REPORT

Linking population size structure, heat stress and bleaching responses in a subtropical endemic coral

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Abstract Anthropocene coral reefs are faced with increasingly severe marine heatwaves and mass coral bleaching mortality events. The ensuing demographic changes to coral assemblages can have long-term impacts on reef community organisation. Thus, understanding the dynamics of subtropical scleractinian coral populations is essential to predict their recovery or extinction post-disturbance. Here we present a 10-yr demographic assessment of a subtropical endemic coral, *Pocillopora aliciae* (Schmidt-Roach et al. in Zootaxa 3626:576–582, 2013) from the Solitary Islands Marine Park, eastern Australia, paired with long-term temperature records. These coral populations are regularly affected by storms, undergo seasonal thermal variability, and are increasingly impacted by severe marine heatwaves. We examined the demographic processes governing the persistence of these populations using inference from size-frequency distributions based on log-transformed planar area measurements of 7196 coral colonies. Specifically, the size-frequency distribution mean, coefficient of variation, skewness, kurtosis, and coral density were applied to describe population dynamics. Generalised Linear Mixed Effects Models were used to determine temporal trends and test demographic responses to heat stress. Temporal variation in size-frequency distributions revealed various population processes, from recruitment pulses and cohort growth, to bleaching impacts and temperature dependencies. Sporadic recruitment pulses likely support population persistence, illustrated in 2010 by strong positively skewed size-frequency distributions and the highest density of juvenile corals measured during the study. Increasing mean colony size over the following 6 yr indicates further cohort growth of these recruits. Severe heat stress in 2016 resulted in mass bleaching mortality and a 51% decline in coral density. Moderate heat stress in the following years was associated with suppressed *P. aliciae* recruitment and a lack of early recovery, marked by an exponential decrease of juvenile density (i.e. recruitment) with increasing heat stress. Here, population reliance on sporadic recruitment and susceptibility to heat stress underpin the vulnerability of subtropical coral assemblages to climate change.

Keywords Population dynamics • Size-frequency distributions • Recruitment • *Pocillopora aliciae* • Heat stress

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Introduction

Marine habitats are under increasing pressure in the Anthropocene due to cumulative stress from multiple local and global stressors (Pandolfi et al. 2003; Hughes et al. 2017a, b; Duarte et al. 2020). Progressive warming of marine habitats under climate change is affecting global biodiversity patterns due to altered species performances, but this issue is further compounded by increasingly common climatic extremes (Smale et al. 2019). As marine ecosystems are comprised of a diversity of taxa with species-specific environmental optima and tolerances, species-level population dynamics and interactions inevitably define high-level ecosystem trends. Predicting ecosystem trajectories relies on disassembling these multi-taxa communities into their distinct species populations (Capdevila et al. 2020).

Populations can react abruptly to stress events, and often follow the disturbance dynamics model (Gilmour 2004; Crabbe 2009; Leray et al. 2012); while some populations decline, others proliferate in the newly available ecological niche space. These dynamics are influenced by species-specific life history strategies and differential responses to stress events. Using advanced quantitative techniques, such as integral projection models, future population trajectories can be determined from basic demographic information on vital rates (survival, growth, reproduction, recruitment) (Cant et al. 2020; Capdevila et al. 2020). Moreover, short-lived changes to vital rates can drive transient population dynamics with long-term impacts on population persistence (Capdevila et al. 2020). Although long-term studies on population dynamics and vital rates are numerous in terrestrial ecology, they are lacking in marine and coral reef ecology (Edmunds and Riegl 2020; Pisapia et al. 2020). In the context of climate change impacts on coral reefs, addressing population dynamics of marine species is an important scientific and monitoring priority (Edmunds and Riegl 2020; Pisapia et al. 2020).

Short sharp periods of anomalous temperature known as marine heatwaves have caused unprecedented damage to marine habitats (Oliver et al. 2018; Holbrook et al. 2019), especially coral reefs (Ainsworth et al. 2016; Hughes et al. 2017b). As these events persist from several weeks to a few months, stress levels manifest in a cumulative way. Thermal stress events can be measured using the Degree Heating Week (DHW) metric by accumulating sea surface temperature (SST) anomalies exceeding an upper threshold of a species thermal tolerance over a multi-month time-window (Liu et al. 2003). Thus, stress magnitude based on DHW depends on both the duration and intensity of the event, and the threshold temperature (Supplementary Materials). Notably, DHW metrics have proven useful for evaluating coral bleaching (Heron et al. 2016; Kim et al. 2019). Excessive thermal stress stimulates a decoupling of the symbiosis between corals, the reef-building organisms on coral reefs, and their zooxanthellae, phototrophic symbiotic algae (Brown 1997). This results in the expulsion of zooxanthellae, coral bleaching, and can lead to mortality. The frequency, duration and scale of mass coral bleaching and mortality events are increasing (Hughes et al. 2017b; Smale et al. 2019) and have devastated numerous tropical coral reefs.

