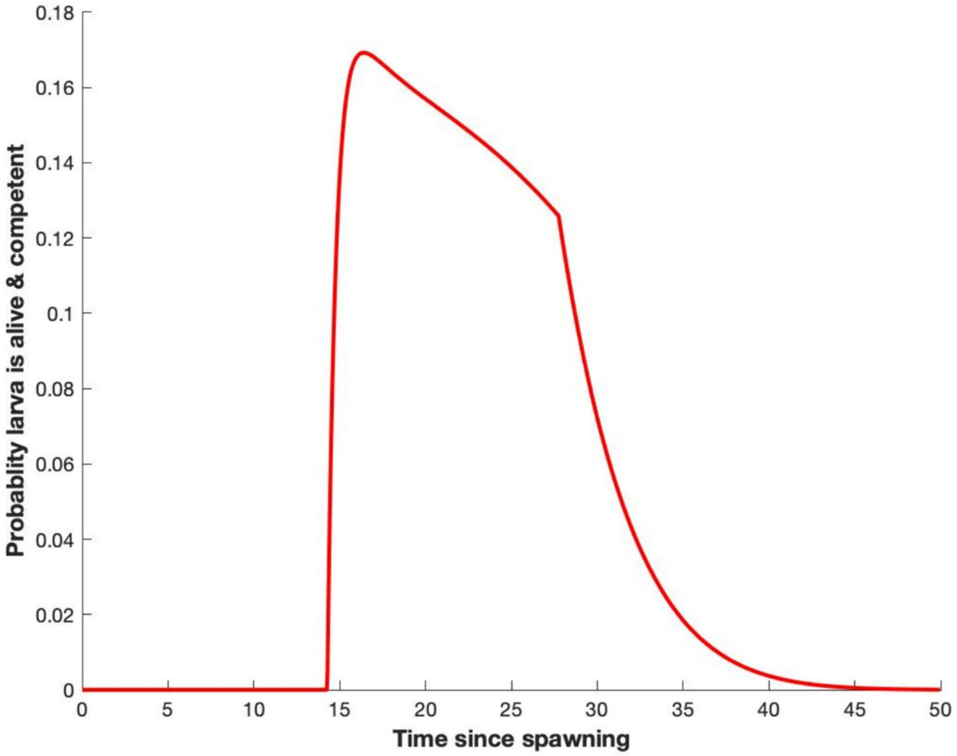

Fig. 1 Proportion of larvae that are both competent and remain alive as a function of days since spawning. This proportion is conditional on not yet having settled. Before 15 days, larvae are too immature to settle, after 40 days, almost all larvae (> 99%) have died

so an effective visualisation of the entire graph—i.e. one that provides an understanding of the network structure, and allows ready comparison between models) is challenging. We therefore focus on sets of small numbers of reefs, in different locations across the GBR.

Comparison 3 calculates the size of the aggregate absolute difference between pairs of models and pairs of years, relative to the total amount of dispersal occurring in the two models. We do not want small differences between low-value connections to appear important (e.g. if $c^n_{ij} = 10^{-5}$, but $c^m_{ij} = 10^{-7}$), and so we base the pairwise comparison (i.e. between c^m_{ijt} and c^n_{ijt}) on the absolute difference between the two model predictions:

$$\Delta^{mn} = \frac{1}{T}\frac{\sum_i \sum_j \sum_t \left| c^m_{ijt} - c^n_{ijt} \right|}{\sum_i \sum_j \sum_t c^m_{ijt} + c^n_{ijt}} \tag{1}$$

The metric Δ^{mn} can be thought of as the number of released larvae that the two models m and n disagree about, as a proportion of the total larvae released in each of the T simulated release events. Equation 1 sets a very precise definition for the amount of agreement between the models—it is not enough for two models to agree approximately on where larval exchange occurs. We therefore repeated this comparison with a less precise definition of agreement (*Supporting Information*).

The second set of comparisons focus on the reefs themselves. In 2017, Hock and colleagues (Hock et al. 2017) proposed a method for identifying priority reefs on the GBR. Their analyses were based on whether five network metrics—calculated using the c^m_{ijt} values of connectivity matrices—were above their median value. We investigate four that are widely used in ecological network analysis. The first is the node out-degree: the number of different reefs that each reef has a direct connection to. The second metric is the total node-strength of each reef: the sum of all outward connections from that reef. The third metric is the number of "strong" links. That is, links that provided more than 10% of settlement to any other reef (including self-recruitment). The fourth metric is the size of the out-component of each reef: the number of reefs that could eventually be reached by the descendants of individuals from each reef, even over multiple generations. We modify this final metric to calculate the number of reefs that could be reached within 3 generations, since almost all of our matrices are irreducible (i.e. the out-component of each reef is the entire system). Reducible matrices (i.e. those in Hock et al. 2017) are generally the result of simulations that release too few larvae. We calculate the values of the metrics for each of the three different hydrodynamic models, and measure the overlap between the priority sets—those reefs with above-median network values. Since we would expect about 25% of above-median values to coincide based on random chance, we compare the observed overlap to this expectation.

Our final set of comparisons are at a regional scale—larger than an individual reef, but smaller than the entire GBR. We use spectral community detection methods from network theory (Girvan and Newman 2002) to identify groups of reefs within the GBR that have high modularity. That is, groups of reefs that exchange a lot of larvae among themselves, but which do not exchange as much larvae with reefs in other groups (Saint-Amand et al. 2023a).

