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

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

Running head: Connectivity and heat tolerance in coral populations

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Keywords: Coral reefs, connectivity, thermal stress, oceanographic modeling, larval dispersal

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

Introduction

Most marine organisms are progressively exposed to rising temperatures associated with climate change, and their survival is often evaluated in terms of their ability to cope via changes in physiology, phenology, and/or colonization (Bellard et al., 2012). Marine larval dispersal via ocean currents is a major component of population connectivity of many marine organisms (Cowen & Sponaugle, 2009), and because of its capacity to increase a species’ range and its ability to recover following local disturbance, species that disperse widely are thought to be less susceptible to global extinction (Jones et al., 2007). Coupled bio-physical dispersal models provide a framework for understanding the patterns of larval dispersal as well as its barriers (Cowen et al., 2006; Kool et al.,
2013; Paris et al., 2013; Treml et al., 2015). Modeling has revealed that connectivity can be complex, particularly at the spatial scales of coral reef systems (e.g., 1-10 km) where topography, eddies, and tides interact to create barriers to dispersal (Werner et al., 2007). They also allow one to quantitatively estimate the probability of dispersal among sites within the connected range of a population (Treml et al., 2008; Mitarai et al., 2009; Kool et al., 2011). For a given population, that range might include a variety of conditions. Mumby et al. (2011), for example, illustrated the potential importance of larval connectivity across different temperature regimes in the Bahamas, as well as considering this in reserve design. However, the capacity of dispersal to deliver individuals adapted to different temperature regimes has not been widely considered.

The temperature tolerance of adult corals is tied to the temperature regime of the local environment (Logan et al., 2014). Corals begin to experience heat stress once temperatures exceed their thermal stress threshold (TST). The TST is typically around 1–2°C above the climatological mean monthly maximum (MMM) for a given location (Liu et al., 2003). During a bleaching event, however, individuals within the same coral species will often exhibit a range of bleaching severity to the same conditions. This reflects variations in environmental factors within the reef (e.g. small changes in depth, shading, currents, etc.) (Berkelmans, 2002; McClanahan et al., 2005; Ulstrup et al., 2006); different clades of algal symbionts (Buddemeier et al., 2004; Silverstein et al., 2015); and differences in coral morphology (Loya et al., 2001) or condition (Fitt et al., 2001). It may also reflect genetic/genomic differences in heat tolerance within the local population (Palumbi et al., 2014).
A subpopulation of corals in any one location represents individuals that are not only offspring of local corals, but also offspring of corals on other reefs that arrived via larval transport. The degree of larval connectivity thus plays a role in determining the genetic makeup of heat tolerance across coral populations. If a coral subpopulation has a high probability of receiving larvae from corals adapted to temperatures higher or lower than those of their own waters, the temperature tolerance of the individuals may differ from that determined solely by local conditions. One recent study suggests that heat tolerance in the reef coral *Acropora hyacinthus*, for example, is determined about equally by acclimation and genetic inheritance (Palumbi *et al.*, 2014), and another showed that larvae of *Acropora millepora*, when exposed to heat stress, had a 10 times greater survival rate if the parents were from warmer waters (Dixon *et al.*, 2015).

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

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

Model simulations

ROMS is an ocean circulation model that is widely used for regional and coastal investigations (Shchepetkin & McWilliams, 2003, 2005). CT-ROMS has a 5-km horizontal resolution and 50 vertical terrain-following levels weighted toward the surface in order to better resolve the mixed layer. The model domain is configured to include as many reefs as possible within the Coral Triangle region, and to minimize edge effects and truncation of connected populations (Fig. 2), although not all such effects can be avoided. The model bathymetry is interpolated from the global SRTM30_PLUS product (Becker et al., 2009), which has a 30-arc second (approximately 1-km) spatial resolution. The model time step is 90 seconds. Tides are explicitly resolved in CT-ROMS, with tidal
forcing naturally implemented at the boundary by providing tidal elevation and barotropic flows from the global model of ocean tides TPXO 7.2 (Egbert & Erofeeva, 2002). An astronomical tide-generating potential is also added as a body force in the momentum equation to ensure correct tidal phasing. Evaluations of CT-ROMS against observations have shown that it has considerable skill in simulating ocean temperature and ocean circulation (Castruccio et al., 2013).

