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Global warming decreases connectivity among coral populations

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Global warming is killing corals; however, the effects of warming on population connectivity, a process fundamental to reef recovery, are largely unexplored. Using a high-resolution (as high as 200 m), empirically calibrated biophysical model of coral larval dispersal for the southern Great Barrier Reef, we show that the increased larval mortality and reduced competency duration under a 2 °C warming alter dispersal patterns, whereas projected changes in large-scale currents have limited effects. Overall, there was on average a 7% decrease in the distance larvae disperse (among-reef interquartile range (IQR), -10% to -4%), an 8% decrease in the number of connections into each reef (IQR, -11% to -3%) and a 20% increase in local retention (IQR, 0% to +49%). Collectively, these shifts imply that 2 °C of warming will reduce inter-reef connectivity, hampering recovery after disturbances and reducing the spread of warm-adapted genes. Such changes make protections more effective locally, but may require reducing spacing between protected areas.

oral reefs have been in decline for centuries due to local human impacts^{1,2}, with ocean warming accelerating these declines in recent decades^{3,4}. Warmer temperatures cause corals to bleach (that is, lose their algal symbionts, and thus a major source of carbon), become less fertile and more likely to die^{5,6}. The ability of coral populations to recover after disturbance is highly dependent on patterns of reef connectivity7. The interchange of larvae among reefs allows and accelerates the (re)colonization of distant habitats. Previous research demonstrates that warmer temperatures increase early larval mortality and reduce the time it takes larvae to settle^{8,9}, causing an increase in the proportion of larvae retained on their natal reef (that is, local retention¹⁰). However, the effect of higher temperatures on long-term larval survival and settlement, and how such changes will affect connectivity, remains unexplored. Additionally, projected changes in ocean circulation in response to global warming have the potential to affect patterns of connectivity worldwide11,12.

In this article we combine experimental calibration of biological models of larval survival and competency for the stony coral *Acropora millepora* with a high-resolution (as high as 200 m) hydrodynamic model of physical transport on the southern Great Barrier Reef to test for the effects of a 2 °C increase in temperature (estimated for 2080–2100 under the Representative Concentration Pathway 4.5 scenario or for 2050 under the Representative Concentration Pathway 8.5 scenario¹³) on patterns of connectivity (Appendix 1). Specifically, we first measure long-term larval survival and competency dynamics of *A. millepora* under current and future temperature conditions in laboratory conditions. We use *A. millepora* as our model species because it has a similar egg size and competence curve (ability to settle over time) as other *Acropora* species^{8,9,10,17,18}, and because Acropora is by far the most abundant genus in the Great Barrier Reef and across much of the Indo-Pacific region. We then simulate water currents through the Great Barrier Reef using the Second-generation Louvain-la-neuve Ice-ocean Model (SLIM) during three recent successive spawning seasons for which good observational data were available (2008-2010), and use biophysical particle tracking to estimate the dispersal of A. millepora larvae and the resultant inter-reef connectivity network. Averaging over all larvae released and over all three spawning seasons, we estimate that temperature-induced changes in larval survival and settlement competence will reduce larval dispersal distance by 6.6% (with an among-reef interquartile range (IQR) of -10.0% to -4.2%; Fig. 1a) and the number of outgoing connections by 8.1% (among-reef IQR, -10.8% to -3.0%; Fig. 1c), that is, larvae will reach fewer reefs (Appendix 1 and Supplementary Table 9). We find that 75% of the reefs in this region will experience a decrease in both connectivity metrics, with some experiencing a very large decrease (>15%, Fig. 1a,c; Appendix 1). In addition, we estimate that a 2°C warming will increase the proportion of larvae produced by a reef that settles back onto that reef (local retention) by 19.5% (among-reef IQR, 0.0% to +49.2%). Similarly, the proportion of settlers on a reef that originated from larvae released by that reef (self-recruitment) will increase on average by 15.0% (among-reef IQR, -0.2% to +43.5%). That is, recruitment back to the natal reef increases both relative to the larval production by each reef, and relative to the number of larvae arriving at that reef from the metapopulation as a whole¹⁹. This means that reefs will become more isolated and more dependent on locally produced larvae for replenishment after disturbances.

While on average warming decreases larval dispersal distances and the number of inter-reef connections, and increases local retention of larvae, there is substantial inter-reef variability in these projected changes, as is evident in Fig. 1. Some reefs are likely to see

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Fig. 1 | Maps showing the effects of a 2 °C increase in water temperature across the southern Great Barrier Reef, Australia, by reef. a, Average source-to-destination reef distance (connection length). **b**, Local retention (proportion of larvae produced on a reef that settle back on that reef). **c**, Number of incoming connections from other reefs. **d**, Current best source reefs, as measured by a source index defined as the number of outgoing connections multiplied by the number of outgoing larvae per reef. **e**, The relative change in the source index for the 2 °C increase scenario. Inset histograms in **a-c** and **e** show normalized distributions of the relative changes shown in the maps; values outside the range of the x axis are included in final bar for readability. **f**, Average water current speeds from the hydrodynamic model for the present-day simulations. All quantities are averaged over the three spawning seasons (2008-2010) modelled.

much larger swings than the average in terms of how isolated from or connected to they are with respect their neighbours, and a small proportion are projected to experience changes opposite in direction to the average. This high spatial heterogeneity is caused by the way that changes in the time taken by larvae to acquire and lose the ability to settle, and changes to their mortality rate, interact with the strength and direction of local currents (Fig. 1f) and the geographic distribution of neighbouring reefs, both of which are highly variable in space. In some areas weakening of inter-reef connectivity occurs much more strongly than the average, for instance, around the reef-dense Whitsunday Islands (>15% decrease in dispersal distance and number of connections; Fig. 1a,c). Conversely, warmer waters can also lead to stronger inter-reef connections where the conditions are right, although this is rare. For example, in areas where strong currents rapidly transport larvae away from their natal reefs, over neighbouring reefs, and then out to reef-sparse areas of open sea, hastening the onset of competence can allow more larvae to settle onto these neighbouring reefs before being lost at sea; this may be the case for the small group of reefs off Cape Palmerston, which see an increase in average dispersal distances (Fig. 1a).

The net weakening of inter-reef connectivity is driven by changes in larval development dynamics. Warmer temperatures increase larval mortality (Appendix 1, Supplementary Tables 1 and 2, and Supplementary Fig. 1a). This effect was especially marked during embryogenesis, after which mortality rates were similar between temperatures, consistent with accelerated rates of cell division during embryogenesis at higher temperatures increasing the frequency of errors that lead to fatal malformations²⁰. Warmer temperatures also alter competence dynamics: how quickly larvae acquire the capacity to settle and metamorphose on a reef habitat (that is, become competent), and how long they retain that capacity (Appendix 1). Specifically, under elevated temperatures, the minimum time for

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Fig. 2 | Relative change in recovery times in the 29 °C scenario (2050-2100) compared to the 27 °C scenario (current) following disturbance. a, Single-reef disturbances. b, Multiple-reef disturbances. Inset histograms show normalized distributions for the changes in recovery times.

larvae to settle is reduced from 4.89 to 3.87 days; however, larvae tend to lose competence much more quickly, halving from peak competence after about 7 weeks at +2 °C compared to 14 weeks at current temperatures (Appendix 1, Supplementary Tables 3 and 4, and Supplementary Fig. 1b). One potential explanation for this is the combination of higher rates of metabolism at warmer temperatures²¹ leading to faster depletion of energy reserves (coral larvae are non-feeding) and thus a shorter time-window during which sufficient energy remains available for successful settlement and metamorphosis.

In contrast to temperature effects on survival and development, projected changes in large-scale water circulation in the Great Barrier Reef (Appendix 1 and Supplementary Fig. 8) have a small effect on connectivity patterns, with average changes to all connectivity indicators being <2.2% (Appendix 1 and Supplementary Table 8). Changes in large-scale circulation through the Coral Sea predicted by the Coupled Model Intercomparison Project 5 (CMIP5) global climate models may affect water flow onto the Great Barrier Reef, with most CMIP5 models projecting increased flow towards the Great Barrier Reef driven by an increase in the strength of the South Pacific subtropical gyre (Appendix 1 and Supplementary Fig 8). The effects of this change on the Great Barrier Reef itself are modelled by modulating the large-scale currents entering the lagoon (Appendix 1, part 3). However, this change is found to have a small effect on current speeds through the Great Barrier Reef (average changes of under 1 cm s⁻¹ over the vast majority of the domain, which is very low compared with typical current speeds; Fig. 1f), and the effect on coral connectivity is roughly an order of magnitude smaller than the biological changes caused by the ocean warming that we document (Appendix 1 and Supplementary Table 9). Other changes to environmental conditions in the region are also possible, such as modulation in the strength of local wind stress during coral spawning seasons, but we have no strong evidence quantifying how they will evolve over the coming decades and hence they are not accounted for here.

Local retention is estimated to increase on average by 19.5% (among-reef IQR, 0.0% to +49.2%) at higher temperature (+2 °C)

because a reduction in the time to settlement overcompensates for an increase in mortality. Seventy-four percent of the reefs in the region are predicted to experience an increase in local retention, with 26% experiencing increases greater than 50% (Fig. 1b). This spatial variability in projected changes in local retention reflects the high degree of geographic variability in water currents (Fig. 1f) and thus residence times in the Great Barrier Reef²². The increased local retention will be more prevalent on reefs with mean water residence times lower than 4 days, such as reefs offshore from Mackay and in the Whitsundays (Fig. 1b), due to the decrease in the minimum time to acquire competence to under 4 days. Therefore, some coral populations are likely to become more vulnerable to local disturbances, but also more responsive to local management, such as control of sedimentation or prohibitions on anchoring¹⁰.

To determine the contribution of warming-driven changes in coral connectivity patterns to recovery rates after disturbances, we developed a simple metapopulation model (Appendix 2). The model projects the time taken for each reef to recover from localized and regional disturbances in both the present day and under the 2°C warming scenario; the change in recovery time was then calculated as the percentage change between the two. Temperature-driven changes in larval dispersal are projected to cause a marginal decrease in average recovery times across all reefs $(-1.8\% \pm 5.9\%$ (mean \pm s.d.) for localized, single-reef disturbances, and $-1.7\% \pm 4.7\%$ for regional, multiple-reef disturbances); however, at the reef-scale there are some important changes (Fig. 2a,b). For example, on isolated reefs, which already receive few larvae from other reefs, reduced long-distance connectivity will further diminish recovery rate (~10% increase in recovery time). At the same time, increased local retention on other reefs, such as those in the reef-dense areas off Mackay, will promote enhanced recovery (~10% decrease in recovery time) primarily because this increased local retention more than offsets the decrease in the strength and number of inter-reef connections. These projected changes in recovery times due to the shifts in connectivity indicated by our study are likely to be underestimates because the changes will be

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compounded by warming-induced decreases in the spawning stock, including increased mortality, decreased fertility and fecundity, and density-dependent reduction in fertilization rates.