Results

The hydrodynamic models were validated against sea surface elevation and current measurements, from seven locations across the Great Barrier Reef. Observations were produced by long-term oceanographic moorings equipped with Acoustic Doppler Current Profilers, from the Integrated Marine Observing System (IMOS) network. Modelled and observed seas surface elevation are in “very good” agreement (Table 2) while the velocity is in “good” to “very good” agreement. In order to evaluate the model’s skill against each other, we used a Taylor diagram that provides a statistical summary of model performances (SI Figure S13), and ADCP comparisons (SI Figure S14–S16). The results showed that the models performed relatively similarly to each other, and exhibited reasonably close agreement with observations.

The larval dispersal patterns predicted by the three models are broadly congruent at the scale of the entire GBR (Fig. 2). Dispersal is strongest between nearby reefs, and decays in strength with distance. The distance decay of dispersal strength is somewhat slower among the northern reefs. The summary statistics, however, reveal substantial variation in connectivity patterns between years and between hydrodynamic models (Table 3).

When comparing between different hydrodynamic models, we observe the most alignment between *GBRL* and *SLIM*, and the greatest divergence between *GBR1* and the other two models. In general, the difference between two models run for the same year is larger than the difference between two different years for the same model. This is concerning, since different models would ideally make similar predictions about dispersal patterns for a particular year, whereas we expect connectivity patterns to vary between years.

The comparisons in Fig. 2 and Table 3 summarise the results across the whole GBR. When we focus on smaller regions (Fig. 3), the divergence between the predictions of the different hydrodynamic models becomes more apparent. Figure 3 shows spatial connectivity patterns from a single year (2018), visualised as graphs, for three different regions of the GBR. In each region, the predictions of the three different hydrodynamic models vary considerably. Many connections between reefs only occur in a single model. The general patterns created are also different. One model predicts large amounts of connectivity, while another predicts fewer, weaker connections. These exemplars are not unusual among locations on the GBR (SI Figures S1–S10).

When we calculate the network metrics for each reef on the GBR, we observe a similarly low amount of agreement between the predictions of the three models (Fig. 4). The rank correlation between the different network metrics is low to moderate; as with the reef-to-reef connections (Table 4). However, in this case, the similarity is not always greatest between *GBRL* and *SLIM*. When we use these metrics to predict high-value reefs, following the median threshold of Hock and colleagues, we observe only limited overlap between the priority sets—generally between 30 and 40% of the reefs are classified as priorities by both models. This value is larger than random expectation, (25%, with 95% confidence bounds of 24–26%) but not dramatically larger. The location of these highest

Table 2 Summary statistics comparing the three models to observations from moorings. Results show linear correlation, and centred root-mean-squared deviation (CRMSD). Comparisons were undertaken at seven sites across the GBR: the Capricorn Channel (GBRCCH), Heron Island (GBRHIS), Lizard Island (GBRLSL), Myrmidon Reef (GBRMYR), One Tree East (GBROTE), Palm Passage (GBRPPS), and Yongala (NRSYON)

	SLIM		GBR1		GBRL	
Site	Correlation	CRMSD	Correlation	CRMSD	Correlation	CRMSD
GBRCCH	0.935	0.304	0.937	0.260	0.982	0.127
GBRHIS	0.972	0.150	0.983	0.128	0.984	0.122
GBRLSL	0.798	0.361	0.797	0.362	0.975	0.146
GBRMYR	0.739	0.448	0.736	0.446	0.894	0.281
GBROTE	0.966	0.160	0.984	0.105	0.954	0.181
GBRPPS	0.982	0.105	0.980	0.110	0.982	0.106
NRSYON	0.766	0.396	0.777	0.362	0.822	0.365