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

**Larval connectivity**

We calculated connectivity – the probability of larval transport between a source and sink reef – over the 47-year period, based on a common and widespread broadcast spawning species (*Acropora millepora*), to quantify the proportion of larvae at each reef that arrived from other source sites (Thompson et al., in prep.). Although the larval release times were based on *A. millepora* spawning parameters (Baird, 2001; Baird et al., 2009; Connolly & Baird, 2010), this calculation mainly addressed the potential connectivity,
that is, the physical component of the transport (see Mitarai et al., 2009; Watson et al., 2012). Recent studies of connectivity, including the work by Treml et al. (2012) and Treml et al. (2015) in the Coral Triangle, illustrate the role of several biological parameters in connectivity, such as fecundity (Baird & Marshall, 2002; Sudek et al., 2012); precompetency period (Heyward et al., 2002; Figueiredo et al., 2014); survivability and pelagic larval duration (Edmunds et al., 2001; Bassim & Sammarco, 2003; Baums et al., 2006; Nozawa & Harrison, 2007; Randall & Szmant, 2009); and settlement (Coles, 1985). Including these factors would produce a more realistic calculation of connectivity (“realized connectivity” of Watson et al., 2012), but limiting our analysis to potential connectivity allows us isolate the role of physics in this first order analysis of the role of connectivity on TST. Given the computational burden of particle tracking between the large number of reef cells within the CT-ROMS domain, and to increase the robustness in the estimated larval transport, we organized contiguous reef and coastal cells into sites of 8x8 cells (number of sites = 2497). Twenty-five particles were released from each reef and coastal cell on each of five consecutive days following the full moons nearest to April 1 and September 1 (spring and fall spawning periods for A. millepora) for each of the 47 years of simulation. Following this approach, up to ~8000 particles were released from each site (depending on the number of non-land cells within each 8x8 site), totaling > 18 million particles per spawning event and > 1.7 billion for the 47-year analysis. Rigid testing of the sample size sensitivity (following an approach similar to Simons et al., 2013), indicated that this sample size was sufficient to accurately sample the Lagrangian probability density function (PDF) used to calculate the potential connectivity.
The Lagrangian particle tracking routine TRACMASS (Döös, 2012) was used to calculate the Lagrangian trajectories from daily average CT-ROMS Eulerian velocity fields. Potential connectivity, the probability of transport between source and sink sites (e.g., probability that a particle released at site $j$ will arrive at site $i$), was calculated for the fall and spring releases of each year and for two dispersal periods: 10 days and 30 days. Potential connectivity was calculated following the methodology of Mitarai et al. (2009) by calculating the PDF at the end of the dispersal period (e.g. the locations of all particles at day 10 and at day 30; see Fig. S1 in Supporting Information). The average potential connectivity was then calculated from all spring and fall releases during the 47-year period (i.e., 94 releases). These results thus provide a long-term average of potential connectivity that includes seasonal to decadal scales of variability. While larvae of *A. millepora* and related species can survive for more than 100 days, most are only competent between 4–30 days following spawning, and most settle within 10 days (Baird, 2001; Connolly & Baird, 2010). The 10-day dispersal period therefore represents a likely timeframe for the peak of larval settlement, but we also determined potential connectivity for the 30-day dispersal period because long-distance dispersal may become more important if mass mortality events over large regions eliminate short-distance larval sources. We did not consider dispersal longer than 30 days because even though rare dispersal events can be important in populations (de Queiroz, 2005), the computational requirements to adequately analyze such rare events increase greatly, particularly if we are to maintain statistical robustness in quantifying potential connectivity.

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

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

\[ TST_{pc,i} = \frac{\sum_j a_{ij} f R_j TST_j}{\sum_j a_{ij} f R_j} \]

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

To quantify the potential impact of including potential connectivity in coral bleaching predictions, TST and TST pc were used to calculate the degree heating week (DHW) (Liu
et al., 2003), a metric of thermal heat stress quantified as the 12-week accumulation of sea surface temperature exceeding the TST (or TST\textsubscript{pc}). Mild bleaching typically occurs at 4–8 DHW (severity = 1), moderate bleaching at 8-12 DHW (severity = 2), and severe bleaching at 12+ DHW (severity = 3). These predictions were compared to bleaching observations from ReefBase (ReefBase-Project, 2007), which also reports bleaching severity on a scale of 0–3. We concentrated on observations during the widespread bleaching event of 1998 (Fig. S2). Bleaching events in some regions within the CTROMS domain were well observed in 1998 (Philippines, Great Barrier Reef) but were under observed in others. Using the 329 reef locations where bleaching observations were available, we compared the distributions of the maximum predicted severity with the observed severity (chi-square test). We also applied the paired t-test to the distances between maximum predicted severity and maximum observed severity (|SEV\textsubscript{PRED} – SEV\textsubscript{OBS}|) to determine if predicted severity improved when using TST\textsubscript{pc} versus TST.

