

Larval connectivity across temperature gradients and its potential effect on heat tolerance in coral populations

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Article begins on next page

1 *Title:* Larval connectivity across temperature gradients, and its potential effect on heat
2 tolerance in coral populations

3 *Running head:* Connectivity and heat tolerance in coral populations

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23 dispersal

24

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26 **Abstract.** Coral reefs are increasingly exposed to elevated temperatures that can cause
27 coral bleaching and high levels of mortality of corals and associated organisms. The
28 temperature threshold for coral bleaching depends on the acclimation and adaptation of
29 corals to the local maximum temperature regime. However, because of larval dispersal,
30 coral populations can receive larvae from corals that are adapted to very different
31 temperature regimes. We combine an offline particle tracking routine with output from a
32 high-resolution physical oceanographic model to investigate whether connectivity of
33 coral larvae between reefs from different thermal regimes could alter the thermal stress
34 threshold (TST) of corals. Our results suggest that larval transport between reefs of
35 widely varying temperatures is likely in the Coral Triangle, and that accounting for this
36 connectivity may be important in bleaching predictions. This has important implications
37 in conservation planning, because connectivity may allow some reefs to have an inherited
38 heat tolerance that is higher or lower than predicted based on local conditions alone.

39 **Introduction**

40 Most marine organisms are progressively exposed to rising temperatures associated with
41 climate change, and their survival is often evaluated in terms of their ability to cope via
42 changes in physiology, phenology, and/or colonization (Bellard *et al.*, 2012). Marine
43 larval dispersal via ocean currents is a major component of population connectivity of
44 many marine organisms (Cowen & Sponaugle, 2009), and because of its capacity to
45 increase a species' range and its ability to recover following local disturbance, species
46 that disperse widely are thought to be less susceptible to global extinction (Jones *et al.*,
47 2007). Coupled bio-physical dispersal models provide a framework for understanding
48 the patterns of larval dispersal as well as its barriers (Cowen *et al.*, 2006; Kool *et al.*,

49 2013; Paris *et al.*, 2013; Treml *et al.*, 2015). Modeling has revealed that connectivity can
50 be complex, particularly at the spatial scales of coral reef systems (e.g., 1-10 km) where
51 topography, eddies, and tides interact to create barriers to dispersal (Werner *et al.*, 2007).
52 They also allow one to quantitatively estimate the probability of dispersal among sites
53 within the connected range of a population (Treml *et al.*, 2008; Mitarai *et al.*, 2009; Kool
54 *et al.*, 2011). For a given population, that range might include a variety of conditions.
55 Mumby *et al.* (2011), for example, illustrated the potential importance of larval
56 connectivity across different temperature regimes in the Bahamas, as well as considering
57 this in reserve design. However, the capacity of dispersal to deliver individuals adapted to
58 different temperature regimes has not been widely considered.

59 The temperature tolerance of adult corals is tied to the temperature regime of the local
60 environment (Logan *et al.*, 2014). Corals begin to experience heat stress once
61 temperatures exceed their thermal stress threshold (TST). The TST is typically around 1–
62 2°C above the climatological mean monthly maximum (MMM) for a given location (Liu
63 *et al.*, 2003). During a bleaching event, however, individuals within the same coral
64 species will often exhibit a range of bleaching severity to the same conditions. This
65 reflects variations in environmental factors within the reef (e.g. small changes in depth,
66 shading, currents, etc.) (Berkelmans, 2002; McClanahan *et al.*, 2005; Ulstrup *et al.*,
67 2006); different clades of algal symbionts (Buddemeier *et al.*, 2004; Silverstein *et al.*,
68 2015); and differences in coral morphology (Loya *et al.*, 2001) or condition (Fitt *et al.*,
69 2001). It may also reflect genetic/genomic differences in heat tolerance within the local
70 population (Palumbi *et al.*, 2014).

71 A subpopulation of corals in any one location represents individuals that are not only
72 offspring of local corals, but also offspring of corals on other reefs that arrived via larval
73 transport. The degree of larval connectivity thus plays a role in determining the genetic
74 makeup of heat tolerance across coral populations. If a coral subpopulation has a high
75 probability of receiving larvae from corals adapted to temperatures higher or lower than
76 those of their own waters, the temperature tolerance of the individuals may differ from
77 that determined solely by local conditions. One recent study suggests that heat tolerance
78 in the reef coral *Acropora hyacinthus*, for example, is determined about equally by
79 acclimation and genetic inheritance (Palumbi *et al.*, 2014), and another showed that
80 larvae of *Acropora millepora*, when exposed to heat stress, had a 10 times greater
81 survival rate if the parents were from warmer waters (Dixon *et al.*, 2015).