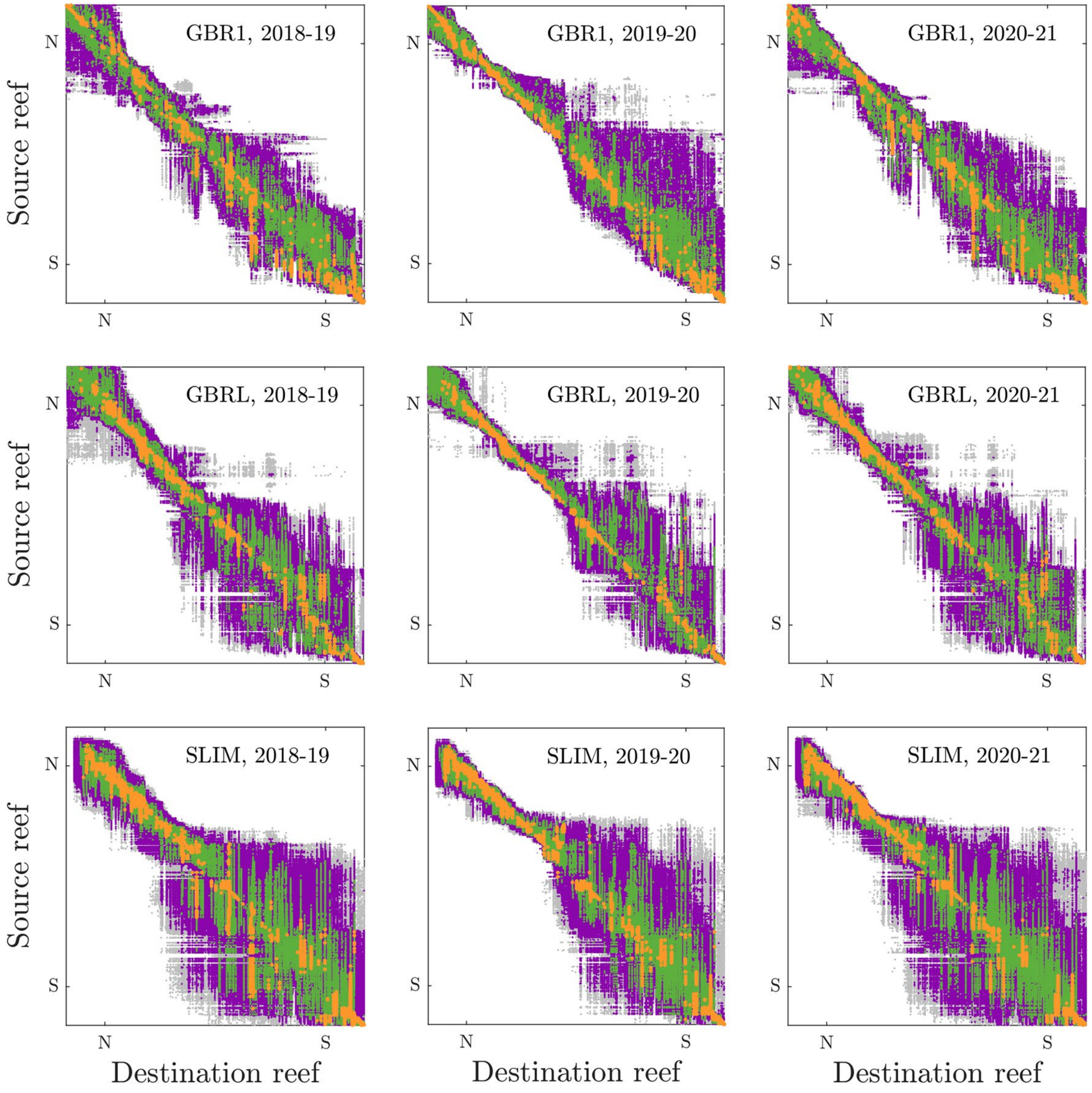

Fig. 2 Each row of panels shows connectivity matrices for three different years, predicted by one of the hydrodynamic models. Reefs are ordered latitudinally, from north (N) to south (S). The first row shows the GBR1 model, the second shows GBRL, the bottom shows SLIM. Each point represents a single nonzero connection, colour-coded by the value of c^{m}_{ij}. Purple points are in the upper 25 percentile of nonzero connections, green points are in the upper 5%, and orange points are in the upper 0.5%

performing reefs have commonalities between some models, for some metrics, but not reliably (SI Figure S17).

We can also compare the model predictions at a regional scale, by identifying strongly connected communities from among the GBR reefs. Figure 5 shows the communities identified by an analysis of the connectivity matrices, for each of the three different biophysical dispersal models in 2019–2020 (SI Figures S11–S12 repeat this process for the other two dispersal years). While there are similarities between the groups, the overall agreement is only 20% stronger than random expectation (*Supporting Information*).

Discussion

Modelling the ocean currents that flow through coastal marine ecosystems and drive the dispersal of pelagic larvae is a challenge, which is at the leading edge of both computational oceanography and marine ecology. During the process of model construction, biophysical modellers

Table 3 Summary difference statistics ($\Delta^{mn}_{t_1t_2}$) between hydrodynamic models m and n in years t_1 and t_2. Values range between zero (where the two models make identical predictions for all larvae) and one (where the models disagree entirely). Cells are coloured from most similar to least similar (blue–green–yellow–red)

		GBR1			*GBRL*			*SLIM*		
		2019	*2020*	*2021*	*2019*	*2020*	*2021*	*2019*	*2020*	*2021*
GBR1	*2019*	0	0.71	0.64	0.86	0.89	0.87	0.81	0.85	0.82
	2020		0	0.64	0.84	0.84	0.83	0.79	0.78	0.78
	2021			0	0.84	0.85	0.84	0.79	0.80	0.78
GBRL	*2019*				0	0.56	0.41	0.69	0.71	0.70
	2020					0	0.41	0.74	0.70	0.73
	2021						0	0.69	0.69	0.69
SLIM	*2019*							0	0.38	0.30
	2020								0	0.31
	2021									0