These comparisons are not intended to measure the predictive power of the bleaching algorithm (Logan et al., 2012) but rather to determine whether predicted bleaching severity based on TST\textsubscript{pc} is significantly closer to observations than that based on local TST.

**Results**

Local TST, calculated here as 2.5\(\sigma\)°C above the MMM, varies considerably across the region, with 95% of sites falling within 27.8–31.3°C (Fig. 3a). Some of the lowest TSTs in the Coral Triangle are near the equator in the well-mixed region of the Sulu and Banda Seas. Relative to the mean local TST, the mean TST\textsubscript{pc} is only slightly elevated (10 days:
0.03±0.38°C; 30 days: 0.04±0.47°C), and the difference is not significant for either the
10 or 30-day dispersal periods (paired t-test: p=0.05 for 10-day; p=0.14 for 30-day).

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

Despite the low probability of any one reef providing larvae to another reef, the few that
do arrive contribute substantially to the total pool. Examples of TST\textsubscript{pc} for specific sites
illustrate how connectivity affects both the average and range of TST at a particular site.

For Site 695 in the northern Great Barrier Reef (Fig. 4) the potential source reefs over 10
days are limited to the middle and northern GBR sites, and TST\textsubscript{pc} based on these sites is
around 0.6°C cooler than the local TST. The source reefs over 30 days are dominated by
more southerly sites, and the average TST\textsubscript{pc} is more than 1.3°C cooler. In both cases, the
TST values of the source reefs span more than 2°C.

The effect of connectivity on TST can vary dramatically even between closely located
sites. The TST\textsubscript{pc} for Site 2394 in the Palawan Region of the Philippines region is only
slightly cooler than the local TST (Fig. S4), but for Site 2138 in the Sulu Archipelago,
TST\textsubscript{pc} is more than 2°C warmer (Fig. S5). In some regions, the effect of connectivity on
mean TST\textsubscript{pc} is minimal, but the range of TST values from the source sites can exceed 3°C (e.g., site 937, Fig. S6).

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

Discussion

Our results indicate that many reefs in the Coral Triangle region are potentially connected to reefs from a wide range of TSTs, and thus have the opportunity to receive larvae that are more or less adapted to elevated temperature than would be suggested by local conditions alone. With longer dispersal periods (and longer dispersal distances), the potential for connectivity to regions of significantly warmer or cooler temperatures increases. The shift to TST distributions with higher skewness and kurtosis (Fig. S3) is therefore expected, since TST\textsubscript{pc} is essentially an average of TST across the connected
reefs. In reality larvae settle over a range of days within the larval competency period, so the true distribution of $TST_{pc}$ would actually reflect a range of dispersal periods, as well as other biological factors. Our analysis therefore represents the physical limits of how much larval connectivity can contribute to TST; and the addition of biological constraints within those physical limits will certainly refine these results. Nonetheless, the results illustrate and expand on the concept originally proposed by Mumby et al. (2011): as long as exogenous larvae originate from reefs with temperatures that differ from the sink reef, they can potentially alter the overall temperature tolerance of a species by increasing the diversity of individuals (or alleles) with respect to temperature tolerance. Thus, both the range and average severity of the bleaching response at any one site could be quite different from that predicted by the locally derived TST.

We show that the 10-day $TST_{pc}$ improves the TST-based predictions of bleaching severity, albeit slightly. This improvement supports the idea that connectivity can affect heat tolerance, but we note that this result is probably biased by the paucity of bleaching observations in the Coral Triangle region, and the concentration of those observations from the Great Barrier Reef (Fig. 5b) where previous studies have shown that in addition to temperature stress, other factors such as local weather and circulation patterns played a role in the 1998 coral bleaching event (Berkelmans et al., 2004). The fact that $TST_{pc}$ resulted in a shift toward more bleaching (Fig. 5a) may reflect that most of the Great Barrier Reef bleaching reports are from reefs that are downstream from cooler reefs. If bleaching observations had been distributed more widely across the Coral Triangle, then the shift would be less extreme. Predictions based on the 30-day $TST_{pc}$ are not significantly better than predictions based on local TST. This difference with the 10-day
based predictions is expected given that larvae of most broadcast spawning corals settle within 10 days (Baird, 2001); therefore restricting dispersal to a 10-day time frame should approximate true dispersal better than at day 30, despite the lack of biological factors (e.g., larval mortality, settlement).

