



Predicting coral metapopulation decline in a changing thermal environment

Daniel M. Holstein¹ · Tyler B. Smith² · Ruben van Hooidonk^{3,4} · Claire B. Paris⁵

Received: 1 March 2021 / Accepted: 25 March 2022
© The Author(s) 2022

Abstract Thermal stress is expected to compromise the persistence of tropical corals throughout their biogeographic ranges, making many reefs inhospitable to corals by the end of the century. We integrated models of local predictions of thermal stress throughout the coming century, coral larval dispersal, and the persistence of a coral's metapopulation(s) in the Caribbean to investigate broad trends in metapopulation fragmentation and decline. As coral reef patches become inhospitable throughout the next century, the metapopulation of *Orbicella annularis* is predicted to fragment, with sub-networks centered around highly connected patches and thermal refuges. Some of these are predicted to include the reefs of Colombia, Panama, Honduras, Guatemala, Belize, Southern and Northern Cuba, Haiti, and the Bahamas. Unknown coral

population demographic parameters, such as lifetime egg production and stock-recruitment rates, limit the model's predictions; however, a sensitivity analysis demonstrates that broadscale patterns of fragmentation and metapopulation collapse before the end of the century are consistent across a range of potential parameterizations. Despite dire predictions, the model highlights the potential value in protecting and restoring coral populations at strategic locations that are highly connected and/or influential to persistence. Coordinated conservation activities that support local resilience at low coral cover have the potential to stave off metapopulation collapse for decades, buying valuable time. Thermal refuges are linchpins of metapopulation persistence during moderate thermal stress, and targeted conservation or restoration that supports connectivity between these refuges by enhancing local population growth or sexual propagation may be critically important to species conservation on coral reefs.

Topic Editor Steve Vollmer

✉ Daniel M. Holstein
dholstein1@lsu.edu

¹ Department of Oceanography and Coastal Sciences, College of the Coast and Environment, Louisiana State University, 2259 Energy Coast and Environment Building, Baton Rouge, LA, USA

² Center for Marine and Environmental Studies, University of the Virgin Islands, St. Thomas, VI, USA

³ Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, Miami, FL, USA

⁴ Atlantic Oceanographic and Meteorological Laboratory, National Oceanic and Atmospheric Administration, Miami, FL, USA

⁵ Department of Ocean Sciences, University of Miami Rosenstiel School of Marine and Atmospheric Science, Miami, FL, USA

Keywords Metapopulations · Coral reefs · Extinction · Persistence · Bleaching · Connectivity

Introduction

Coral reefs have emerged as an unfortunate contemporary example of how climate change challenges the persistence of essential biomes. Under thermal stress, photosynthetic coral holobionts can experience thermal bleaching, a process in which the symbiotic relationship between coral host and algal symbiont breaks down, potentially resulting in coral mortality (Glynn 1996; Loya et al. 2001). When corals experience bleaching in consecutive years, it is associated with higher probabilities of mortality and local extinctions (Pandolfi et al. 2011; Grottoli et al. 2014),

which has and will continue to occur with increasing frequency over the next century (van Hooidonk et al. 2013, 2015). Human societies world-wide depend on coral reefs for the provisioning of ecosystem goods and services, and those goods and services are also at risk as coral reefs degrade (Moberg and Folke 1999; Costanza et al. 2017). A challenge to our ability to forecast the futures of coral reefs and to generate effective conservation strategies is that most projections and conservation activities occur at local or reef (patch) scales, but the mechanisms that promote species persistence, such as migration, occur over larger biogeographic scales. Thus, local conservation or restoration activities may not be deployed spatially or temporally where it is regionally most needed or effective.

A metapopulation is a patchwork of incompletely isolated populations (or patches), which are connected through the migration of individuals. The persistence of a metapopulation depends on processes of local persistence (or self-persistence, potentially through the retention of individuals between generations), and on processes of network persistence, like migration (Hastings and Botsford 2006). In theory, a metapopulation may persist if a single sub-population is self-persistent and provides itself with enough recruits to replace reproductive adults before those adults perish (Hastings and Botsford 2006). Network persistence can be achieved even when this condition is not met through the supplement of recruits from connected sub-populations. Models of marine migrations and metapopulations are useful in understanding how patchworks of habitats interact with each other (Treml et al. 2008; Holstein et al. 2014; Schill et al. 2015), how migration supports persistence or fisheries (Hastings and Botsford 2006; Botsford et al. 2009), the design of marine protected areas (Steneck et al. 2009; White et al. 2010a, 2014; Kininmonth et al. 2011), and how the removal of habitats can have cascading effects (Bode et al. 2008). Corals are sessile as adults, and migration occurs during a pelagic larval life phase. Coral planulae larvae are poor swimmers (Hata et al. 2017) and connectivity between patches depends highly on ocean currents and on the timing of adult reproduction (Holstein et al. 2014, 2016; Limer et al. 2020). Migration between reefs can be highly asymmetric (Beger et al. 2010; Holstein et al. 2014; Limer et al. 2020) and species-specific (Treml et al. 2012; Holstein et al. 2014).

Coral reefs are expected to experience intensification of thermal stress throughout the next century (Pandolfi et al. 2011; Maynard et al. 2015; van Hooidonk et al. 2015) and that stress is not expected to be homogenous geographically (van Hooidonk et al. 2013, 2015; Logan et al. 2014). Distinct coral reefs experience heterogeneous environmental conditions and disturbance regimes, resulting in localized perturbations or extinctions (Hastings and Botsford 2006;

Mumby et al. 2011; Smith et al. 2014). Habitat patches that are removed from an environmental stressor and/or experience elevated resistance or resilience may behave as “refuges” from that stressor and support enhanced metapopulation resilience (Mumby et al. 2011). Refuges support metapopulation persistence through sustained adult or larval migrations to less resistant patches during or following disturbance (Keppel et al. 2012; Smith et al. 2014; Keppel and Wardell-Johnson 2015).

How habitat connectivity and the distribution of thermal refuges will play a role in the persistence of coral reefs is a longstanding but unanswered question (Glynn 1996; Mumby et al. 2011). Here, we have used a spatially realistic abundance-based metapopulation model to understand the seascape interactions of thermal stress and biophysical migration in a coral. This model synthesizes projections of thermal stress and the probability of coral larval exchanges between Caribbean coral reefs to assess metapopulation persistence throughout the current century. We focused on a threatened foundational species, the boulder star coral *Orbicella annularis*, but expect patterns to be similar for species with comparable life histories, distributions, and thermal tolerances. Because there is little empirical evidence for the demographic thresholds of local coral population collapse (e.g., minimum thresholds of recruitment or coral cover to maintain persistence), we have tested an array of potential thresholds in a model sensitivity analysis, which also highlights how conservation or restoration activities that bolster local demographics can influence region-wide persistence. We have identified regions of the Western Atlantic that could be targeted for species conservation and/or restoration and predicted the fragmentation and decline of the metapopulation of this important coral species throughout the most acute phases of global warming.