This model projects how coral larval dispersal patterns and connectivity will be altered by climate change. In the process, the potential for each reef to act as a source of larvae to the region and the extent to which warming would alter this were also projected. Previous work on the Great Barrier Reef has focused on identifying 'robust source reefs' based on present-day connectivity and history of disturbance^{23,24}. Comparing the outputs of the various models, it is evident that as resolution increases, from 4 km (ref. 23) to 1.6 km (ref. ²⁴) to 200 m in our model, the potential role of nearshore reefs as sources for the system becomes more evident^{23,24} (Fig. 1d). The high resolution around reefs (200 m) of our model resolves hydrodynamics at the reef scale more effectively, particularly nearshore, and therefore enhances our capacity to anticipate the potential impacts of local-scale management interventions. We opted for a depth-integrated model, without waves, to simulate flow through the mainly shallow, well-mixed waters of the Great Barrier Reef to achieve a combination of high spatial resolution around reefs (needed to capture reef-scale retention processes such as lee reef eddies) and a relatively large model domain (needed to capture the inter-reef dispersal that drives metapopulation dynamics).

From a management perspective, reduced connectivity and increased local retention suggest that a greater number of reefs, particularly reefs contributing most to the overall supply of larvae (source reefs), will require greater levels of protection, and protected areas will have to be closer together, to increase the ability of the system to replenish itself following natural and anthropogenic disturbances. Concomitantly, the stronger local retention might benefit persistence as more larvae recruit to favourable habitats^{25,26}, and stronger stock-recruitment relations will enhance the potential impacts of local management interventions^{10,25}. The recovery of disturbed areas can be achieved by reducing local anthropogenic stressors (through reduction/elimination of overfishing of herbivores, regulated sewage discharge or elimination of mechanical damage such as dredging) or protecting surrounding undisturbed reefs to maximize the supply of larvae to the disturbed reefs and thus facilitate colonization. In the southern Great Barrier Reef, many of the best source reefs lie in the outer/easternmost portion of the continental shelf (Fig. 1d), due to the high reef density and strong currents facilitating inter-reef connections. These reefs are projected to be weaker sources of larvae in the future (Fig. 1a,c). However, in most cases, they are projected to remain the best sources in the system (Fig. 1e). While our model projects that changes in connectivity would allow some reefs to recover more rapidly following disturbance, this would only be true if the growth rates, post-settlement survival, fertility and fecundity of corals were not compromised by warming, whereas prior work indicates that such adverse effects are likely²⁷⁻²⁹. Additionally, isolated reefs with very low mean water residence times (that is, high self-recruitment but low local retention) will become more vulnerable to local extinction and therefore need greater protection from localized disturbances, and would have to be actively restored (larval seeding and/or outplanting) if disturbed.

The changes in inter-reef connectivity projected here for *A. millepora* in the southern Great Barrier Reef could diminish the capacity of these coral populations to adapt and are likely not to be exclusive to this species or region^{8–10,30–33}. A reduction in long-distance dispersal is likely to reduce the migration of temperature-tolerant genes from lower latitudes. Our results are also likely to be robust for most reefs on a global scale because the great majority of reefs worldwide have similar mean water residence times^{30–32}, *Acropora* is the most abundant coral genus in the Indo-Pacific (and was once the most abundant in the Atlantic) and the response to warming of the early-life-history stages of all other coral species studied to date is similar to that of *Acropora*^{8–10,33}. Most reefs of the future will

be less connected and this reduction in connectivity needs to be considered when choosing how best to respond to global warming, and in evaluating the extent to which the dispersal of warm-adapted genotypes will be sufficient to allow coral populations to cope with increasing temperatures.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/ s41558-021-01248-7.

Received: 3 November 2020; Accepted: 10 November 2021; Published online: 30 December 2021

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Methods

We first measured long-term larval survival and competency dynamics of the coral A. millepora under current and future temperature conditions in laboratory conditions (Appendix 1, part 1). This species was used because Acropora species are the most abundant in the Great Barrier Reef and the rest of the Indo-Pacific, and have similar egg size and larval development rates (~532-604 µm mean egg diameter; 4-6 days to larval competency). Eggs and sperm of six A. millepora colonies were mixed to allow fertilization. To obtain the survival curve, four replicates of 50 embryos per temperature treatment (ambient temperature (27 °C) and +2 °C (29 °C)) were stocked in 200 ml glass jars. Every day for 134 days, embryos/larvae were counted and water was renewed. The survival data were fitted to alternative models to determine whether mortality rates were constant over time (exponential model), increased or decreased monotonically over time (Weibull model), or whether they first decreased, then increased, or vice versa (generalized Weibull: see Appendix 1 for details). To obtain the competency curve, embryos were reared at 27 °C (ambient temperature) and 29 °C (+2 °C), and each day from days 3 to 9 postfertilization, and then on days 11, 13, 16, 23, 30, 37, 44, 58, 72 and 99, three replicates of 20 larvae from each of the temperature treatments were placed in 200 ml glass jars with a preconditioned settlement tile at the same temperature. A day later, the number of larvae that had settled and metamorphosed was recorded. As with survival, we considered exponential, Weibull and generalized Weibull functional forms for the loss of competence (see Appendix 1 for details). We then integrated the estimated survival and competency parameters for each temperature into a stochastic model that estimates the probability that a larva is alive and competent at any given time for each temperature.

The flow of ocean currents through the Great Barrier Reef was simulated using an unstructured mesh, depth-integrated hydrodynamic model (SLIM) forced by tides, wind and large-scale oceanographic currents³⁴ during the spawning season in three successive recent years (2008-2010). The mesh resolution was very high around reefs (200 m), and coarser in deeper areas with more uniform bathymetry (up to 5 km). The use of a depth-integrated model necessarily omits any variation in flow with depth, which can be relevant for larval dispersal when flow changes markedly with depth, and depth distributions change due to swimming behaviour or shifts in buoyancy with development³⁵. However, observational and modelling studies over the past four decades have consistently found Great Barrier Reef waters to be vertically well-mixed throughout most of the shelf for most of the year, with upwelling events and stratification being relatively limited in space and time (Appendix 1, part 2). In addition, coral larval swimming speeds are orders of magnitude lower than measurements of water flow both on and off reefs (vertical and horizontal currents), and thus cannot swim against currents³⁶. Although our model may therefore be missing some relevant three-dimensional effects, for example, localized upwelling at the shelf break which may affect flow near some outer barrier reefs, focusing finite computational resources on resolving reef-scale horizontal flow allows us to better resolve flow features that are crucial to circulation throughout the shelf, such as eddies that form behind reefs which can trap larvae in their vicinity, while still being able to characterize dynamics over a spatial scale appropriate to the inter-reef connectivity patterns of corals. The present-day hydrodynamics were validated using local measurements of current strength and direction from mooring locations on the shelf, and the model was found to reproduce realistic currents (Appendix 1, part 2).

To obtain estimates of connectivity between reefs, an individual based model was then used to simulate particle transport using currents from three recent years (2008–2010) in the weeks immediately following spawning in the Great Barrier Reef (November) and larval survival and competency dynamics for present and future sea temperature scenarios. The model assumes that when a larva is alive and competent, if it passes on top of a reef it will detect the presence of the reef (through chemical and physical cues³⁷), settle and metamorphose (Appendix 1, general methods). Particle transport was modelled separately for each spawning season using currents simulated for that specific period (Appendix 1, part 2). To simulate the impact of changing large-scale ocean circulation on larval connectivity, the biophysical model was also forced with modified low-frequency currents at the model boundaries to mimic the changes predicted to ocean circulation in the Coral Sea by CMIP5 climate models (see Appendix 1, part 3). Connectivity metrics for the three years were averaged to make the results more robust to annual variations (Appendix 1, part 4). The estimated connectivity matrices for each year are available at https://doi.org/10.5061/dryad.4f4qrfjbk.

To determine the contribution of warming-driven changes in coral connectivity patterns to recovery rates after disturbances, we developed a simple metapopulation model of coral cover accounting for density-dependent growth (budding) and recruitment, using the connectivity matrices from the biophysical dispersal model (Appendix 2). Previously reported biological data on fecundity and post-settlement survival of coral recruits are used to set realistic model parameters,

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and all corals are assumed to have equal fecundity and post-settlement mortality. Fecundity, initial abundance and growth and mortality rates were set to be equal at 27 °C and 29 °C because the aim was to predict changes in recovery times following disturbances due exclusively to the impact of changes in connectivity. We simulated two different types of disturbance: single-reef disturbances, where initial coral cover was reduced by 85% over one reef at a time, mimicking events such as crown-of-thorns outbreaks, and regional disturbances, where initial coral cover was reduced by 75% over a 30-km-wide cross-shore strip, and by 40% in 30-km-wide strips to either side, mimicking the passage of a severe tropical cyclone across the Great Barrier Reef. The model was run, in turn, using the connectivity matrices obtained from the 27 °C and 29 °C biophysical model runs. The model projects the time taken for each reef to recover from localized and regional disturbances for both the present day and under the 2 °C warming scenario, and the change in recovery time was then calculated as the percentage change between the two.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Yearly connectivity matrices and the processed data used to construct Figs. 1a–e and 2 are available at https://doi.org/10.5061/dryad.4f4qrfjbk. Larval survival and competency is provided in the Appendix 1 (Supplementary Fig. 1) and can be obtained from the authors on request.

Code availability

The SLIM model source code can be found at https://git.immc.ucl.ac.be/dg/dg. Larval dynamics modelling is provided in the Appendix 1, and references therein, and can be obtained from the authors on request.

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Acknowledgements

Major funding for this research was provided by the Australian Research Council (DP110101168) (J.F., A.H.B.), a Queensland Government Smart Futures Fellowship (J.F.), the Australian Research Council's Centre of Excellence for Coral Reef Studies (A.H.B., S.R.C.), Federation Wallonie-Bruxelles ARC grant 10/15-028 (C.J.T.), the Belgian Fund for Scientific Research (FRS-FNRS) (J.L.), and Université catholique de Louvain, Belgium (E.H., E.D., J.L.). High-performance computing resources were provided by the Université catholique de Louvain (CISM/UCL) and the Consortium des Équipements de Calcul Intensif en Fédération Wallonie-Bruxelles (CÉCI) funded by the FRS-FNRS under grant number 2.5020.11 and by the Walloon Region.

Author contributions

J.F., C.J.T., S.R.C. and A.H.B. conceptualized the study. J.F. collected the data. J.F. and C.J.T. wrote the original manuscript. S.R.C., A.H.B., E.H. and E.D. edited the article. C.J.T., E.H., E.D. and J.L. developed the model. All authors participated in funding acquisition.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41558-021-01248-7.

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Last updated by author(s): November 9, 2021

Reporting Summary

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		Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.

