



The projected degradation of subtropical coral assemblages by recurrent thermal stress

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Abstract

1. Subtropical coral assemblages are threatened by similar extreme thermal stress events to their tropical counterparts. Yet, the mid- and long-term thermal stress responses of corals in subtropical environments remain largely unquantified, limiting our capacity to predict their future viability.
2. The annual survival, growth and recruitment of 311 individual corals within the Solitary Islands Marine Park (Australia) was recorded over a 3-year period (2016–2018), including the 2015/2016 thermal stress event. These data were used to parameterise integral projection models quantifying the effect of thermal stress within a subtropical coral assemblage. Stochastic simulations were also applied to evaluate the implications of recurrent thermal stress scenarios predicted by four different Representative Concentration Pathways.
3. We report differential shifts in population growth rates (λ) among coral populations during both stress and non-stress periods, confirming contrasting bleaching responses among taxa. However, even during non-stress periods, the observed dynamics for all taxa were unable to maintain current community composition, highlighting the need for external recruitment sources to support the community structure.
4. Across all coral taxa, projected stochastic growth rates (λ_s) were found to be lowest under higher emissions scenarios. Correspondingly, predicted increases in recurrent thermal stress regimes may accelerate the loss of coral coverage, species diversity and structural complexity within subtropical regions.
5. We suggest that these trends are primarily due to the susceptibility of subtropical specialists and endemic species, such as *Pocillopora aliciae*, to thermal stress. Similarly, the viability of many tropical coral populations at higher latitudes is

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highly dependent on the persistence of up-current tropical systems. As such, the inherent dynamics of subtropical coral populations appear unable to support their future persistence under unprecedented thermal disturbance scenarios.

KEYWORDS

coral reefs, demography, high-latitude, integral projection model, life table response experiment, population dynamics, stochastic projections

1 | INTRODUCTION

Climate change and anthropogenic disturbance are reshaping the structure of biological communities and modifying the global distribution of abiotic regimes (Newman, 2019; Pecl et al., 2017). These disturbances are exposing many organisms to increasingly novel environments to which they are often not adapted (Hoffmann & Sgró, 2011). In coral reef ecosystems, shifts from natural reef systems towards alternative degraded states are becoming commonplace (Graham et al., 2014; Hughes et al., 2003; Pandolfi et al., 2003). Despite comprehensive evidence of climate stress impacting reefs (Hughes et al., 2019; Hughes, Kerry, et al., 2018), we lack the mechanistic understanding to predict how changing environments will affect global coral population dynamics (Edmunds & Riegl, 2020). Thus, it is crucial we define the link between environmental conditions and population performance, and identify drivers enhancing the resilience of corals to future environmental shifts (Benton et al., 2006; Darling & Côté, 2018).

State-based demographic modelling allows for examining whether, which and how the characteristics of individuals reflect on the viability and condition of natural populations (Caswell, 2001; Lefkovitch, 1965). These demographic approaches can therefore quantify the resilience of natural populations following environmental disturbance (Ellner et al., 2016; Kayal et al., 2018). In the 1980s, state-based demographic tools were first used to investigate the relationship between coral size and demographic characteristics, and thereby the varying population-level contributions of individual colonies (see Hughes, 1984; Hughes & Connell, 1987). Demographic approaches applied to corals have since served to identify trends in vital rates that underpin localised population trajectories (Hughes & Tanner, 2000; Precoda et al., 2018; Riegl et al., 2018). However, few coral studies use these models to project the future impacts of changing environmental regimes on the viability of coral populations (Edmunds & Riegl, 2020; but see Kayal et al., 2018). Without simulations that embrace the heterogeneity of coral assemblages, assessments of the future status of global coral populations will lack realism (Edmunds et al., 2014; Madin et al., 2012).

Local environmental regimes, together with physiological limitations, enforce trade-offs within an individual's vital rate characteristics of survival, growth and reproduction (Stearns, 1992). Thus, environmental filtering influences the relative abundance of local populations based on differential abiotic tolerances and increases the prevalence of characteristics best suited to local conditions (Gallego-Fernández & Martínez, 2011). However, demographic characteristics can undergo various adjustments (Jongejans et al., 2010;

Pfister, 1998), and the extent to which organisms can modify their vital rate trade-offs defines the capacity of different populations to exploit new environments and respond to varying conditions (Benton et al., 2006; Tuljapurkar et al., 2009).

Extensive subtropical coral assemblages can be found at latitudes far beyond the typical range of coral reef development (>23.5 Beger et al., 2014; Harriott & Smith, 2002). At higher latitudes, enhanced seasonality, broader spectra in abiotic conditions, a high frequency of storm events, and reduced light availability exposes corals to stronger environmental filtering than their tropical counterparts (Beger et al., 2014; Mizerek et al., 2016; Muir et al., 2015; Sommer et al., 2014, 2017, 2018). Subtropical assemblages, therefore, represent ideal systems for quantifying the mechanistic link between coral dynamics and ecological performance (Camp et al., 2018; Kleypas et al., 1999; Mizerek et al., 2016). Yet, with the impacts of thermal stress becoming increasingly apparent within subtropical communities (Abdo et al., 2012; Celliers & Schleyer, 2002; Goyen et al., 2019; Harrison et al., 2011; Kim et al., 2019), how does the ability of subtropical corals to tolerate natural variability influence their capacity to withstand increasingly frequent acute disturbances?

Many studies have assessed the response of tropical coral assemblages to thermal stress (e.g. Adjeroud et al., 2018; Hughes et al., 2019; Hughes, et al., 2018; Kayal et al., 2018). However, there exist multiple fundamental differences between the dynamics of tropical and subtropical coral species (Baird et al., 2009; Woolsey et al., 2015). Presently, the genus-specific collapse and recovery responses of subtropical corals and their drivers, following thermal stress events, remain largely unknown (Kim et al., 2019). This limited perspective regarding the future viability and condition of subtropical coral communities around the globe is hindering our capacity to predict their future and manage them effectively.

Here, we utilised integral projection models (IPMs; Easterling et al., 2000) and stochastic simulations to examine the impact of recurrent thermal stress on subtropical coral assemblages, providing insight into the potential future trajectories of subtropical coral assemblages. IPMs provide a robust framework for incorporating individual heterogeneity into population-level assessments and projections (Merow et al., 2014). As such, IPMs are ideal for quantifying and simulating population responses to varying environments and gaining insight into the viability of natural populations faced with changing climates (Ellner et al., 2016; Kayal et al., 2018). Thermal stress is expected to reduce the size and condition of different populations, whereas non-stress conditions may allow for recovery and population growth (see Adjeroud et al., 2018). We therefore also

conducted stochastic projections to investigate the effects of future thermal stress patterns, predicted by the different representative concentration pathways (RCPs), on the long-term condition of a subtropical coral assemblage.

2 | MATERIALS AND METHODS

2.1 | Field site description and census design

The Solitary Islands Marine Park (SIMP; -30.3° , 153.143° ; Figure 1a) is located off the coast of New South Wales, Australia. The SIMP consists of rocky coastal islands and shallow benthic communities characterised by a relatively high cover (up to 50%) of scleractinian

corals (Dalton & Roff, 2013). During the 2015/2016 global bleaching event, extensive bleaching occurred throughout subtropical eastern Australia (Kim et al., 2019). Within the SIMP, the extent of bleaching was comparable to that of the Great Barrier Reef (GBR; Hughes et al., 2017).