Methods

We have integrated two independent models into a numerical metapopulation model. The first is a thermal projection model of the Caribbean which projects the number of severe bleaching years, defined as years with greater than 8 degree heating weeks (DHW) (Gleeson and Strong 1995), expected in a decade at $\sim 0.1^\circ$ resolution throughout the current century. These projections were calculated from The Geophysical Fluid Dynamics Laboratory (GFDL) Modular Ocean Model version 4.1 (MOM4.1: Griffies et al. 2004), sensu van Hooidonk et al. (2015). The second is a coral larval dispersal and connectivity model for *Orbicella annularis* covering the same region (see Holstein et al. 2014) and which includes 3,103 64 km² gridded polygons to represent coral reef habitat

patches. The density of *O. annularis* within these patches was assumed to be homogenous throughout the model domain and the amount of reef (%area) within each polygon (determined from Andrefouet & Guzman 2004) was used to approximate the available *O. annularis* habitat area within a patch. Virtual larvae were allowed to disperse from each habitat patch in 5 yr of three-dimensional currents obtained from three nested hydrodynamic models, all based in the community code of the Hybrid Coordinate Ocean Model (HYCOM; Bleck 2002), including Global (HYCOM-Global, 1/12°), Gulf of Mexico (GoM-HYCOM, 1/25°), and Florida Keys (FKeyS-HYCOM, 1/100°, Kourafalou & Kang (2012)) models.

The output of the dispersal model used to build the numerical metapopulation model was $3,103 \times 3,103$ matrices describing the mean probability of larval arrival from any patch (*i*) to any other patch (*j*). These probabilities were averaged across 5 yr of simulation time. The dispersal model included adult spawning times, the time to larval competency (first ability to settle), the maximum pelagic larval duration, larval mortality and larval buoyancy characteristics. Further information is provided in the supplementary material (Table S1-S3), and in Holstein et al. (2014). Thermal projections were interpolated for each decade onto a 64 km² grid to correspond spatially with the output from the coral dispersal and connectivity model.

The initial connectivity probability matrix, *D*, describes the mean probability of larval dispersal connection (probability of arrival) between any two patches. *D* was projected in time over each decade of the thermal projection model, and connection probabilities were influenced by the habitability of both source and sink patches, to approximate demographic connectivity matrices (Hastings and Botsford 2006) for *O. annularis* over the next eight decades. The demographics of most corals, including *O. annularis*, within a given reef are not well-understood beyond simple size-class distributions or broad estimates of rates of recruitment. Thus, in order to build our demographic model, and approximate thresholds that describe in what circumstances an *O. annularis* sub-population will collapse, we utilized the Beverton–Holt function to establish a range of proportional patch coral cover below which local populations would be expected to collapse (sensu Garavelli et al. 2018). Lifetime egg production (*LEP*) is a demographic parameter important for understanding both local patch persistence and a patch's contributions to migration in a metapopulation network (O'Farrell and Botsford 2005; White 2010). However, *LEP* is largely unknown for corals, and thus, we have chosen to express *LEP* as the fraction of a theoretical maximum lifetime egg production assuming no thermal stress, *FLEP* (White et al. 2010b; Garavelli et al. 2018). Similarly, there are no known estimates of the

stock-recruitment relationships for any coral, and so we used a range of values of (the slope at the origin of the stock-recruitment curve at low population density, sensu White (2010)) to test a range of critically low coral cover values at which a local population would collapse (*FLEP_{crit}*) (Sissenwine and Shepherd 1987). To do so, we have followed the methods of White (2010) and set $\lambda_{crit} = 1/(FLEP_{crit} \times \lambda_D)$. λ_D is the leading eigenvalue of the connectivity probability matrix *D*. Values of *FLEP_{crit}* tested were 0.01, 0.05, 0.10, 0.15 and 0.20 (1–20% of maximum *LEP*). We consider *FLEP* and proportional “coral area” to be interchangeable quantities.

Metapopulation persistence was then estimated by calculating a demographic connectivity matrix, *C*, from each patch, *i*, to any other patch, *j*, at each decadal timestep, *t*:

$$C_{i,j} = A_i D_{i,j} FLEP_i \alpha_{crit} \times (1 - V_{t,i}) \times (1 - V_{t,j})$$

where *A_i* is the proportional reef area of production patch and *V_t* is a vector containing the annual thermal vulnerability of each patch at each decadal time step. These thermal vulnerabilities are extracted from datasets published in van Hooidonk et al. (2015) which describe the expected annual bleaching events at each location per decade. These decadal vulnerabilities have been divided by 10 and can be interpreted as the probability of annual bleaching in each decade.

Thermal stress thus affected not only population egg production (a theoretical maximum was scaled by $1 - V_{t,i}$), but also settlement and recruitment (incoming connectivity probabilities were scaled by $1 - V_{t,j}$). It was assumed that annual bleaching over a decade ($V_{t,i} = 1$) would result in zero connectivity to or from the affected patch due to mortality, energy limitations (Grottoli et al. 2014), and/or collapsed reproductive synchrony (Shlesinger and Loya 2019). Any $V_t = 1$ should be interpreted as an extirpated local population that does not support coral recruitment. Thus, the effect of *V_t* on a local patch's habitat quality can be approximated by an exponentially decreasing decay function (Fig. 1), influenced by a loss of local adults (egg producers) and by a collapse of the local recruitment environment. The metapopulation was considered persistent in a given decade if any patch was expected to be persistent, or if the leading eigenvalue, $\lambda_{C,t} \geq 1$ (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001; Hastings and Botsford 2006).

As thermal stress reduces connectivity, the metapopulation may fragment into separate isolated metapopulations or populations. These were found in *C_t* by searching for strongly connected components (SSCs), within which all potential directional connections between patches were realized (even if over multiple “stepping stone” connections). If found, the persistence of each SSC was assessed by subsetting *C_t* into sub-matrices (*C_{t,SSC,n}*), and again