Software and code

olicy information about availability of computer code					
Data collection	raw data is available on figures and can be requested to authors.				
Data analysis	R code will be publicly available on dryad				

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
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Outputs of connectivity matrix are available on dryad

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Projection of the connectivity in the Southern region of the Great Barrier Reef using a empirically calibrated bio-physical dispersal model
Research sample	Coral larvae survival had 4 replicates of 50 embryos per treatment. Competency was measured using 3 replicates of 20 larvae daily.
Sampling strategy	Larvae were selected haphazardly, and larval jars were randomly allocated to the treatments and/or replicates
Data collection	Larval survival data was collected daily for 134 days. Competency data was collected on days 11, 13, 16, 23, 30, 37, 44, 58, 72 and 99.
Timing and spatial scale	The biophysical model was run using hydrodynamics of 3 years in the southern region of the Great Barrier Reef.
Data exclusions	No data was excluded.
Reproducibility	Experiment can be repeated following the methods described. The dispersal model can be reconstructed using the SLIM model links.
Randomization	Larval jars which were randomly allocated to the treatments and/or replicates, and measured in random order daily.
Blinding	No blinding was used.
Did the study involve fiel	d work? Yes X No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

NΛ	ho	de
1 V	пu	us

n/a	Involved in the study	n/a	Involved in the study
\boxtimes	Antibodies	\boxtimes	ChIP-seq
\boxtimes	Eukaryotic cell lines	\ge	Flow cytometry
\boxtimes	Palaeontology and archaeology	\boxtimes	MRI-based neuroimaging
	Animals and other organisms		
\boxtimes	Human research participants		
\boxtimes	Clinical data		
\ge	Dual use research of concern		

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals.
Wild animals	Six wild coral colonies were collected a few days before spawning and kept in recirculating aquaria.
Field-collected samples	Coral gametes were collected in the lab from six wild collected colonies 9as described above)
E .1.1.	
Ethics oversight	No etnical approval or guidance required.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Supplementary information

Global warming decreases connectivity among coral populations

In the format provided by the authors and unedited

Additional Information for

Global warming decreases connectivity among coral populations

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This file includes:

Appendix 1: Methods and Results for Connectivity (Fig. S1-S8, Tables S1-S10) Appendix 2: Metapopulation model and details of model simulations (Fig. S9-S12)

Other Supplementary Materials for this manuscript include:

External Database: Connectivity matrices at https://doi.org/10.5061/dryad.4f4qrfjbk

Appendix 1: Methods and Results for Connectivity

General Methods

We first measured long-term larval survival and competency dynamics of the coral *Acropora millepora* under current and future temperature conditions in laboratory conditions (Part 1). *Acropora* species are the most abundant in the Great Barrier Reef (GBR) and the rest of the Indo-Pacific, and were formerly dominant in the Caribbean (Veron 2000).

The flow of ocean currents through the GBR was simulated using an unstructured mesh, depth-integrated hydrodynamic model (SLIM) forced by tides, wind and large-scale oceanographic currents (Thomas et al. 2014) during 3 successive years' spawning seasons (2008-2010). The mesh resolution was very high around reefs (200m), and coarser in deeper areas with more uniform bathymetry (up to 5km) (Part 2). The very high spatial resolution around reefs allowed the model to capture small scale circulation dynamics, such as eddies that form behind reefs which can trap larvae in their vicinity. Failure to resolve reef-scale dynamics would lead to underestimates of local retention and overestimates of long-distance dispersal; this is particularly pertinent where the bathymetry is very complex and reef-dense such as in the southern GBR. The present-day hydrodynamics were validated for each spawning season using local measurements (Part 2). To obtain estimates of connectivity between reefs, an individual based model was then used to simulate particle transport using currents from 3 recent years in the weeks immediately following spawning in the GBR (Table S11) and larval survival and competency dynamics for present and future sea temperature scenarios. Particle transport was modelled separately for each spawning season using currents simulated for that specific period, and the connectivity measures calculated for each season were averaged to obtain the values reported in Table S9. Full by-year connectivity measures are also reported in Table S10.

The model assumes that when a larva is alive and competent, if it passes on top of a reef it will detect its presence (through chemical and physical cues, Gleason and Hoffman 2011), settle and metamorphose, consistent with previous work on coral larval dispersal. By definition, a competent larva is defined as a larva that once exposed to a good settlement cue (reef), it will settle and undergo metamorphosis. That is, model parameters were estimated by measuring the proportion of larvae that commenced metamorphosis after being exposed to a settlement cue. Given that clay tiles pre-conditioned by deployment on reefs generally developed communities sufficient to induce settlement within a matter of weeks, we believe that it is reasonable to expect that competent larvae encountered by a reef would seek to settle and metamorphose. Additionally, to simulate the impact of changing large-scale ocean circulation on larval connectivity, the biophysical model was also forced with modified low-frequency currents at the model boundaries to mimic the changes predicted to ocean circulation in the Coral Sea by CMIP5 climate models (see Part 3, below for details and justification). The estimated dispersal patterns and connectivity matrices are presented in Part 4.

Data collection

Six colonies of *Acropora millepora* were collected from the reef at Orpheus Island, Great Barrier Reef, on the full moon of November 2011. The colonies were transported to James Cook University where spawning occurred. The eggs and sperm from all colonies were mixed to allow fertilization. Two hours after spawning, the embryos were washed to remove the sperm and split into three temperature treatments: 25° C (2° C below ambient), 27° C (ambient temperature at Orpheus Island during spawning season) and 29° C (2° C above ambient temperature). Embryos/larvae were raised under a natural photoperiod in 2L plastic bowls at a density <1 larvae.mL⁻¹. Ceramic tiles that had been left for 2 months on the reef at the depth adult corals occur were used as settlement cues. Note: for the biophysical dispersal model we only used the 27 and 29°C temperatures (ambient, and ambient + 2° C, respectively), as these were the two realistic scenarios.

Survival

After fertilisation (2h after spawning), four replicates of fifty embryos per temperature treatment were stocked in 200ml glass jars. Every day for 134 days (nearly 5 months), embryos/larvae were counted and water was renewed. The experiment stopped on day 134, because the remaining larvae settled on the glass jar in the absence of a settlement cue.

Competency

Each day from days 3 to 9 post-fertilization, and then on days 11, 13, 16, 23, 30, 37, 44, 58, 72 and 99, three replicates of twenty larvae (that had been maintained in the absence of any settlement cue) were collected from each of the temperature treatments, placed in 200mL glass jars with a pre-conditioned settlement tile, and kept at the same temperature. A day later, the number of larvae that had settled and metamorphosed was recorded.

Model

In our model, larvae suffer mortality at stochastic rate $\mu_T(t)$, where *t* denotes time after spawning and *T* denotes temperature dependence. Larvae acquire competence at stochastic rate $\alpha_T(t)$ and lose competence at stochastic rate $\beta_T(t)$. Since the survival and competence data sets were collected separately, survival and competence modelling was also performed separately.

Survival

We used a standard likelihood formulation for our survival analysis. Since no larvae were removed during the study, and larvae were censused at fixed points in time, our design was interval-censored. Thus, the log-likelihood is:

$$\log L = \sum_{t=0}^{t_f} \left(\left[A(t-1) - A(t) \right] \log \left[P_a(t-1) - P_a(t) \right] \right) + A(t_f) \log \left[P_a(t_f) \right]$$

where *t* is time (days since fertilization), t_f is the last day larvae were censused, A(t) is the number of individuals alive at time *t*, A(t-1)-A(t) is the number of larvae that died from one day to the next (i.e. between time *t*-1 and *t*), $P_a(t)$ is the probability of being alive at time *t*, and $P_a(t-1)-P_a(t)$ is the probability to dying from one day to next (i.e. between time *t*-1 and *t*). The probability of being alive at time *t* is given by:

$$P_a(t) = e^{-\int\limits_{\omega=0}^{t} \mu_{T(\omega)d\omega}}$$

For mortality, our most general model is the "generalized Weibull", according to which the mortality rate is:

$$\mu_T(t) = \frac{\lambda_T \nu_T (\lambda_T t)^{\nu_T - 1}}{1 - \sigma_T (\lambda_T t)^{\nu_T}}$$

This model allows for "bathtub-shaped" mortality curves, where mortality is high initially, decreases as larvae age, and then increases again as larvae become very old. Such mortality patterns are plausible *a priori*: we might expect high mortality as larvae develop, low mortality once development is complete but energy stores are plentiful, and then high mortality as energy reserves become depleted. Moreover, bathtub-shaped mortality patterns have been observed in previous work on corals. We also consider special cases of the generalized Weibull. For instance, the standard Weibull survival model, which allows monotonic increases or decreases in mortality rate over time, is the limiting case of the generalized Weibull as $\sigma \rightarrow 0$:

$$\mu_{T}(t) = \lambda v (\lambda t)^{v-1}$$

and the exponential model, according to which mortality rate is constant over time, is the special case of the Weibull model when $\nu=1$:

$$\mu_T(t) = \lambda$$

To assess which distribution (exponential, Weibull or Generalised Weibull) best described the survival dynamics, we fitted the survival data at different temperatures to all three possible distributions, estimating the parameters with maximum likelihood methods and using AICc

(Akaike's Information Criterion with the small-sample bias-correction term) to select the model that best described the survival dynamics. After selecting the functional form for survival, we assessed whether there was support for temperature-dependent mortality rates by comparing a model where all parameters were independent of temperature with models where different combinations of survival parameters were dependent on temperature, using AICc. Further, we estimate model selection uncertainty by calculating Akaike weights for each model. These terms can be understood as an estimate of the probability that the given model is actually the best one for the population from which the sample was taken (or, more strictly, the probability that a given model would end up as the best-performing model if the experiment were repeated with an independent sample from the same study population).

We found that there was very strong support for modelling survival data with a generalised Weibull distribution (Table S1), and for modelling all parameters as explicit functions of temperature, as evidenced by the very high Akaike weights associated with these models (Tables S1 and S2, see best fit model in Fig. S1).

FUNCTIONAL FORM OF THE SURVIVAL MODEL						TEMPERATURE DEPENDENCE			
Nr. par.	MLL	AICc	Akaike weights	Model parameters	Nr. par.	MLL	AICc	Akaike weights	
		4320.8		$\lambda_T, \mathbf{v}_T, \mathbf{\sigma}_T$	9	-2151.4	4320.8	>0.999	
			>0.999	λ _T , ν, σ	5	-2163.7	4337.4	< 0.001	
				λ_T, ν_T, σ	7	-2161.8	4337.6	< 0.001	
0	2151 4			λ_T, ν, σ_T	7	-2163.2	4340.5	< 0.001	
9	-2131.4			λ, ν, σ_T	5	-2167.4	4344.8	< 0.001	
				λ, ν_T, σ_T	7	-2165.9	4345.9	< 0.001	
				λ, ν _T , σ	5	-2168.0	4345.9	< 0.001	
				λ, ν, σ	3	-2170.2	4346.5	< 0.001	
6	-2173.9	4359.8	< 0.001						
3	-2484.0	4973.9	< 0.001						
	AL F(Nr. par. 9 6 3	AL FORM OF 7 MODEL Nr. MILL 9 -2151.4 6 -2173.9 3 -2484.0	AL FORM OF THE SUF MODEL MILL AICc 9 -2151.4 4320.8 6 -2173.9 4359.8 3 -2484.0 4973.9	AL FORM OF THE SURVIVAL MODEL Nr. par. MLL AICc Akaike weights 9 -2151.4 4320.8 >0.999 6 -2173.9 4359.8 <0.001	AL FORM OF THE SURVIVAL MODELTEMINr. par.MLLAICcAkaike weightsModel parameters9-2151.44320.8>0.999 λ_T, v_T, σ_T λ_T, v_T, σ λ_T, v, σ λ, v, σ_T λ, v_T, σ_T λ, v_T, σ λ, v_T, σ λ, v, σ 9-2173.94359.8<0.001	AL FORM OF THE SURVIVAL MODEL TEMPERAT Nr. par. MLL AICc Akaike weights Model Nr. parameters Nr. par. 9 -2151.4 4320.8 >0.999 λ_T, v_T, σ_T 9 λ_T, v, σ 5 λ_T, v_T, σ_T 9 λ_T, v, σ 5 λ_T, v_T, σ_T 7 λ, v, σ_T 5 λ, v, σ_T 5 λ, v, σ_T 5 λ, v_T, σ_T 7 λ, v, σ_T 5 λ, v, σ 3 6 -2173.9 4359.8 <0.001	AL FORM OF THE SURVIVAL MODEL TEMPERATURE DEI Nr. par. MLL AICc Akaike weights Model parameters Nr. par. MLL 9 -2151.4 A320.8 >0.999 λ_T, v_T, σ_T 9 -2151.4 λ_T, v, σ 5 -2163.7 λ_T, v, σ 7 -2163.2 λ_T, v, σ_T 7 -2163.2 λ, v, σ_T 5 -2167.4 λ, v, σ_T 5 -2165.9 λ, v, σ_T 7 -2165.9 λ, v, σ_T 5 -2168.0 λ, v, σ 3 -2170.2 6 -2173.9 4359.8 <0.001	AL FORM OF LIFE SURVIVAL MODEL TEMPERATURE DEPENDENT Nr. par. MILL AICc Akaike weights Model parameters Nr. par. MLL AICc 9 -2151.4 4ICc $\Lambda_{T, v, \sigma_{T}}$ 9 -2151.4 4320.8 $\Lambda_{T, v, \sigma_{T}}$ 5 -2163.7 4337.4 $\Lambda_{T, v, \sigma_{T}}$ 7 -2163.2 4340.5 $\Lambda_{T, v, \sigma_{T}}$ 7 -2163.2 4340.5 $\Lambda_{V, v, \sigma_{T}}$ 5 -2167.4 4344.8 $\Lambda, v, r, \sigma_{T}$ 5 -2165.9 4345.9 $\Lambda, v, r, \sigma_{T}$ 5 -2168.0 4345.9 $\Lambda, v, r, \sigma_{T}$ 5 -2168.0 4345.9 Λ, v, σ_{T} 3 -2173.9 4359.8 <0.001	