In April 2016, during the 2015/2016 bleaching period, we set up 31 permanent coral plots across four islands within the SIMP (Figure 1a). Each plot consisted of a numbered tag fixed into an area of bare reef substrate, surrounded by coral colonies (Figure 1b). At each location, plots were placed haphazardly in the coral habitat, at depths between 8 and 11 m to capture the diversity and spatial arrangement of this subtropical coral assemblage. Photographs were used to identify corals within each plot and capture their initial size and position. During these primary surveys, plots were

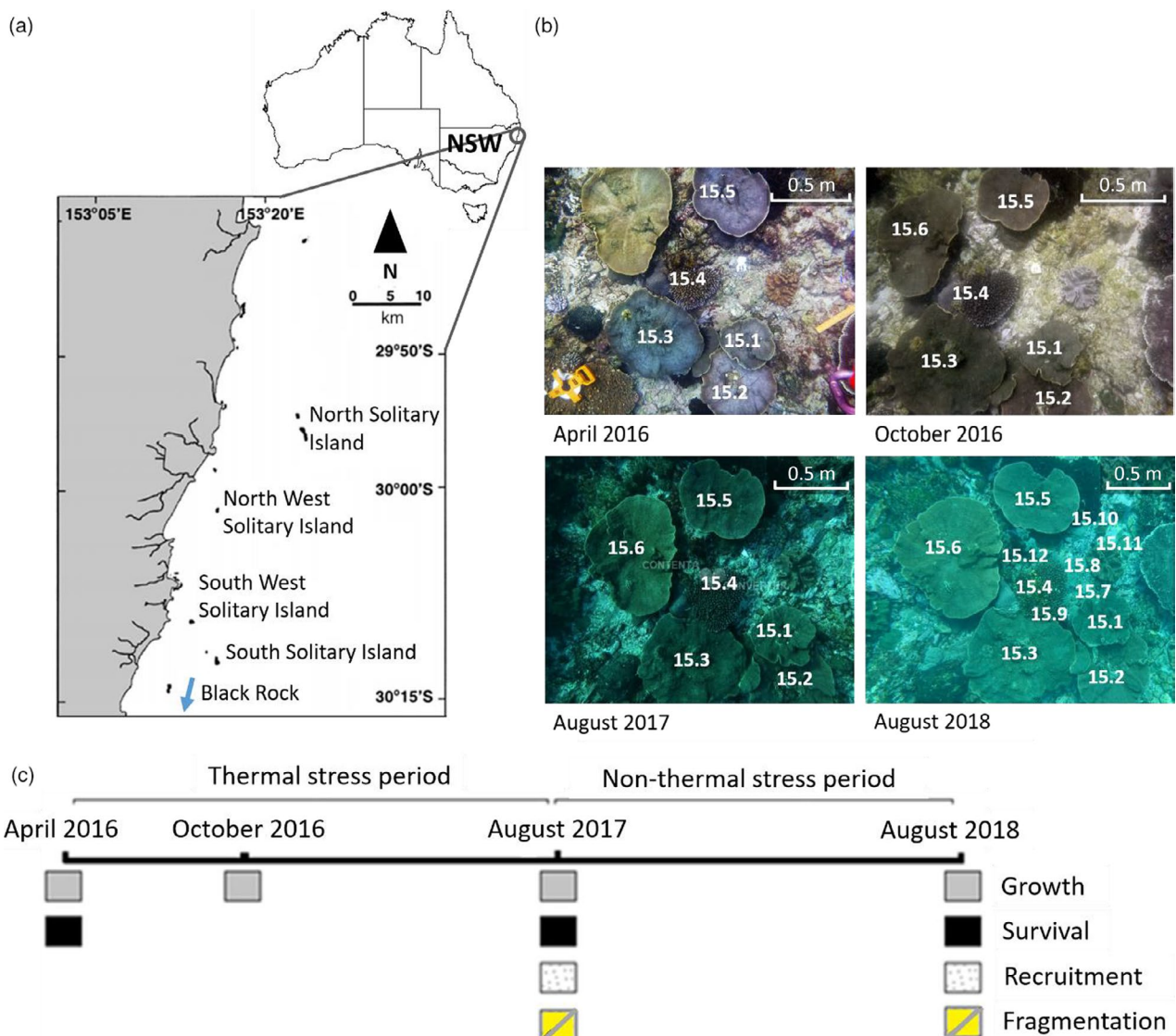


FIGURE 1 (a) The Solitary Islands Marine Park (SIMP) in New South Wales (NSW), Australia, showing the location of North Solitary Island, North West Solitary Island, South Solitary Island and South West Solitary Island, with Black Rock at South West Rocks (SWR) located to the south. (b) The general layout of a permanent coral plot with tagged colonies (numbered) arranged around a numbered tag, and the process of resurveying plots with new colonies added to track recruitment and to supplement the loss of tagged colonies. (c) Census schedule showing the frequency at which the different demographic variables of survival, growth, fragmentation and recruitment were measured, allowing for the construction of models comparing the dynamics of the population between thermal stress and non-stress periods

classified as either offshore or inshore depending on location. We initially surveyed 149 individual coral colonies, belonging to 24 species. We revisited all tagged colonies in October 2016, and again in August 2017, recording their survival, size and fragmentation, to capture the dynamics of this community during and after a bleaching event (Figure 1b,c). During surveys in August 2017, new plots and corals were added to replace those lost due to storms and mortality (Supporting Information S1), which increased the number of tagged colonies to 311 and included the setup of additional plots at Black Rock, to the south of the SIMP (Figure 1a). During August/September 2018, the survival, size and fragmentation of all tagged colonies were re-measured, on this occasion reflecting dynamics during a non-stress period (Figure 1c).

2.2 | Demographic measurements

During each census, demographic information was collected from each individual colony. We recorded the size of each colony using top-down photographs including a millimetre scale bar to minimise measurement error. Colony sizes were then measured as the visible horizontal surface area (z , see Equation 1; cm^2), using the area calculation function in ImageJ (Schneider et al., 2012). Colony growth (γ) was then defined as the difference in size between successive surveys. Prior to use in analyses, the size data collected in April 2016 required 'advancing' by four months. This adjustment was necessary to standardise an inconsistency in the census intervals between April 2016–August 2017 (16 months) and August 2017–August/September 2018 (~12 months). To correct for this mismatch, a grouped mean monthly growth rate of tagged corals was calculated for the 16-month period between April 2016 and August 2017 (Supporting Information S2). We then used this monthly growth rate to estimate the size of each coral in August 2016 given their size in April 2016. Carrying out the size adjustment in this way ensured that all further analyses represented annual intervals, and accounted for any seasonal variation in colony growth. Finally, colony size data were log transformed.

Colony survival (σ) and fragmentation (κ) were measured as the presence/absence of each colony and whether fragmentation had occurred, respectively. As with growth, the survival and fragmentation probabilities recorded for the period between April 2016 and August 2017 required adjusting to account for mismatches in census timings. This adjustment was carried out during model construction (see Section 2.3). In the event of fragmentation, colony fragments were measured and included as new individuals, but marked as a product of colony fragmentation, with the largest fragment retaining the parent colony's identity.

Finally, during each of the 2017 and 2018 surveys, the size of new recruits within the tagged plot areas was recorded to capture a measure of recruitment (Figure 1c). Here, we assumed that all new recruits were produced during the census interval in which they were observed. The fecundity (φ) of tagged colonies was not directly measured as part of the field surveys. Instead, a relationship between

colony size and fecundity was obtained using data collected from tropical corals by Hall and Hughes (1996) sourced from the Coral Trait Database (Madin et al., 2016; see Supporting Information S3). This relationship described an exponential association between fecundity and colony size, and allowed us to estimate the fecundity of our tagged colonies based on their size. We defined fecundity as the combined density of eggs & testes (Hall & Hughes, 1996), so per capita larval density (φ) was estimated to be half a colony's fecundity (Supporting Information S3).