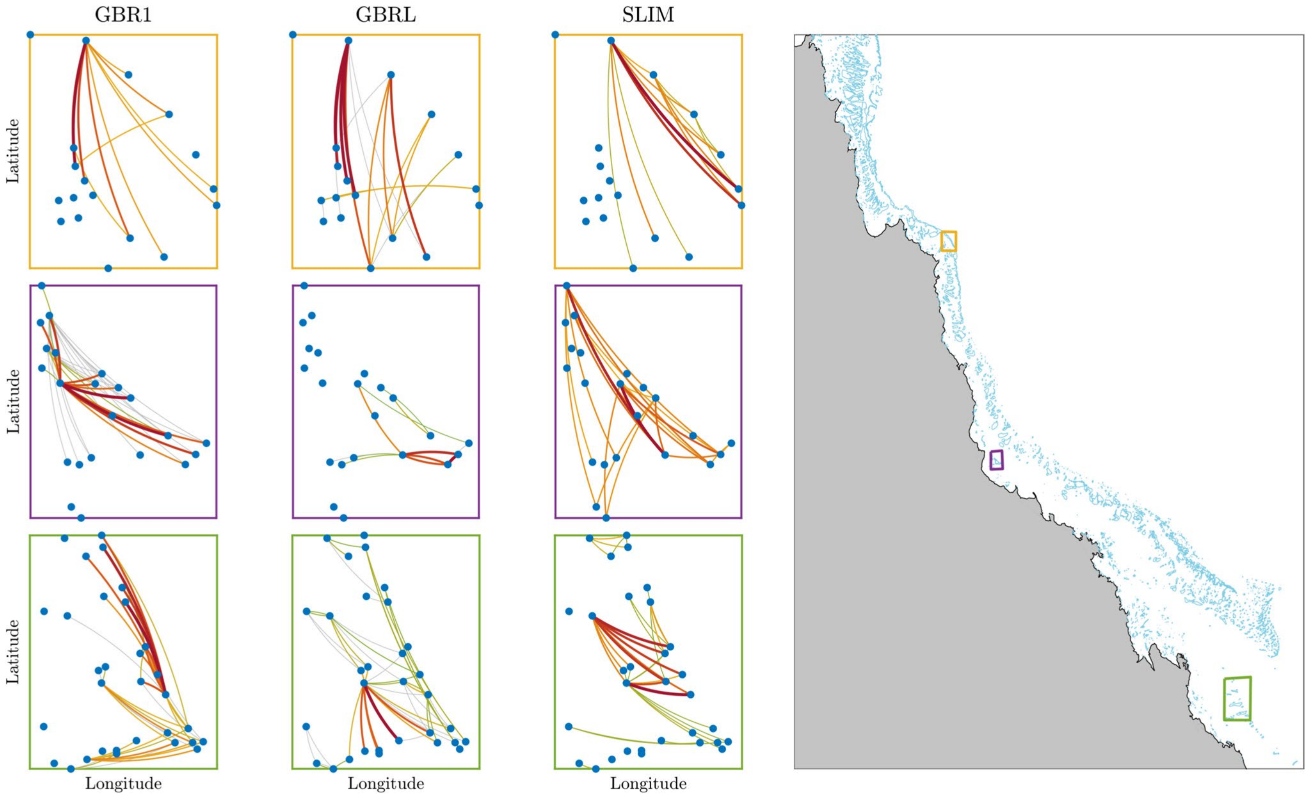

Fig. 3 Local-scale connectivity patterns among three groups of reefs, for each of the three biophysical models. Top row shows connections among 18 reefs in the northern section; middle row shows connections among 31 reefs in the central section; bottom row shows connections among 22 reefs in the southern Capricorn Bunkers region. Lines show the strongest 10% of connections in each location, with colours showing the relative strength from red (strongest) to green (weakest)