82 Whether immigrants can increase the fitness of a local population depends not only on
83 genetics, but also on demographic factors, behavior, and environment (Tallmon *et al.*,
84 2004). Our study quantifies the potential for connectivity to bring immigrants from
85 different temperature regimes to a particular reef. We are specifically interested in
86 whether the overall temperature stress threshold (TST) of a coral species on a particular
87 reef could be significantly different when one accounts for the thermal stress thresholds
88 of larvae it receives from different temperature regimes. This is the first step in testing
89 the degree to which connectivity can shift temperature tolerance in corals. The main
90 hypothesis is that a population receiving larvae from cooler regimes will have an overall
91 lower tolerance to heat stress; and those receiving larvae from warmer regions will have a
92 higher tolerance (Fig. 1).

93 **Materials and methods**

94 We base our analysis on temperature and ocean circulation output from a 47-year
95 hindcast run (1960–2006) of the Regional Ocean Model System for the Coral Triangle
96 region (CT-ROMS; Fig. 2). We use the offline Lagrangian particle tracking routine,
97 TRACMASS (Döös, 2012), to calculate the physical transport of particles released in a
98 manner consistent with a widespread broadcasting species (e.g., *Acropora millepora*),
99 and track the particles in the surface layer for two dispersal periods: 10 days and 30 days.
100 We calculate the thermal stress threshold for each reef based on its local sea surface
101 temperature (SST) climatology, and then recalculate it based on the TST of all of the
102 source reefs (including self-seeding). Finally, we test whether accounting for
103 connectivity leads to better prediction of the observed patterns of coral bleaching during
104 the widespread bleaching event of 1998.

105 ***Model simulations***

106 ROMS is an ocean circulation model that is widely used for regional and coastal
107 investigations (Shchepetkin & McWilliams, 2003, 2005). CT-ROMS has a 5-km
108 horizontal resolution and 50 vertical terrain-following levels weighted toward the surface
109 in order to better resolve the mixed layer. The model domain is configured to include as
110 many reefs as possible within the Coral Triangle region, and to minimize edge effects and
111 truncation of connected populations (Fig. 2), although not all such effects can be avoided.
112 The model bathymetry is interpolated from the global SRTM30_PLUS product (Becker
113 *et al.*, 2009), which has a 30-arc second (approximately 1-km) spatial resolution. The
114 model time step is 90 seconds. Tides are explicitly resolved in CT-ROMS, with tidal

115 forcing naturally implemented at the boundary by providing tidal elevation and
116 barotropic flows from the global model of ocean tides TPXO 7.2 (Egbert & Erofeeva,
117 2002). An astronomical tide-generating potential is also added as a body force in the
118 momentum equation to ensure correct tidal phasing. Evaluations of CT-ROMS against
119 observations have shown that it has considerable skill in simulating ocean temperature
120 and ocean circulation (Castruccio *et al.*, 2013).

121 The hindcast simulation (1960–2007) described in Kleypas *et al.* (2015) was forced at the
122 oceanographic boundaries with data from the Simple Ocean Data Assimilation (SODA,
123 Carton & Giese, 2008) and at the atmospheric boundary with data from the Coordinated
124 Ocean-Ice Reference Experiments (CORE2, Large & Yeager, 2004). Reef locations were
125 obtained from the Global Distribution of Coral Reefs (UNEP-WCMC *et al.*, 2010), which
126 merges data from the Millennium Coral Reef Mapping Project (IMaRS-USF, 2005;
127 IMaRS-USF & IRD, 2005) and the World Atlas of Coral Reefs (Spalding *et al.*, 2001).
128 The data were converted from ArcGIS shape files to 30 m resolution raster files, which
129 were then used to estimate percent reef area for each CT-ROMS grid cell.