Our methods for measuring recruitment and colony fecundity involved making several key assumptions regarding the reproductive biology of scleractinian corals. Firstly, we assume that recruits are produced during the annual phase in which they are observed. Yet, with coral recruits only discernible at a size that may reflect a longer growth period than the frequency of our surveys (~4 cm^2), this may not be the case. Secondly, we are assuming a relationship between larval output and colony size measured in tropical corals can be applied to subtropical assemblages. The formulation of this fecundity-size relationship also involves the grouping of gonochoristic and hermaphroditic taxa, and uses larval density (combined density of eggs & testes/ mm^3) as a measure of colony fecundity. Thirdly, including fecundity in our demographic assessments in this way implies the assumption that we are dealing with a closed system; this is despite both local and external recruitment processes occurring within the SIMP (Harriott, 1998; Harriott & Banks, 1995). However, these assumptions were addressed through the inclusion of a recruit settlement factor (ψ) in our demographic models (see Section 2.3). This settlement factor operates as a ratio that weights all reproductive functions by the actual number of observed recruits for each taxon/coral group. Subsequently, fecundity enabled us to include a link between adult and recruit dynamics, with the settlement factor then translating larval density estimates into a taxon-specific measure of 'the number of individuals surviving to an observable size in a subtropical setting'.

2.3 | Demographic model construction

We used IPMs to evaluate the impact of thermal stress on the dynamics of different coral populations within the SIMP and to assess the future implications of different disturbance scenarios. IPMs bypass the need to artificially force continuous state variables (e.g. size) into discrete classes, a requirement in size-based matrix population models (Easterling et al., 2000). IPMs are therefore well suited for populations structured by continuous state variables where small state transitions can result in large changes in demographic characteristics (Burgess, 2011).

With many unresolved taxonomic inconsistencies occurring throughout the Scleractinia, the identification of coral species can be problematic (Fukami et al., 2004), particularly without voucher specimens. Consequently, coral studies tend to focus on higher taxonomic levels (Darling et al., 2019). Compared to species identity, functional traits provide a superior capacity for understanding

patterns and processes at the community- or assemblage-level, and the implications of changing abiotic conditions (McGill et al., 2006). Coral colony morphology strongly correlates with demographic characteristics and dictates how individuals interact with their environment, underpinning their success and vulnerability to varying abiotic conditions (Álvarez-Noriega et al., 2016; Zawada et al., 2019). Thus to evaluate the dynamics of the coral assemblage in the SIMP, we pooled tagged colonies based on distinct morphological characteristics to construct separate IPMs for four coral groups reflecting the structural diversity of subtropical coral communities. While we recognise these morphological clusters do not resemble true 'populations', we will henceforth refer to them as such, to aid clarity when discussing the outputs of our IPMs in a demographic context.

The four morphological coral groups we used accounted for approximately 90% of our tagged sample (88% of corals tagged in April 2016, and 90.5% of colonies surveyed in August 2017). Three of these groups comprised the three most common coral taxa found within the SIMP: *Acropora* spp., *Turbinaria* spp. and *Pocillopora aliciae*. For our fourth group (henceforth 'Encrusting') we pooled corals exhibiting sub-massive/encrusting growth forms from multiple genera (*Acanthastrea*, *Astrea*, *Dipsastraea*, *Goniopora*, *Micromussa*, *Montipora* and *Paragoniastrea*). The coral species found within the SIMP belonging to these encrusting genera exhibit cosmopolitan distributions and are found across 41%–74% of global coral habitats (Veron et al., 2016). Therefore, although this final coral cluster represents a diverse range of species, it does not reflect contrasting abiotic tolerances.

The remaining ~10% of our tagged sample consisted of *Porites heronensis* and *Stylophora pistillata* colonies. During the 2015/2016 thermal stress event, we lost 85% of our tagged *P. heronensis* colonies through mortality. With low survival unrepresentative of its closest morphological group (Encrusting), including *P. heronensis* would unreasonably skew patterns for the 'Encrusting' group; therefore, this species was excluded from this group. Equally, despite both belonging to the *Pocilloporidae* and sharing similar morphological traits, *S. pistillata* could not be grouped with *P. aliciae*. *Stylophora pistillata* is a characteristic tropical species, with the Solitary Islands located close to the southern extent of this species' geographical range (Veron et al., 2016). *Pocillopora aliciae* is instead a subtropical endemic (Schmidt-Roach et al., 2013), and therefore grouping these two coral species together would mask the differences underlying their contrasting distributions. Hence colonies of both *P. heronensis* and *S. pistillata* were excluded from further analyses.

An IPM (Equation 1) describes changes in the structure and size of a population n over a discrete period in time (time t to $t + 1$). This model is defined by the IPM kernel K , which in this study was formulated from three sub-kernels P , H and F (Equation 2). The sub-kernel P outlines the probabilities of non-fragmenting corals surviving and retaining or changing their size (from z to z'). H combines the likelihood of corals undergoing fragmentation, and the eventual quantity, and size, of any fragments produced. F is the recruitment contribution of established individuals at time $t + 1$. L and U are then the minimum and maximum size over which these properties of survival, growth, fragmentation

and reproduction were modelled, and are typically 10% above and below actual observed size boundaries (Merow et al., 2014).

$$n(z', t + 1) = \int_L^U K(z', z) n(z, t) \Delta z, \quad (1)$$

$$K(z', z) = P(z', z) + H(z', z) + F(z', z). \quad (2)$$

Here, we incorporated a discrete size class representing the dynamics of the largest colonies into our IPMs (Figure 2). This was done to overcome statistical challenges in model convergence of vital rates due to the limited sample size for colonies at the large end

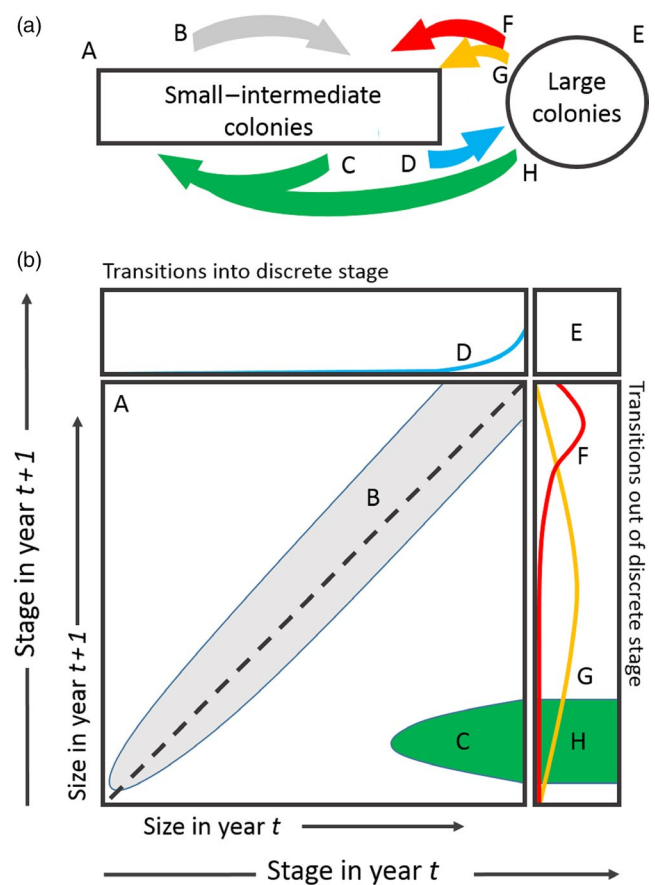


FIGURE 2 (a) Diagram depicting the coral life cycle structure used in this study, containing both a continuous (A) and a discrete (E) size class. (b) The representation of this life cycle in a two-stage IPM format. Here the demographic characteristics of the life cycle are represented by the growth (B) and reproduction (C) of individuals within the continuous size class, the progression of individuals from the continuous class into the discrete stage (D), the survival of discrete stage individuals (E), and the retrogression (F), fragmentation (G) and reproduction (H) of discrete stage individuals back into the continuous class. The dashed line represents null growth within the continuous class. The threshold size between continuous and discrete size classes in each model was calculated as the point of intersection between bleaching and non-bleaching growth trends for each species. This two-stage format ensured the accurate representation of large colony dynamics

of the size spectrum (*Acropora*: $z > 665 \text{ cm}^2$; *Turbinaria*: $z > 330 \text{ cm}^2$; *Pocillopora*: $z > 244 \text{ cm}^2$; Encrusting: $z > 706 \text{ cm}^2$; see Supporting Information S4 for details on how this size threshold was imposed for the continuous and discrete parts of the IPM, and for assessments of model sensitivity to threshold positioning). Correspondingly, additional vital rates were incorporated into our IPM sub-kernels to include between-stage transitions (Figure 2).