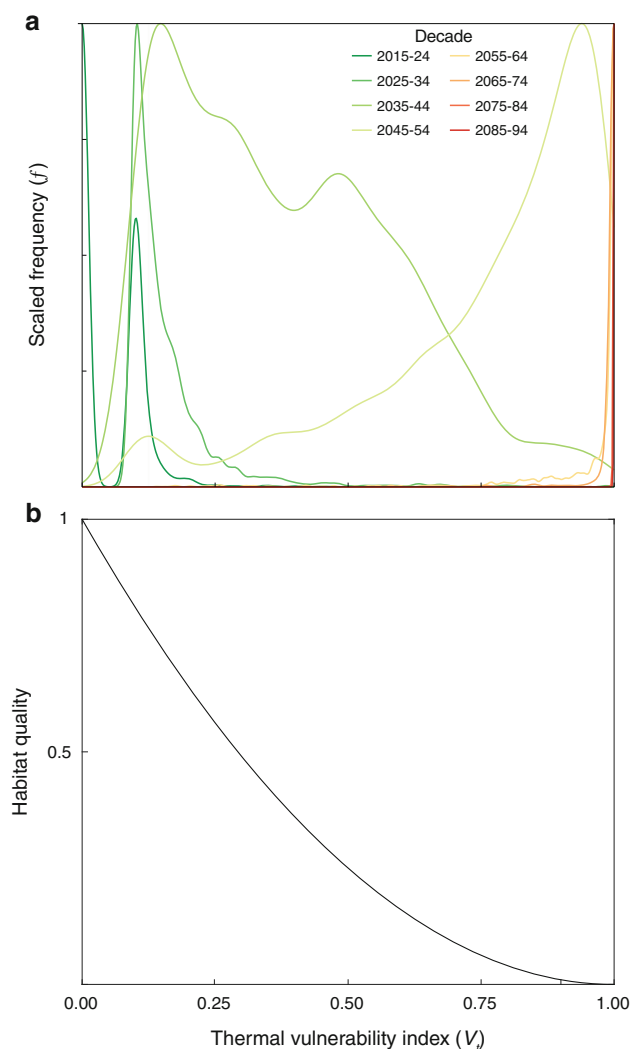


Fig. 1 Distributions of predicted Caribbean coral thermal stress and the resulting effect of thermal vulnerability on the model's estimation of habitat quality. **a**) Decadal coral habitat thermal vulnerability (V_t) frequency distribution kernels (sensu Maynard et al. 2015; van Hooijdonk et al. 2015), scaled for interpretation. Each kernel (indicated by color) indicates the frequency distribution of annual bleaching vulnerability (V_t) across the Caribbean in a given decade. Note that V_t is scaled between 0 and 1, where 1 indicates 10 bleaching years in a decade. **b**) An approximation of the effect of thermal stress (expressed as V_t) on habitat quality in the model, scaled by thermal stress at both larval production and settlement habitat. For simplicity, the curve assumes larvae are produced and settle within the same habitat patch

assessing if the leading eigenvalue of each SCC $\lambda_{C,T,SCC,n} \geq 1$. In order to identify patches that inordinately support connectivity and persistence, in each decade an eigenvector-like measure, patch PageRank centrality (Page et al. 1999) was estimated for each node in each decadal time step using MATLAB software ($\sim \lambda_{C,T,i}$). There are many available centrality measures to describe the relative influence or “importance” of a patch on or to its metapopulation network. The most obvious to use when

discussing persistence (as measured using the leading eigenvalue of the connectivity matrix) may be eigenvector centrality, which should identify nodes (patches) that most contribute to the eigenvalue. However, in directed and asymmetric networks like the ones analyzed here, eigenvector centrality is difficult or impossible to calculate. Thus, we have opted to utilize PageRank centrality, which provides an eigenvector-like measure that in undirected networks is equivalent to eigenvector centrality, and a reliable measure in directed networks (Page et al. 1999).

Results

Metapopulation persistence ($\lambda_{C,i}$) predictably declines as thermal stress increases throughout the century, and the rate of that decline depends on the minimum coral cover that will allow local patches to remain persistent ($FLEP_{crit}$) (Fig. 2). This decline begins to manifest mid-century and falls precipitously as thermal stress becomes extreme late in the century, corresponding to a basin-wide shift in the distribution and extremity of thermal stress (Fig. 1A). All $FLEP_{crit}$ tested, from 1 to 20% maximum coral cover, resulted in collapsed metapopulations by 2075. If coral $FLEP_{crit}$ is as high as 0.20, the model predicts that metapopulation collapse will begin in the current decade. (High $FLEP_{crit}$ implies a low barrier to local population

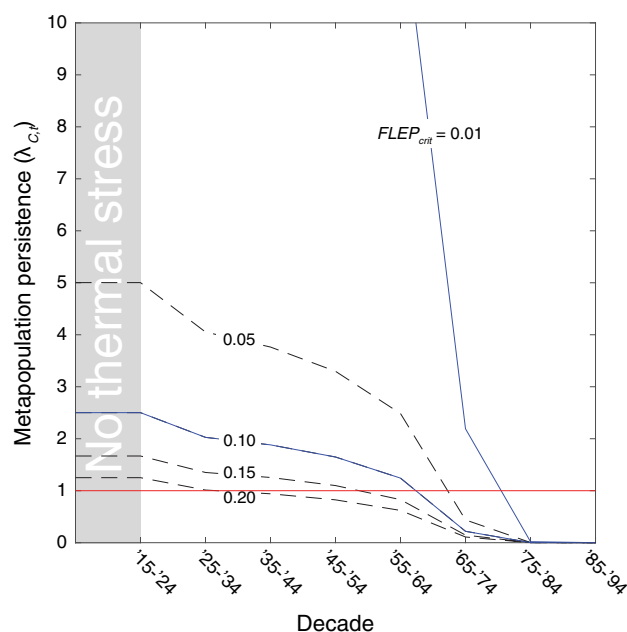


Fig. 2 Predicted changes in metapopulation persistence due to increasing thermal stress and loss of connectivity, according to the minimum coral cover required for local population persistence ($FLEP_{crit}$). The minimum $FLEPs$ used in Fig. 3 & 4 ($FLEP_{crit} = [0.01, 0.10]$) are shown in blue. A red line indicates when and where $\lambda_{C,i}$ falls below 1

collapse.) $FLEP_{crit}$ lower than 0.10 staves off collapse until the second half of the century. Even a very low $FLEP_{crit}$, which assumes that local coral populations are persistent at 1% of their maximum coral cover, would result in shrinking non-persistent metapopulations by the last few decades of the century.

Extreme thermal stress effectively eliminates population connectivity in the model by the end of the century due to severe reductions in habitat quality metapopulation-wide (Fig. 3 and 4). A large regional metapopulation that encompasses most of the Caribbean Sea begins to fragment near the middle of the century (Fig. 3 and 4). The pattern of fragmentation is independent of $FLEP_{crit}$ and is determined by the spatial distribution of extremes in V_t . V_t approaching 1 eliminates migration and connectivity, and thermal refuges with lower V_t support fragmented SCCs. The largest SCC includes the Greater Antilles, Florida Keys, and Bahamas, with smaller enclave metapopulations distributed throughout the Caribbean, centered around thermal refuges (patches that have lower-than-mean V_t). The most persistent of these enclaves is predicted to occur off the coasts of Colombia and Panama. The locations of thermal refuges (lower-than-mean V_t) in the fourth decade of the model (2045–2054) are particularly useful in predicting the locations of SCCs in the following decade (Fig. 3 and 4).

The persistence of newly fragmented metapopulations (SCCs) depends on $FLEP_{crit}$, with lower $FLEP_{crit}$ leading to stronger connectivity within SCCs and greater persistence at each time step (Fig. 3 & 4). Regardless of $FLEP_{crit}$, SCCs continue to shrink and fragment as thermal stress increases throughout the remainder of the century, and the fates of *O. annularis* metapopulations with different $FLEP_{crit}$ converge in the last two decades (Fig. 2, 3 & 4).

Thermal refuges begin to disproportionately support metapopulation persistence in the fourth decade of the simulation (Fig. 5), and the spatial distribution of patch PageRank centrality ($\sim \lambda_{C,t}$) is consistent between metapopulations with different $FLEP_{crit}$ (Fig. 3 and 4). Patches that have lower-than-mean decadal thermal vulnerability ($\bar{V}_t$) have disproportionately large relative PageRank centrality ($\sim \lambda_{C,t,i}$), especially as thermal stress begins to make some patches inhospitable (Fig. 5). As thermal stress becomes more extreme near the end of the decade, thermal refuges become isolated, and connectivity dissolves.

