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Global warming decreases connectivity among coral populations

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Abstract:

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 200m), 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 an average 7% decrease in the distance larvae disperse (among-reef interquartile range (IQR): -10% to -4%), 8% decrease in the number of connections into each reef (IQR: -11% to -3%), and 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 of protected areas.

43 **Main text:**

44 Coral reefs have been in decline for centuries due to local human impacts^{1,2}, with ocean
45 warming accelerating these declines in recent decades^{3,4}. Warmer temperatures cause corals to
46 bleach (i.e., lose their algal symbionts, and thus a major source of carbon), become less fertile
47 and more likely to die^{5,6}. The ability of coral populations to recover after disturbance is highly
48 dependent on patterns of reef connectivity⁷. The interchange of larvae among reefs allows and
49 accelerates the (re)colonization of distant habitats. Previous research demonstrates that warmer
50 temperatures increase early larval mortality and reduce the time it takes them to settle^{8,9}, causing
51 an increase in the proportion of larvae retained on their natal reef (i.e. local retention¹⁰).
52 However, the effect of higher temperatures on long-term larval survivorship and settlement, and
53 how such changes will affect connectivity remains unexplored. Additionally, projected changes
54 in ocean circulation in response to global warming have the potential to affect patterns of
55 connectivity worldwide^{11,12}.

56 Here, we combine experimental calibration of biological models of larval survival and
57 competency for the stony coral *Acropora millepora* with a high-resolution (as high as 200m)
58 hydrodynamic model of physical transport on the southern Great Barrier Reef to test for the
59 effects of a 2°C increase in temperature (estimated for 2080-2100 under Representative
60 Concentration Pathway [RCP] 4.5 scenario or 2050 under RCP 8.5 scenario¹³) on patterns of
61 connectivity (Appendix 1). Specifically, we first measure long-term larval survival and
62 competency dynamics of the coral *Acropora millepora* under current and future temperature
63 conditions in laboratory conditions. We use *Acropora millepora* as our model species because it
64 has a similar egg size and competence curve (ability to settle over time) as other *Acropora*
65 species¹⁴⁻¹⁸, because it has qualitatively similar responses to temperature in survival and

66 competence to many other coral species^{17,19-22}, and because *Acropora* is by far the most abundant
67 genus in the Great Barrier Reef and across much of the Indo-Pacific region. We then simulate
68 water currents through the Great Barrier Reef using the Second-generation Louvain-la-neuve
69 Ice-ocean Model (SLIM) during 3 recent successive spawning seasons for which good
70 observational data were available (2008-2010), and use biophysical particle tracking to estimate
71 the dispersal of *Acropora millepora* larvae and the resultant inter-reef connectivity network.
72 Averaging over all larvae released and over all 3 spawning seasons, we estimate that
73 temperature-induced changes in larval survival and settlement competence will reduce larval
74 dispersal distance by 6.6% (with an among-reef interquartile range [IQR] of -10.0% to -4.2%;
75 Fig 1a) and the number of outgoing connections by 8.1% (among-reef IQR of -10.8% to -3.0%;
76 Fig 1c), i.e. larvae will reach fewer reefs (Appendix 1, Table S9). We find that 75% of the reefs
77 in this region will experience a decrease in both connectivity metrics, with some experiencing a
78 very large decrease (>15%, Fig. 1a, c; Appendix 1). In addition, we estimate that a 2°C warming
79 will increase the proportion of larvae produced by a reef that settles back onto that reef (local
80 retention) by 19.5% (among-reef IQR of 0.0% to +49.2%). Similarly, the proportion of settlers
81 on a reef that originated from larvae released by that reef (self-recruitment) will increase on
82 average by 15.0% (among-reef IQR of -0.2% to +43.5%). That is, recruitment back to the natal
83 reef increases both relative to the larval production by each reef, and relative to the number of
84 larvae arriving to that reef from the metapopulation as a whole²³. This means that reefs will
85 become more isolated and more dependent on locally-produced larvae for replenishment after
86 disturbances.