Responses of coral assemblages to thermal stress differ markedly between high and low latitudes, due to various reasons, including environmental variation, bleaching history, and taxonomic composition (West and Salm 2003). In the tropics, branching Acropora spp. are generally more vulnerable to thermal stress and bleaching, with slow-growing massive taxa (e.g. Porites spp.) more stress tolerant (Marshall and Baird 2000; McClanahan et al. 2020, but see Guest et al. 2012). In contrast, Acropora spp. in high-latitude reefs appear to be more resistant to thermal stress (Schleyer et al. 2008; Harrison et al. 2011; Dalton et al. 2020), and Porites spp. less resilient (Dalton and Carroll 2011; Harrison et al. 2011; Kim et al. 2019). While anomalous temperatures and resulting bleaching-induced mortality decimated tropical coral populations in the north and mid-Great Barrier Reef in 2016, 2017 and 2020 (Ainsworth et al. 2016; Hughes et al. 2017b; Hughes and Pratchett 2020), lesser bleaching impacts were recorded at high eastern Australian latitudes (Kim et al. 2019). Nonetheless, episodes of coral bleaching at high-latitudes are becoming increasingly severe, with localised minor events in the 1980s and 1990s (Cook et al. 1990; Celliers and Schleyer 2002; Schleyer et al. 2008; Hongo and Yamano 2013) superseded by more destructive events in the 2010s (Dalton and Carroll 2011; Harrison et al. 2011; Kim et al. 2019). These bleaching and mortality events have long-term implications on coral reef composition (Dalton and Carroll 2011; Hongo and Yamano 2013), population dynamics, and demographic processes (Cant et al. 2020).

The impact of low-magnitude thermal stress on coral populations (i.e. elevated temperatures below bleaching thresholds) remains poorly known, as it is difficult to detect in situ. Coral stress responses can be accurately quantified in laboratory experiments by measuring rates of calcification, photosynthesis or respiration to determine thermal optima (i.e. optimal and threshold temperatures for metabolic function) (Edmunds and Burgess 2018; Silbiger et al. 2019). However, unless bleaching occurs, these coral responses cannot be detected by visual census in the field. Evidence of high-magnitude thermal stress responses (i.e. coral bleaching and mortality) are more common (Crabbe 2009; Kim et al. 2019; McClanahan et al. 2020),
highlighting the urgent need to quantify the role of low-magnitude thermal stress in driving coral population dynamics.

Coral size-frequency distributions provide valuable insights into population processes and the vital rates of survival, growth, and recruitment (Babcock 1991; Bak and Meesters 1998; Gilmour 2004; Smith et al. 2005; Adjeroud et al. 2007; Alvarado-Chacón and Acosta 2009; Crabbe 2009; Leray et al. 2012; Bauman et al. 2013; Anderson and Pratchett 2014; Zhao et al. 2014; Dietzel et al. 2020; Pisapia et al. 2020), because colony size is strongly associated to changes in other vital rates (Madin et al. 2020). In general, strong positive or negative skewness of size-frequency distributions can be indicative of greater recruitment processes, aging populations, or disproportionate mortality of either the small or large colonies (Bak and Meesters 1998; Adjeroud et al. 2007; Zhao et al. 2014). Temporal changes in mean coral size can reflect cohort growth or size-specific mortality, while changes to variance can indicate high mortality throughout size classes (Bak and Meesters 1998; Anderson and Pratchett 2014). These inferences can be used to assess spatial and interspecific variation in demographic processes (Dietzel et al. 2020), indicate population health (Smith et al. 2005), and identify limitations to population persistence (Precoda et al. 2018). However, disentangling the demographic drivers of given size-frequency distributions can be difficult (i.e. recruitment, growth or mortality). While assuming a constant supply of recruits can help interpret growth and mortality (Babcock 1991), such assumptions may be invalid in the subtropics (Harriott 1999b).