Discussion

Here, we have demonstrated that the Caribbean metapopulation of the major reef-building coral *O. annularis* may be in serious jeopardy without major changes to the

trajectory of climate change by the end of the next century. The coral's network of connected sub-populations in the Caribbean will be prone to extreme fragmentation and extinction risk, with trends that depend on the spatial distribution of thermal refuges and network connectivity. The main findings—that thermal stress fragments the metapopulation and reduces persistence—are an obvious one based on the model formulation. The results that are potentially of greater interest are patterns of this fragmentation over space and time, and how these patterns change (or do not) with different assumptions regarding local coral demographic thresholds. The fact that our model predicts coral declines throughout the century corroborates those of countless recent studies (e.g., Pandolfi et al. 2003; Carpenter et al. 2008; Descombes et al. 2015), but the metapopulation context provided here adds considerable spatial and temporal granularity to understand and potentially mitigate the risk of climate changes to a coral's persistence. It should be noted clearly that this model focuses on only one coral reef stressor, sea surface temperature, among many climate and anthropogenic stressors that are known to be synergistic in their deleterious effects on corals and coral reefs (Nyström et al. 2000). Thus, this model provides context to understand the spatial and temporal influence of thermal stress on the metapopulation fragmentation of a coral, and the potential to extend the current model with additional environmental or biological datasets is considerable.

At what point does a local coral population collapse? Although there is evidence of local near-loss or extirpation of coral species following perturbations like storms (Adjeroud et al. 2002), outbreaks of coral predators (Kayal et al. 2012), or thermal stress (Glynn and de Weerd 1991; Razak and Hoeksema 2003; Adjeroud et al. 2009; Glynn 2011), population collapse due to low adult abundance or cover is not well documented or understood. Further, it is likely dependent on the severity and periodicity of disturbance (Riegl et al. 2018). For example, frequent disturbance-driven losses of highly fecund large size-classes of *Acropora downingi*, and the simultaneous loss of connectivity due to thermal stress was predicted to cause recruitment failures both locally and across a metapopulation in the Arabian/Persian Gulf (Riegl et al. 2018). It is not currently clear to what extent coral cover can become denuded within a coral reef before populations can no longer persist, and this threshold may be population-specific. The threshold of local egg production below which a coral population can no longer sustain itself (assuming no immigration) is an important component of our metapopulation model's assumptions and is expressed as a fraction of a theoretical maximum. This fraction can be thought of as the minimum fraction of lifetime egg production that must be maintained after or during thermal stress, or more

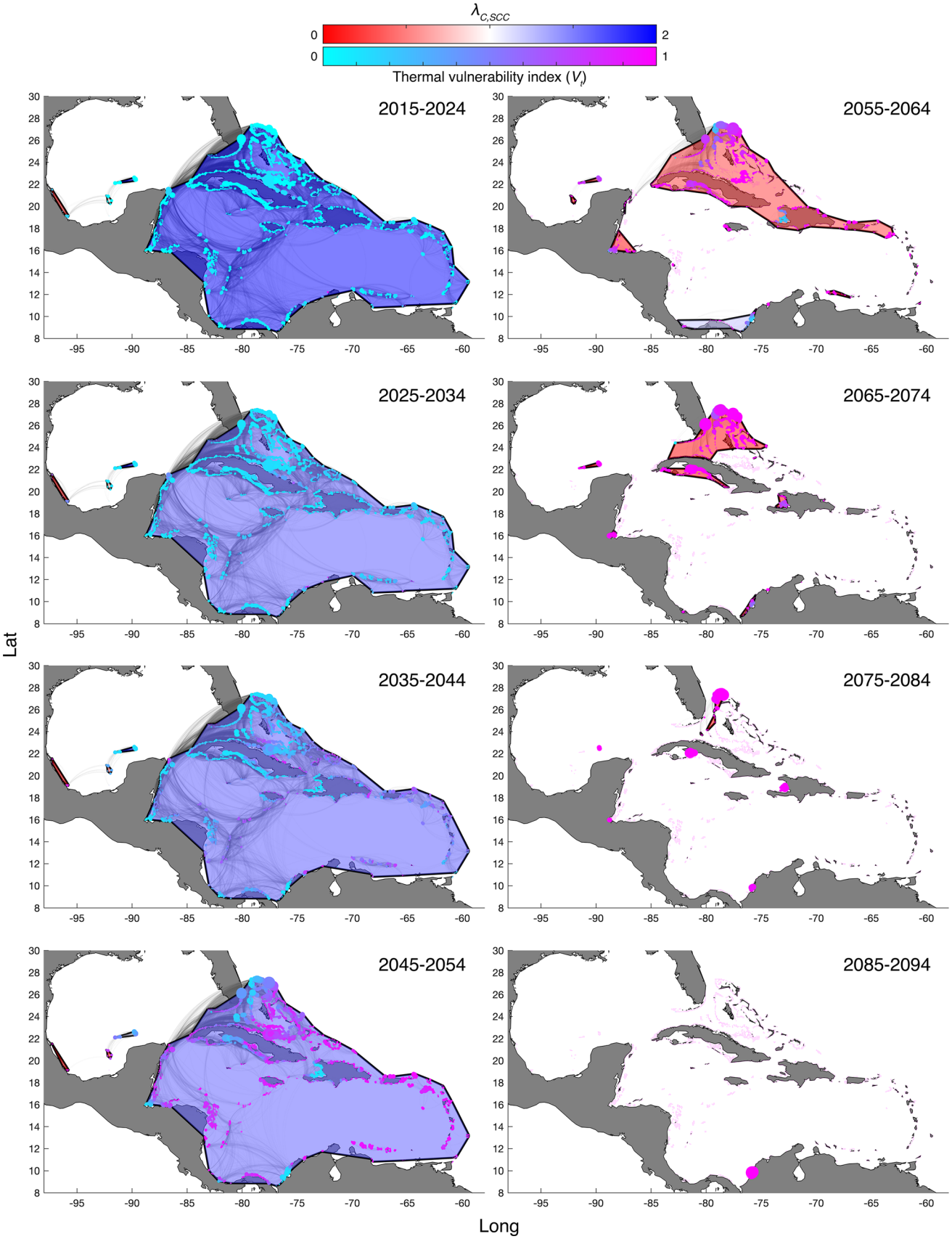


Fig. 3 Maps detailing *Orbicella annularis* metapopulation decline due to thermal stress over a century of predicted warming, including patch-specific thermal vulnerability (V_p , node color), patch connectivity (edges), patch PageRank centrality ($\sim \lambda_{C,i}$, node size), and the boundaries and persistence ($\lambda_{C,SCC}$, shaded color) of each strongly connected component (SCC) during each decade assuming a minimum $FLEP_{crit}$ of 0.10. An identical data representation using $FLEP_{crit}$ of 0.01 is shown in Fig. 4. Connection direction is represented by clockwise arcs

simply, as the fraction of maximum coral cover (tissue area) that must remain following that thermal stress for the population to persist (if we assume that egg production per polyp in adults is consistent regardless of colony size, and thus, colony egg production scales linearly with coral tissue area, e.g., Hall and Hughes 1996; Sakai 1998; Holstein et al. 2015, Alvarez-Noriega et al. 2016). These coral loss thresholds determine in what decade the *O. annularis* metapopulation collapses in our metapopulation model, with lower thresholds—or greater tolerance to loss in abundance or coral cover – delaying collapse by decades.