In our models, sub-kernel P contains the size-based probability of survival (σ_1), and colony growth (γ) from size z to size z' , for non-fragmenting colonies within the continuous stage class (Equation 3). Sub-kernel P then also describes the size-based probability of colonies surviving and progressing into the discrete (large) size class (δ), and the survival of large discrete-size colonies (σ_2 ; Equation 3). Lastly, sub-kernel P also outlines colony shrinkage from the large discrete size class into the continuous size class (ρ), as well as the size distribution of corals produced by this retrogression (S_2 ; Equation 3). Sub-kernel H consists of the probability of fragmentation (κ_1), and the number (τ_1), and size of any fragments (f_1) produced by colonies in the continuous class (Equation 4). These rates are combined with the likelihood of fragmentation within the discrete class (κ_2), the quantity (τ_2) and size (f_2), of any fragments produced (Equation 4). Sub-kernel F contains the per capita larvae density production by colonies in both the continuous (φ_1) and discrete stages (φ_2 ; Equation 5). These demographic processes are combined with a factor that converts larval density into a number of successfully settling recruits (ψ), and the size distribution of surviving recruits (C_1 ; neither of which are dependent on the size class of the parent colony; Equation 5). Lastly, with data collection occurring post breeding, colony survival is also built into both sub-kernels H and F .

$$P(z', z) = \begin{cases} (1 - \delta(z)) ((1 - \kappa_1(z)) \sigma_1(z) \gamma(z', z)) \\ \delta(z) \sigma_1(z) \\ (1 - \rho) (1 - \kappa_2) \sigma_2 \\ \rho \sigma_2 S_2(z') \end{cases}, \quad (3)$$

$$H(z', z) = \begin{cases} (1 - \delta(z)) (\kappa_1(z) \sigma_1(z) \tau_1(z) f_1(z')) \\ \kappa_2 \sigma_2 \tau_2 f_2(z') \end{cases}, \quad (4)$$

$$F(z', z) = \begin{cases} (1 - \delta(z)) (\sigma_1(z) \varphi_1(z) \psi C_1(z')) \\ \sigma_2 \varphi_2 \psi C_1(z') \end{cases}. \quad (5)$$

Given the low density of the coral assemblages within the SIMP (Supporting Information S4, Figure S6), all vital rates were modelled as density-independent. Growth (γ) was analysed as the relationship between size z at time t and size at time $t + 1$. The variance in growth was then fitted as a function of size at time t , using a gamma distribution to allow for a quadratic relationship while ensuring variance remained positive. Survival (σ_1) and fragmentation (κ_1) were both

modelled as a function of colony size using logistic regressions. For the period between April 2016 and August 2017, these probabilities were also multiplied by the exponent 1.333 to ensure they were adjusted to represent transitions during a 12-month interval rather than the observed 16 months. The number of eggs produced was determined using a nonlinear least squares regression, which allowed for an exponential relationship with colony size. Fragment size and quantity were modelled as a linear function of initial colony size, with the variance in fragment size modelled as a function of initial colony size using a gamma distribution. Recruit size distributions were also calculated, though kept independent of parent colony size as parental lineage could not be determined for each recruit. We then determined the recruit settlement factor (ψ), using the estimated density of larvae produced per colony (φ) and the total number of observed recruits (R ; Equation 6).

$$\psi = \frac{\sum \varphi(z)}{R}. \quad (6)$$

All vital rate analyses were conducted with time as a fixed effect to allow us to separate models for both thermal stress and non-stress periods; this ensured we could empirically measure the effects of thermal stress and forecast the future implications of recurrent stress events. Then, to ensure that all analyses accounted for similarities resulting from random nesting in the data, island identity, island location (Inshore or Offshore; see Supporting Information S1), bleached state and colony ID were also included as random effects in vital rate regressions. AIC scores were used to determine the most appropriate model structures.

2.4 | Population growth rates and life table response experiments

To quantify the effect of thermal stress on the coral assemblage within the SIMP, we calculated the growth rate (λ) for each of our constructed IPMs. Values of λ exist on a scale of 0 to 2, with $\lambda < 1$ reflecting decline and $\lambda > 1$ representing growth. We obtained estimates of the variance in λ by repeating jack-knife resampling 1,000 times, each time omitting 5% of our sample without replacement. One-way life table response experiment analyses (LTREs; Caswell, 1989) were then used to quantify the vital rate drivers behind any differences in λ observed between bleached and non-bleached models. For LTRE analysis, the non-stress state was set as the control group. Our LTRE analysis therefore defined λ during thermal stress as approximately equal to the sum of its corresponding value during non-stress, plus the relative contributions (α) of any changes in the different vital rate regression parameters used to construct our IPMs (Equation 7).

$$\lambda_{\text{bleaching}} \approx \lambda_{\text{non-bleaching}} + \alpha^{(\text{parameter}^1)} + \alpha^{(\text{parameter}^2)} + \dots + \alpha^{(\text{parameter}^i)}. \quad (7)$$

To determine α for each parameter, we first constructed an IPM equal to the mean of our associated bleaching and non-bleaching models

$K^{(i)}$. The parameter-level sensitivities (S) of $K^{(i)}$ were then calculated (Equation 8), using the stepwise change in λ for the mean model ($\Delta\lambda_k$) following small perturbations to each parameter (Δi). Multiplying these sensitivities of mean model $K^{(i)}$ by the observed differences in each parameter (i) between associated bleaching and non-bleaching models then returned the parameter-level contributions (Equation 9).

$$S = \frac{\Delta\lambda_k}{\Delta i}, \quad (8)$$

$$\alpha = S (i_{\text{bleaching}} - i_{\text{non-bleaching}}). \quad (9)$$

2.5 | Model projections and bleaching simulations

Stochastic projections were used to evaluate the long-term viability of our subtropical coral assemblages given the dynamics observed during regular and thermal stress periods. The value of λ calculated from an IPM refers to asymptotic growth trends (Caswell, 2001) and assumes environments are constant. Thus, λ is unlikely to reflect the true dynamics of systems exposed to varying environments (Ellner et al., 2016). For each of our coral groups, we therefore also calculated λ_s (Equation 10). This variable is a stochastic measure of growth rate accounting for the transient nature of natural environments (Ellner et al., 2016), with N_t the total population size at time t , and equal to $\sum n_t$.

$$\log(\lambda_s) = E \left[\log \left(\frac{N_{t+1}}{N_t} \right) \right]. \quad (10)$$

We used sea surface temperature (SST) data from an ensemble of CMIP5 climate models (Supporting Information S5) to simulate future temperature trajectories for the Solitary Islands region. The model ensemble we used was selected to ensure our future SST estimates were comparable with projections used in other studies simulating future thermal stress responses in corals (see van Hooijdonk et al., 2014). Corresponding with Liu et al. (2003), we used these simulations to determine degree heating week (DHW) projections for the period 2018–2100 under each of the four different IPCC RCP scenarios (2.6, 4.5, 6.0 and 8.5; Supporting Information S5; IPCC, 2014). Typically, estimating DHWs only involves mean weekly SSTs that exceed the mean monthly maximum (MMM) by a threshold of 1°C (Liu et al., 2003). However, following the work of Kim et al. (2019), we removed the 1°C threshold, as this alternative approach captures the impact of low-level thermal stress found to affect subtropical corals (see also van Hooijdonk & Huber, 2009). Binomial regression analysis was then used to determine the annual likelihood of DHWs ≥ 4 , from which we constructed a series of future annual thermal stress probabilities for each RCP scenario.