87 While on average warming decreases larval dispersal distances and the number of inter-
88 reef connections, and increases local retention of larvae, there is substantial inter-reef variability

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

104 The net weakening of inter-reef connectivity is driven by changes to larval development
105 dynamics. Warmer temperatures increase larval mortality (Appendix 1, Tables S1, S2, Fig. S1A).
106 This effect was especially marked during embryogenesis, after which mortality rates were
107 similar between temperatures, consistent with accelerated rates of cell division during
108 embryogenesis at higher temperatures increasing the frequency of errors that lead to fatal
109 malformations²⁴. Warmer temperatures also alter competence dynamics: how quickly larvae
110 acquire the capacity to settle and metamorphose on reef habitat (i.e. become competent), and
111 how long they retain that capacity (Appendix 1). Specifically, under elevated temperatures, the

112 minimum time for larvae to settle is reduced from 4.89 to 3.87 days; however, larvae tend to lose
113 competence much more quickly, halving from peak competence after about 7 weeks at +2°C
114 compared to 14 weeks at current temperatures (Appendix 1, Tables S3, S4, Fig. S1B). One
115 potential explanation for this is the combination of higher rates of metabolism at warmer
116 temperatures²⁵ leads to faster depletion of energy reserves (coral larvae are non-feeding) and thus
117 a shorter time-window during which sufficient energy remains available for successful
118 settlement and metamorphosis.

119 In contrast to temperature effects on survival and development, projected changes in
120 large-scale water circulation in the Great Barrier Reef (Appendix 1, Fig. S8) have a small effect
121 on connectivity patterns, with average changes to all connectivity indicators being < 2.2%
122 (Appendix 1, Table S8). Changes in large-scale circulation through the Coral Sea predicted by
123 the Coupled Model Intercomparison Project 5 (CMIP5) global climate models may affect water
124 flow onto the Great Barrier Reef, with most CMIP5 models projecting increased flow towards
125 the Great Barrier Reef driven by an increase in the strength of the South Pacific sub-tropical gyre
126 (Appendix 1, Fig S8). The effects of this change on the Great Barrier Reef itself are modelled by
127 modulating the large-scale currents entering the lagoon (Appendix 1, Part 3). However, this
128 change is found to have a small effect on current speeds through the Great Barrier Reef (average
129 changes of under 1cm/s over the vast majority of the domain, i.e. very low compared to typical
130 current speeds, Fig. 1f), and the effect on coral connectivity is roughly an order of magnitude
131 smaller than the biological changes caused by ocean warming that we document (Appendix 1,
132 Table S9). Other changes to environmental conditions in the region are also possible, such as
133 modulation in the strength of local wind stress during coral spawning seasons, however we have

134 no strong evidence quantifying how they will evolve over the coming decades and hence they are
135 not accounted for here.

136 Local retention is estimated to increase on average by 19.5% (among-reef IQR of 0.0% to
137 +49.2%) at higher temperature (+2°C) because a reduction in the time to settlement over-
138 compensates for an increase in mortality. Seventy four percent of the reefs in the region are
139 predicted to experience an increase in local retention, with 26% experiencing increases greater
140 than 50% (Fig. 1b). This spatial variability in projected changes in local retention reflects the
141 high degree of geographic variability in water currents (Fig. 1f) and thus residence times in the
142 Great Barrier Reef²⁶. The increased local retention will be more prevalent on reefs with mean
143 water residence times lower than 4 days, such as reefs offshore from Mackay and in the
144 Whitsundays (Fig. 1b), due to the decrease in the minimum time to acquire competence to under
145 4 days. Therefore, some coral populations are likely to become more vulnerable to local
146 disturbances, but also more responsive to local management, such as control of sedimentation or
147 prohibitions on anchoring¹⁰.