Estimations from the early 2000s were that Caribbean scleractinian coral cover was less than $\sim 20\%$ of 1970s levels (Gardner et al. 2003). Judging by estimates of annual rates of decline (Côté et al. 2005), contemporary coral cover is likely far less. Whether these perturbed communities are locally persistent is not known, which compromises our ability to make local and metapopulation predictions of persistence. Complicating this is that some corals, particularly branching forms, can be highly clonal within a population. While this may result in seemingly persistent local populations (which appear to have high population growth due to fragmentation), these populations may also carry an “extinction debt,” owing to a reduced capacity for sexual propagation and reduced genetic diversity (Honney and Bossuyt 2005; Baums et al. 2006). Coral reef decline is also often characterized by non-linear shifts in stable states between coral dominance and algal dominance (Scheffer et al. 2001). Algal dominance can limit the recruitment of new corals (Hughes et al. 2007) and low calcium carbonate accretion associated with low coral cover can result in the erosion of reef framework, further limiting the recruitment and recovery of coral-dominated communities (Perry et al. 2013). These non-linear dynamics at low coral densities have not been explicitly parameterized in the current metapopulation model, and if shifts to macroalgal dominated states are expected at $FLEPs$ greater than parameterized here, the result could be even more rapid metapopulation fragmentation.

The model results suggest that coral metapopulation fragmentation may be major even if local populations are extremely resistant to coral loss. No matter the $FLEP_{crit}$

chosen, the pattern and form of metapopulation decline in the current model is the same, due to the distribution of thermal stress (V_t), its influence on habitat quality, and patterns of connectivity. The regional metapopulation fragments in the middle of the century, a major component is centered in the Greater Antilles, Florida Keys and Bahamas, and smaller persistent enclaves are centered around thermal refuges, before ultimate collapse. These include the reefs of Colombia, Panama, Honduras, Guatemala, and Belize. If thermal stress is not reduced, the model predicts dire outcomes. However, the existence of thermal refuges even late in the century and the tendency of these refuges to support $SCCs$ through “propagule rain” (Gotelli 1991) could help resource managers in the design and implementation of effective mitigations. Should mitigations exist that could bolster these populations (restoration, assisted evolution, reduction of synergistic stressors, shading, assisted reproduction, assisted recruitment, etc.) these locations may be good candidates due to their thermal environment and their connectivity. Further, although species have different dispersal capabilities and environmental requirements, these patterns may be indicative of the patterns of fragmentation for other species that are similarly sensitive to thermal stress and/or have similar life histories.

While the model predicts shrinking, non-persistent metapopulations near the end of the century in every $FLEP_{crit}$ scenario, the time at which the metapopulation switches from persistent to non-persistent equilibria is pushed to a later date when local populations can tolerate greater coral losses. Not only does this stress the importance of understanding the local demographics of perturbed coral reefs, but it also suggests that local mitigations that either enhance local coral cover or enhance sexual propagation at low cover have the potential to slow the rate of metapopulation-wide decline. These mitigations could potentially keep local populations from collapsing (coral cover $> FLEP_{crit}$) and/or locally reduce $FLEP_{crit}$, respectively. This is intuitive, but models such as the one described here can provide conservation practitioners with meaningful local and regional goals. For example, spatially targeted mitigations to reduce common coral stressors like excess terrestrial nutrients or sedimentation, or meaningful coral restorations that maintain functioning local populations, may buy decades of critical time toward the middle and end of the current century and allow re-expansion of the metapopulation assuming climate change is mitigated. A similar effect would be achieved if populations could better tolerate thermal stress.

Not all populations contribute equally to persistence throughout the century. Although we caution that these results carry many assumptions regarding the distribution of thermal stress (sensu van Hooidonk et al. 2015), local