For each of our coral groups, we used these thermal stress simulations to investigate the relative impact of recurrent thermal stress regimes of varying intensities on the future condition of their population. Colony size distributions recorded in August 2018 for each population were set as the initial size distributions (n_0) for each

projection. Then, using the corresponding IPMs, we projected each population to the end of the century (Equation 11) to determine their future n_t distributions.

$$n_{t+1} = \mathbf{K}n_t. \quad (11)$$

Here n_t is a probability distribution defining the size of individuals in the population at time t as a function of their size, and \mathbf{K} is a discretised IPM matrix, with the number of iterations relating to the time frame over which the population is being assessed. During each annual iteration, the thermal stress probability associated with that step was used to determine whether the bleached or non-bleached IPM was selected. Following each iteration, the vector n_{t+1} was retained, allowing for a series of N_t values to be calculated and used in determining λ_s , and enabling us to record the temporal change in the coverage of each coral population. The coefficients of variance for all calculated metrics were also estimated, and a one-way ANOVA was used to test the effect of RCP scenario selection on the estimates of λ_s for each coral group.

3 | RESULTS

3.1 | Population growth rates (λ) and LTRE analysis

The impact of thermal stress on population performance varied, with λ differing between non-stress and thermal stress periods across all four coral groups. Values of λ for both *Acropora* and *P. aliciae* reflected a state of population decline during the thermal stress period ($\lambda < 1$; *Acropora*: $\lambda_{\text{bleaching}} = 0.8688$, 95% CI [0.8685, 0.8692]; *Pocillopora*: $\lambda_{\text{bleaching}} = 0.2989$ [0.2980, 0.2998]). Despite a large increase in λ for *P. aliciae* during non-bleaching, both the *Acropora* and *P. aliciae* populations then remained in a state of decline throughout the non-stress period (*Acropora*: $\lambda_{\text{non-bleaching}} = 0.8767$ [0.8752, 0.8782]; *Pocillopora*: $\lambda_{\text{non-bleaching}} = 0.8126$ [0.8110, 0.8142]). In contrast, the *Turbinaria* group maintained relatively stable dynamics during the thermal stress period ($\lambda \approx 1$; $\lambda_{\text{bleaching}} = 0.9989$ [0.9983, 0.9995]), though experienced a slight decline in population growth during the non-stress period ($\lambda_{\text{non-bleaching}} = 0.9859$ [0.9857, 0.9862]). Lastly, the Encrusting group remained at equilibrium throughout both thermal stress and non-stress periods, showing marginal improvements during the non-stress phase ($\lambda_{\text{bleaching}} = 1.0002$ [0.9998, 1.0007], $\lambda_{\text{non-bleaching}} = 1.0008$ [1.0002, 1.0014]).

Our LTRE analysis provided an approximation as to the relative contribution changes in the processes of growth, survival and recruitment had on the observed differences in λ reported between the stress and non-stress periods. In the *Acropora* and *P. aliciae* populations, differences in λ between bleached and non-bleached periods involved changes in the parameters relating to survival (Figure 3a,c). For *Acropora*, the survival of very large colonies (σ_2) was highest during thermal stress (Figure 3a), however, this corresponded with a decline in estimates of λ . This disparity indicates that improvements in large colony survival were unable to counteract the cumulative impacts of changes in the survival and growth dynamics of smaller

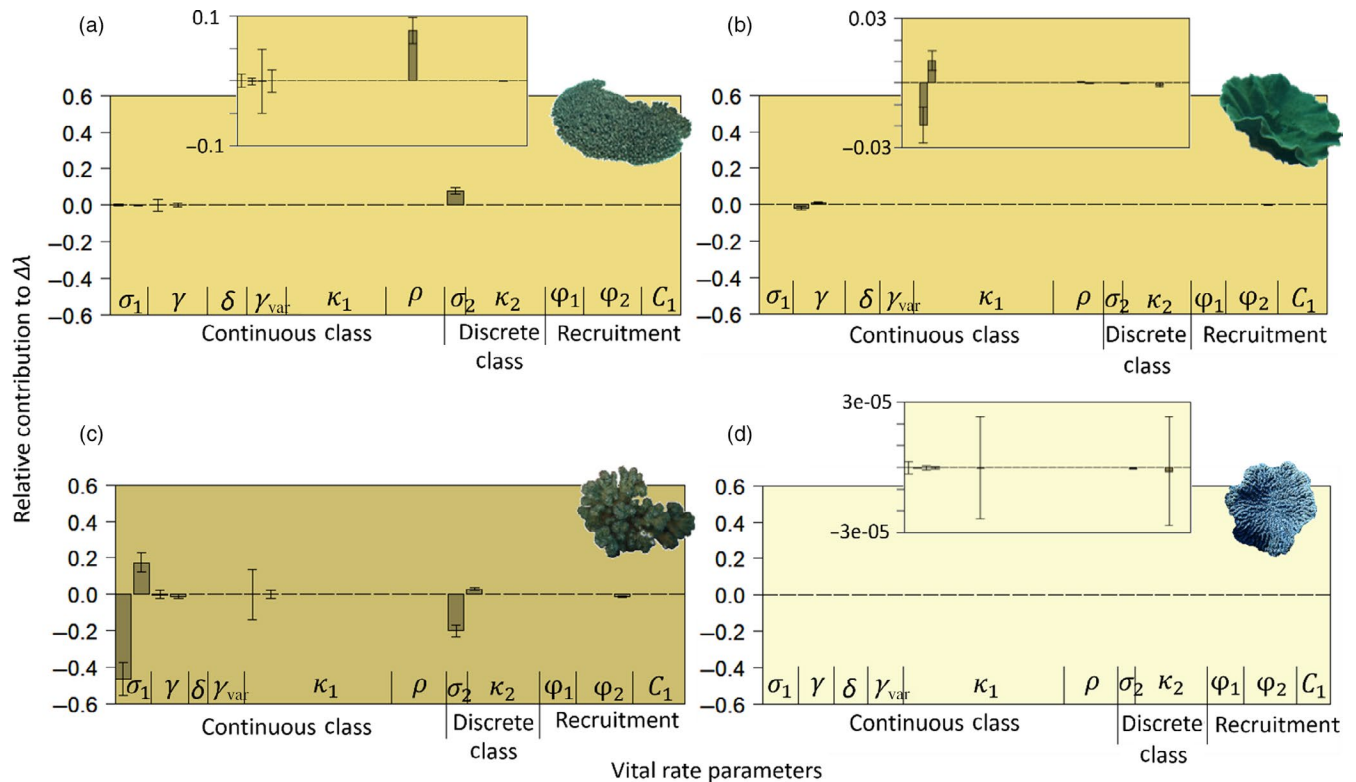


FIGURE 3 Life table response experiment analysis showing the standardised parameter-level contributions of each vital-rate, towards the observed differences in population growth rates ($\Delta\lambda$) between bleaching and non-bleaching for the (a) *Acropora*, (b) *Turbinaria*, (c) *Pocillopora aliciae* and (d) Encrusting populations. Each parameter corresponds with a regression coefficient (left: intercept; right: slope) used in determining the size structured vital rates of survival (σ_1), growth (γ), growth variance (γ_{var}), fragmentation (κ_1), and recruitment within the continuous class, (ρ) progression into discrete class, and the survival (σ_2), fragmentation (κ_2) and recruitment of discrete class individuals. Inset panels highlight the contributions relative to each coral population. Panel colours reflect the absolute magnitude of $\Delta\lambda$, with darker shades representing greater dissimilarity between bleaching and non-bleaching dynamics