Temporal demographic assessments are key to capturing short-lived population dynamics. Most published coral size-structure assessments use once-off spatial surveys (e.g. Alvarado-Chacón and Acosta 2009; Anderson and Pratchett 2014), with very few temporal assessments exceeding 2 yr (Babcock 1991; Gilmour 2004; Crabbe 2009; Leray et al. 2012). These temporal studies emphasize greater stress responses in juveniles and smaller size classes, in line with the classification of corals as r-strategists (Loya 1976). Higher susceptibility of smaller size classes is often linked to the disturbance dynamics model, with causes including storms (Gilmour 2004; Crabbe 2009), sedimentation (Gilmour 2004), Crown-of-Thorns starfish outbreaks (Leray et al. 2012), and bleaching episodes (Crabbe 2009; Leray et al. 2012). Reinforcing this model, population size-frequency distributions often remain relatively stable during disturbance-free periods (Babcock 1991; Gilmour 2004). These studies demonstrate the valuable inference possible from temporal assessments of population size-frequency distributions. However, they all focus on tropical reefs, supporting the urgent need for equivalent long-term coral demographic studies in the subtropics to understand coral population trajectories in these vulnerable marginal environments.

Here we investigate the population dynamics of the subtropical endemic coral Pocillopora aliciae (Schmidt-Roach et al. 2013) in a region of rapidly changing climate in subtropical eastern Australia over a 10-yr period (2010–2019) during which this species suffered severe bleaching and mortality in response to heat stress (Kim et al. 2019; Cant et al. 2020). Specifically, we address three questions: (1) How do survival, growth, and recruitment vary temporally, as indicated by population size-frequency distributions? (2) How does mass coral bleaching affect long-term population trends, as inferred from coral densities? (3) Do coral population processes such as coral recruitment correlate with marine heatwave intensity, and does this effect vary spatially?

Methods

Study site and species

The present study was conducted at the Solitary Islands Marine Park (30° South) in subtropical eastern Australia. In situ sea water temperature and coral size-frequency distributions were assessed at 4 sites ranging from 2 to 11 km offshore (Fig. 1). The physical and chemical oceanography of this region is primarily influenced by the warm East Australian Current (EAC), which flows poleward approximately 50 km offshore following the continental margin at the 1500 m isobath (Malcolm et al. 2011). Accordingly, offshore islands are more strongly influenced by seasonal eddies and periodic warming, and have water temperatures that are more variable and on average 0.5 °C and 1.0 °C warmer than mid-shelf and inshore islands, respectively (Malcolm et al. 2011). This drives strong cross-shelf gradients in biotic communities, with distinct fish communities between offshore, mid-shelf and inshore islands (Malcolm and Ferrari 2019), and a greater prevalence of tropical species of coral and fish offshore (Harriott et al. 1994; Sommer et al. 2014; Malcolm and Ferrari 2019). In this study we surveyed 2 replicate offshore islands (North Solitary Island and South Solitary Island) and 2 replicate mid-shelf islands (Northwest Solitary Island and Southwest Solitary Island) in line with previously established cross-shelf island classifications (Malcolm et al. 2011; Malcolm and Ferrari 2019) (Fig. 1).

We use the subtropical endemic Pocillopora aliciae (Schmidt-Roach et al. 2013) as a model organism to understand demographic associations with thermal stress. In 2016, Pocilloporidae bleached more severely than other coral taxa at the Solitary Islands (Kim et al. 2019) and in other areas globally (Dalton et al. 2020; McClanahan et al.
2020). *Pocillopora aliciae* was recently separated from *Pocillopora damicornis* based on genetic analyses (Schmidt-Roach et al. 2013) and is the most common species of *Pocilloporidae* in the Solitary Islands. *Pocillopora aliciae* are facultative brooders, observed to release fully developed planulae following the December new moon (Schmidt-Roach et al. 2013), similar to closely related *P. damicornis*, which also have high localised self-recruitment (Figueiredo et al. 2014). *Pocillopora aliciae* is found between Cape Byron (28.6° S) and Sydney (33.8° S).

