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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.

Coral 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 connectivity[7]. 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 retention[10]). 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 worldwide[11,12].

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 scenario[13]) 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[8,9,14,15,16], because it has qualitatively similar responses to temperature in survival and competence to many other coral 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 whole[19]. 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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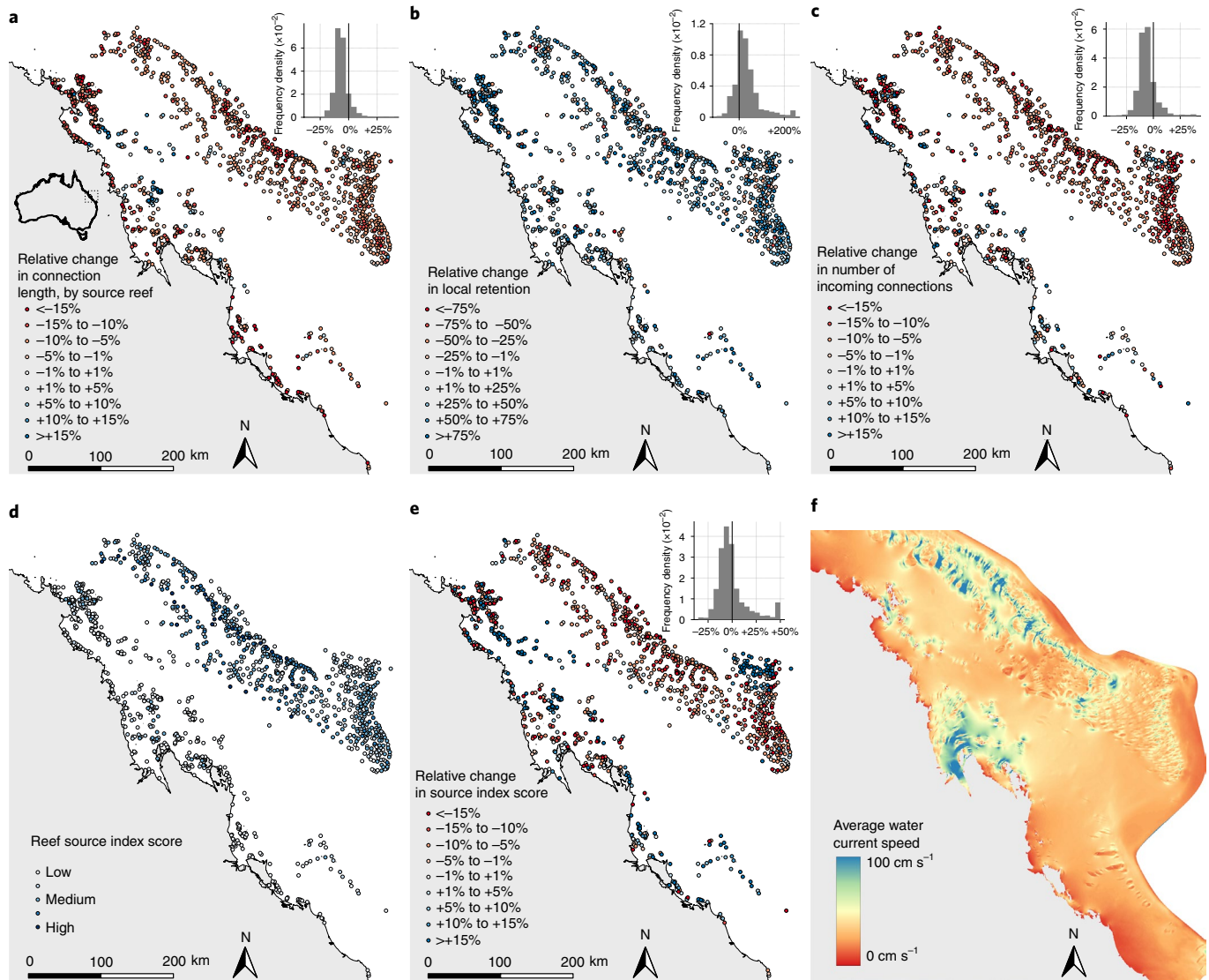
Fig. 1 | Maps showing the effects of a 2 °C increase in water temperature across the southern Great Barrier Reef, Australia, by reef. a, Average source-to-destination reef distance (connection length). **b**, Local retention (proportion of larvae produced on a reef that settle back on that reef). **c**, 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 malformations[20]. 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
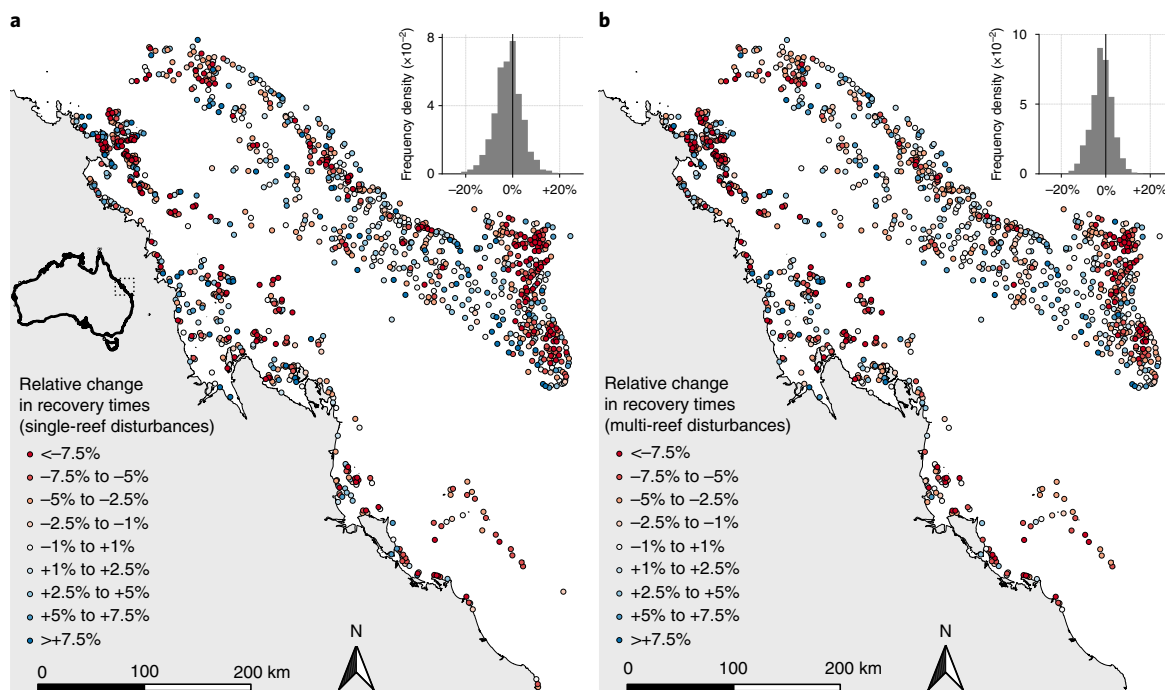
Fig. 2 | Relative change in recovery times in the 29 °C scenario (2050–2100) compared to the 27 °C scenario (current) following disturbance.
a, Single-reef disturbances. **b**, Multiple-reef disturbances. Inset histograms show normalized distributions for the changes in recovery times.

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 temperatures[21] 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 Reef[22]. 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 anchoring[10].

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% ± 5.9% (mean ± s.d.) for localized, single-reef disturbances, and −1.7% ± 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

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 likely[27–29]. 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.

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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 currents[34] 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 development[35]. 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 currents[36]. 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 cues[37]), 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,

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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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

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Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy 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

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

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
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Outputs of connectivity matrix are available on dryad

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

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 field work?   ☐ Yes   ☒ 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

n/a	Involved in the study
☒	Antibodies
☒	Eukaryotic cell lines
☒	Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	Human research participants
☒	Clinical data
☒	Dual use research of concern

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging

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)
Ethics oversight	No ethical approval or guidance required.

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