Table S1. Selection of the functional form of the survival model and temperature dependence of its parameters. Maximum log-likelihoods (MLL) and Akaike Information Criteria (AIC) were used to select the models.

Danamatana	Temperature						
Parameters	25°C	27°C	29°C				
2 (1 ⁻¹)	0.02954	1.38x10 ⁻⁴	1.25x10 ⁻⁵				
λ(d)	[0.02117 - 0.04098]	$[2.0x10^{-6} - 2.31x10^{-3}]$	$[0 - 1.85 \times 10^{-3}]$				
	0.4612	0. 2069	0.1386				
V	[0.3789 - 0.508]	[0.134 - 0.307]	[0.0892 - 0.2019]				
	1.275x10 ⁻⁷	2.1545	2.3833				
ω	[0 - 0.3617]	[1.6623 - 2.1634]	[2.2419 - 2.3557]				

Table S2. Estimates of the survival model parameters. Between parentheses are the 95% confidence intervals of the parameters calculated using profile likelihood.

Competence dynamics

For the acquisition of competence, since there is a minimum period of time required for individuals to complete embryogenesis and develop the structures needed for settlement, we assume that $\alpha_T(t) = 0$ when $t < t_{c,T}$ and afterwards larvae acquire competence at a constant stochastic rate $a_T(14)$. After acquiring competence, larvae lose competence at a stochastic rate $\beta_T(t)$. The competence likelihood is given by the probability of being competent at each of the sampling days (*t*), which is given by the probability density of having acquired competence between time $t_{c,T}$ and *t*, and remained competent until at least time *t*:

$$P_{c}(t) = \int_{\tau=t_{c_{T}}}^{t} a_{T} e^{-aT\left(\tau-t_{c_{T}}\right)} e^{-\int_{\gamma=0}^{t-\tau} \beta_{T}(\gamma)d\gamma} d\tau$$

For the loss of competence, our most general model is the "generalized Weibull", according to which the loss of competence rate is:

$$\beta_{T}(t) = \frac{b_{T}\eta_{T}(b_{T}t)^{\eta_{T}-1}}{1 - \omega_{T}(b_{T}t)^{\eta_{T}}}$$

This model allows for "bathtub-shaped" loss of competence curves, where the rate of loss of competence is high initially, decreases as larvae age, and then increases again as larvae become very old. However, we might expect instead that loss of competence increases over time as larvae become very old and eventually deplete their energy reserves. Therefore, we also consider special cases of the generalized Weibull. For instance, the standard Weibull model, which allows monotonic increases or decreases in mortality rate over time, is the limiting case of the generalized Weibull as $\omega \rightarrow 0$:

$$\beta_T(t) = b \, \eta(bt)^{\eta-1}$$

and the exponential model, according to which rate of loss of competence is constant over time, is the special case of the Weibull model when $\eta=1$:

$$\beta_T(t) = b$$

To assess which distribution (exponential, Weibull or Generalised Weibull) best described the loss of competence, we fitted the competence data to models assuming all three possible distributions. For each one of them, the parameters were estimated using maximum likelihood, and then we used AIC to select the model that best described the loss of competence dynamics. After selecting the functional form for the loss of competence, we assessed whether there was support for temperature-dependent competence rates by comparing a model where all parameters were independent of temperature with models where different combinations of competence parameters were dependent on temperature, using the AIC.

The loss of competence was best characterised by a Weibull distribution (Table S3, see best fit model in Fig. S1b). In our best-fitting model, temperature decreases the minimum time to competence (t_c) and increases the per capita rate of loss of competence (b) (Tables 3 and 4), meaning larvae develop (acquire competence) faster at higher temperatures and lose the ability to settle earlier on. The per capita rate of acquisition of competence (a) and the shape parameter of the loss of competence (η) do not differ among temperatures (Tables S3 and S4). Akaike weights indicated strong support for the Weibull functional form, especially relative to the simpler exponential form. In the model selection for temperature dependence, there was some model selection uncertainty, with the model including only temperature effects on t_c , and the model including temperature effects on t_c and a but not b, receiving some support in the model selection. However, overall evidence for temperature-dependent competence dynamics was very strong: the model with no temperature-dependent parameters had essentially zero support in the model selection (Table S3). **Table S3.** Selection of the functional form of the loss of competence model and temperature dependence of its parameters. Maximum log-likelihoods (MLL) and Akaike Information Criteria (AIC) were used to select the best fitting model. $_T$ signifies that the parameter varies with temperature (i.e. temperature dependence); when absent, the parameter is constrained to be equal for all temperatures (i.e. independent of temperature), e.g. t_{cT} , a, b_T , η_T signify that a is independent of temperature, while t_{cT} , b_T and η_T are dependent of temperature.

FUNCTIO COMPET	OSS OF FENCE	TEMPERATURE DEPENDENCE OF ALL COMPETENCE PARAMETERS							
Model	Nr. par.	MLL	AICc	Akaike weights	Model parameters	Nr. par.	MLL	AICc	Akaike weights
Generalised Weibull	15	-285.0	605.6	0.017					
					$t_{cT,} a_T, b_T, \eta_T$	12	-285.0	597.5	0.029
					$t_{c,} a_T, b_T, \eta_T$	10	-296.5	615.4	< 0.001
					$t_{cT,}a, b_T, \eta_T$	10	-285.5	593.3	0.234
	12 -2				t_{cT} , a_T , b_{J} , η_T	10	-288.1	598.7	0.016
		-285.0	597.5		$t_{cT,} a_T, b_T, \eta$	10	-286.6	595.5	0.078
				0.983	$t_{c,} a, b_{T}, \eta_{T}$	8	-304.3	626.2	< 0.001
					$t_{c,} a_T, b, \eta_T$	8	-299.6	616.7	< 0.001
Wathall					$t_{c,} a_{T}, b_{T}, \eta$	8	-296.9	611.4	< 0.001
weibuli					$t_{cT,}a,b,\eta_T$	8	-289.0	595.5	0.078
					$t_{cT,}a,b_{T},\eta$	8	-287.4	592.3	0.386
					$t_{cT,} a_T, b, \eta$	8	-290.2	597.9	0.023
					$t_{c,} a, b, \eta_T$	6	-309.7	632.4	< 0.001
					$t_{c,} a, b_{T}, \eta$	6	-312.3	637.6	< 0.001
					$t_{c,} a_{T}, b, \eta$	6	-302.1	617.2	< 0.001
					$t_{cT,} a, b, \eta$	6	-290.6	594.1	0.157
					$t_{c,}a,b,\eta$	4	-312.3	632.7	< 0.001
Exponential	9	-339.2	698.4	< 0.001					

Table S4. Estimates of the competence model parameters. Between parentheses are the 95% confidence intervals of the parameters calculated using profile likelihood. The mean time to competence (mtc) was calculated as $t_c + 1/a$. * denotes that this parameter was dependent on temperature in the best-fitting model selected by AIC.

	ě		
Parameters	25°C	27°C	29° C
* (1)	5.38	4.89	3.87
t^{c} (d)	(5.04 - 5.74)	(4.77 – 5.01)	(3.74 - 4.01)
a (d-l)	0.4497	0.4497	0.4497
<i>a</i> (u)	(0.3672 - 0.5497)	(0.3672 - 0.5497)	(0.3672 - 0.5497)
1 * (1 ⁻¹)	0.01623	0.02669	0.02996
<i>b</i> ⁺ (d)	(0.01047 - 0.02559)	(0.01847 - 0.03770)	(0.02126 - 0.04094)
	0.3981	0.3981	0.3981
η	(0.3236 - 4988)	(0.3236 - 4988)	(0.3236 - 4988)
	7.60	7.12	6.10
mic (d)	(7.19 - 8.05)	(6.73-7.61)	(5.70-6.57)



Fig. S1. Larval survival (a) and competency (b) over time at 27°C (current) and 29°C (2050-2100). The circles represent the observations, and the lines represent the best fitted models. Note: observations on B were slightly offset to allow visualization of all replicates of both treatments that would otherwise be overlapped.

Part 2: Hydrodynamic model and validation of present-day hydrodynamics

Hydrodynamic model

Larval dispersal was modelled using the depth-averaged version of the ocean model SLIM¹ and its particle-tracking module, following the same approach as Thomas et al. (2015). SLIM is a finite element, unstructured mesh ocean model. SLIM's use of an unstructured mesh allows the model resolution to be varied in space (Legrand et al. 2006). The mesh was generated with the Gmsh software package (Geuzaine and Remacle 2009), and was made very fine close to reefs and coastlines, where small-scale flow features are known to be important, whilst being kept coarser in open-sea areas, where the flow is more uniform and high resolution is not essential. The mesh resolution ranged from 200 m to 5 km, the time step used was 44 seconds, and the model was able to explicitly resolve small-scale features such as tidal eddies forming in the wakes of reefs. Given the topographic complexity of the region, resolving these features is essential to accurately model larval dispersal, as they are known to have a significant impact on retaining larvae close to their natal reef (Burgess et al. 2007). Details of the model equations and the paramaterisations used can be found in Thomas et al. (2014). The depth-averaged SLIM model has previously been shown to be able to realistically reproduce large-scale flow through different regions in the GBR (Andutta et al. 2012; Thomas et al. 2014; Thomas et al. 2015; Wolanski et al. 2013), as well as propagation of tides (Lambrechts et al. 2008; Thomas et al. 2014), salinity concentration (Andutta et al. 2011), suspended sediment concentration (Lambrechts et al. 2010) and small-scale features in the wakes of islands (Lambrechts et al. 2008). The use of a depth-integrated model for our study region is justified by the fact that waters in the GBR are generally vertically well-mixed throughout the year and over most of the shelf where observations exist (e.g. see Middleton and Cunningham 1984; Wolanski 1983, Luick et al. 2007; Dimassa et al., 2010; Mao and Luick, 2014), especially over reefs, where larval dispersal is concentrated, and where bottom roughness is at least an order of magnitude greater than elsewhere (this is accounted for in the model), further facilitating rapid vertical mixing (Lugo-Fernández et al. 1998).