Coral data

Coral population surveys were conducted in the austral spring of 2010, 2012, 2016 (referred to as 2016a), 2018, and 2019, and during a coral bleaching event in April 2016 (referred to as 2016b) (Fig. S1). At each site, three consecutive haphazardly placed 30-m belt transects were run at 8–10 m water depth. Downward-facing photographs were taken every metre, forming a 1-m-wide belt, and each photograph included a 50 cm calibration stick (Sommer et al. 2011, 2014). Individual coral sizes were extracted from the photographs using ImageJ region of interest (ROI) tools and R (Version 1.2.1335), with any dead portions excluded and the incidence of partial mortality recorded, although very rare (Supplementary Materials). Bleaching severity was homogeneous across each colony and was recorded as normal, moderate, or severe whitening (< 25%, 26–75%, > 76% respectively). *Pocillopora aliciae* colonies were categorised as adults or juveniles, with a cut-off of 10 cm², the minimum planar area at onset of sexual maturity (10 cm²) for a closely related species, *Stylophora pistillata* (Hall and Hughes 1996) (Supplementary Materials). Demographic processes were inferred from size-frequency distributions, as individual coral colonies were not followed through time, preventing direct measurements of growth and mortality rates.

Temperature data

To examine effects of cumulative thermal stress on coral colony density, we calculated thermal stress using an adaptation of the Degree Heating Weeks (DHW) metric for in situ temperature data (as opposed to remotely sensed SST), based on an 18-yr in situ temperature record and a 34-yr remotely sensed SST record (Supplementary
Materials). This approach resulted in two in situ DHW metrics calculated using different temperature accumulation thresholds (DHW_{IC} and DHW_{OC}). Further information is in the Supplementary Materials. NOAA Coral Reef Watch (CRW) relate DHW values to bleaching alert levels: No Bleaching (DHW = 0 °C-weeks), Possible Bleaching (0 > DHW > 4 °C-weeks), Significant Bleaching Likely (4 > DHW > 8 °C-weeks), Severe Bleaching and Significant Mortality Likely (DHW > 8 °C-weeks). Since bleaching in this study was not observed below in situ DHW_{IC} of 10 °C-weeks, we consider thermal stress < 10 °C-weeks as a low-magnitude thermal stress. The maximum thermal stress experienced by juvenile corals (up to approx. 2 yr old) was measured using the maximum juvenile thermal stress metric (DHW_{IC-max} & DHW_{OC-max}). This metric was calculated as the maximum in situ DHW experienced in the two pre-survey years and was computed by site and time-point. Juvenile corals in this study were up to approximately 2 yr old based on P. aliciae growth rates (Harriott 1999a). Notably, DHW trends were only retained in this manuscript for the DHW metric which provided best-fitting models based on the Akaike Information Criterion (c.f. next section).

Statistical analysis

How do survival, growth, and recruitment vary temporally, as indicated by population size-frequency distributions? Variation in size-frequency distributions were compared among years and sites based on probability density curves and the following descriptive statistics: mean colony area (i.e. size-frequency distribution mean), coefficient of variation, skewness, and kurtosis (Peterson and Carl 2020). All summary statistics were computed on log-transformed colony area measurements (Bak and Meesters 1998; Anderson and Pratchett 2014). We used colony planar area to estimate size as it relates to age and fecundity (Babcock 1991; Madin et al. 2020). Changes in mean colony area may indicate cohort growth but can be masked by high recruitment and mortality processes (Bak and Meesters 1998). Coefficient of variation (CV = σ/µ) can be used to compare populations with different mean colony sizes (Bak and Meesters 1998) and skewness to measure the asymmetry of size-frequency distributions, which can indicate recruitment and large-colony mortality processes (Bak and Meesters 1998; Grinyó et al. 2016). Specifically, positive skewness can reflect a high proportion of recruits/juveniles compared to large colonies, with the opposite true for negative skewness. High kurtosis can suggest slow growth transitions or low recruitment and large-colony survival (Anderson and Pratchett 2014), while low kurtosis describes a flat distribution undergoing fast growth transitions or high recruitment and large colony survival. Temporal variations in size-frequency distributions were tested among years (fixed effect) and among transects (random effect) using mixed effect ANOVAs paired to Tukey tests (Bates et al. 2015) for each site independently.

How does mass coral bleaching affect long-term population trends, as inferred from coral densities? Coral colony density (m⁻²) was calculated as the number of corals per photo for all size classes together, and again for adult and juvenile size classes separately (Fig. S1a, b), as juvenile coral density is closely linked to recruitment processes. Temporal variations in colony density among years (fixed effect) and among sites and transects (nested random effects: transect within site) were tested using Negative Binomial generalised linear mixed effect models (GLMM) paired to Tukey tests (see below for validation steps) (Bates et al. 2015). These tests were carried out independently for offshore and mid-shelf regions due to striking cross-shelf differences in P. aliciae abundance and known cross-shelf gradients in coral assemblage (Harriott et al. 1994; Sommer et al. 2014; Dalton and Carroll 2011).