130 ***Larval connectivity***

131 We calculated connectivity – the probability of larval transport between a source and sink
132 reef – over the 47-year period, based on a common and widespread broadcast spawning
133 species (*Acropora millepora*), to quantify the proportion of larvae at each reef that
134 arrived from other source sites (Thompson *et al.*, in prep.). Although the larval release
135 times were based on *A. millepora* spawning parameters (Baird, 2001; Baird *et al.*, 2009;
136 Connolly & Baird, 2010), this calculation mainly addressed the potential connectivity,

137 that is, the physical component of the transport (see Mitarai *et al.*, 2009; Watson *et al.*,
138 2012). Recent studies of connectivity, including the work by Treml *et al.* (2012) and
139 Treml *et al.* (2015) in the Coral Triangle, illustrate the role of several biological
140 parameters in connectivity, such as fecundity (Baird & Marshall, 2002; Sudek *et al.*,
141 2012); precompetency period (Heyward *et al.*, 2002; Figueiredo *et al.*, 2014);
142 survivability and pelagic larval duration (Edmunds *et al.*, 2001; Bassim & Sammarco,
143 2003; Baums *et al.*, 2006; Nozawa & Harrison, 2007; Randall & Szmant, 2009); and
144 settlement (Coles, 1985). Including these factors would produce a more realistic
145 calculation of connectivity (“realized connectivity” of Watson *et al.*, 2012), but limiting
146 our analysis to potential connectivity allows us isolate the role of physics in this first
147 order analysis of the role of connectivity on TST. Given the computational burden of
148 particle tracking between the large number of reef cells within the CT-ROMS domain,
149 and to increase the robustness in the estimated larval transport, we organized contiguous
150 reef and coastal cells into sites of 8x8 cells (number of sites = 2497). Twenty-five
151 particles were released from each reef and coastal cell on each of five consecutive days
152 following the full moons nearest to April 1 and September 1 (spring and fall spawning
153 periods for *A. millepora*) for each of the 47 years of simulation. Following this approach,
154 up to ~8000 particles were released from each site (depending on the number of non-land
155 cells within each 8x8 site), totaling > 18 million particles per spawning event and > 1.7
156 billion for the 47-year analysis. Rigid testing of the sample size sensitivity (following an
157 approach similar to Simons *et al.*, 2013), indicated that this sample size was sufficient to
158 accurately sample the Lagrangian probability density function (PDF) used to calculate the
159 potential connectivity.

160 The Lagrangian particle tracking routine TRACMASS (Döös, 2012) was used to
161 calculate the Lagrangian trajectories from daily average CT-ROMS Eulerian velocity
162 fields. Potential connectivity, the probability of transport between source and sink sites
163 (e.g., probability that a particle released at site j will arrive at site i), was calculated for
164 the fall and spring releases of each year and for two dispersal periods: 10 days and 30
165 days. Potential connectivity was calculated following the methodology of Mitarai *et al.*
166 (2009) by calculating the PDF at the end of the dispersal period (e.g. the locations of all
167 particles at day 10 and at day 30; see Fig. S1 in Supporting Information). The average
168 potential connectivity was then calculated from all spring and fall releases during the 47-
169 year period (i.e., 94 releases). These results thus provide a long-term average of potential
170 connectivity that includes seasonal to decadal scales of variability. While larvae of *A.*
171 *millepora* and related species can survive for more than 100 days, most are only
172 competent between 4–30 days following spawning, and most settle within 10 days (Baird,
173 2001; Connolly & Baird, 2010). The 10-day dispersal period therefore represents a likely
174 timeframe for the peak of larval settlement, but we also determined potential connectivity
175 for the 30-day dispersal period because long-distance dispersal may become more
176 important if mass mortality events over large regions eliminate short-distance larval
177 sources. We did not consider dispersal longer than 30 days because even though rare
178 dispersal events can be important in populations (de Queiroz, 2005), the computational
179 requirements to adequately analyze such rare events increase greatly, particularly if we
180 are to maintain statistical robustness in quantifying potential connectivity.