Stratification of the water column is known to occur under specific conditions on the GBR shelf, for example due to episodic river plumes, or due to local upwelling at the shelf break (Mao and Luick, 2014), and whilst a full 3D model would be necessary to simulate flow during these specific episodes, such conditions would not be expected to encompass any significant number of reefs in our domain. As currents at the water surface can be different to lower water layers during periods of sustained winds, it is possible that omitting this detail could lead to underestimating the "noise" in particle dispersal for larvae that spend significant amounts of time at the surface; whilst this effect can be paramaterised in a 2D model, the range of uncertainty in

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

parameters such as the length of time spent at the surface, is so great that it is impossible to do so with any useful certainty without risking artificially biasing the results. Furthermore, it is not clear that omitting this effect would systematically bias the modelled relative difference between different temperature scenarios.

Depth-integrated models have been shown to compare favourably with full 3D models on the GBR shelf (Black et al. 1991; Luick et al. 2007). Using a depth-integrated model therefore allowed us to focus finite computing resources to resolving reef-scale horizontal flow dynamics which strongly affect larval dispersal throughout the GBR, as well as capturing their effect on large-scale flow through the GBR, rather than on resolving 3D effects, which would generally be expected to affect dispersal dynamics in our domain on a more local level. Finally, whilst accounting for fine-scale 3D effects around reefs could yield more accurate estimates of connectivity metrics such as local retention (as long as reef-scale horizontal resolution is maintained), we have no reason to believe that the modelled effect of a temperature change, or modulation in low-frequency currents, would be substantially different with a 3D model.

External forcings were applied to the hydrodynamic model to account for the effects of the tides (OSU TOPEX/Poseidon Global Inverse Solution 7.2 dataset; Egbert and Erofeeva (2002)) and the wind (NCEP Climate Forecast System Reanalysis [CFSR] v2; Saha et al. (2014)) as described in Appendix S1 of Thomas et al. (2015). Water exchange with the neighbouring Coral Sea was accounted for by applying an additional water inflow along the central section of the open sea boundary (between 15°S and 17.6°S), with a corresponding outflow through the southern sections, resulting in the creation of a southward residual circulation (in the absence of other forcings). During periods of intense northward wind-driven currents, the direction of the net residual current was found to reverse and flow northward, in line with observations (Wolanski and Pickard 1985). The exact strength and position of the inflowing and outflowing currents were calibrated using current meter data from moorings of the Great Barrier Reef Ocean Observing System (GBROOS; IMOS (2013)) located close to the domain boundaries. Simulations were carried out for the 35 days following coral mass spawning in 3 successive years (2008, 2009, 2010), and calibration was carried out separately for each spawning season simulated, as the strength of the inflow from the Coral Sea can exhibit inter-annual variability (Burrage et al. 1997); total inflow applied for the 3 spawning years was 0.7 Sverdrups (2008), 1.1 Sv (2009) and 1.6 Sv (2010). These three forcings (tides, winds and low-frequency exchanges with the Coral Sea) are known to be the main drivers of water circulation on the GBR shelf (Wolanski and Pickard 1985, Thomas 2015). The model was validated for each spawning season simulated (shown below) and was found to realistically reproduce flow through the domain under present-day conditions.

Averaged simulated current speeds across all 3 simulations are shown in Figure 1f, which illustrates the complexity of the currents in the region, with currents increasing greatly in strength towards the large Herbert Creek estuary located roughly halfway along the coastline in the figure, which contains many nearshore reefs, and strong water speed gradients are visible

around a large number of offshore reefs, particularly in the more northerly half of the domain. It should be noted this map does not directly show transient features such as tidal reef-wake eddies as they would be visible in a given snapshot in time, though these would still contribute to increasing average current speeds.

Particle-tracking Module

The dispersal of larvae through the region was modelled using a Lagrangian particle tracking module integrated into SLIM. Details of the model equations and parameterisations can be found in Thomas et al. (2014); particles were released into the domain gradually over 2 days following coral mass spawning dates, simultaneously over all reef locations, with particle density proportional to the reef surface area, and their transport was modelled using a random walk formulation of the 2D advection-diffusion equation (Spagnol et al., 2002). The horizontal diffusivity coefficient used for the random walk was calculated using the formulation in de Brye et al. (2010), which contains a dependence on the local element size of the hydrodynamic mesh using the formula of Okubo (1971), reflecting the fact that larger mesh elements contain a greater range of unresolved water motion than smaller elements. This approach has been applied in numerous studies of coastal seas using multi-scale modelling (e.g. see Andutta et al. 2011; de Brauwere et al. 2011; Pham Van et al. 2016). Details of particle release and the diffusivity coefficient used can be found in Table S11. The particle tracking model used a time step of 120 seconds, and outputs from the hydrodynamic model were read in at a time interval of 25 minutes.

The positions of reefs are taken from the Great Barrier Reef Marine Park Authority Features shapefile layer (GBRMPA 2013). Only reef areas shallower than 10 m were considered in the present study, as reefs at greater depths in the domain are not yet consistently included in this map, and selective exclusion of deeper reefs can lead to a significant misrepresentation of connectivity patterns (Thomas et al. 2015). The number of reefs over which larvae were released was 1,223. Data on larval mortality and development rates at different water temperatures are presented in Appendix 1. The virtual larvae released in the model were considered to acquire and lose competency at the (temperature-dependent) rates give in Part 1. Additionally, temperaturedependent mortality was applied using the data given in the same appendix. Because our main conclusions concern how warming alters early larval development, a piecewise approach in which different survival parameters are applied to early (embryogenesis) vs. late development (Moneghetti et al. 2019) was not needed. Present-day water temperatures in the region focused on in this study (i.e. the southern GBR) are typically in the range of 26°-28°C during the coral mass spawning period in Nov-Dec (McLeod et al. 2015); in the model the water temperature was considered to be uniform at 27°C in the present day, and at 29°C for the future scenario. A larva was considered to settle onto the first reef it passed over once it was competent. By the end of the particle-tracking simulations (30 days) the number of remaining particles still alive and competent to settle was of small enough demographic significance -10-15 times smaller than the total number of settled particles – that they could no longer have any materially significant effect

on the connectivity metrics we report. Whilst such low levels of larval exchange would be unlikely to affect local rates of population growth or decline on reefs with extant populations, they could nevertheless be relevant over long-time scales (e.g., facilitating colonization after local extinction and allowing gene flow, which might for example be relevant for the spread of warm-adapted genes).

The domain-wide connectivity measures calculated from the output of the simulations are reported in Tables S9 and S10. In particular, Table S9 reports the values of key connectivity measures for the 2 temperature scenarios (27°C and 29°C) averaged over the 3 spawning seasons simulated (2007, 2008 and 2009), as well as the relative change in these values across the 2 temperature scenarios. Alongside this, Table S9 also reports inter-reef interquartile ranges of these changes, as a measure of inter-reef variability. Table S10 reports the values of the same connectivity measures by spawning season simulated (2007, 2008 and 2009), and by temperature scenario (27°C and 29°C), as well as the relative change in these measures between the 2 temperature scenarios by year, in order to show the inter-annual variability in these measures for the 3 seasons simulated. As can be seen, the changes reported in the connectivity measures between the 2 temperature scenarios were qualitatively consistent across all 3 years, with some variability in the size of the changes between years.

Validation of present-day hydrodynamics

Validation data for the hydrodynamic model are presented in this section. Specifically, we evaluated whether the model's hydrodynamics under present-day conditions reproduced realistic circulation patterns in the modelled domain. Tables S5-S7 report observed and predicted depth-averaged current speeds and directions at different mooring sites in the GBR for each spawning season simulated. Observed data were obtained from the Great Barrier Reef Ocean Observing System (GBROOS; IMOS (2013)).

Each table reports unfiltered values averaged over the length of the 35-day simulation indicated in the caption. These data showed good overall model performance in recreating realistic net residual currents at the mooring locations, which included one site in an open-sea area (Capricorn Channel), where flow is relatively spatially uniform, and 2 others close to an island (Heron Island North and South), where smaller-scale flow features become more important. In all cases the predicted average current speeds and directions were close to the observed values, and within their standard deviations. Looking specifically at the standard deviations, the open-water Capricorn Channel site exhibits less modelled variability than observations, likely due to the coarse spatial resolution of the wind forcing data missing smallerscale features, whilst at the two Heron Island sites where flow has higher spatial gradients and is more strongly influenced by local topography, the modelled variability is closer to observations. There is a slight eastward bias in the current direction estimated at the Heron Island South site, which is very likely due to localized inaccuracies in the local bathymetry dataset used: given the close proximity of the site to Heron Island, even a small misrepresentation of the topography could result in the current direction diverging from the observed values. Whilst such mismatches may be expected to occur at various locations throughout the GBR, we would not expect this to introduce systemic biases in the reported connectivity metrics at the domain-scale, given it contains well over 1,000 reefs.

Table S5: Observed $(|U_{obs}|)$ and simulated $(|U_{SLIM}|)$ depth-averaged absolute current speeds averaged in time over the length of the simulation for 2008, reported in ms⁻¹ with their standard deviations, at GBROOS mooring sites in the southern GBR. Average observed $(|\alpha_{obs}|)$ and simulated $(|\alpha_{SLIM}|)$ current directions are also reported, in degrees relative to North, along with their standard deviations. Time-series plots of these data are shown in Figures S2-S7 (with tides filtered out). CCH: Capricorn Channel; HIN: Heron Island North; HIS: Heron Island South.

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

Table S6. Validation data for the 2009 simulation. Observed data for HIN were unavailable. See Table S5 caption for legend.

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

Table S7. Validation data for the 2010 simulation. See Table S5 caption for legend.

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

In order to assess the ability of the model to reproduce realistic flow over time-scales longer than the semi-diurnal tidal component (which dominates the variability at most locations on the shelf), time-series plots of observed and predicted depth-averaged current speeds and directions, averaged over a 24-hour period, are shown in Figures S2-S4 (speed) and S5-S7 (direction). Additionally, we calculated several error metrics to quantify model performance:

• **Bias**: For <u>Speed</u>, model biases are small (at most ±3cm/s, and under ±1cm/s for 5 out of 8 plots, compared with average speeds on the order of 20-35cm/s), and generally neither very strongly positive or negative (2 sites out of 3 have equal numbers of positive and negative years, whereas Heron Island South exhibits a slight negative bias every year).

For <u>Angle</u>, likewise 2 out of 3 sites have a very small bias (single digits, which as a proportion of 360° is <5%), which varies between positive and negative depending on the year, whilst Heron Island South exhibits a larger bias consistently to the East, which suggests there is a systemic issue introducing this error. This phenomenon appears very localised around this site, since the nearby Heron Island North doesn't exhibit the same systemic bias, and is likely to be caused by inaccuracies in the bathymetry, or underresolved coastal processes at this specific location.