Do coral population processes such as coral recruitment correlate with marine heatwave intensity, and does this effect vary spatially? The effect of maximum juvenile thermal stress (DHW_{IC-max}, fixed effect) on coral density among years, sites, and transects (nested random effects: transect within site within year) was tested using GLMMs with a log link Negative Binomial variance structure suitable for zero-inflated count data (Fig. S8 & Fig. S9 for DHW and Temporal models respectively). Variations in the DHW_{IC-max} effect between offshore and mid-shelf positions were tested using an interaction term (DHW_{IC-max} * shelf position). Routine model validation steps included checking residuals versus fitted values, nonlinear residual patterns, overdispersion, and zero-inflation. Independent GLMMs were built for juvenile and adult coral density. Pseudo-$R^2$ values were calculated to determine percentage of explained variation. The models using the 1 °C temperature threshold filter (DHW_{IC-max}) outperformed models without the 1 °C filter (DHW_{OC-max}) shown by lower AIC values (Chi-sq, $χ = 0.5$, $P < 0.01$; AIC_{OC–AIC_{IC}} = 2.0).

Results

Temperature

In situ water temperatures from the baseline period 2001–2009 ranged from 17.7 to 26.8 °C and 17.5–26.1 °C for offshore and mid-shelf sites, respectively (Fig. 2, grey points). The annual mean baseline temperature trend ranged from 19.0 ± 0.2 °C in August to 24.7 ± 0.2 °C in March. Throughout the year, difference in daily
temperatures between offshore and mid-shelf sites varied by 0.5 ± 0.2 SD °C, with warmer islands offshore and cooler islands mid-shelf. Notably, variations in daily baseline temperatures were much higher between years (1.8 SD) than among sites (0.4 SD), supporting the decision to assess temperature trends as among-site averages.

Between 2009 and 2014, accumulated heat stress (DHW$_{1C}$) was low, not exceeding 8 °C-weeks (Fig. 2). Across sites, mean DHW$_{1C}$ reached 12.2 °C-weeks in 2015 (14.1, 13.5, NA, and 8.6 °C-weeks for North, South, Northwest, and Southwest Solitary Islands, respectively) and 14.0 °C-weeks in 2016 (18.0, 13.5, 12.6, and 12.1 °C-weeks for North, South, Northwest, and Southwest Solitary Islands, respectively).
Islands, respectively). The rate of onset of the heatwave in 2016 was considerably faster than in 2015, where high-level heat stress (> 10 °C-weeks among sites) was reached in 42 days, compared with 60 days. In 2017 and 2018, maximum DHW values were below 8 °C-weeks. However, in 2019, values were again higher, exceeding 9.3 °C-weeks. During 2016, when coral bleaching occurred at all study sites, 221 days were hotter than baseline mean temperatures but only 69 days were cooler (i.e. outside the 95% CI, Fig. 2). The heatwave persisted for 41 days (06/02/16–19/03/16) at daily temperature anomalies > 1 °C, 20 days of which were 0°C weeks. During 2016, when coral bleaching occurred at all study sites, 221 days were hotter than baseline mean temperatures but only 69 days were cooler (i.e. outside the 95% CI, Fig. 2). The heatwave persisted for 41 days (06/02/16–19/03/16) at daily temperature anomalies > 1 °C, 20 days of which were > 2 °C and with a maximum of 2.9 °C (27/02/16). Notably, all DHW values were scaled higher for DHW0°C; however, the main trends remained the same as for DHW1C.

**Demographic time series**

A total of 1558 images were annotated comprising 7196 P. aliciae colonies. The distribution of coral colony sizes ranged from 0.2 to > 2000 cm² (circular diameter equivalent: 0.5 to > 50 cm) (Fig. S4). Given their small size, the smallest corals detected were re-examined; however, no mistakes were found from image analyses. Moreover, neither the removal of smallest corals from analyses (diameter < 1 cm) nor setting a lower juvenile-adult size cutoff (5 cm²) made qualitative changes to overall results (Fig. S7). Under a loge transformation, which standardised coral sizes and increased the resolution of highly abundant small colonies (Bak and Meesters 1998), the size-frequency distribution data ranged from -1.8 to 7.7 loge values. Distributions varied significantly through time (Fig. 3 & Table S1) and information on coral density for juveniles and adults (Fig. 4), five distinct patterns emerged from the time-series dataset, with distinct differences between offshore and mid-shelf coral populations. Notably, these population-level patterns are unlikely to be influenced by partial mortality, which was present in < 5% of surveyed coral colonies (Fig. S5).