148 To determine the contribution of warming-driven changes in coral connectivity patterns
149 to recovery rates after disturbances, we developed a simple metapopulation model (Appendix 2).
150 The model projects the time taken for each reef to recover from localized and regional
151 disturbances in both the present day and under the 2°C warming scenario; the change in recovery
152 time was then calculated as the percent change between the two. Temperature-driven changes in
153 larval dispersal are projected to cause a marginal decrease in average recovery times across all
154 reefs (-1.8±5.9% SD for localized, single-reef disturbances, and -1.7±4.7% for regional,
155 multiple-reef disturbances), however, at the reef-scale there are some significant changes (Fig.
156 2a, b). For example, on isolated reefs, which already receive few larvae from other reefs, reduced

157 long-distance connectivity will further diminish recovery rate (ca. 10% increase in recovery
158 time). At the same time, increased local retention on other reefs, like those in reef-dense areas off
159 Mackay, will promote enhanced recovery (ca. 10% decrease in recovery time) primarily as this
160 increased local retention more than offsets the decrease in the strength and number of inter-reef
161 connections. These projected changes in recovery times due to the shifts in connectivity
162 indicated by our study are likely to be underestimates because the changes will be compounded
163 by warming-induced decreases in the spawning stock, including increased mortality, decreased
164 fertility and fecundity, and density-dependent reduction in fertilization rates.

165 This model is the first to project how coral larval dispersal patterns and connectivity will
166 be altered by climate change. In the process, the potential for each reef to act as a source of
167 larvae to the region and the extent to which warming would alter it were also projected. Previous
168 work on the Great Barrier Reef has focused on identifying ‘robust source reefs’ based on
169 present-day connectivity and history of disturbance^{27,28}. Comparing the outputs of the various
170 models, it is evident that as resolution increases, from 4 Km²⁷ to 1.6 Km²⁸ to 200 m in our
171 model, the potential role of nearshore reefs as sources for the system becomes more evident^{27,28}
172 (Fig. 1d). The high resolution around reefs (200m) of our model resolves hydrodynamics at the
173 reef scale more effectively, particularly nearshore, and therefore enhances our capacity to
174 anticipate the potential impacts of local-scale management interventions. We opted for a depth-
175 integrated model, without waves, to simulate flow through the mainly shallow, well-mixed
176 waters of the Great Barrier Reef, in order to achieve a combination of high spatial resolution
177 around reefs (needed to capture reef-scale retention processes such as lee reef eddies) and
178 relatively large model domain (needed to capture the inter-reef dispersal that drives
179 metapopulation dynamics).

180 From a management perspective, reduced connectivity and increased local retention
181 suggest that a greater number of reefs, particularly reefs contributing most to the overall supply
182 of larvae (source reefs), will require greater levels of protection, and protected areas will have to
183 be closer together, to increase the ability of the system to replenish itself following natural and
184 anthropogenic disturbances. Concomitantly, the stronger local retention might benefit persistence
185 as more larvae recruit to favourable habitats^{32,33}, and a stronger stock-recruitment relationships
186 will enhance the potential impacts of local management interventions^{10,32}. The recovery of
187 disturbed areas can be achieved by reducing local anthropogenic stressors (through
188 reduction/elimination of overfishing of herbivores, regulated sewage discharge or elimination of
189 mechanical damage such as dredging) or protecting surrounding undisturbed reefs to maximize
190 the supply of larvae to the disturbed reefs and thus facilitate colonization. In the southern Great
191 Barrier Reef, many of the best source reefs lie in the outer/eastern-most portion of the continental
192 shelf (Fig. 1d), due to the high reef density and strong currents facilitating inter-reef connections.
193 These reefs are projected to be weaker sources of larvae in the future (Fig. 1a, c). However, in
194 most cases, they are projected to remain the best sources in the system (Fig. 1e). While our
195 model projects that changes in connectivity would allow some reefs to recover more rapidly
196 following disturbance, this would only be true if the growth rates, post-settlement survival,
197 fertility and fecundity of corals was not compromised by warming, whereas prior work indicates
198 that such adverse effects are likely²⁹⁻³¹. Additionally, isolated reefs with very low mean water
199 residence times (i.e. high self-recruitment, but low local retention) will become more vulnerable
200 to local extinction and therefore need greater protection from localized disturbances, and would
201 have to be actively restored (larval seeding and/or outplanting) if disturbed.