181 ***Thermal Stress Threshold (TST)***

182 We used TST as the metric for temperature tolerance because it accounts for the
 183 climatological maximum temperature as well as its variability at each site. The MMM at
 184 each reef location was calculated from the CT-ROMS weekly SSTs for the 1960–1979
 185 period of the hindcast simulation. Based on a previous analysis of temperature stress in
 186 this region (Kleypas *et al.*, 2015), we calculated for each site the local-based temperature
 187 stress threshold (TST) as the MMM + 2.5 σ °C (where σ = the standard deviation of the
 188 MMM). This is a common modification of the NOAA heat stress calculation that takes
 189 into account the natural variability in annual maximum temperature (Donner, 2009).
 190 Compared to the standard metric of MMM + 1°C, this metric was previously determined
 191 to better predict observed bleaching in the Coral Triangle, at least in those regions where
 192 bleaching was well observed (Kleypas *et al.*, 2015).

193 We also calculated TST_{pc}, which is based on the TST and potential connectivity of larvae
 194 of each source reef. TST_{pc} was calculated for each reef (*i*) as:

$$TST_{pc,i} = \frac{\sum_j a_{ij} f R_j TST_j}{\sum_j a_{ij} f R_j} \quad (1)$$

196 where a_{ij} is the potential connectivity between reefs *i* and *j*, *f* is fecundity, R_j is the
 197 percent reef cover at reef *j*, and TST_j is the TST at reef *j*. We assumed fecundity to be
 198 constant at all sites; thus, while it cancels out of this equation *f* would be relevant if one
 199 were to consider differences in fecundity from site to site. R_j scales the potential
 200 connectivity based on the area of each source reef.

201 To quantify the potential impact of including potential connectivity in coral bleaching
 202 predictions, TST and TST_{pc} were used to calculate the degree heating week (DHW) (Liu

203 *et al.*, 2003), a metric of thermal heat stress quantified as the 12-week accumulation of
204 sea surface temperature exceeding the TST (or TST_{pc}). Mild bleaching typically occurs
205 at 4–8 DHW (severity = 1), moderate bleaching at 8–12 DHW (severity = 2), and severe
206 bleaching at 12+ DHW (severity = 3). These predictions were compared to bleaching
207 observations from ReefBase (ReefBase-Project, 2007), which also reports bleaching
208 severity on a scale of 0–3. We concentrated on observations during the widespread
209 bleaching event of 1998 (Fig. S2). Bleaching events in some regions within the
210 CTROMS domain were well observed in 1998 (Philippines, Great Barrier Reef) but were
211 under observed in others. Using the 329 reef locations where bleaching observations
212 were available, we compared the distributions of the maximum predicted severity with
213 the observed severity (chi-square test). We also applied the paired t-test to the distances
214 between maximum predicted severity and maximum observed severity ($|SEV_{PRED} -$
215 $SEV_{OBS}|$) to determine if predicted severity improved when using TST_{pc} versus TST.
216 These comparisons are not intended to measure the predictive power of the bleaching
217 algorithm (Logan *et al.*, 2012) but rather to determine whether predicted bleaching
218 severity based on TST_{pc} is significantly closer to observations than that based on local
219 TST.

220 **Results**

221 Local TST, calculated here as $2.5\sigma^{\circ}C$ above the MMM, varies considerably across the
222 region, with 95% of sites falling within 27.8–31.3°C (Fig. 3a). Some of the lowest TSTs
223 in the Coral Triangle are near the equator in the well-mixed region of the Sulu and Banda
224 Seas. Relative to the mean local TST, the mean TST_{pc} is only slightly elevated (10 days:

225 $0.03\pm 0.38^{\circ}\text{C}$; 30 days: $0.04\pm 0.47^{\circ}\text{C}$), and the difference is not significant for either the
226 10 or 30-day dispersal periods (paired t-test: $p=0.05$ for 10-day; $p=0.14$ for 30-day).

227 The distributions of TST_{pc} relative to TST, however, are increasingly positively skewed
228 and leptokurtic with increasing time of dispersal, reflecting the averaging of the TSTs
229 across the larval source regions of each site (Fig. S3). The spatial patterns of TST_{pc} are
230 similar for the 10-day and 30-day dispersal periods (Fig. 3). TST_{pc} is higher than TST in
231 regions that are downstream of warmer reefs, and lower in regions that are downstream
232 of cooler reefs (Figs. 3b-c). The differences between TST_{pc} and TST are more extreme
233 for the 30-day versus 10-day dispersal period.