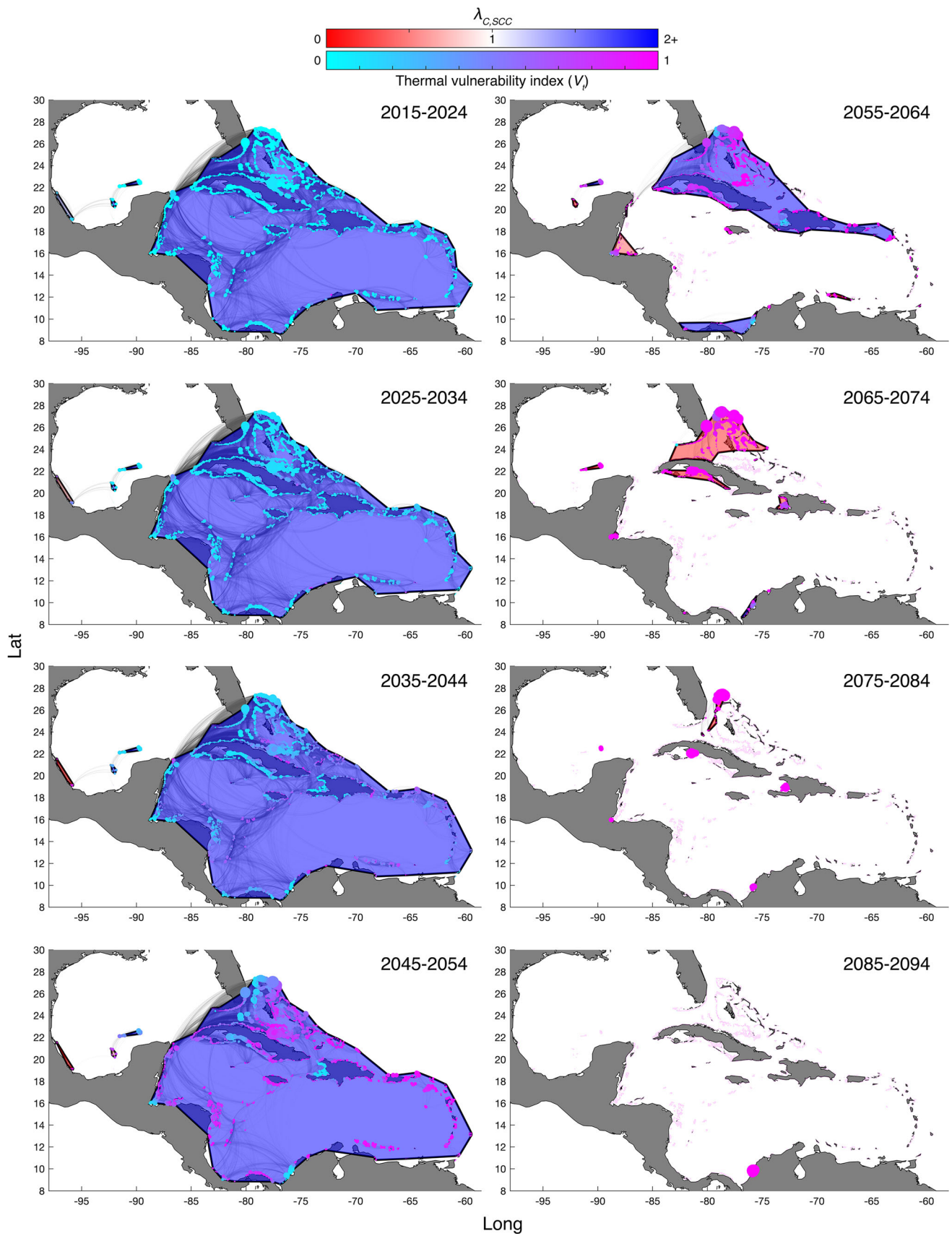


Fig. 4 Maps detailing *Orbicella annularis* metapopulation decline due to thermal stress over a century of predicted warming, including patch-specific thermal vulnerability (V_t , node color), patch connectivity (edges), patch PageRank centrality ($\sim \lambda_{C,i}$, node size), and the boundaries and persistence ($\lambda_{C,SCC}$, shaded color) of each strongly connected component (SCC) during each decade assuming a minimum $FLEP_{crit}$ 0.01. Connection direction is represented by clockwise arcs. Note that the maximum $\lambda_{C,SCC}$ is greater than 2, but the color scale of Fig. 3 is preserved for the sake of comparison

habitat quality, and the dispersal of coral propagules (sensu Holstein et al. 2014), this model has identified habitat patches that behave as linchpins to metapopulation persistence through time. Well-connected refuge habitats appear to be the most critical. This corroborates findings that in metapopulations experiencing perturbation, network centrality becomes spatially condensed (Grilli et al. 2015), and refuges become essential to effectively resisting extinction (Heard et al. 2015). However, isolated “oases” that do not support demographic exchanges with neighboring habitats have limited potential to support metapopulation persistence (Thomas et al. 2001; Moilanen and Nieminen 2002) and thus, the connectedness of both natural and artificial refuges (i.e., preserves and protected areas) has implications for extinction risk and for conservation planning. Our findings show that refuge habitat patches become disproportionately important to maintaining metapopulation persistence when thermal perturbation is

moderate in mid-century; however, by the end of the century, when perturbation is predicted to be so extreme it disrupts network connectivity, isolated refuges cannot support continued persistence. That said, our model does not preclude the potential for re-invasion of habitats from these refuges—or from unknown refuges—if and when metapopulation-wide conditions improve (Ovaskainen and Hanski 2001). Notably, coral populations can and do persist without annual recruitment. Coral individuals may also persist on a reef without recruitment even when population tissue area has fallen below $FLEP_{crit}$. Thus, it is possible that isolated reefs remain persistent, but also that seemingly “persistent” coral populations are effectively extirpated.

If climate change conditions are chronic, adaptation will likely be necessary for metapopulation persistence (Hughes et al. 2003; Baker et al. 2004; Grottoli et al. 2014). Correspondingly, refuge habitats removed from perturbation may not provide effective evolutionary refuge (Smith et al. 2016), as populations are not sufficiently exposed to selective pressures. Neither the potential for adaptation nor any realistic spatial heterogeneity in that potential were included in the model described here. Adaptation to thermal stress could reduce the vulnerability of populations or reduce the minimum coral cover necessary to persist locally, both of which would stave off or reduce the rate of habitat fragmentation that could ultimately lead to metapopulation collapse.

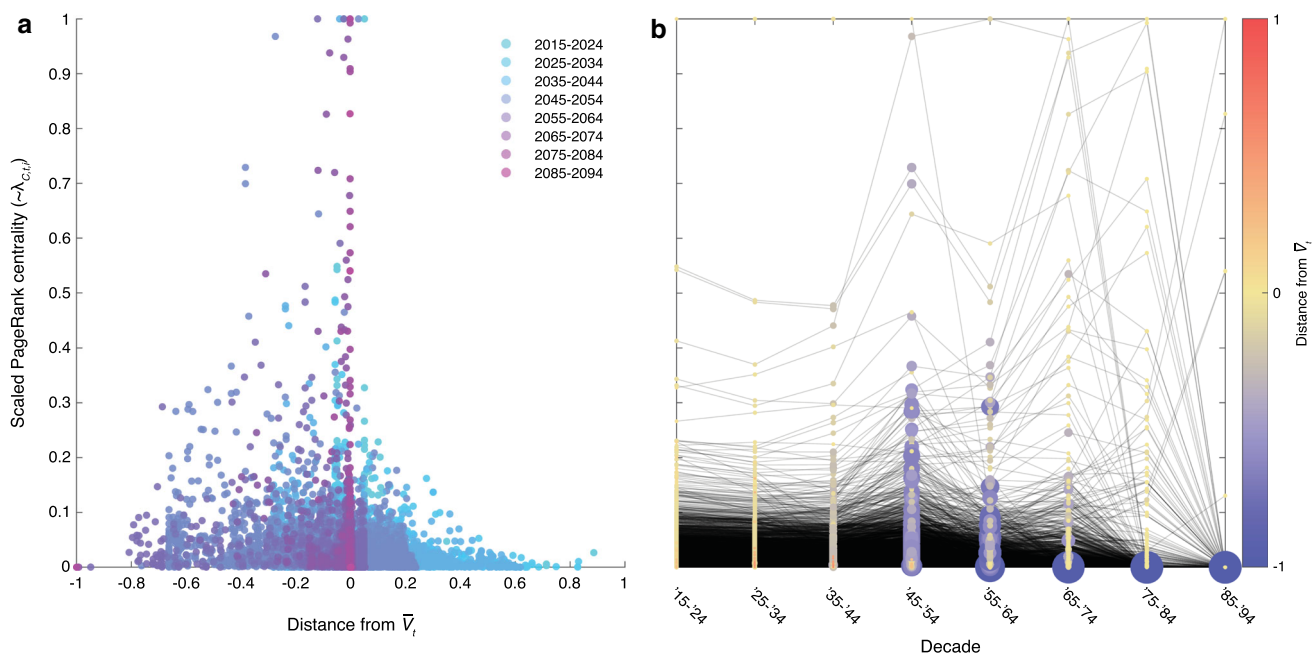


Fig. 5 Changes in relative *Orbicella annularis* patch PageRank centrality with increasing metapopulation-scale perturbation, shown according to **a**) the patch-specific thermal vulnerability (distance from $\bar{V}_t$) and **b**) by decade. Resistant patches, or refuges, have negative

distances from $\bar{V}_t$. $\sim \lambda_{C,i}$ is scaled to 1 in each decade. In **b**), lines connect the same patch through decadal timesteps and points are both colored and scaled by distance from $\bar{V}_t$

Changes in coastal and oceanic hydrodynamics are expected throughout the next century due to altered balances in atmospheric and sea surface warming (Bindoff et al. 2007). Predicting these changes is a developing science, and thus, this important feature of future larval dispersal and connectivity was not integrated into the current model. Along with changing surface currents, the physiology of dispersing larvae is also likely to change with increasing temperature (Munday et al. 2009) and favor shorter dispersal durations and larval retention (Figueirido et al. 2014), rather than migration. These changes to larval dispersal and connectivity are expected to further increase coral population fragmentation (Munday et al. 2009), but may also lead to enhanced local larval retention (Figueirido et al. 2014), which could bolster local populations for a time. However, in a changing environment with increasing perturbations to hospitable conditions on coral reefs, this increasing habitat isolation is likely to have negative effects on species persistence (Opdam and Wascher 2004).