202 The changes in inter-reef connectivity projected here for *A. millepora* in the southern
203 Great Barrier Reef could diminish the capacity of these coral populations to adapt and are likely
204 not to be exclusive to this species or region^{8-10,34-37}. A reduction in long distance dispersal is
205 likely to reduce the migration of temperature tolerant genes from lower latitudes. Our results are
206 also likely to be robust for most reefs on a global scale because the great majority of reefs
207 worldwide have similar mean water residence times³⁴⁻³⁶, *Acropora* is the most abundant coral
208 genus in the Indo-Pacific (and was once the most abundant in the Atlantic), and the response to
209 warming of the early life history stages of all other coral species studied to date is similar to the
210 *Acropora*^{8-10,37}. Most reefs of the future will be less connected and this reduction in connectivity
211 needs to be considered when choosing how best to respond to global warming, and in evaluating
212 the extent to which the dispersal of warm-adapted genotypes will be sufficient to allow coral
213 populations to cope with increasing temperatures.

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333 **Methods**

334 We first measured long-term larval survival and competency dynamics of the coral
335 *Acropora millepora* under current and future temperature conditions in laboratory conditions
336 (Appendix 1, Part 1). This species was used because *Acropora* species are the most abundant in
337 the Great Barrier Reef (GBR) and the rest of the Indo-Pacific, and have similar egg size and larval
338 development rates (~532-604µm mean egg diameter, and 4-6 days to larval competency). Eggs
339 and sperm of six *A. millepora* colonies were mixed to allow fertilisation. To obtain the survival
340 curve, four replicates of fifty embryos per temperature treatment (ambient temperature [27°C], and
341 +2°C [29°C]) were stocked in 200ml glass jars. Every day for 134 days, embryos/larvae were
342 counted and water was renewed. The survival data was fit to alternative models to determine
343 whether mortality rates were constant over time (exponential model), increased or decreased
344 monotonically over time (Weibull model), or whether they first decreased, then increased, or vice-
345 versa (Generalized Weibull: see Appendix 1 for details). To obtain the competency curve,
346 embryos were reared at 27°C (ambient temperature) and 29°C (+2°C), and each day from days 3
347 to 9 post-fertilisation, and then on days 11, 13, 16, 23, 30, 37, 44, 58, 72 and 99, three replicates of
348 twenty larvae from each of the temperature treatments were placed in 200mL glass jars with a pre-
349 conditioned settlement tile at the same temperature. A day later, the number of larvae that had
350 settled and metamorphosed was recorded. As with survival, we considered exponential, Weibull,
351 and generalized Weibull functional forms for the loss of competence (see Appendix 1 for details).
352 We then integrated the estimated survival and competency parameters for each temperature into a
353 stochastic model that estimates the probability that a larva is alive and competent at any given time
354 for each temperature.

355 The flow of ocean currents through the Great Barrier Reef was simulated using an
356 unstructured mesh, depth-integrated hydrodynamic model (SLIM) forced by tides, wind and
357 large-scale oceanographic currents³⁸ during 3 successive recent years' spawning seasons (2008-
358 2010). The mesh resolution was very high around reefs (200m), and coarser in deeper areas with
359 more uniform bathymetry (up to 5km). The use of a depth-integrated model necessarily omits any
360 variation in flow with depth, which can be relevant for larval dispersal when flow changes
361 markedly with depth, and depth distributions change due to swimming behaviour or shifts in
362 buoyancy with development³⁹. However, observational and modelling studies over the past 4
363 decades have consistently found Great Barrier Reef waters to be vertically well-mixed throughout
364 most of the shelf for most of the year, with upwelling events and stratification being relatively
365 limited in space and time (Appendix 1, Part 2). In addition, coral larval swimming speeds are
366 orders of magnitude lower than measurements of water flow both on and off reefs (vertical and
367 horizontal currents), and thus cannot swim against currents⁴⁰. Whilst our model may therefore be
368 missing some relevant 3D effects, for example localised upwelling at the shelf break which may
369 affect flow near some outer barrier reefs, focusing finite computational resources on resolving
370 reef-scale horizontal flow allows us to better resolve flow features that are crucial to circulation
371 throughout the shelf, such as eddies that form behind reefs which can trap larvae in their vicinity,
372 while still being able to characterize dynamics over a spatial scale appropriate to the inter-reef
373 connectivity patterns of corals. The present-day hydrodynamics were validated using local
374 measurements of current strength and direction from mooring locations on the shelf, and the
375 model was found to reproduce realistic currents (Appendix 1, Part 2).