- Mean Absolute Error & RMSE: MAE is included as a guide to the average size of model divergence from observations, and RMSE is included as a standard measure to allow comparison with other models. RMSE is more prone to be affected by short durations of very large discrepancies between the 2 datasets. For <u>Speed</u>, both metrics show that model error does vary between years, with MAE at Capricorn Channel varying from 2cm/s in 2008 to 4cm/s in 2009 and 2010. Whilst these values are small relative to the size of the mean observed current speeds (~25cm/s at Capricorn Channel), confirming that modelled current speeds are well within the bounds of typical observations, some years and sites show absolute errors which can nonetheless approach ~15-20% of observed currents at these specific locations. In particular, the time series plots show some model-observation divergence events lasting ~ 2-3 days at a time, which is mainly driving these MAE values, particularly at the Capricorn Channel site.
- Index of agreement (d) from Willmott (1981): This dimensionless index reflects the degree to which the observed data are accurately estimated by the modelled data, and is defined as:

$$d = 1 - \frac{\sum_{i=1}^{N} (P_i - O_i)}{\sum_{i=1}^{N} [|\dot{P}_i| + |\dot{O}_i|]^2}$$

where P_i and O_i are respectively the predicted and observed data points, $\dot{P}_i = P_i - \bar{P}$ and $\dot{O}_i = O_i - \bar{O}$, with \bar{P} and \bar{O} being respectively the means of the predicted and observed data. *d* therefore is a measure for the quality of the model predictions, varying from 0 to 1, with 0 indicating no relationship between observed and predicted values, and 1 indicating a perfect reproduction of observations.

For <u>Speed</u>, this index exhibits most inter-annual variability at the Capricorn Channel site, ranging from 0.92 in 2008 to 0.71 in 2010. Indeed 2008 is the year with highest *d* values across all 3 sites. In both 2009 and 2010, the Capricorn Channel site has a lower *d* value, reflecting the more prolonged departures from the tidal cycle which are evident in the observed line, but not well reproduced in the modelled line; these mismatches remain generally fairly contained in size (typically $\leq \sim$ 5cm/s in magnitude) and well distributed both above and below the observed values, resulting in net biases of only 0 cm/s and +2 cm/s in 2009 and 2010 respectively, whilst MAE for both these years is at 4cm/s, corresponding to 15-16% of the mean observed speeds. Given the location of the Capricorn Channel site, in open waters away from islands or reefs, the departures between modelled and observed currents are likely due to a combination of unresolved features in the wind forcing, and potentially unresolved multi-day features in water exchanges with the nearby Coral Sea.

As can be seen from the plots at the Heron Island sites, the model accuracy as measured by d in open water (at Capricorn Channel) does not appear very strongly correlated with model performance at the more bathymetrically complex sites close to Heron Island, where local topographic features are likely to be important in influencing the speed and direction of flow in a non-linear way with respect to the flow in open waters. Whilst modelled speed at Heron Island North does match observations better in 2008, when Capricorn Channel also had a high d value, than in 2010, when modelled overshoots in speed in the spring phase of the spring-neap tidal cycle at both sites led to lower d values, the same cannot be said for Heron Island South, which instead matched observations better in 2009 and 2010 than in 2008.

The plots of flow <u>Angle</u> show less variability generally at the Capricorn Channel site in open water, whereas at the Heron Island sites we see small-scale observed departures from the mean value ($< \sim 1-2$ days and $< \sim 25^{\circ}$ from the mean) which are not well reproduced by the model - again the most likely explanations are unresolved small-scale processes in the forcing data, in combination with likely small-scale inaccuracies in bathymetry data and potentially flow features (particularly at Heron Island South) affecting flow at these complex, high-gradient sites.

Taken together, the departures between model and observations would reasonably be expected to affect modelled dispersal of larvae to the extent that we should use care in not overinterpreting the model estimated connectivity on the spatial scale of individual reefs and temporal scale of a few days, since the validation shows the model cannot be expected to consistently reproduce flow speed and direction at these scales, all of the time. This is both due to errors introduced by inaccuracies in the forcing data, and unresolved features and inaccuracies in the model bathymetry; this is an inevitable issue when modelling flow in a region as topographically complex as the GBR. However, these same validation data also show that on the temporal scale of typical larval dispersal processes - roughly a month - departures between modelled and observed flow tend to even out, such that the net bias is close to zero, and on the temporal scale of *multiple* spawning seasons, in our case 3, net biases in modelled larval dispersal will be driven even lower.

Furthermore, these results also underline the importance of modelling larval dispersal at large spatial scales, in our case encompassing well over a thousand reefs distributed over hundreds of kilometres, in order to make the overall conclusions robust to small-scale inaccuracies in modelled flow. Whilst observational data was obtained for only 3 locations, it is reasonable to assume that on the spatial scale of the entire southern GBR region included in our domain, net biases and errors will be driven vastly lower to the point where the larval dispersal metrics and connectivity matrices obtained from these simulations can be considered as robust. Whilst this doesn't exclude that systemic domain-wide sources of error in modelled flow could and inevitably will still be present, the validation plots and metrics show these should be contained to reasonable levels.

Further validation of the SLIM-based biophysical model applied to other parts of the Great Barrier Reef can be found in Thomas et al. (2014) and Thomas et al. (2015).



Figure S2. Time-series plot of observed (blue) and predicted (orange) depth-averaged current speed at different mooring sites for the 2008 simulation. A running boxcar filter is applied with a period of 24 hours to filter out short-frequency variability. Dotted lines show mean values. MAE: Mean Absolute Error, RMSE: Root Mean Square Error, d: index of agreement (Willmott, 1981)



Figure S3. Time-series plot of observed (blue) and predicted (orange) depth-averaged current speed at different mooring sites for the 2009 simulation. See caption to Figure S2 for detail and acronyms.



Figure S4. Time-series plot of observed (blue) and predicted (orange) depth-averaged current speed at different mooring sites for the 2010 simulation. See caption to Figure S2 for detail and acronyms.



Figure S5. Time-series plot of observed (blue) and predicted (orange) depth-averaged current direction at different mooring sites for the 2008 simulation. See caption to Figure S2 for detail and acronyms.



Figure S6. Time-series plot of observed (blue) and predicted (orange) depth-averaged current direction at different mooring sites for the 2009 simulation. See caption to Figure S2 for detail and acronyms.



Figure S7. Time-series plot of observed (blue) and predicted (orange) depth-averaged current direction at different mooring sites for the 2010 simulation. See caption to Figure S2 for detail and acronyms.

Part 3: Estimating projected changes in water flows into the GBR

Context

Many large-scale climate models predict a strengthening of the South Pacific sub-tropical gyre, of which the westward-flowing South Equatorial Current (SEC) is the northern branch. The SEC crosses the Coral Sea and approaches the Great Barrier Reef (GBR) continental shelf roughly between 11° and 20°S (Kessler and Cravatte 2013), causing a flow onto the shelf which has been observed between 14° and 20°S (Andrews and Clegg 1989; Brinkman et al. 2001; Church 1987), and which in turn drives a southward residual flow on the shelf known as the Coastal Sea Lagoonal Current (CSLC; Wolanski et al. (2013)). A strengthening of the SEC would be expected to cause a corresponding increase in the strength of the poleward-flowing East Australian Current (EAC), which flows parallel to the Australian coastline (Sen Gupta et al. 2012, 2016; Sun et al. 2012). Whilst the effects of the strengthening EAC along its central area and southern extension have been extensively studied (e.g. Oliver and Holbrook 2014), such studies rarely extend to include the nascent EAC off the GBR. Furthermore, the model resolution used in global climate models is generally much too coarse to be able to study coastal processes such as those tackled in this article.

An increase in the flow onto the GBR continental shelf would not necessarily lead to stronger currents through the whole shelf, as the net water circulation through the GBR is governed by a complex interplay between the tidal currents, which vary in strength along the shelf and which can significantly modulate the strength of longshore residual currents through the mechanism of tidal friction, wind-driven currents which can overpower the CSLC during periods of prolonged south-easterly trade winds, and the CSLC itself (Wolanski et al. 2003; Wolanski and Spagnol 2000). The relative importance of these three factors is not constant and can change significantly in time and space; for example tidal currents often dominate over scales of minutes to hours in the Southern GBR (SGBR), whereas wind-driven and low-frequency currents dominate over time scales of days to weeks (Wolanski and Pickard, 1985). There can also be variability in the strength and relative dominance of wind-driven currents from one spawning season to the next. The timescales of larval dispersal – hours to weeks – is such that all three factors play important roles, with their relative importance changing depending on the connectivity metric being observed. In the SGBR specifically, the relatively strong tides can be expected to affect local retention most significantly by driving the flushing of larvae from their natal reefs, with peak tidal currents generally being much larger than residual currents (e.g. see Andutta et al., 2012), while wind-driven and low-frequency currents would be expected to more strongly drive longer-distance dispersal and connectivity, particularly between clusters of disparate reefs.

Considering how the main drivers of circulation in the GBR may change in future decades, tidal forcing can reasonably be expected to remain unchanged, whilst changes to bottom roughness and sea level can reasonably be expected to not significantly alter currents on a large

scale, though reef degradation may locally have an impact where it leads to reduction in bottom roughness. In the case of large-scale flow in the South Pacific affecting circulation in the GBR, the scale of the flow features involved is such that they can be modelled by global climate models, and as outlined above many models suggest a strengthening of the SEC in the coming decades; here we model how these changes may influence flow on the GBR.

This is, of course, not to deny that other small-or large-scale environmental changes not accounted for in these climate models could potentially affect the low-frequency circulation through the GBR. Of the 3 drivers of water circulation outlined above, changes to wind stress also have the potential to affect currents through the region and thus larval dispersal, in particular for larvae that mainly inhabit the upper water layers. However, the uncertainty around any future changes to the wind field on the scale of the southern GBR's continental shelf, which is relatively small compared to the scales resolved by global climate models, and specifically during the limited annual time window of coral larval dispersal, mean we currently lack robust, quantitative, regional-scale projections of future wind stress at sufficient resolution, and as such it is not currently possible to estimate if and how any such changes could affect larval dispersal with any useful degree of confidence. Thus, the results presented in this study represent our best estimate of future changes at the current time.

Method

Estimates for the change in water fluxes entering the GBR shelf were obtained by analysing the output of 27 CMIP5 global climate model versions² (Taylor et al. 2012). Zonal water currents were obtained for the top 200 m of the transect between 10° and 20°S (roughly corresponding to the known range of the SEC liable to impinge on the GBR shelf [Thomas 2015]) at a longitude of 155°E for a) present-day simulated circulation, and b) projected circulation for 2080-2100 assuming a "business as usual" global climate scenario (corresponding to the Representative Concentration Pathway [RCP]8.5), in order to assess the greatest possible impact of climate change on water circulation on the shelf. Whilst the bulk of the impinging water does not enter the GBR shelf, we assume that the change in water transport onto the shelf is proportional to the change in transport impinging on the shelf.