234 Despite the low probability of any one reef providing larvae to another reef, the few that
235 do arrive contribute substantially to the total pool. Examples of TST_{pc} for specific sites
236 illustrate how connectivity affects both the average and range of TST at a particular site.
237 For Site 695 in the northern Great Barrier Reef (Fig. 4) the potential source reefs over 10
238 days are limited to the middle and northern GBR sites, and TST_{pc} based on these sites is
239 around 0.6°C cooler than the local TST. The source reefs over 30 days are dominated by
240 more southerly sites, and the average TST_{pc} is more than 1.3°C cooler. In both cases, the
241 TST values of the source reefs span more than 2°C .

242 The effect of connectivity on TST can vary dramatically even between closely located
243 sites. The TST_{pc} for Site 2394 in the Palawan Region of the Philippines region is only
244 slightly cooler than the local TST (Fig. S4), but for Site 2138 in the Sulu Archipelago,
245 TST_{pc} is more than 2°C warmer (Fig. S5). In some regions, the effect of connectivity on

246 mean TST_{pc} is minimal, but the range of TST values from the source sites can exceed 3°C
247 (e.g., site 937, Fig. S6).

248 Predicted coral bleaching severity for the 1998 La Niña event, regardless of using TST or
249 TST_{pc} , are significantly different from the maximum observed bleaching (chi-square
250 value = 147.4 for TST; 177.7 for $TST_{pc} - 10d$; 84.4 for $TST_{pc} - 30d$) (Fig. 5). Comparing
251 the accuracy of predicted bleaching to observed bleaching, however, indicates that
252 bleaching predicted using TST_{pc} for the 10-day dispersal period is significantly closer to
253 observations than that using TST (paired t-test, $p < 0.0001$). This was not the case when
254 comparing predictions using the 30-day TST_{pc} versus TST ($p = 0.2556$). In general, the
255 TST_{pc} -based predictions were of higher-level bleaching. Even in the 10-day bleaching
256 predictions, however, the improvements were almost entirely in the Great Barrier Reef
257 region (Fig. 5b). Outside of this region, bleaching reports were few and scattered, and
258 most of the predictions remained unchanged (39 observations), while the remainder was
259 almost evenly split between better (18), and worse (16).

260 **Discussion**

261 Our results indicate that many reefs in the Coral Triangle region are potentially connected
262 to reefs from a wide range of TSTs, and thus have the opportunity to receive larvae that
263 are more or less adapted to elevated temperature than would be suggested by local
264 conditions alone. With longer dispersal periods (and longer dispersal distances), the
265 potential for connectivity to regions of significantly warmer or cooler temperatures
266 increases. The shift to TST distributions with higher skewness and kurtosis (Fig. S3) is
267 therefore expected, since TST_{pc} is essentially an average of TST across the connected

268 reefs. In reality larvae settle over a range of days within the larval competency period, so
269 the true distribution of TST_{pc} would actually reflect a range of dispersal periods, as well
270 as other biological factors. Our analysis therefore represents the physical limits of how
271 much larval connectivity can contribute to TST; and the addition of biological constraints
272 within those physical limits will certainly refine these results. Nonetheless, the results
273 illustrate and expand on the concept originally proposed by Mumby *et al.* (2011): as long
274 as exogenous larvae originate from reefs with temperatures that differ from the sink reef,
275 they can potentially alter the overall temperature tolerance of a species by increasing the
276 diversity of individuals (or alleles) with respect to temperature tolerance. Thus, both the
277 range and average severity of the bleaching response at any one site could be quite
278 different from that predicted by the locally derived TST.

279 We show that the 10-day TST_{pc} improves the TST-based predictions of bleaching
280 severity, albeit slightly. This improvement supports the idea that connectivity can affect
281 heat tolerance, but we note that this result is probably biased by the paucity of bleaching
282 observations in the Coral Triangle region, and the concentration of those observations
283 from the Great Barrier Reef (Fig. 5b) where previous studies have shown that in addition
284 to temperature stress, other factors such as local weather and circulation patterns played a
285 role in the 1998 coral bleaching event (Berkelmans *et al.*, 2004). The fact that TST_{pc}
286 resulted in a shift toward more bleaching (Fig. 5a) may reflect that most of the Great
287 Barrier Reef bleaching reports are from reefs that are downstream from cooler reefs. If
288 bleaching observations had been distributed more widely across the Coral Triangle, then
289 the shift would be less extreme. Predictions based on the 30-day TST_{pc} are not
290 significantly better than predictions based on local TST. This difference with the 10-day

291 based predictions is expected given that larvae of most broadcast spawning corals settle
292 within 10 days (Baird, 2001); therefore restricting dispersal to a 10-day time frame
293 should approximate true dispersal better than at day 30, despite the lack of biological
294 factors (e.g., larval mortality, settlement).