376 To obtain estimates of connectivity between reefs, an individual based model was then
377 used to simulate particle transport using currents from 3 recent years (2008-2010) in the weeks

378 immediately following spawning in the Great Barrier Reef (November) and larval survival and
379 competency dynamics for present and future sea temperature scenarios. The model assumes that
380 when a larva is alive and competent, if it passes on top of a reef it will detect the presence of the
381 reef (through chemical and physical cues⁴¹), settle and metamorphose (see Appendix 1, General
382 Methods). Particle transport was modelled separately for each spawning season using currents
383 simulated for that specific period (Appendix 1, Part 2). To simulate the impact of changing large-
384 scale ocean circulation on larval connectivity, the biophysical model was also forced with
385 modified low-frequency currents at the model boundaries to mimic the changes predicted to ocean
386 circulation in the Coral Sea by CMIP5 climate models (see Appendix 1, Part 3). Connectivity
387 metrics for the 3 years were averaged to make the results more robust to annual variations
388 (Appendix 1, Part 4). The estimated connectivity matrices for each year are available⁴² at
389 <https://doi.org/10.5061/dryad.4f4qrfjbjk>.

390 To determine the contribution of warming-driven changes in coral connectivity patterns
391 to recovery rates after disturbances, we developed a simple metapopulation model of coral cover
392 accounting for density-dependent growth (budding) and recruitment, using the connectivity
393 matrices from the biophysical dispersal model (Appendix 2). Previously reported biological data
394 on fecundity and post-settlement survival of coral recruits is used to set realistic model
395 parameters, and all corals are assumed to have equal fecundity and post-settlement mortality.
396 Fecundity, initial abundance and growth and mortality rates were set to be equal at 27 °C and 29
397 °C, as the aim was to predict changes in recovery times following disturbances due exclusively to
398 the impact of changes in connectivity. We simulated 2 different types of disturbance: single-reef
399 disturbances, where initial coral cover was reduced by 85% over one reef at a time, mimicking
400 events such as crown-of-thorns outbreaks, and regional disturbances, where initial coral cover

401 was reduced by 75% over a 30-km wide cross-shore strip, and by 40% in 30-km wide strips to
402 either side, mimicking the passage of a severe tropical cyclone across the GBR. The model was
403 run, in turn, using the connectivity matrices obtained from the 27°C and 29°C biophysical model
404 runs. The model projects the time taken for each reef to recover from localized and regional
405 disturbances in both the present day and under the 2°C warming scenario, and the change in
406 recovery time was then calculated as the percent change between the two.

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408

409 **Method References:**

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417 *Biol. Ecol.* **408**, 42-57 (2011).
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419 <https://doi.org/10.5061/dryad.4f4qrfjvk>.

420

421 **Data Availability Statement:** Yearly connectivity matrices and the processed data used to
422 construct Figs 1a-e and Fig 2 are available at <https://doi.org/10.5061/dryad.4f4qrfjbjk>. Larval
423 survival and competency is provided in appendix (Figure S1) and by request to the authors.

424

425 **Code Availability Statement:** The SLIM model source code can be found at
426 <https://git.immc.ucl.ac.be/dg/dg>. Larval dynamics modeling is provided in appendix, references
427 within, and by request to the authors.

428

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438

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461 **Figure legends**

462 **Fig. 1.** Maps showing the effects of a 2°C increase in water temperature across the southern Great
463 Barrier Reef, Australia, by reef. (a) average source-to-destination reef distance (connection
464 length), (b) local retention (proportion of larvae produced on a reef that settle back on that reef),
465 (c) number of incoming connections from other reefs. (d) shows current best source reefs, as
466 measured by a source index defined as the number of outgoing connections multiplied by the
467 number of outgoing larvae per reef, and (e) the relative change in the source index for the 2°C
468 increase scenario. Inset histograms for (a-c) & (e) show normalised distributions of the relative
469 changes shown in the maps; values outside range of x-axis are included in final bar for readability.
470 (f) shows average water current speeds from the hydrodynamic model for the present-day
471 simulations. All quantities are averaged over the 3 spawning seasons (2008-2010) modelled.