The relative change in net westward zonal water velocity was calculated for each model, and a multi-model median of the relative change was calculated, as well as upper and lower quartiles of the distribution. Simulations were then run of the hydrodynamics on the GBR shelf using SLIM for future scenarios using the approach outlined in Appendix Part 2, but with the following modification: the residual currents entering the shelf at the open sea boundaries (i.e. representing water exchange with the neighbouring Coral Sea) were modulated by the multi-

² CMIP5 model versions: ACCESS1.0, ACCESS1.3, CanESM2, CCSM4, CESM1-CAM5, CMCC-CESM, CMCC-CM, CMCC-CMS, CNRM-CM5, CSIRO Mk3.6, FIO-ESM, GFDL-ESM2G, GFDL-ESM2M, GISS-E2-H, GISS-E2-R, HadGEM2-CC, HadGEM2-ES, IPSL-CM5A-LR, IPSL-CM5A-MR, MIROC5, MIROC-ESM, MPI-ESM-LR, MPI-ESM-MR, MRI-CGCM3, MRI-ESM1, NorESM1-ME, NorESM1-M

model median relative change, as well as the lower and upper quartiles, to obtain a set of 3 simulations which are representative of the range of relative changes predicted by the models; this was done to account for the significant inter-model variation. All other model parameters were not modified compared with the present-day simulations, either because they are not expected to change in a way significant enough to affect large-scale water circulation (such as tidal forcing or bottom roughness), or because the uncertainty is too great to currently estimate potential changes with any confidence (such as local wind stress over the GBR during the specific time windows of coral spawning periods). The aim was to quantify the impact of changes in water circulation alone on larval connectivity. For each present-day simulation (i.e. 2008, 2009 and 2010), a set of three future scenario simulations was run. Larval dispersal simulations were then carried out using these "future scenario" hydrodynamic simulations, and connectivity matrices were obtained. Connectivity indicators were calculated separately for each of these future scenario simulations and were then compared with the equivalent indicators in the corresponding "present day" scenario to obtain a value for relative change in the indicator. These values were averaged over the 3 years simulated for each of the 3 types of simulation (i.e. a) those forced by the multi-model-median change, b) those forced by the upper quartile change and c) those forced by the lower quartile change) to obtain a single set of 3 change indicators representing change due to median, upper and lower quartile predictions.

Results

Analysis of the output of 27 CMIP5 climate models showed that the net zonal flow towards the GBR shelf was expected to exhibit strengthened westward transport, although variability in predictions between models was significant, as shown in Figure S8. The multi-model median was a westward increase in current strength of 10%, and the upper and lower quartiles were an increase of 28% and a decrease of 3%, respectively.

Simulations of the hydrodynamics on the GBR shelf were run with the residual currents at the boundaries modified by these three values to obtain three sets of modelled water circulations (accounting for inter-model variation), and the outputs from these simulations were used to drive the larval dispersal model at a water temperature of 27°C. The change in the main connectivity indicators caused by the change in circulation patterns are shown in Table S8, along with respective standard errors that provide a measure of uncertainty around these changes due to present-day levels of inter-annual variability. The results show that changing the water in- and outflow at the boundaries had a minimal effect on larval dispersal; however, the uncertainty is relatively significant for dispersal distance. Changes in the speed of simulated water currents through the GBR's shelf were small, with even the more extreme of the scenarios – increasing low-frequency inflow by 28% – resulting in average water speeds changing by less than 1cm/s over the vast majority of the domain, with no great spatial heterogeneity in this response. These changes are small compared with the typical current speeds in the region which are >20cm/s, rising to over 50 cm/s in the immediate vicinity of certain reefs, as shown in Fig1f, mainly driven

by vigorous tidal currents. As such, the effect on connectivity patterns was minimal overall, with average changes in most quantities being smaller than 1% relative to the present-day scenario. Changes of the order of magnitude of 1% or smaller are relatively insignificant given the limitation in precision of large-scale models such as the one employed in this study, and as such it is not possible to conclude with any significant confidence that the changes in flow simulated in these experiments would likely lead to a significant change in these connectivity metrics in reality. Furthermore, the spatial variation in the changes was low, meaning that the whole domain saw similarly small changes. Given the changes to the connectivity indicators were around an order of magnitude smaller than the effect of 2°C warmer waters, we can conclude that even if low-frequency flow through the GBR changes more dramatically than the projected scenarios modelled here, the effect on connectivity for A. *millepora* would still likely be very small compared to the effects of warming waters. Furthermore, the changes to the connectivity indicators were smaller than their inter-annual variations in the present-day scenario (Table S10), suggesting that inter-annual variations in the wind field during spawning seasons have a stronger influence in causing inter-annual changes in connectivity than projected future changes to boundary currents, at least within the range of plausible changes projected by the CMIP5 models.

It is nonetheless worth pointing out changes to a couple of the connectivity metrics. For example, stronger inflow currents led to a small increase in the source-to-destination reef distance (+1.2% to +2.2%), implying that stronger inflowing currents led to slightly increased potential for travelling further from natal reefs. Interestingly, the weaker inflow current also led to a small increase in source-to-destination distance, albeit an insignificantly small one of +0.3%, which illustrates the non-linear nature of currents in the GBR: small changes to a particular current do not necessarily result in a linear response in particle dispersal, due to the vast complexity of the topography, and the interaction between low-frequency currents from the Coral Sea, wind-driven currents, and the strong tidal currents which flow through the domain (Wolanski et al., 2003, Wolanski & Spagnol, 2000). In this case, it may also be that weakening the inflowing current facilitated stronger wind-driven northerly currents during periods of southeasterly trade winds, which can occur during the spawning season, whilst having no discernible strengthening effect on the southerly currents during periods of low trade winds. This being the case, years with stronger south-easterly trade winds during the spawning season would be expected to see a different response to the modulation in low-frequency inflow than years with little or no wind. This is supported by the relatively high uncertainty around this change caused by present-day levels of inter-annual variability in the currents (standard error of 2.7% to 3.8%). It is therefore possible that if the typical wind regime during coral spawning season over the GBR changes significantly in the future, this could have a non-linear effect on the response of larval dispersal to stronger water exchanges with the Coral Sea, and in particular a drop in the strength of south-easterly trade winds could lead to changes in low-frequency flow onto the shelf having a larger impact on larval dispersal than if we assume present-day wind conditions, whereas an increase in their strength would likely lead to an even smaller impact on larval dispersal from increased flow onto the shelf.

Local retention also saw a small increase in the stronger current scenarios, presumably due to a small increase in water residence times over some reefs; again part of the explanation lies with the non-linear interaction between the currents and the topography, as imposing stronger currents at the boundaries does not necessarily lead to stronger currents over all the domain, and can even lead to a decrease in certain areas. For instance an increase in the current strength can cause an increase in residence times in areas sufficiently dense with reefs, due to increased steering of residual currents around reefs by the so-called "Sticky Water" effect (Wolanski & Spagnol, 2000; Andutta et al., 2012), facilitating increased local retention of larvae close to their natal reef. The self-recruitment rates exhibited a decrease, albeit of similarly very small magnitude, meaning that whilst there was a small increase in larvae settling on their natal reefs, this was also accompanied by an increase in larvae from other reefs. It should be borne in mind whilst interpreting these results that many of the main connectivity indicators, and particularly local retention and self-recruitment, are mostly affected by the flushing time of reefs, which in the southern GBR is mainly controlled by tidal rather than Coral Sea-driven or winddriven flows (see Andutta et al. 2012, Table 2; peak tidal currents at all mooring sites in the GBR are much greater than residual currents). For comparison, these changes are roughly an order of magnitude smaller than the impact of increasing the water temperature by 2°C (cf. results reported in the main text). Thus, the effect of the altered circulation patterns was considered insignificant compared with the effect of the temperature increase, particularly given the large uncertainty surrounding these changes in large-scale circulation.



Figure S8. Histogram showing the distribution of the projected relative changes in westward zonal currents between 10°S and 20°S, averaged over the top 200m of the water column, extracted from 27 CMIP5 models.

Table S8. Change in connectivity measures for different circulation scenarios, compared with the present-day scenario. The 3 scenarios listed correspond to a modulation of residual currents flowing through the domain of -3%, +10% and +28% relative to the present-day scenario. Data shown are for a water temperature of 27°C. Δ self-rec.: change in self-recruitment; Δ dist: change in average distance between source & destination reefs; Δ local ret.: change in local retention. The standard errors represent a measure of uncertainty around these changes due to present-day levels of inter-annual variability.

Scenario	$\Delta local ret. (\pm SE)$	$\Delta self$ -rec. ($\pm SE$)	$\Delta dist (\pm SE)$
-3% inflow	+0.1% (±1.2%)	-1.2% (±1.1%)	+0.3% (±2.7%)
+10% inflow	+0.5% (±0.4%)	-0.8% (±1.4%)	+2.2% (±2.7%)
+28% inflow	+1.3% (±1.4%)	-0.9% (±1.4%)	+1.2% (±3.8%)

Part 4: Current and future dispersal patterns and connectivity matrices

The changes to dispersal patterns estimated using the bio-physical dispersal model are summarized in Tables S9 and S10. The actual by-reef estimates (connectivity matrices) can be found at https://doi.org/10.5061/dryad.4f4qrfjbk

Table S9. Connectivity measures for different temperature scenarios simulated, averaged over all larvae, and over the 3 different years simulated. Relative changes are computed per year as the change in the averaged connectivity measures between the 2 temperature scenarios, then averaged over all years such that each spawning season had an equal contribution, meaning they do not represent the arithmetic difference between the year-averaged values reported for 27°C and 29°C. The 25th, 50th and 75th percentiles of relative changes are reported for year-averaged by-reef changes, with equal weight given to each reef, and are included as a measure of among-reef variability.

Temperature	Average source- to-destination reef distance	Local retention	Self-recruitment	Average number of incoming connections per reef
27°C	26.4 km	2.6%	6.9%	47.8
29°C	24.7 km	3.1%	7.9%	44.0
Relative change	-6.6%	+19.5%	+15.0%	-8.1%
[25 th , 50 th , 75 th] percentiles of among- reef relative changes	[-10.0%, -7.1%, - 4.2%]	[0.0%, +21.4%, +49.2%]	[-0.2%, +17.4%, +43.5%]	[-10.8%, -7.1%, - 3.0%]

Table S10. Connectivity measures for different temperature scenarios simulated, by year (columns 3-6), and relative change in each metric between the 2 temperature scenarios, by year (columns 7-10). The bottom row gives the average changes across all 3 years. LR: average local retention, SR: average self-recruitment, Cx/reef: average number of connections per reef, Length: average source-to-destination reef distance, d(LR): percent change in local retention between the 2 temperature scenarios, d(SR): percent change in self-recruitment between the 2 temperature scenarios, d(NC): percent change in the number of connections between the 2 temperature scenarios, d(Len): average percent change in the source-to-distance reef distance

Year	Temp	LR(%)	SR(%)	Cx/reef	Length (km)	d(LR) (%)	d(SR) (%)	d(NC) (%)	d(Len) (%)
2008	27	2.59%	7.01%	51.7	23.76				
	29	2.85%	7.71%	49.1	22.49	+10.4%	+9.9%	-4.9%	-5.3%
2009	27	2.05%	6.15%	53.9	32.88				
	29	2.53%	7.01%	47.2	31.51	+23.3%	+13.9%	-12.4%	-4.2%
2010	27	3.04%	7.38%	68.6	22.55				
	29	3.79%	8.93%	63.8	20.22	+24.9%	+21.1%	-7.1%	-10.3%
Yr-AVE						+19.5%	+15.0%	-8.1%	-6.6%

Table S11. Parameters used with the Lagrangian particle-tracking model to simulate dispersal of larvae in each spawning season.