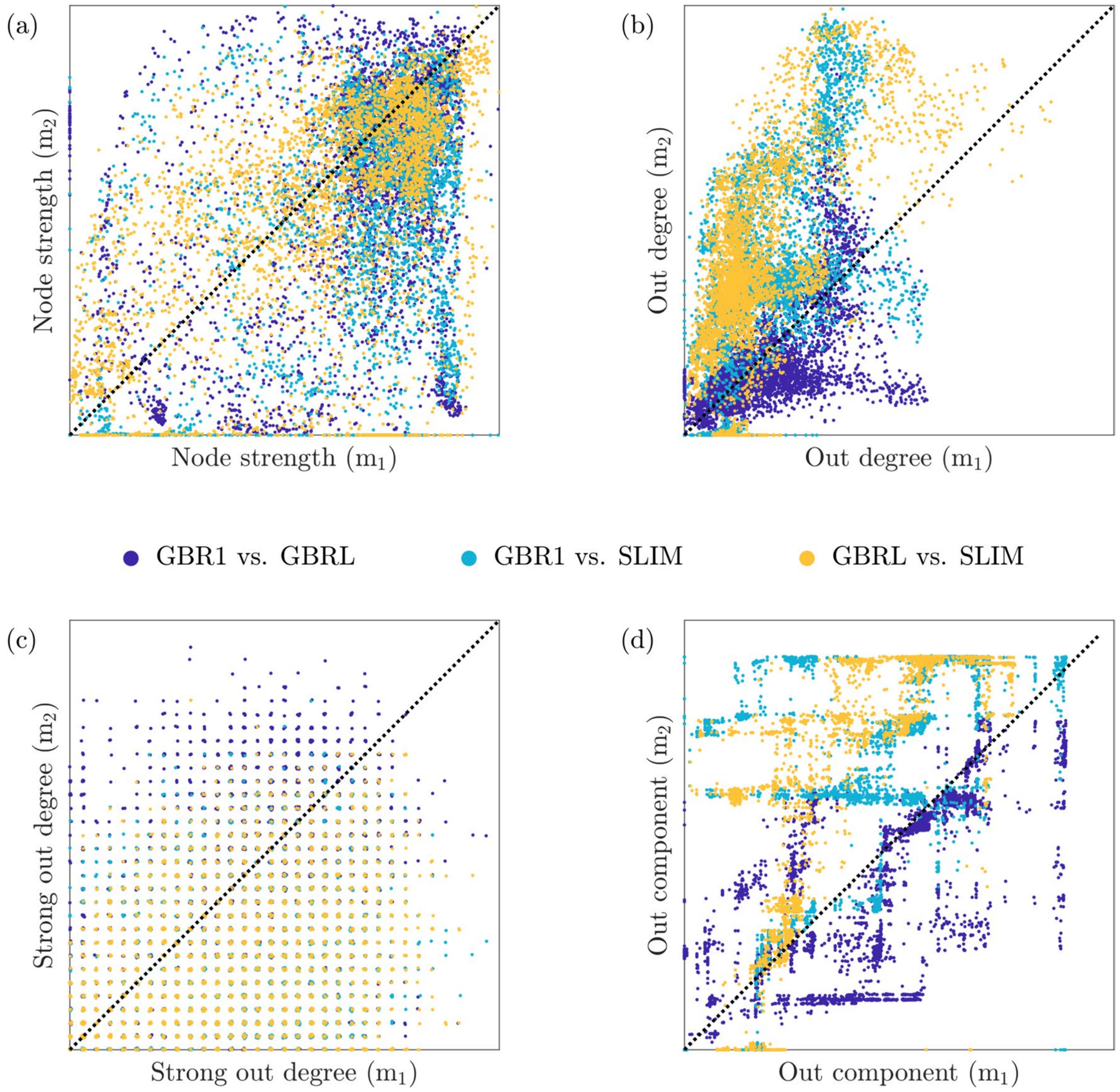

Fig. 4 Each point in these panels shows a network metric calculated for an individual reef on the GBR, compared between two different hydrodynamic models. The three different colours show pairwise comparisons between the three hydrodynamic models. **a** Compares node strengths. **b** Compares node out degrees. **c** Compares node strong out degrees. **d** Compares the size of each node's out component

are faced with a series of choices with no single correct option, due either to unavoidable trade-offs, or to unresolved uncertainty. Although these choices are encountered in both the biological and hydrodynamic components of dispersal modelling, the sensitivity of model predictions to hydrodynamic choices is less studied.

At the scale of the entire GBR, our three different hydrodynamic models show broad agreement, and predict similar overall dispersal patterns. Connections are strongest between reefs in the same region (i.e. within a few hundred kilometres of each other), and the reefs in the northern GBR are connected at greater distances than those in the southern GBR (Fig. 2). However, at smaller scales, the strength of different dispersal pathways, and the relative larval dispersal strengths of different reefs (Fig. 3; SI Figures S1–S10), are substantially different. This smaller scale is most relevant to managers, whose decisions are more likely to be affected by the dispersal patterns in the immediate vicinity of their actions. Our three models also disagree on which reefs should be prioritised for COTS control actions (Fig. 4; Table 4).

These results represent the first in-depth comparison between biophysical models that are based on different hydrodynamic models of the same coastal marine ecosystem. It is possible that more agreement would be observed between models of other marine ecosystems, even in other

Table 4 Blue columns show the rank correlation between the network metrics calculated for each reef in the GBR, according to different hydrodynamic models. Green columns show the fractional overlap between priority sets calculated based on different hydrodynamic models. Both values are relatively low

	Rank correlation		*Overlap percentage*	
	GBRL	*SLIM*	*GBRL*	*SLIM*
Node Out Degree				
GBR1	0.30	0.28	0.30	0.30
GBRL		0.52		0.35
Node Out Strength				
GBR1	0.63	0.59	0.36	0.33
GBRL		0.61		0.34
Node Out Component				
GBR1	0.70	0.62	0.40	0.37
GBRL		0.78		0.46

coral reef systems. The GBR is characterised by high-volume tidal flows across a wide continental shelf, whose drainage is complicated by shallow-water reefs separated by high-velocity channels. These unique dynamics may amplify the differences between the model predictions. Moreover, the differences we observe are primarily at the reef-to-reef scale; from a sufficient distance, the models produce quite similar dispersal patterns. Our findings therefore specifically caution against using these models to make decisions about individual reefs—which reefs should become marine reserves, for example, or which reefs should be prioritised for coral restoration projects. It is possible that comparisons between the models at larger scales (e.g. larval exchange between clusters of reefs, or regions of the GBR), or comparisons that focus on distance and direction (e.g. dispersal kernels fitted to the model predictions) would show less divergence. However, we note that our two limited attempts to compare the models at a larger spatial scale did not resolve their differences particularly well (Fig. 5).

Despite our attempts to harmonise the larval component of the three biophysical models, there were differences in the timing and number of egg releases between GBR1, and GBRL/SLIM. Slight though these differences were (releases were only a few days apart, and within the same spawning window), larval dispersal predictions are known to be highly sensitive small differences in timing (Donahue et al. 2015). As a consequence, we may be overestimating the differences