colonies (Figure 3a). In contrast, in *P. aliciae*, the survival of both large colonies (σ_2), and those within the continuous size class (σ_1), were considerably lower during bleaching, prompting a large decline in λ (Figure 3c). This LTRE analysis also shows that *P. aliciae* did not benefit from improvements in recruitment dynamics; this is despite an elevation in the number of *P. aliciae* recruits reported during the non-bleaching period (Table S2). Alternatively, the change in λ reported for the *Turbinaria* population, albeit small, appears to have been largely a result of changes in the growth (γ) dynamics of this population (Figure 3b). Estimates of λ for the Encrusting population varied little between the stress and non-stress periods. This consistency in λ is reflected in the LTRE analysis, with vital rate parameters for the Encrusting group remaining stable throughout both the stress and non-stress periods, at least compared to the scale of the changes observed in the other three coral groups (Figure 3d).

3.2 | Stochastic growth rate (λ_s) and community projections

Regional CMIP5 model projections indicate that the frequency of future thermal stress leading to bleaching responses will increase over time within SIMP, but that the exact prevalence of thermal

stress will differ among the four RCP pathways (time: $p < 0.001$; RCP: $p < 0.001$; time \times RCP: $p < 0.001$; Nagelkerke r^2 : 0.593. See Supporting Information S5). Under RCP pathways 2.6, 4.5 and 6.0, future increases in the frequency of thermal stress events will be less severe than those predicted under RCP 8.5 (Tukey's HSD: RCP 2.6 = 4.5 = 6.0 < 8.5). In both the 6.0 and 8.5 RCP scenarios, annual thermal stress events that are capable of inducing bleaching within the SIMP are expected before the end of the current century (Supporting Information S5: Figure S7), although under both scenarios annual bleaching is not expected until after 2090. The RCP 4.5 scenario presents a more optimistic outlook with a maximum annual bleaching probability of 46% expected by the year 2100 within the SIMP. Unsurprisingly, RCP 2.6 offers the most encouraging future for the SIMP with thermally induced bleaching remaining low, and forecast once every 6.8 years by the end of the century.

RCP scenario selection was found to have a statistically significant effect on the stochastic growth rate of each coral group (ANOVA: *Acropora*: $F = 6,124$, $p < 0.001$; *Turbinaria*: $F = 4,962$, $p < 0.001$; *Pocillopora*: $F = 29,808$, $p < 0.001$; Encrusting: $F = 2,738$, $p < 0.001$). However, the relative impact of this effect differed among populations (Table 1). The greatest effect occurred in *P. aliciae*, with scenarios of heightened carbon emissions resulting in a severe reduction in λ_s (Table 1; Tukey's HSD:

TABLE 1 The impact of the future thermal stress regimes predicted under each representative concentration pathway scenario on the stochastic growth rates (λ_s) of each coral population. Variance displayed as 95% CI

Population	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
<i>Acropora</i>	0.8725 [0.8727, 0.8722]	0.8636 [0.8637, 0.8634]	0.8604 [0.8604, 0.8603]	0.8632 [0.8633, 0.8632]
<i>Turbinaria</i>	1.0157 [1.0157, 1.0157]	1.0150 [1.0150, 1.0149]	1.0151 [1.0151, 1.0151]	1.0137 [1.0137, 1.0137]
<i>Pocillopora aliciae</i>	0.7212 [0.7230, 0.7193]	0.6395 [0.6415, 0.6376]	0.5243 [0.5254, 0.5232]	0.4123 [0.4133, 0.4113]
Encrusting	0.9863 [0.9866, 0.9860]	0.9804 [0.9807, 0.9802]	0.9759 [0.9759, 0.9758]	0.9758 [0.9759, 0.9758]

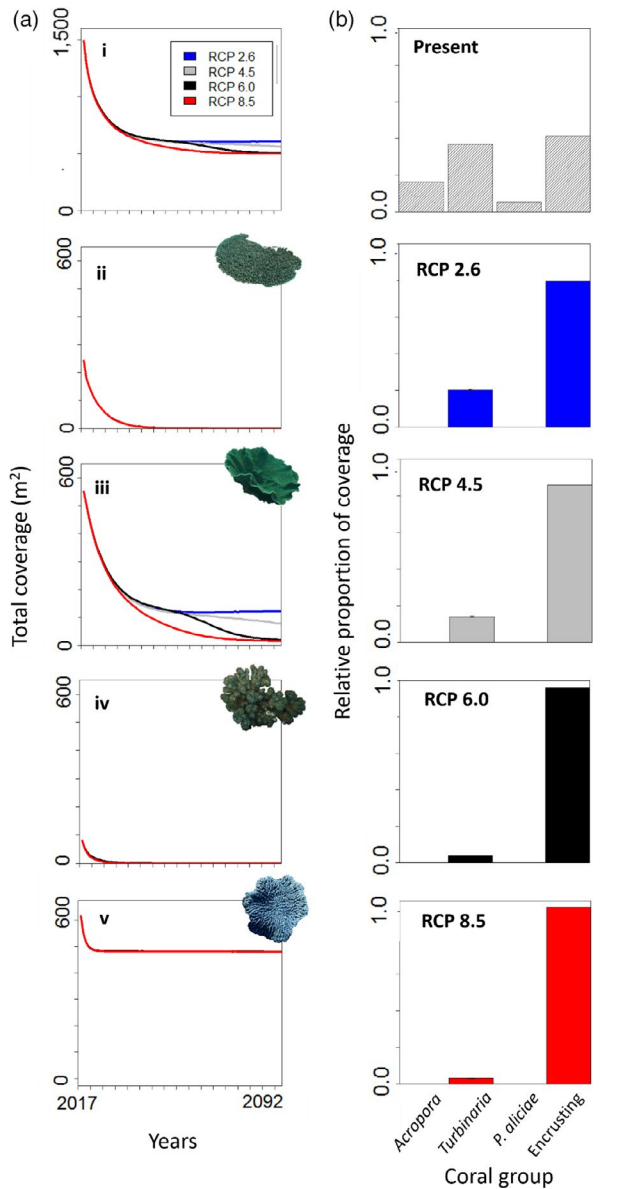


FIGURE 4 (a) Simulated trends in coral coverage within tagged plots under the different Representative Concentration Pathway scenarios showing (i) overall coverage, and the coverage of each separate population (ii) *Acropora*, (iii) *Turbinaria*, (iv) *Pocillopora aliciae* and (v) Encrusting. (b) Comparison of the relative contribution towards overall coverage by each population between present coverage and projected coverage in 2100 under the four different Representative concentration pathway scenarios (RCP)

RCP 2.6 > 4.5 > 6.0 > 8.5). Similarly, for each of the other coral groups, scenario RCP 2.6 always resulted in larger λ_s values; however, higher emission scenarios resulted in only minimal declines, with the exact trend varying among populations (Table 1; Tukey's HSD: *Acropora* = RCP 2.6 > 4.5 > 6.0 < 8.5; *Turbinaria* = RCP 2.6 > 4.5 < 6.0 > 8.5; Encrusting = RCP 2.6 > 4.5 > 6.0 = 8.5). Across all populations, only *Turbinaria* was projected to exhibit positive population growth under any of the emission scenarios (Table 1).