295 An important and logical assumption of the TST_{pc} approach is that heat tolerance in
296 corals is primarily based on genetic inheritance. Palumbi *et al.* (2014) determined that
297 about half the heat tolerance in *A. hyacinthus* is attributable to genetic differences. Thus,
298 the role of connectivity in determining heat tolerance depends on how strong a role the
299 genetic factor plays. In addition, locations with the greatest connectivity to other reefs
300 within a population of a species are more likely to have greater genetic diversity than
301 more isolated locations (Liggins *et al.*, 2014). If that genetic diversity includes different
302 levels of adaptation to heat stress, then the bleaching response should reflect that. In a
303 coral subpopulation with connectivity across a narrow range of temperatures (e.g., Fig.
304 S4), for example, one should find a narrow range of tolerance to heat stress and therefore
305 a more uniform bleaching response, while in a population with connectivity to reefs from
306 a diversity of temperature regimes the bleaching response should be more varied (e.g.,
307 Figs. S5, S6). We are unable to test this because the diversity of bleaching responses was
308 not adequately documented in the observations.

309 Whether larval transport actually affects temperature tolerance in the real world depends
310 on many factors. First, the work presented here focuses on the physical aspects of
311 connectivity, while the actual connectivity is also affected by biological factors such as
312 reproductive output, precompetency period, larval mortality, settlement, and post-
313 settlement mortality. Usually, biological factors reduce connectivity, but not always.

314 Successful recruitment, for example, is limited by available space. A local mortality
315 event can increase available space while simultaneously decreasing the level of self-
316 seeding, so that the probability of successful recruitment from non-local sources increases.
317 Thus, where coral cover has been greatly reduced (e.g. mass mortality following a
318 bleaching event), newly settling corals may be disproportionately sourced from non-local
319 temperature regimes (Fig. 1c). Successful recruitment between reefs with different
320 environmental conditions may also be affected by “phenotype-environment mismatch,”
321 which can naturally bias recruitment against exogenous colonizers (Marshall *et al.*, 2010).
322 On the other hand, if local environments are changing, then some exogenous larvae may
323 be better adapted than endogenous larvae, such as suggested for *A. millepora* (Dixon *et*
324 *al.*, 2015).

325 Connectivity can thus lead to increased heat tolerance simply through the sourcing of
326 exogenous individuals from regions where corals are adapted to heat stress, but it can
327 also lead to an increase in population fitness via immigration of new alleles (“genetic
328 rescue” sensu Tallmon *et al.*, 2004). Coral larvae appear to inherit heat tolerance from
329 parents, and experience selection based on their genetic heat-stress capacity (Dixon *et al.*,
330 2015). If true, then selection would skew the impact of connectivity on TST to screen for
331 larval genotypes that are best able to survive the temperatures during transit as well as at
332 the destination reef. Considering future increases in surface temperatures, if selection
333 favors larvae from warmer regions, then larvae sourced from warmer water reefs should
334 be more successful than those from cooler reefs. Unfortunately, immigration can also
335 lead to reduced fitness in a population (e.g. founder effects, outbreeding depression,

336 Tallmon *et al.*, 2004), but so far there has been little research on these effects in coral
337 populations (Baums, 2008).

338 The time scale over which successful recruitment of exogenous larvae occurs is also
339 extremely important. Successful recruitment is stochastic, with strong variability from
340 year to year (Siegel *et al.*, 2008). To account for these effects, we base our calculations
341 on a nearly 50-year hindcast simulation. Future work should also take into account the
342 effects of disturbance and recolonization, which are likely to become more important in
343 the future given predictions of more frequent bleaching events in this region over the next
344 50 years.