Crucially, although the current model suggests a dramatic decline in *O. annularis* metapopulation persistence in the middle of the century, the metapopulation persistence predictions for each decade are temporally independent from each other, and highly dependent on predicted thermal stress. What this implies is that the persistent metapopulation(s) predicted around mid-century in most scenarios would remain persistent, or even expand, if thermal stress does not further increase or is reduced. This is a strong argument for immediate global reductions in carbon emissions to avoid the extreme heating scenarios predicted for the end of the current century, and this model provides an example of an ecological target for those initiatives.

Although this simulation study focused on thermal stress, coral and other marine metapopulations face more than a single challenge to their persistence, and these challenges will interact in complex ways (Nyström et al. 2000) and be species-specific (Loya et al. 2001; Grottoli et al. 2014; Shlesinger and Loya 2019). Thus, these *O. annularis* metapopulation simulations are speculative, rather than truly predictive of the future of *O. annularis* or of coral reefs in general. While these results warn of Caribbean *O. annularis* metapopulation extinction by the end of the century, our results also suggest that carefully targeted conservation, the identification and protection of natural refuges and, of course, a global effort to reduce carbon emissions and warming, have the potential to mitigate extinction risk despite dire environmental predictions. The protection of coral reefs from climate changes is still within our grasp—and modeling exercises that integrate spatial projections of the future environment with biological and population models provide a scaffold for addressing this multifaceted environmental problem.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00338-022-02252-9>.

Acknowledgements The authors thank Sarah H. Groves and the reviewers for constructive manuscript comments, and Lysel Garavelli for discussion of metapopulation model construction.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data availability The datasets and software code generated during and/or analyzed during the current study are available in a Github repository, https://github.com/seascapelab/CoralMetapop_01.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Adjeroud M, Augustin D, Galzin R, Salvat B (2002) Natural disturbances and interannual variability of coral reef communities on the outer slope of Tiahura (Moorea, French Polynesia): 1991 to 1997. *Mar Ecol Prog Ser* 237:121–131
- Adjeroud M, Michonneau F, Edmunds PJ, Chancerelle Y, de Loma TL, Penin L, Thibaut L, Vidal-Dupiol J, Salvat B, Galzin R (2009) Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs* 28:775–780
- Alvarez-Noriega M, Baird AH, Dornelas M, Madin JS, Cumbo VR, Connolly SR (2016) Fecundity and the demographic strategies of coral morphologies. *Ecology* 97:3485–3493
- Andreouet S, Guzman HM (2004) Coral reef distribution, status and geomorphology-biodiversity relationship in Kuna Yala (San Blas) archipelago, Caribbean Panama. *Coral Reefs* 24:31–42
- Baker AC, Starger CJ, McClanahan TR, Glynn PW (2004) Corals' adaptive response to climate change. *Nature* 430:741–741
- Baums IB, Miller MQ, Hellberg ME (2006) Geographic variation in clonal structure in a reef-building Caribbean coral, *Acropora palmata*. *Ecol Monogr* 76:503–519
- Beger M, Linke S, Watts M, Game E, Treml E, Ball I, Possingham HP (2010) Incorporating asymmetric connectivity into spatial decision making for conservation. *Conserv Lett* 3:359–368
- Bindoff NL, Willebrand J, Artale V, Cazenave A, Gregory J, Gulev S, Hanawa K, Quéré C Le, Levitus S, Nojiri Y, Shum CK, Talley LD, Unnikrishnan A (2007) Observations: Oceanic Climate Change and Sea Level. In: Solomon S, Qin D, Manning M., Chen Z., Marquis M., Averyt K.B., Tignor M., Miller H.L. (eds) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge

- University Press, Cambridge, United Kingdom and New York, NY, USA
- Bode M, Burrage K, Possingham HP (2008) Using complex network metrics to predict the persistence of metapopulations with asymmetric connectivity patterns. *Ecol Modell* 214:201–209
- Botsford LW, White JW, Coffroth M, Paris CB, Planes S, Shearer TL, Thorrold SR, Jones GP, (2009) Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* 28:327–337
- Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E (2008) One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts. *Science* 321:560–563
- Costanza R, de Groot R, Braat L, Kubiszewski I, Fioramonti L, Sutton P, Farber S, Grasso M (2017) Twenty years of ecosystem services: How far have we come and how far do we still need to go? *Ecosyst Serv* 28:1–16
- Côté I, Gill J, Gardner T, Watkinson A (2005) Measuring coral reef decline through meta-analyses. *Philos Trans R Soc B Biol Sci* 360:385–395
- Descombes P, Wisz MS, Leprieux F, Parravicini V, Heine C, Olsen SM, Swingedouw D, Kulbicki M, Mouillot D, Pellissier L (2015) Forecasted coral reef decline in marine biodiversity hotspots under climate change. *Glob Chang Biol* 21:2479–2487
- Figueiredo J, Baird AH, Harii A, Connolly SR (2014) Increased local retention of reef coral larvae as a result of ocean warming. *Nat Clim Chang* 4:498–502
- Garavelli L, White JW, Chollett I, Chérubin LM (2018) Population models reveal unexpected patterns of local persistence despite widespread larval dispersal in a highly exploited species. *Conserv Lett* 11(5):e12567
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Gleeson MW, Strong AE (1995) Applying MCSST to coral reef bleaching. *Adv Sp Res* 16:151–154
- Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. *Glob Chang Biol* 1:177–509
- Glynn PW (2011) In Tandem Reef Coral and Cryptic Metazoan Declines and Extinctions. *Bull Mar Sci* 87:767–794
- Glynn PW, de Weerd WH (1991) Elimination of Two Reef-Building Hydrocorals Following the 1982–83 El Niño Warming Event. *Science* 253:69–71
- Gotelli NJ (1991) Metapopulation models: the rescue effect, the propagule rain and the core-satellite hypothesis. *Am Nat* 138:768–776
- Griffies SM, Winton M, Samuels BL (2004) The Large and Yeager (2004) dataset and CORE. NOAA Geophysical Fluid Dynamics Laboratory 1–9
- Grilli J, Barabás G, Allesina S (2015) Metapopulation Persistence in Random Fragmented Landscapes. *PLOS Comput Biol* 11(5):e1004251
- Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, McGinley M, Baumann J, Matsui Y (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Glob Chang Biol* 20:3823–3833
- Hall VR, Hughes TP (1996) Reproductive Strategies of Modular Organisms: Comparative Studies of Reef-Building Corals. *Ecology* 77:950
- Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. *Nature* 404:755–758
- Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. *Proc Natl Acad Sci* 103:6067–6072
- Hata T, Madin JS, Cumbo VR, Denny M, Figueiredo J, Harii S, Thomas CJ, Baird AH (2017) Coral larvae are poor swimmers and require fine-scale reef structure to settle. *Sci Rep* 7:2249
- Heard GW, Thomas CD, Hodgson J, a., Scroggie MP, Ramsey DSL, Clemann N, (2015) Refugia and connectivity sustain amphibian metapopulations afflicted by disease. *Ecol Lett* 18:853–863
- Holstein D, Paris C, Mumby P (2014) Consistency and inconsistency in multispecies population network dynamics of coral reef ecosystems. *Mar Ecol Prog Ser* 499:1–18
- Holstein DM, Paris CB, Vaz AC, Smith TB (2016) Modeling vertical coral connectivity and mesophotic refugia. *Coral Reefs* 35:23–37
- Honnay O and Bossuyt B, (2005) Prolonged clonal growth: escape route or route to extinction? *Oikos* 108:427–432
- Hughes TP (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science* 301:929–933
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. *Curr Biol* 17:360–365
- Kayal M, Vercelloni J, Lison de Loma T, Bosserelle P, Chancerelle Y, Geoffroy S, Stievenart C, Michonneau F, Penin L, Planes S, Adjerdou M (2012) Predator Crown-of-Thorns Starfish (*Acanthaster planci*) Outbreak, Mass Mortality of Corals and Cascading Effects on Reef Fish and Benthic Communities. *PLOS ONE* 7(10):e47363
- Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob Ecol Biogeogr* 21:393–404
- Keppel G, Wardell-Johnson GWR, Refugial capacity defines holdouts, microrefugia and stepping-stones: a response to Hannah, et al (2015) *Trends Ecol Evol* 30:233–234
- Kininmonth S, Beger M, Bode M, Peterson E, Adams VM, Dorfman D, Brumbaugh DR, Possingham HP (2011) Dispersal connectivity and reserve selection for marine conservation. *Ecol Modell* 222:1272–1282
- Kourafalou VH, Kang H (2012) Florida Current meandering and evolution of cyclonic eddies along the Florida Keys Reef Tract: Are they interconnected? *J Geophys Res Ocean* 117:1–25
- Limer BD, Bloomberg J, Holstein DM (2020) The Influence of Eddies on Coral Larval Retention in the Flower Garden Banks. *Front Mar Sci* 7:1–16
- Logan CA, Dunne JP, Eakin CM, Donner SD (2014) Incorporating adaptive responses into future projections of coral bleaching. *Glob Chang Biol* 20:125–139
- Loya Y, Sakai K, Nakano Y, Van WR (2001) Coral bleaching: the winners and the losers. *Ecology* 4:122–131
- Maynard J, van Hooidonk R, Eakin CM, Puotinen M, Garren M, Williams G, Heron SF, Lamb J, Weil E, Willis B, Harvell CD (2015) Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. *Nat Clim Chang* 5:688–694
- Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. *Ecol Econ* 29:215–233
- Moilanen A, Nieminen M (2002) Simple Connectivity Measures in Spatial Ecology. *Ecology* 83:1131–1145
- Mumby PJ, Elliott IA, Eakin CM, Skirving W, Paris CB, Edwards HJ, Enriquez S, Iglesias-Prieto R, Cherubin LM, Stevens JR (2011) Reserve design for uncertain responses of coral reefs to climate change. *Ecol Lett* 14:132–140

- Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. *Coral Reefs* 28:379–395
- Nyström M, Folke C, Moberg F, Nyström M (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- O'Farrell MR, Botsford LW (2005) Estimation of change in lifetime egg production from length frequency data. *Can J Fish Aquat Sci* 62:1626–1639
- Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biol Conserv* 117:285–297
- Ovaskainen O, Hanski I (2001) Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theor Popul Biol* 60:281–302
- Page L, Brin S, Motwani R, Winograd T (1999) The PageRank Citation Ranking: Bringing Order to the Web. Technical Report. Stanford InfoLab
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjørndal K, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC, (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting Coral Reef Futures Under Global Warming and Ocean Acidification. *Science* 333:418–422
- Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ (2013) Caribbean-wide decline in carbonate production threatens coral reef growth. *Nat Commun* 4:1402
- Razak TB, Hoeksema BW (2003) The hydrocoral genus *Millepora* (Hydrozoa: Capitata: Milleporidae) in Indonesia. *Zool Verh* 345:313–336
- Riegl B, Johnston M, Purkis S, Howells E, Burt J, Steiner SCC, Sheppard CRC, Bauman A (2018) Population collapse dynamics in *Acropora downingi*, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. *Glob Chang Biol* 24:2447–2462
- Sakai K (1998) Effect of Colony Size, Polyp Size, and Budding Mode on Egg Production in a Colonial Coral. *Biol Bull* 195:319–325
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596
- Schill SR, Raber GT, Roberts JJ, Treml EA, Brenner J, Halpin PN (2015) No Reef Is an Island: Integrating Coral Reef Connectivity Data into the Design of Regional-Scale Marine Protected Area Networks. *PLoS ONE* 10(12):e0144199
- Shlesinger T, Loya Y (2019) Breakdown in spawning synchrony: A silent threat to coral persistence. *Science* 365:1002–1007
- Sissenwine MP, Shepherd JG (1987) An Alternative Perspective on Recruitment Overfishing and Biological Reference Points. *Can J Fish Aquat Sci* 44:913–918
- Smith TB, Glynn PW, Maté JL, Toth LT, Gyory J (2014) A depth refugium from catastrophic coral bleaching prevents regional extinction. *Ecology* 95:1663–1673
- Smith TB, Gyory J, Brandt ME, Miller WJ, Jossart J, Nemeth RS (2016) Caribbean mesophotic coral ecosystems are unlikely climate change refugia. *Glob Chang Biol* 22:2756–2765
- Steneck RS, Paris CB, Arnold SN, Ablan-Lagman MC, Alcala a. C, Butler MJ, McCook LJ, Russ GR, Sale PF, (2009) Thinking and managing outside the box: coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. *Coral Reefs* 28:367–378
- Szmant AM (1985) The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea Annularis* (Ellis and Solander). *Proc Fifth Int Coral Reef Congr* 4:295–300
- Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger B (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc R Soc London Ser B Biol Sci* 268:1791–1796
- Treml E, a, Roberts JJ, Chao Y, Halpin PN, Possingham HP, Riginos C, (2012) Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. *Integr Comp Biol* 52:525–537
- Treml EA, Halpin PN, Urban DL, Pratson LF (2008) Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landsc Ecol* 23:19–36
- Van Hooidonk R, Maynard JA, Planes S (2013) Temporary refugia for coral reefs in a warming world. *Nat Clim Chang* 3:508–511
- van Hooidonk R, Maynard JA, Liu Y, Lee S-K (2015) Downscaled projections of Caribbean coral bleaching that can inform conservation planning. *Glob Chang Biol* 21:3389–3401
- White JW (2010) Adapting the steepness parameter from stock–recruit curves for use in spatially explicit models. *Fish Res* 102:330–334
- White J, Botsford L, Hastings A, Largier J (2010a) Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal. *Mar Ecol Prog Ser* 398:49–67
- White JW, Botsford LW, Moffitt EA, Fischer DT (2010b) Decision analysis for designing marine protected areas for multiple species with uncertain fishery status. *Ecol Appl* 20:1523–1541
- White WJ, Schroeger J, Drake PT, Edwards CA (2014) The Value of Larval Connectivity Information in the Static Optimization of Marine Reserve Design. *Conserv Lett* 7:533–544

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.