In comparison to projected population size, simulations of coral cover reveal a different future outlook for the diversity and condition of coral assemblages within the SIMP (Figure 4). At present, coverage within our plots is primarily dominated by *Turbinaria* and Encrusting colonies, with *Acropora* and *P. aliciae* together contributing <30% cover. Given the dynamics we observed across our tagged corals, coral cover within our plots is projected to decline to approximately half its current level, regardless of RCP scenario (Figure 4a.i). Across all simulations this loss of coverage initially occurs very rapidly, driven by declines in all of our coral groups (Figure 4a.ii-v). These declines result in the loss of *Acropora* and *P. aliciae* populations from the plots (Figure 4). However, projected cover does eventually plateau as the cover of the *Turbinaria* and Encrusting groups achieves more stable levels (Figure 4a). For the Encrusting group the stable coverage level remains uniform across RCP scenarios; yet for *Turbinaria* the threshold is highly dependent on the RCP scenario, with the higher emission scenarios of RCP 6.0 and 8.5 resulting in minimal coverage levels (Figure 4). Ultimately, it is the variation in *Turbinaria* coverage that drives the projected variance in overall plot diversity and coverage under the different RCP scenarios (Figure 4).

4 | DISCUSSION

Our capacity to manage global coral reef ecosystems in the face of rapidly changing climates relies on robust predictions of how environmental shifts influence the long-term viability of coral communities (Edmunds et al., 2014; Edmunds & Riegl, 2020). Here, we show that within a subtropical assemblage, *Turbinaria* spp. and most corals displaying encrusting and massive morphologies possess enhanced resistance towards thermal stress events. In comparison, populations of *Acropora* spp. and *Pocillopora aliciae* are particularly sensitive to thermal stress. However, we illustrate that, regardless of

this taxon-specific resistance, an increasing frequency of recurrent thermal stress events will reduce the coverage, complexity, diversity and viability of subtropical coral assemblages.

4.1 | Contrasting trajectories among coral groups

The contrasting responses of coral taxa to thermal stress needs to be considered in future ecosystem-level assessments and predictions for high-latitude coral communities. Indeed, *P. aliciae* is the least viable population within the SIMP due to a high susceptibility to thermal stress (Kim et al., 2019) and limited recovery during non-stress conditions. *Pocillopora aliciae* is a subtropical specialist, endemic to the east coast of Australia (Schmidt-Roach et al., 2013) between the Cook Island Aquatic Reserve (−28.1956, 153.5781; B. Sommer, 2017, pers. obs.), and Sydney (−33.8688, 151.2093; Booth & Sears, 2018). Corals adapted to a subtropical existence tolerate greater seasonal variance, and broader scales in abiotic measures than tropical assemblages (Camp et al., 2018; Sommer et al., 2018). However, the response of *P. aliciae* within the SIMP, following elevated temperature stress, illustrates that the enhanced stress tolerance expected of corals exposed to frequent abiotic variability (Oliver & Palumbi, 2011) appears not to have benefitted this subtropical population. The accumulated thermal exposure experienced by corals in the SIMP during the 2015/2016 bleaching event exceeded the thermal tolerances of some subtropical corals (Kim et al., 2019); as such subtropical and other marginal species are highly vulnerable to future recurrent heat stress (Schoepf et al., 2015). Nevertheless, with *P. aliciae* exhibiting recent poleward range expansions (Booth & Sears, 2018), our results may also reflect the reduced ability of this coral species to further alter its energetic trade-offs at the northern extent of its distribution (Sheth & Angert, 2018).

Through our stochastic projections, the emerging models predict a reduction in the coverage of *Acropora* spp. within the SIMP. *Acropora* spp. typically constitute a large majority of the structural complexity in global reef environments (Nyström, 2006). With *P. aliciae* also providing a considerable structural contribution (Harriott et al., 1994), a decline in the coverage of these corals will reduce benthic complexity within the Solitary Islands region where there is already a low diversity of branching coral species (Sommer et al., 2014). This loss of structural complexity will likely have cascading effects on the diversity of other taxa associated with these coral assemblages, and subsequently the overall resilience of the local ecosystem (Graham & Nash, 2013). However, this perspective assumes that other branching, more thermally tolerant tropical species will be unable to establish subtropical populations capable of fulfilling this structural role (Baird et al., 2012).

Thermal stress is not the only impact acting upon coral assemblages within the SIMP. The subtropical coastline of eastern Australia experiences frequent extratropical cyclones known as east coast lows (ECLs; Harley et al., 2017). Therefore, it is not possible to fully attribute our projected reduction in *Acropora* coverage to the consequences of thermal stress. During the 2015/2016 thermal stress event, the observable symptoms of bleaching were minimal within

the *Acropora* assemblage of the SIMP (Kim et al., 2019). In June 2016, the coastline of NSW was subjected to a non-typical ECL system which produced uncharacteristic wave patterns and resulted in high levels of coastal erosion and coral damage (Mortlock et al., 2017). With their brittle, tabular structure highly susceptible to physical damage and abrasion, it is likely that this subtropical storm event contributed to the diminished survival of *Acropora* spp. reported in this study, and must also be remembered when evaluating survival patterns across the other coral groups.

Corals exhibiting encrusting morphologies are forecasted to experience relative stability in terms of substrate coverage within the SIMP. The less complex morphologies of sub-massive and encrusting corals may provide them with a physiological advantage during thermal stress events (Woesik et al., 2012), enhancing their viability under future recurrent thermal stress scenarios. However, *Porites heronensis*, which exhibits sub-massive and encrusting growth forms (Veron et al., 2016), was excluded from the Encrusting group for this analysis. The cause of this exclusion was the high mortality recorded for this species during the 2015/2016 bleaching event, which was unrepresentative of the rest of the Encrusting group and prevented us modelling this species independently. Therefore, while relative stability is expected for the encrusting coral assemblage within the SIMP, the high level of bleaching vulnerability observed for *P. heronensis* does not follow this trend (Kim et al., 2019).

The subtropical *Turbinaria* assemblage within the SIMP also appeared to display high resistance during the 2015/2016 thermal stress event. *Turbinaria* spp. are known to possess a high tolerance threshold for a range of abiotic stressors (Morgan et al., 2017; Sofonia & Anthony, 2008). While *Turbinaria* is capable of maintaining relatively stable population dynamics, our simulations indicate that extended, recurrent thermal disturbance will still elicit a decline in the coverage of this taxon. These contrasting trends suggest an accumulation of smaller sized colonies, which is a scenario often observed in coral communities following disturbance (Loya et al., 2001; Riegl & Purkis, 2015). Akin to corals with reduced morphological complexity, increased rates of mass transfer in smaller colonies can enhance their survival during thermal stress events in comparison to larger conspecifics (Shenkar et al., 2005). Yet, a reduction in average colony size can also result in a decline in reproductive output (Álvarez-Noriega et al., 2016). Reef communities increasingly dominated by small and intermediately sized corals are therefore expected to display reduced recovery potential following future disturbances (Pisapia et al., 2019; Riegl & Purkis, 2015).