1. At offshore sites, coral densities were consistently higher than at mid-shelf sites (+ 3.5 ± 1.4 m⁻²; Mann–Whitney U, W = 0, P < 0.01).
2. Depending on shelf position, recruitment pulses were temporally isolated with higher skewness for offshore coral populations. Recruitment (inferred from juvenile coral densities) was likely the main driver of skewness offshore, shown by a positive linear relationship between both variables (Fig. S10). However, this was not the case for mid-shelf populations (Fig. S10). A bimodal size-frequency distribution biased toward juvenile corals (skew = 1.14) was detected at North Solitary Island in 2010, suggesting a considerable offshore recruitment pulse. This is supported by a similar but smaller peak at South Solitary Island (skew = 0.30). In contrast, no recruitment pulses were detected at mid-shelf populations in 2010 (Northwest Solitary Island skew = −0.22, Southwest Solitary Island skew = 0.01). However, an increase in mid-shelf skewness (Northwest Solitary Island skew = 0.25, Southwest Solitary Island skew = 0.04) and juvenile coral density (+ 0.2 m⁻²) in 2012 suggests a marginal increase in recruitment during that period. As partial mortality was rare, it was unlikely that pulses in the density of juvenile size-class corals were caused by processes other than recruitment (Fig. S5).
3. Multiannual growth transitions from juvenile to adult stages were indicated by decreasing skewness and increasing mean colony size (Table 1) and adult colony density (Fig. 4) with time. This trend was striking for offshore size-frequency distributions following the offshore recruitment pulse (2010–2016). During this period, adult colony density increased from 2.2 to 4.7 m⁻² (Fig. 4 & Table S2; GLMM Tukey, P > 0.05), suggesting cohort growth of juveniles and thus offshore recruitment success. However, there was a lack of cohort growth in mid-shelf populations. Despite the potential of increased recruitment in 2012 (Fig. 3 inferred from skewness and mean size), adult colony density had declined by 2016, 4 yr later.
4. Coral bleaching in 2016 (Fig. S1 & S3) caused substantial declines in Pocillopora populations across the Solitary Islands. Six months post-bleaching, juvenile density had declined by 88% compared to 2012 levels (3.2–0.4 m⁻²; Fig. 4 & Table S2; GLMM Tukey, P > 0.05), while adult colony density had declined by 47% compared to 2016a levels (Fig. 4 & Table S2; GLMM Tukey, P > 0.05). This represents a 51% decline in total coral density post-bleaching (5.9–2.9 m⁻²; Fig. 4 & Table S2; GLMM Tukey, P > 0.05). Coral bleaching in 2016 was recorded across all sites, but with higher incidences of severe bleaching in South and Southwest Solitary Islands (Fig. S3).
5. Early recovery of juvenile density post-bleaching (by 2018) was higher for offshore coral populations (42%; 0.4–0.7 m⁻²; Fig. 4 & Table S2; GLMM Tukey, P < 0.05) than for mid-shelf populations (23%; 0.13–0.16 m⁻²; Fig. 4 & Table S2; GLMM Tukey, P > 0.05). However, by the following year, offshore juvenile density had fallen back to the level immediately post-bleaching (Fig. 4 & Table S2; GLMM Tukey, P < 0.05).
Demographic effect of thermal stress

Maximum juvenile thermal stress (DHW_{1C-max}) and shelf position explained 60% of variation in *P. aliciae* recruitment, inferred by the exponential decay of juvenile coral density with increasing maximum juvenile thermal stress offshore (Fig. 5a). The effect size ($\beta = \text{slope}$) of maximum juvenile thermal stress (DHW_{1C-max}) at offshore reefs ($\beta = -0.20$) was double that of mid-shelf reefs ($\beta = 0.20 + 0.12 = -0.08$), shown by a significant interaction term (GLMM, term = DHW_{1C-max} * shelf position, $\beta = -0.12, z = -3.0, P < 0.005$). This indicates that recruitment processes (i.e. larval settlement and growth to juvenile stages) were more successful offshore and at low levels of maximum juvenile thermal stress. There was no effect of maximum juvenile thermal stress on adult colony density (GLMM, term = DHW_{1C-max}, $z = -1.4, P > 0.05$), and only a marginal effect of shelf position (GLMM term, $z = 1.9, P = 0.09$).