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

Whether larval transport actually affects temperature tolerance in the real world depends on many factors. First, the work presented here focuses on the physical aspects of connectivity, while the actual connectivity is also affected by biological factors such as reproductive output, precompetency period, larval mortality, settlement, and post-settlement mortality. Usually, biological factors reduce connectivity, but not always.
Successful recruitment, for example, is limited by available space. A local mortality event can increase available space while simultaneously decreasing the level of self-seeding, so that the probability of successful recruitment from non-local sources increases. Thus, where coral cover has been greatly reduced (e.g. mass mortality following a bleaching event), newly settling corals may be disproportionately sourced from non-local temperature regimes (Fig. 1c). Successful recruitment between reefs with different environmental conditions may also be affected by “phenotype-environment mismatch,” which can naturally bias recruitment against exogenous colonizers (Marshall et al., 2010). On the other hand, if local environments are changing, then some exogenous larvae may be better adapted than endogenous larvae, such as suggested for A. millepora (Dixon et al., 2015).

Connectivity can thus lead to increased heat tolerance simply through the sourcing of exogenous individuals from regions where corals are adapted to heat stress, but it can also lead to an increase in population fitness via immigration of new alleles (“genetic rescue” sensu Tallmon et al., 2004). Coral larvae appear to inherit heat tolerance from parents, and experience selection based on their genetic heat-stress capacity (Dixon et al., 2015). If true, then selection would skew the impact of connectivity on TST to screen for larval genotypes that are best able to survive the temperatures during transit as well as at the destination reef. Considering future increases in surface temperatures, if selection favors larvae from warmer regions, then larvae sourced from warmer water reefs should be more successful than those from cooler reefs. Unfortunately, immigration can also lead to reduced fitness in a population (e.g. founder effects, outbreeding depression,
Tallmon et al., 2004), but so far there has been little research on these effects in coral populations (Baums, 2008).

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

Finally, our model results are based on the thermal stress response of a model broadcasting species, while observations of bleaching severity reflect the degree of pigment loss in coral colonies across the entire species composition as well as the percentage of colonies affected (Marshall & Schuttenberg, 2006). A better approach would be to compare the model results to observed bleaching within a single species (e.g. A. millepora), but this reduces the number of observations to a very small subset. Despite this bias, the analysis does suggest that exogenous colonization via connectivity, and using normal dispersal periods, can alter the thermal tolerance of local populations. Thus, verifying the impact of connectivity on thermal stress thresholds of corals is important, because if significant, it will aid the identification of suitable sites for conservation. The simplest approach to verifying the impact is to examine temperature tolerances downstream of warmer areas (such as with increasing latitudes of boundary currents; e.g. Kuroshio Current), which should be higher than expected; or downstream of colder areas (e.g., the northward flowing Hiri Current along the northern Great Barrier Reef). The
Banda Sea, for example, is a relatively cool region of the Coral Triangle surrounded by warmer regions, and connectivity from those warmer regions should lead to an increase in the thermal tolerance of the coral populations there (Fig. 3). This could explain why this region has so few reports of bleaching despite the heat stress conditions (Kleypas et al., 2015).

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

Acknowledgements

This work was funded in part by the National Science Foundation and the Integrated Science Program of NCAR. Computational resources were provided by NSF-MRI Grant CNS-0821794, MRI-Consortium: Acquisition of a Supercomputer by the Front Range Computing Consortium (FRCC); and on Yellowstone (ark:/85065/d7wd3xhc) by NCAR’s Computational and Information Systems Laboratory, sponsored by NSF. We greatly appreciate Dr. Bror Jönsson for his assistance with the TRACMASS code. We also thank Kris Karnauskas and two anonymous reviewers for valuable comments.
References


Figures

Figure 1. Illustration of how dispersal across temperature gradients can cause variations in a species’ TST. Arrow thickness represents strength of connectivity, $a$; note that self-seeding typically provides the largest contribution. (a) Recruitment of larvae from site $j_1$ to site $i$ will introduce individuals with higher thermal tolerance relative to reef $i$ natives; (b) Recruitment of larvae from site $j_2$ to site $i$ will introduce individuals with lower thermal tolerance; (c) Following a mortality event at site $i$, recruitment from $j_1, j_2$ becomes proportionately higher; (d) Where connectivity increases immigration from sites spanning a range of temperature regimes, the TST at site $i$ should reflect the TSTs at sites $j_1$ through $j_4$, as well as site $i$. $R_j$ is the reef area at site $j$. $TST_{pc,i}$ is the TST at site $i$ adjusted for potential connectivity.

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

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

Figure 4. Potential connectivity for site 695 (indicated with an arrow) on the Great Barrier Reef, following 10 and 30-day dispersal periods (a, c). Probability density function of the relative contributions $TST_j$ of connected sites ($j$) to the $TST_{pc}$ are binned
into 0.5°C intervals (b, d). Black line indicates the local TST. Dashed line indicates the TST\textsubscript{pc} based on the TSTs of the connected reefs.

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