472

473 **Fig. 2.** Relative change in recovery times in the 29°C scenario (2050-2100) compared to the 27°C
474 scenario (current) following disturbance. (a) single-reef disturbances and (b) multiple-reef
475 disturbances. Inset histograms show normalised distributions for the changes in recovery times.

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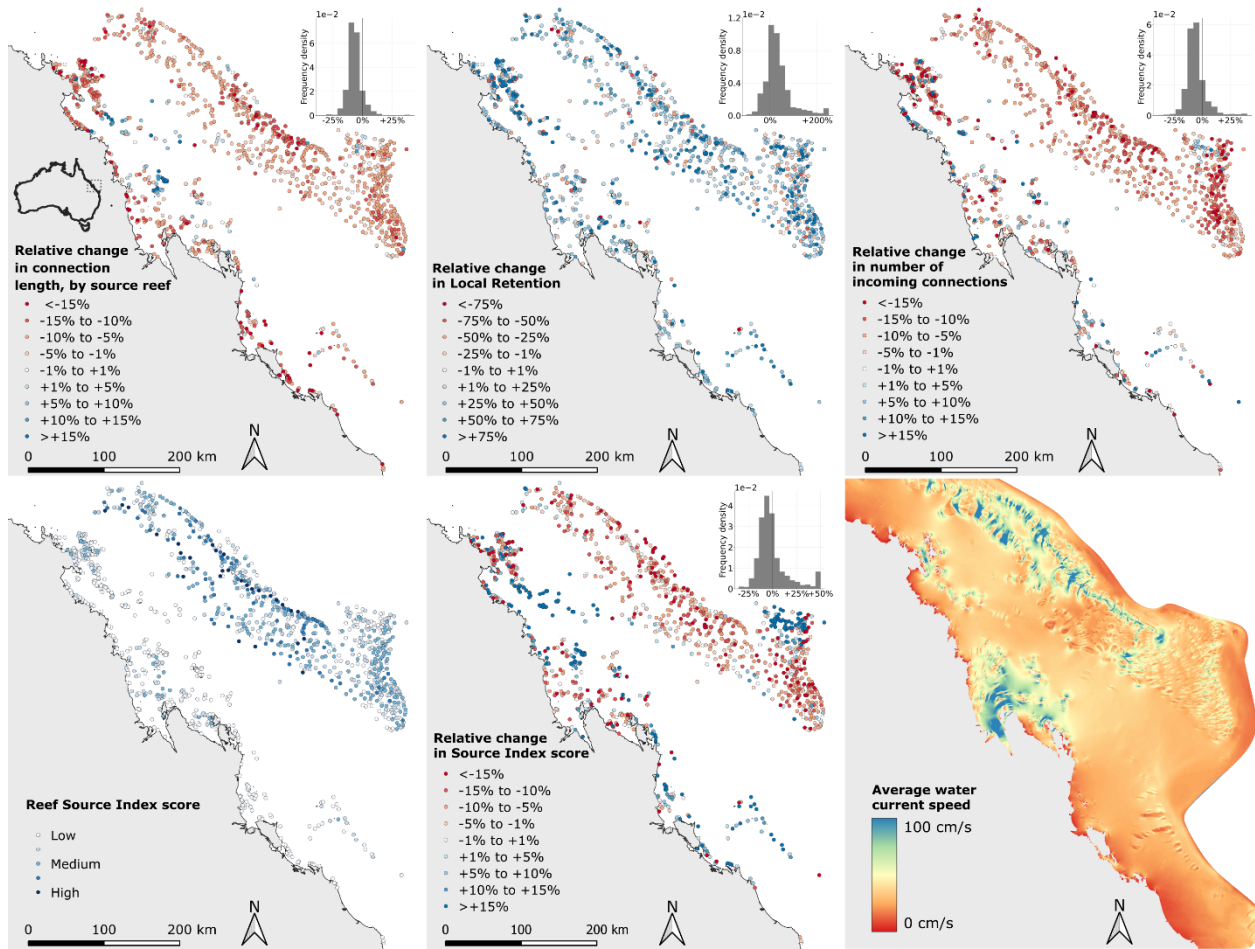
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Figure 1



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Figure 2