345 Finally, our model results are based on the thermal stress response of a model
346 broadcasting species, while observations of bleaching severity reflect the degree of
347 pigment loss in coral colonies across the entire species composition as well as the
348 percentage of colonies affected (Marshall & Schuttenberg, 2006). A better approach
349 would be to compare the model results to observed bleaching within a single species (e.g.
350 *A. millepora*), but this reduces the number of observations to a very small subset. Despite
351 this bias, the analysis does suggest that exogenous colonization via connectivity, and
352 using normal dispersal periods, can alter the thermal tolerance of local populations. Thus,
353 verifying the impact of connectivity on thermal stress thresholds of corals is important,
354 because if significant, it will aid the identification of suitable sites for conservation. The
355 simplest approach to verifying the impact is to examine temperature tolerances
356 downstream of warmer areas (such as with increasing latitudes of boundary currents; e.g.
357 Kuroshio Current), which should be higher than expected; or downstream of colder areas
358 (e.g., the northward flowing Hiri Current along the northern Great Barrier Reef). The

359 Banda Sea, for example, is a relatively cool region of the Coral Triangle surrounded by
360 warmer regions, and connectivity from those warmer regions should lead to an increase
361 in the thermal tolerance of the coral populations there (Fig. 3). This could explain why
362 this region has so few reports of bleaching despite the heat stress conditions (Kleypas *et*
363 *al.*, 2015).

364 If connectivity is indeed a factor determining heat tolerance in corals, then two general
365 rules of thumb will help identify reefs that are likely to fare better with future warming:
366 1) reefs that are consistently downstream from warmer water reefs (see also Mumby *et al.*,
367 2011); and 2) reefs that receive larvae from a diverse range of temperature regimes,
368 providing higher probability that some of those immigrants will be better adapted to
369 warmer regimes. These results provide a framework that can be directly tested as
370 advances in genomics increases our capacity to link ecological, evolutionary and
371 physiological processes to determine how organisms respond to thermal stress (Barshis *et*
372 *al.*, 2013; Porcelli *et al.*, 2015).

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558 **Figures**

559 **Figure 1.** Illustration of how dispersal across temperature gradients can cause variations
560 in a species' TST. Arrow thickness represents strength of connectivity, a ; note that self-
561 seeding typically provides the largest contribution. (a) Recruitment of larvae from site $j1$
562 to site i will introduce individuals with *higher* thermal tolerance relative to reef i natives;
563 (b) Recruitment of larvae from site $j2$ to site i will introduce individuals with *lower*
564 thermal tolerance; (c) Following a mortality event at site i , recruitment from $j1, j2$
565 becomes proportionately higher; (d) Where connectivity increases immigration from sites
566 spanning a range of temperature regimes, the TST at site i should reflect the TSTs at sites
567 $j1$ through $j4$, as well as site i . R_j is the reef area at site j . $TST_{pc,i}$ is the TST at site i
568 adjusted for potential connectivity.

569 **Figure 2.** The Coral Triangle and surrounding regions, showing the CT-ROMS domain
570 and major oceanographic currents. Reef locations are highlighted in pink. Modified
571 from Castruccio *et al.* (2013).

572 **Figure 3.** The temperature stress threshold (TST) for coral based on local TST (a) as
573 determined by the $MMM+2.5\sigma^{\circ}C$. The differences between TST and TST_{pc} based on a
574 10-day dispersal period (b) and a 30-day dispersal period (c) illustrate the potential
575 impact of connectivity on the TST of a local population for a typical broadcasting coral
576 (e.g. *Acropora millepora*). Red values show where stress thresholds are higher due to
577 connectivity and blue areas where stress thresholds are lower.

578 **Figure 4.** Potential connectivity for site 695 (indicated with an arrow) on the Great
579 Barrier Reef, following 10 and 30-day dispersal periods (a, c). Probability density
580 function of the relative contributions TST_j of connected sites (j) to the TST_{pc} are binned

581 into 0.5°C intervals (b, d). Black line indicates the local TST. Dashed line indicates the
582 TST_{pc} based on the TSTs of the connected reefs.

583 **Figure 5.** Comparison of bleaching predictions to observations when using TST_{pc} versus
584 TST. (a) Histograms of observed maximum bleaching severity (0 = no bleaching; 1 =
585 mild bleaching; 2 = moderate; 3 = severe) from 329 sites, and maximum predicted
586 bleaching severity based on TST, TST_{pc} 10-days, and TST_{pc} 30-days at the same sites. (b)
587 Locations where bleaching severity predicted by the 10-day TST_{pc} is the same, better or
588 worse than by TST.