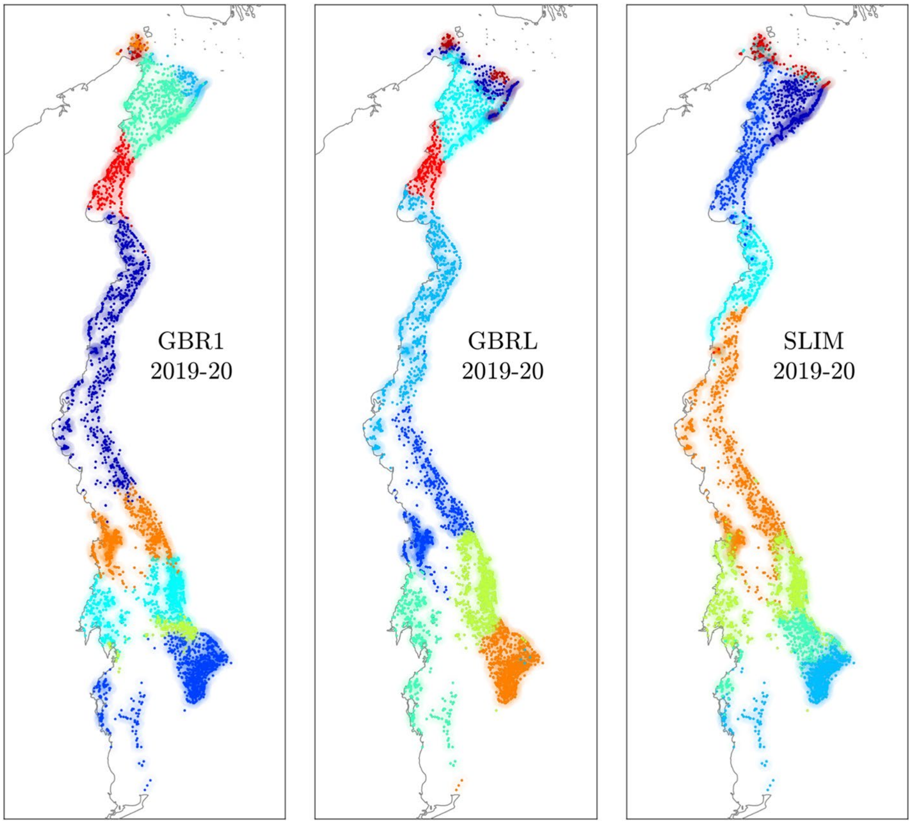

Fig. 5 Dispersal communities in the GBR with high modularity. Reefs with the same colour belong to the same community. Colouring is not consistent across panels, because the communities are not directly analogous. Results are compared for GBR1, GBRL, and SLIM

between GBR1 and the other two models. The differences between the model predictions could be partly resolved by data assimilation being applied to the fine-scale hydrodynamic models, rather than their forcings.

The differences between our models parallel the results of other studies that compared the larval dispersal predictions made by multiple hydrodynamic models. Ross and colleagues (Ross et al. 2020) used two comparable hydrodynamic models to predict the dispersal of deep-sea invertebrates, and found substantial differences between their predictions. These differences went beyond slight differences in connectivity patterns—the authors measured notably different predictions in the average distance travelled by larvae, the spatial extent of dispersal from any given reef, and even in the mean direction of travel by larvae. Bode et al. (2018) performed an *ex post* analysis of two quite different dispersal models on the GBR (Bode et al. 2018; Mumby et al. 2018), and also found considerable divergence between the two models, and their ecological and conservation implications. In both cases, as in our analyses, the predictions of different hydrodynamic models were so different that they raise questions about whether single models can be trusted to support decision-making.

Whenever substantial divergence has been observed between biophysical dispersal models, a common response is that the problem can be solved by choosing the "best" model. Forecasts and decisions would then be based on the predictions of this single model (Mumby et al. 2018). In situations where the performance of dispersal models can be assessed with validation data, this solution may be reasonable. However, we believe that the "single best model" solution may be inapplicable to many coral reef contexts. First, in other contexts with better validation data than larval dispersal (e.g. weather, seasonal climate, hurricanes), model ensembles still remain the preferred solution (Hermann and Marzocchi 2023). Second, as we emphasise in the introduction, there is no single "best" biophysical model. Models with higher horizontal spatial resolution are better; models with higher vertical resolution are also better. Both choices cannot be made simultaneously because computational resources are finite, and it is not possible to determine a priori which choice is best. Third, while a validation comparison with empirical data on larval dispersal could theoretically identify the best model a posteriori, this is not possible in practice. Empirical data on larval dispersal is enormously costly to collect, and does not have enough statistical power to unambiguously identify a single best model (Nolasco et al. 2018; Bode et al. 2019). Moreover, marine ecosystems are sufficiently large and varied that it is highly unlikely that any model can outperform all others everywhere, under all conditions, and for all decisions. Thus, even if a single biophysical model could be shown to be superior according to one empirical dataset, this would not justify the exclusion of the other models.

We developed a set of three different biophysical larval dispersal models to predict the dispersal of COTS on the GBR, with the specific purpose of assessing the sensitivity of model predictions to equally defensible hydrodynamic modelling choices. Despite shared input datasets and assumptions about larval biology, these models failed to agree on the structure of the resulting larval dispersal patterns, or on the role and relative contributions of individual reefs. These results suggest that larval dispersal patterns are sensitive to hydrodynamic model assumptions. However, we believe that our results should not be used as the basis of a model comparison—that is, as an opportunity to identify which model is most accurate, or which is best suited to support decisions on the GBR. Nor do we believe they should be used as the basis for a standard sensitivity analysis: to identify which uncertain dimensions of a model should be better-resolved. When we use sensitivity analyses in this way—when we call for "better" representations of particular elements of the biophysics—we are ignoring the constrained nature of many of these choices. Instead, we suggest that no single biophysical or hydrodynamic model should be used to support management decisions. The results provide support for recent calls for applying an ensemble approach to larval dispersal modelling, where the predictions of different, divergent models are collated into a multi-model ensemble (Bode et al. 2018; Ross et al. 2020; Krueck et al. 2022).

Acknowledgements Funding support was provided by the *COTS Control Innovation Program*. The Program is a collaboration between the Great Barrier Reef Foundation, Australian Institute of Marine Science, CSIRO, James Cook University and the University of Queensland, and is funded by the partnership between the Australian Government's Reef Trust and the Great Barrier Reef Foundation.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions.