4.2 | Climate simulations for the Solitary Islands region

Relative to other subtropical communities, the Solitary Islands region may be afforded more time before bleaching becomes an annual occurrence. Under RCP 8.5 simulations, annual bleaching conditions in the subtropics could be expected from 2054 (van Hooidonk et al., 2014), whereas annual bleaching conditions under RCP 4.5 will

occur ~25 years later (van Hooidonk et al., 2016). In contrast, our climate simulations suggest that under RCPs 4.5, 6.0 and 8.5 annual thermal stress events are not expected within the SIMP until much closer to the end of the 21st century (Supporting Information S5, Figure S7). Therefore, within the SIMP, corals may experience more buffered thermal regimes over the next century. This restrained warming of SSTs could provide corals in the SIMP with marginally more time to adapt to warming conditions. However, future shifts in the activity of destructive storms may offset this adaptive potential (Ji et al., 2015).

4.3 | Recruitment limitation

The dynamics observed in our tagged coral populations, following the 2015/2016 bleaching event, point to a future reduction in the coverage of coral assemblages within the SIMP, even under low emission scenarios. The continued viability of subtropical coral assemblages is highly dependent on larval supply from lower latitudes (Beger et al., 2014), which supplements their existing genetic diversity and enhances their ability to recover from disturbance events (Noreen et al., 2009). Thus, evaluation of recruitment patterns is necessary when predicting trends in the future viability of subtropical corals.

Within the Solitary Islands region, recruitment at a scale large enough to support growing populations may be reliant on larval supply from the north (Harriott & Banks, 1995; Sommer et al., 2014). Throughout our study, recruitment across all coral groups remained low, except in the endemic *P. aliciae* population. With larval supply in the subtropics often sporadic and asynchronous (Harrison, 2011), our simulations could potentially be under-representing recruitment dynamics. However, the 2015/2016 bleaching event caused a severe reduction in recruitment on the GBR (Hughes et al., 2019). With the GBR a key contributor to the larval influx in eastern Australia's subtropical coral assemblages (Noreen et al., 2009), it is unlikely the viability of coral populations in the SIMP will improve following future recurrent bleaching events of similar or greater magnitudes. Alternatively, with *P. aliciae* a known brooding species, new recruits typically settle close to their parent colony, enhancing colonisation potential while reducing dependency on external recruitment sources (Figueiredo et al., 2013; Harriott & Banks, 1995; Schmidt-Roach et al., 2013).

Globally, coral populations have extended the poleward limits of their distributions into higher latitudes (Baird et al., 2012; Precht & Aronson, 2004; Yamano et al., 2011). These expansions have occurred despite the presence of numerous abiotic restrictions, which limit the genetic and species diversity of the shifting assemblages, and reduce the continual supply of larvae to higher latitudes (Nakabayashi et al., 2019; Sommer et al., 2014). Coral species originating from the tropics are likely to be rarer in the subtropics and so more dependent on external sources of recruitment for maintaining viability, whereas for species with subtropical orientated distributions locally sourced larvae are likely more important in maintaining

populations and genetic diversity (Ayre & Hughes, 2000; Keith et al., 2015). It is important, therefore, to consider the role of local limitations on the larval stock dynamics within the SIMP when defining the observed trends in the viability of the local coral populations.

4.4 | Environmental legacy effects

Some aspects of coral physiology, particularly those relating to the production of viable larvae, can require multiple years to recover from thermal stress (Hagedorn et al., 2016). Correspondingly, recovery of corals within the SIMP may have been incomplete during the collection of data reflecting population dynamics during a non-stress period. Our simulations would therefore be underestimating the viability of subtropical coral assemblages within the Solitary Island region. However, with the return times of thermal stress events decreasing, corals are unlikely to be afforded sufficient recovery time in the future (Hughes, Anderson, et al., 2018).

Delayed effects can also apply to the negative impacts of thermal stress, as often the full extent of bleaching is not observed until well after the actual thermal stress event (McClanahan et al., 2009). Indeed, across each of the four coral groups we examined in this study, fragmentation was more readily observed during the non-stress phase (Supporting Information S4). Though, with the thermal stress period occurring first in our survey sequence, increasing colony fragmentation likely represents delayed partial mortality in response to the thermal stress, rather than a reaction to the conditions experienced during the non-stress period. Subsequently, the more resilient dynamics reported here for both the Encrusting and *Turbinaria* groups may not persist in reality over extended timeframes.

4.5 | The caveats of an IPM framework

While IPMs represent a powerful mathematical tool, the findings we present here must be considered in the context of the challenges encountered when implementing an IPM framework for a coral community. Our survey, conducted over two consecutive years, represents a comparatively restricted timeline. However, IPMs demand a data-heavy approach which, coupled with the operational challenges facing the collection of long-term demographic data in coral communities, restricts the feasibility of this technique for use in assessments of scleractinian coral populations (Edmunds & Riegl, 2020). To that extent, the temporal coverage of our work is comparable with previous efforts to construct IPM frameworks for coral populations using empirically derived data (Elahi et al., 2016; Kayal et al., 2018; Precoda et al., 2018; Scavo Lord et al., 2020). Additionally, in contrast to much of this previous work, we collected data for all vital rates simultaneously, thereby ensuring all estimates are subject to identical abiotic pressures. Although no model can completely satisfy the complexity of natural environments (Gertsev & Gertseva, 2004), we need to understand the demographic characteristics of coral populations if we are to comprehend their viability,

and responses to future climate shifts (Edmunds et al., 2014). We have therefore endeavoured to ensure logistical obstacles have not hindered the efficacy, or pertinence of our study, while advocating for the expanded use of IPMs in coral research.

5 | CONCLUSIONS

We have quantified the impact of thermal stress within a subtropical coral assemblage to evaluate the long-term viability of subtropical corals in the SIMP. The demographic approach we have applied transcends the purely correlative approaches previously used to evaluate the thermal stress responses of global coral assemblages (Edmunds & Riegl, 2020). We demonstrate that despite prior exposure to variable abiotic environments, and a slow pace of thermal stress increase, subtropical coral assemblages will likely be subject to substantial degradation by future recurrent thermal stress events. In fact, the future reduction in complex morphologies that we forecast for the subtropical coral assemblage within the SIMP closely resembles observations in tropical reef communities (Loya et al., 2001); although poleward shifts in tropical coral species may temper this loss of complexity in the short term (McIlroy et al., 2019; Yamano et al., 2011).

While there was considerable variation in the actual responses observed among different coral taxa, the overall expected loss of coverage, diversity, and complexity in this subtropical region will hinder the functioning of the wider ecosystem that relies on this coral community (Graham & Nash, 2013). Abiotic conditions within the SIMP may provide some buffering against the detrimental impacts of future warming. However, the susceptibility of subtropical specialist species to thermal stress (Kim et al., 2019), coupled with the high dependency on larval supply from tropical environments for many species with tropical origins (Sommer et al., 2014), is ultimately impeding the viability of subtropical coral assemblages. This vulnerability presents a challenge for the future management of these marginal environments, and diminishes the potential for high-latitude locations to act as climate refugia for many coral species.

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AUTHORS' CONTRIBUTIONS


M.B. and R.S.-G. conceived the project ideas and M.B., S.W.K., C.A.S., B.S., H.A.M. and J.M.P. designed the field methodology; J.C., C.A.S., J.M.P., S.W.K., H.A.M., B.S. and M.B. collected data in the field, and J.C., M.Br. and R.S.-G. analysed the data; J.C., R.S.-G. and M.B. led the writing of the manuscript, with all authors contributing critically to the writing and giving final approval for publication.

DATA AVAILABILITY STATEMENT

The IPM models used in this study will be digitised in the Madrina IPM database. The Madrina IPM database is aimed at providing a central open source repository for IPMs constructed for animal populations, corresponding with the COMADRE database of Matrix populations models. At the time of submission the Madrina IPM database was under development, however, code detailing the implementation of all demographic models and analyses used in this study have been published on Zenodo: <https://doi.org/10.5281/zenodo.4015167> (Cant, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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