Date/times of particle release	2008: 17 November, (00:00)
initiation	2009: 7 November, (00:00)
	2010: 26 November, (00:00)
Duration of particle release	48 hours; gradual release
Locations of particle release	Release occurred simultaneously over 1,223 reefs in the
	domain; reef extents obtained from GBRMPA shallow reefs
	layer (GBRMPA, 2013); reef centre coordinates used are
	contained in data deposited at Dryad – cf. link above
Extents of seeding habitats	Reef areas ranged from 0.02km ² to 155.2km ²
Particle tracker time step	120 seconds; hydrodynamic fields updated every 25 minutes
Particle tracker diffusivity	$K = α\Delta^{1.15}$ (following Okubo, 1973),
coefficient	with $\alpha = 0.041 \text{m}^{0.85}$ (following Andutta et al., 2011)

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Appendix 2:

Metapopulation model and details of model simulations

The metapopulation model estimates coral cover (based on number of polyps) on each reef over time and accounts for density-dependent growth (budding) and recruitment, using the connectivity matrices from the bio-physical dispersal model (Appendix 1). Previously reported biological data on fecundity and post-settlement survival of coral recruits is used to set realistic model parameters (details in Appendix 1), and all corals are assumed to have equal fecundity and post-settlement mortality. Fecundity, initial abundance and growth and mortality rates were set to be equal at 27 °C and 29 °C, as the aim was to predict changes in recovery times following disturbances due exclusively to the impact of changes in connectivity. We simulated 2 different types of disturbance: single-reef disturbances, where initial coral cover was reduced by 85% over one reef at a time, mimicking events such as crown-of-thorns outbreaks, and regional disturbances, where initial coral cover was reduced by 75% over a 30-km wide cross-shore strip, and by 40% in 30-km wide strips to either side, mimicking the passage of a severe tropical cyclone across the GBR. The model was run, in turn, using the connectivity matrices obtained from the 27°C and 29°C biophysical model runs, and we recorded the relative change in recovery times at each reef between the two scenarios.

Model description and parameters

To gauge the effect of the altered connectivity patterns on the time taken for coral populations on reefs to recover from disturbances, a polyp metapopulation model was utilised. The model is described by the following equation:

$$\frac{dS_i}{dt} = (1 - c_i(t)) \left(RS_i(t) + r(t)s \sum_j C_{ji}(t) \right)$$

discretised as:

$$S_{i,n+1} = S_{i,n} \left[1 + \Delta t R \left(1 - c_{i,n} \right) \right] + \Delta t r_n \left(\sum_j C_{ji,n} \right) s \left(1 - c_{i,n} \right)$$

where:

- $S_{i,n}$ is the size of the coral population on reef *i* at iteration *n*, counted as the number of coral polyps,
- Δt is the time step from iteration *n* to iteration n+1 (a value of $\Delta t = \frac{1}{96}$ years was used as this was found to be the largest value which resulted in stable model runs),

- *R* is the net clonal growth rate per coral polyp, estimated from the literature as R = 0.145 year⁻¹ (based on Gilmour et al. 2013, where the growth of an isolated coral reef system was measured during a period of minimal recruitment),
- c_{i,n} is the coral cover fraction on reef *i* at iteration *n*, i.e. the proportion of the reef's available space covered by coral polyps, given by c_{i,n}= (S_{i,n}A_{polyp}) /A_i, where A_{polyp} = 1 mm² is the surface area of a polyp (from Anthony 1999), and A_i is the surface area on reef *i* available for corals, assumed to be equal to 40% of the reef's total surface area, a typical coral cover proportion for a reasonably healthy reef in the GBR,
- r_n , herein referred to as the recruitment timing factor, is the value of a step function, labelled r(t) in the undiscretised model equation, at iteration n, which accounts for the fact that recruitment is concentrated into a limited time period. r(t) is a normalised step function indicating which period of the year recruitment occurs, and so is =0 outside the

spawning season, >0 during the spawning season, and has the property that $\int_{1 \text{ year}} r(t)dt=1$. For simplicity, recruitment is considered to occur during 1 month of the year, therefore $r_n = 12.0 \text{ year}^{-1}$ during the coral spawning season and $r_n = 0 \text{ year}^{-1}$ during the other 11 months of the year,

- *s* is the proportion of coral larvae settling which survive to maturity, taken to be s = 0.13 (Penin et al. 2010),
- C is the connectivity matrix, whose elements represent the number of larvae from origin reef *j* settling on destination reef *i*, per year. The term $\Delta t \sum_j C_{ji,n}$ therefore sums the total number of incoming larvae at reef *i* from all reefs (including reef *i* itself) during time step *n*.

The evolution of the population on a reef is therefore driven by asexual growth which continuously occurs throughout the year and recruitment which only occurs during the spawning season and is limited by the space available on the reef. The elements in the original connectivity matrices produced by the larval dispersal simulations gave the *proportion* of larva released at reef *j* arriving at reef *i* whilst competent, assuming all reefs had full coral cover. To obtain $C_{ji,n}$ – the *number* of larvae from reef *j* arriving at reef *i* per year – the following equation was used:

$$C_{ji,n} = P_{ji}c_{j,n}\frac{A_j}{A_{polyp}}e_{polyp}$$
(3)

where $c_{j,n}$ is the source reef's coral cover fraction, A_j is its surface area, A_{polyp} is the surface area of a polyp, taken as before to be 1 mm² based on Anthony (1999) and e_{polyp} is the number of eggs produced per polyp, estimated as 6/year from Hall and Hughes (1996). Only polyps aged 3 years or older were considered to contribute eggs.

The model accounts for the possibility of coral growing as exually via the term $\Delta t S_{i,n} R(1 - c_i)$, and through recruitment via the term multiplied by the connectivity matrix. The recruitment timing factor r_n ensures that recruitment is not allowed to occur all year round, but only during one month per year; in the remaining 11 months recruitment does not contribute to population growth. It should be noted that the net clonal growth rate R implicitly accounts for natural mortality as well as clonal growth. The factor of $(1 - c_i)$ accounts for the fact that space on a reef is limited, and as the free space available diminishes, coral growth slows down and settlement success also decreases. The surface area available to coral polyps was considered to be 40% of the reef's total surface area, a figure which represents the typical coral cover for a reasonably healthy reef in the GBR.

These parameters represent our best estimates, as more detailed data is scarce at present. The model makes a number of simplifications, such as assuming that coral growth will be 2dimensional, and that *R* and *s* are constant in space and time. However, it should be considered that the goal was to calculate the magnitude of the relative change in recovery times between different scenarios, rather than to accurately predict present-day recovery times per se. Model sensitivity analysis showed the main results presented in the main text are broadly insensitive to small uncertainties in the biological model parameters (see later section on Sensitivity of model to biological parameters). Furthermore, keeping the growth and survival rates constant allowed us to isolate the effect of the change in connectivity on recovery times, which was the specific aim of this study.

Model simulations and scenarios

Disturbances were simulated by reducing coral cover over certain reefs. Recovery times were obtained by recording how many iterations it took for the disturbed reefs to regain 99% of their initial coral cover. Two types of disturbance were simulated:

- a) Single reef disturbances, whereby initial coral cover was reduced by 85% over a single reef, mimicking the effect of a highly localized severe disturbance affecting a reef. This was repeated, independently, for every reef in the domain, to obtain recovery times for each reef. The aim was to mimic the effect of a highly-localised severe disturbance on a single reef, such as physical damage or destruction from coastal development, dredging, quarrying, destructive fishing practices and gear, boat anchors and groundings, and recreational misuse (touching or removing corals).
- b) Multiple reef disturbances, whereby coral cover was reduced on groups of reefs at a time. These groups were composed of 3 neighbouring cross-shelf strips 30 km wide (shown in Fig S9); all reefs in the outer strips had coral cover reduced by 40%, whilst reefs in the central strip had coral cover reduced by 75%, mimicking the effect of a severe tropical cyclone (TC) passing cross-shore through the GBR. This type of track and the area affected is consistent with what has been observed for several TCs in the GBR, most recently Severe TC Debbie (2017), which crossed over the GBR as a Category 4 storm and made landfall at Airlie Beach, just to the North of the study region, following a

similar type of cross-shore track, and had winds classed as "very destructive" (Category 3 or above) across a strip at least 90-100km wide whilst passing over the GBR (BoM, 2018). In general, the study area commonly sees TCs follow roughly cross-shore tracks crossing the GBR and approaching the coast from the Coral Sea (recent examples in the southern GBR include Erica, 2003; Ului, 2010; Anthony, 2011; Debbie, 2017), though some TCs do follow other tracks (notably Hamish, 2009, which followed an unusual long-shore track passing through most of the GBR).

In total this resulted in a set of 15 different parallel cyclone tracks being simulated (Figure S9 shows the cross-shelf strips). No reefs were disturbed in the southernmost 60km of the domain due to the very small number of reefs in this sector (4).

The reductions in coral cover were chosen to be on the more severe end of the level of damage which could be envisaged to occur on a coral reef in order to clearly test the impact that a change in connectivity could potentially have on recovery. For the Tropical Cyclone-like disturbance (type b in the list above), simple assumptions were made based on the fact that damage is expected to be greatest towards the middle of the TC's path and lower further out, and that observed damage to reefs following severe TCs can be both very extensive and variable in space, with some reefs almost entirely stripped of marine life whilst other reefs can show much lower levels of damage (GBRMPA, 2011; Beeden et al., 2015). Our model simplifies this out of necessity, but it should be borne in mind that we are not aiming to recreate the damage profile of a particular TC, but rather mimic the potential effects of a very severe TC.

For each of the 2 disturbance types, the model was run 3 times, each time using the connectivity matrix obtained from a different year's dispersal simulation, for a given temperature scenario (27 or 29°C). This process was repeated for both temperature scenarios, with the only difference between the 2 scenarios being the connectivity matrices used, allowing us to identify the impact of changing connectivity patterns on coral recovery times. The percent change in recovery times between the 27 and 29°C scenarios was calculated for each reef for each simulated year, and these percent changes were then averaged over all reefs to obtain a single percent change value per year. These values were then averaged over all simulated years to obtain a single figure, representing the year-averaged change in recovery times between the 27 and 29°C scenarios.



Figure S9: Southern GBR domain with cross-shelf strips used to disturb groups of reefs at a time shown in grey (see "Model simulations and scenarios" item b) in the main text for context). Reefs centroids are shown in red, for reference.

Sensitivity of model to biological parameters

To ascertain the sensitivity of model results to uncertainty in the biological input parameters, a sensitivity analysis was carried out whereby the population model was run for scenario *a*) described above (single-reef disturbances), using the same 3 years' connectivity matrices as used to obtain the results described in the main text, with the biological input parameters which affected the results reported in the text varied in turn (the results we are interested in being mean and standard deviation of changes in recovery times across all reefs). Parameters *R* (clonal growth rate), *s* (proportion of larval recruits surviving to maturity) and *e_polyp* (the number of eggs per polyp) were varied in turn by +/-10%, 25% and 50%. The change in recovery times between the 27°C and 29°C scenarios was calculated for each reef, and mean and standard deviations across all reefs were calculated. The results of this analysis, shown in Figures S10 to S12, show these results have limited sensitivity to uncertainties in the biological parameters. The fact that we are interested in changes in recovery times between the



two scenarios, rather than absolute recovery times helps to limit the impact of parameter uncertainty on the results.

Figure S10: Sensitivity of mean change in recovery time (left axis), and standard deviation in change of recovery times across all reefs (right axis), to variation in the clonal growth rate (R).



Figure S11: Sensitivity of mean change in recovery time (left axis), and standard deviation in change of recovery times across all reefs (right axis), to variation in the parameter value for the proportion of larvae settling which survive to maturity (*s*).



Figure S12: Sensitivity of mean change in recovery time (left axis), and standard deviation in change of recovery times across all reefs (right axis), to variation in the parameter value for the number of eggs released per polyp (e_{polyp}).

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