Data availability All connectivity matrices are available at https://github.com/MikeBode/Biophysical_model_comparison.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Almany GR, Planes S, Thorrold SR et al (2017) Larval fish dispersal in a coral reef seascape. Nature Ecol Evolution 1:1–7

Andutta F, Kingsford M, Estuarine EW, Shelf C (2012) Sticky water'enables the retention of larvae in a reef mosaic. Estuarine Coastal Shelf Sci 101:54

Armsworth PR (2002) Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. Ecology 83:1092–1104

Beger M, Simon L, Game E, Ball I, Treml E, Watts M, Possingham HP (2010) Incorporating asymmetric connectivity into spatial decision making for conservation. Conserv Lett 3:359–368

Black KP (1993) The relative importance of local retention and inter-reef dispersal of neutrally buoyant material on coral reefs. Coral Reefs 12:43–53. https://doi.org/10.1007/BF00303783

Bode L, Mason LB, Middleton JH (1997) Reef parameterisation schemes with applications to tidal modelling. Prog Oceanogr 40:285–324. https://doi.org/10.1016/S0079-6611(98)00006-8

Bode M, Armsworth PR, Fox HE, Bode L (2012) Surrogates for reef fish connectivity when designing marine protected area networks. Mar Ecol Prog Ser 466:155–166. https://doi.org/10.3354/meps09924

Bode M, Bode L, Choukroun S, James MK, Mason LB (2018) Resilient reefs may exist, but can larval dispersal models find them? PLoS Biol 16:e2005964

Bode M, Leis JM, Mason LB, Williamson DH, Harrison HB, Choukroun S, Jones GP (2019) Successful validation of a larval dispersal model using genetic parentage data. PLoS Biol. https://doi.org/10.1371/journal.pbio.3000380

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4:144–150

Burchard H, Petersen O, Rippeth TP (1998) Comparing the performance of the mellor-yamada and the κ-ε two-equation turbulence models. J Geophys Res Oceans 103:10543–10554. https://doi.org/10.1029/98JC00261

Burgess S, Bode M, Leis J, Mason L (2022) Individual variation in marine larval-fish swimming speed and the emergence of dispersal kernels. Oikos. https://doi.org/10.1111/oik.08896

Caballes CF, Byrne M, Messmer V, Pratchett MS (2021) Temporal variability in gametogenesis and spawning patterns of crown-of-thorns starfish within the outbreak initiation zone in the northern Great Barrier Reef. Mar Biol 168:1–13. https://doi.org/10.1007/S00227-020-03818-3/FIGURES/6

Chamberlain MA, Oke PR, Brassington GB, Sandery P, Divakaran P, Fiedler RAS (2021) Multiscale data assimilation in the Bluelink ocean reanalysis (BRAN). Ocean Model 166:101849. https://doi.org/10.1016/J.OCEMOD.2021.101849

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Ann Rev Mar Sci 1:443–466. https://doi.org/10.1146/annurev.marine.010908.163757

Criales MM, Chérubin L, Gandy R, Garavelli L, Ghannami MA, Crowley C (2019) Blue crab larval dispersal highlights population connectivity and implications for fishery management. Mar Ecol Prog Ser 625:53–70. https://doi.org/10.3354/MEPS13049

D'Aloia CC, Bogdanowicz SM, Francis RK, Majoris JE, Harrison RG, Buston PM (2015) Patterns, causes, and consequences of marine larval dispersal. Proc Natl Acad Sci USA 112:13940–13945. https://doi.org/10.1073/pnas.1513754112

Dauhajre DP, McWilliams JC, Renault L (2019) Nearshore lagrangian connectivity: submesoscale influence and resolution sensitivity. J Geophys Res Oceans 124:5180–5204. https://doi.org/10.1029/2019JC014943

De'Ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27 year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.1208909109

Deloitte (2013) Economic contribution of the Great Barrier Reef, GBRMPA

Dight IJ, Bode L, James MK (1990) Modelling the larval dispersal of Acanthaster planci - I. large scale hydrodynamics, cairns section, great barrier reef marine park. Coral Reefs 9:115–123. https://doi.org/10.1007/BF00258222

Donahue MJ, Karnauskas M, Toews C, Paris CB (2015) Location isn't everything: timing of spawning aggregations optimizes larval replenishment. PLoS ONE 10:e0130694. https://doi.org/10.1371/JOURNAL.PONE.0130694

Durran D R (2010) Numerical Methods for Fluid Dynamics https://doi.org/10.1007/978-1-4419-6412-0

Girvan M, Newman MEJ (2002) Community structure in social and biological networks. Proc Natl Acad Sci U S A 99:7821–7826

Herrmann M, Marzocchi W (2023) Maximizing the forecasting skill of an ensemble model. Geophys J Int 234:73–87. https://doi.org/10.1093/GJI/GGAD020

Herzfeld M (2006) An alternative coordinate system for solving finite difference ocean models. Ocean Model 14:174–196. https://doi.org/10.1016/J.OCEMOD.2006.04.002

Hock K, Wolff NH, Ortiz JC, Condie SA, Anthony KRN, Blackwell PG, Mumby PJ (2017) Connectivity and systemic resilience of the great barrier reef. PLoS Biol. https://doi.org/10.1371/journal.pbio.2003355

James MK, Armsworth PR, Mason LB, Bode L (2002) The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. Proc Royal Soc B: Biol Sci 269:2079–2086. https://doi.org/10.1098/RSPB.2002.2128

Jones G P (2015) Mission impossible: unlocking the secrets of coral reef fish dispersal., p. 16–27. In: C. Mora [ed.], Ecol Fishes Coral Reefs. Cambridge University Press

Kininmonth S, Beger M, Bode M, Peterson E, Adams VM, Dorfman D, Brumbaugh DR, Possingham HP (2011) Dispersal connectivity and reserve selection for marine conservation. Ecol Modell 222:1272–1282. https://doi.org/10.1016/j.ecolmodel.2011.01.012

Krueck NC, Tong C, Cox C et al (2022) Benefits of measurable population connectivity metrics for area-based marine management. Mar Policy 144:105210. https://doi.org/10.1016/J.MARPOL.2022.105210

Lambrechts J, Hanert E, Deleersnijder E, Bernard PE, Legat V, Remacle JF, Wolanski E (2008) A multi-scale model of the hydrodynamics of the whole great barrier reef. Estuar Coast Shelf Sci 79:143–151. https://doi.org/10.1016/J.ECSS.2008.03.016

Leis J M, and M McCormick (2002) The biology, behaviour and ecology of the pelagic, larval stage of coral reef fishes, In: P.F. Sale [ed.], Coral Reef Fishes: diversity and dynamics in a complex ecosystem. Academic Press

Luick JL, Mason L, Hardy T, Furnas MJ (2007) Circulation in the great barrier reef lagoon using numerical tracers and in situ data. Cont Shelf Res 27:757–778. https://doi.org/10.1016/j.csr.2006.11.020

Matthews SA, Mellin C, Pratchett MS (2020) Larval connectivity and water quality explain spatial distribution of crown-of-thorns starfish outbreaks across the great barrier reef. Adv Mar Biol 87:223–258. https://doi.org/10.1016/bs.amb.2020.08.007

Mitarai S, Siegel DA, Winters KB (2008) A numerical study of stochastic larval settlement in the California current system. J Mar Syst 69:295–309. https://doi.org/10.1016/j.jmarsys.2006.02.017

Moneghetti J, Figueiredo J, Baird AH, Connolly SR (2019) High-frequency sampling and piecewise models reshape dispersal kernels of a common reef coral. Ecology. https://doi.org/10.1002/ECY.2730

Mumby PJ, Hock K, Condie SA, Ortiz JC, Wolff NH, Anthony KRN, Blackwell PG (2018) Response to bode and colleagues:'resilient reefs may exist, but can larval dispersal models find them?'. PLoS Biol. https://doi.org/10.1371/journal.pbio.2007047

Nolasco R, Gomes I, Peteiro L, Albuquerque R, Luna T, Dubert J, Swearer SE, Queiroga H (2018) Independent estimates of marine population connectivity are more concordant when accounting for uncertainties in larval origins. Sci Rep 8:2641. https://doi.org/10.1038/s41598-018-19833-w

Nolasco R, Dubert J, Acuña JL et al (2022) Biophysical modelling of larval dispersal and population connectivity of a stalked barnacle: implications for fishery governance. Mar Ecol Prog Ser 694:105–123. https://doi.org/10.3354/MEPS14097

Pelc RA, Warner RR, Gaines SD, Paris CB (2010) Marine reserves special feature: detecting larval export from marine reserves. Proc Natl Acad Sci USA 107:18266–18271. https://doi.org/10.1073/pnas.0907368107

Pratchett MS, Dworjanyn S, Mos B, Caballes CF, Thompson CA, Blowes S, Uthicke S, Wink M (2017) Larval survivorship and settlement of crown-of-thorns starfish (Acanthaster cf. solaris) at varying algal cell densities. Diversity. https://doi.org/10.3390/d9010002

Ross RE, Nimmo-Smith WAM, Torres R, Howell KL (2020) Comparing deep-sea larval dispersal models: a cautionary tale for ecology and conservation. Front Mar Sci. https://doi.org/10.3389/FMARS.2020.00431/FULL

Saint-Amand A, Lambrechts J, Hanert E (2023a) Biophysical models resolution affects coral connectivity estimates. Sci Rep. https://doi.org/10.1038/s41598-023-36158-5

Saint-Amand A, Lambrechts J, Thomas CJ, Hanert E (2023b) How fine is fine enough? effect of mesh resolution on hydrodynamic simulations in coral reef environments. Ocean Model 186:102254. https://doi.org/10.1016/J.OCEMOD.2023.102254

Simons RD, Siegel DA, Brown KS (2013) Model sensitivity and robustness in the estimation of larval transport: a study of particle tracking parameters. J Mar Syst 119–120:19–29. https://doi.org/10.1016/J.JMARSYS.2013.03.004

Steven ADL, Baird ME, Brinkman R et al (2019) eReefs: an operational information system for managing the great barrier reef. Taylor Francis 12:S12–S28. https://doi.org/10.1080/1755876X.2019.1650589

Treml EA, Ford JR, Black KP, Swearer SE (2015) Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. Mov Ecol 3:1–16. https://doi.org/10.1186/S40462-015-0045-6/TABLES/3

Vercelloni J, Caley M, Mengersen K (2017) Crown-of-thorns starfish undermine the resilience of coral populations on the great barrier reef. Global Ecol Biogeogr 26:846–853. https://doi.org/10.1111/geb.12590

Weersing K, Toonen RJ (2009) Population genetics, larval dispersal, and connectivity in marine systems. Mar Ecol Prog Ser 393:1–12. https://doi.org/10.3354/meps08287

Westcott DA, Fletcher CS, Kroon FJ, Babcock RC, Plagányi EE, Pratchett MS, Bonin MC (2020) Relative efficacy of three approaches to mitigate Crown-of-Thorns Starfish outbreaks on Australia's great barrier reef. Sci Rep. https://doi.org/10.1038/s41598-020-69466-1

Whomersley P, Van der Molen J, Holt D, Trundle C, Clark S, Fletcher D (2018) Modeling the dispersal of spiny lobster (Palinurus elephas) larvae: Implications for future fisheries management and conservation measures. Front Mar Sci. https://doi.org/10.3389/FMARS.2018.00058/FULL

Williamson DH, Harrison HB, Almany GR et al (2016) Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park. Mol Ecol 25:6039–6054. https://doi.org/10.1111/mec.13908