Discussion

We investigated demographic patterns of a subtropical endemic coral over a 10-yr period and linked these patterns to in situ accumulated thermal stress. Together, our results reveal demographic processes and acute ontogenetic stage-specific associations with thermal stress for offshore coral populations at this high-latitude climate change hotspot. *Pocillopora aliciae* populations in the Solitary Islands are likely supported by large infrequent recruitment pulses that maintain population persistence and the high number of...
adult colonies recorded in our study (Fig. 3). The low density of P. aliciae at mid-shelf islands suggests that, although the populations may be viable, they rely heavily on sporadic recruitment from outside, likely nearby sources, congruent with the findings of Cant et al. (2020). Thermal stress associations were observed, whereby suppressed recruitment processes occurred during periods of high heat stress and even moderate levels of heat stress (Fig. 5) not normally considered detrimental for corals. We also recorded a 51% decline in P. aliciae colony density post-2016 and the most intense marine heatwave (in terms of DHW1C) at the Solitary Islands since at least 1985 (Fig. 3). The inherent reliance on sporadic recruitment pulses, combined with recruitment suppression under moderate heatwaves, has the potential to severely reduce this subtropical endemic population.

Population dynamics

Pocillopora aliciae populations appear to have followed the disturbance dynamics model (Gilmour 2004; Crabbe 2009; Leray et al. 2012), which proposes that disturbances, such as storms, sedimentation and Crown-of-Thorns starfish outbreaks, can cause abrupt changes in coral populations and size-frequency distributions. In this study, abrupt changes to P. aliciae size structure were noted after severe bleaching during a marine heatwave in 2016; however, other changes in P. aliciae size structure could have been missed due to a data gap from 2012 to 2016. We demonstrate a strong association between heat stress and declines in P. aliciae population density and recruitment but cannot imply causation since other potential disturbances were not measured in this study. For instance, storm damage has impacted coral assemblages in eastern Australia (Harriott and Smith 2000; Sommer et al. 2018) and may be important in driving some observed patterns. The Coffs Harbour Waverider Buoy, located 16 km due south of South Solitary Island, recorded severe storm events with maximum wave heights exceeding 11 m twice during this study period, in January 2013 and June 2016 (Manly Hydraulics Laboratory, NSW Government).

Recovery dynamics for coral populations are under intensifying pressure due to the increasing frequency of marine heatwaves and mass coral bleaching events, which are forcing ever shorter recovery intervals (Hughes et al. 2017b; Oliver et al. 2018). Over several years, coral populations can naturally recover from disturbances including storms (Gilmour 2004; Crabbe 2009), sedimentation (Gilmour 2004), Crown-of-Thorns starfish outbreaks (Leray et al. 2012), and coral bleaching mortality (Babcock 1991;
Table 1 Summary statistics of log-transformed size-frequency distributions by site and year, showing sample size (n), colony density (No./m²), mean log-transformed colony size (cm²), coefficient of variation (CV), skewness (Skew), kurtosis (Kurt), and the Tukey group assigned from site-specific GLMMs testing size-frequency distributions between years for offshore (North and South) and mid-shelf (Northwest and Southwest) Solitary Islands.

| Shelf position | Site       | Year | n   | No./m² | Mean size (cm²) | CV | Skew | Kurt | Tukey group |
|----------------|------------|------|-----|--------|-----------------|----|------|------|-------------|
| Offshore       | North      | 2010 | 891 | 9.91   | 1.06            | 1.64 | 1.14 | 0.18 | D           |
|                |            | 2012 | 745 | 10.51  | 2.23            | 0.5 | 0.19 | 0.13 | A           |
|                |            | 2016a| 600 | 6.87   | 3.13            | 0.4 | −0.29 | 0.37 | B           |
|                |            | 2016b| 348 | 3.92   | 3.46            | 0.31 | 0.4 | 0.13 | C           |
|                |            | 2018 | 252 | 2.83   | 3.24            | 0.37 | −0.3 | 0.25 | BC          |
|                |            | 2019 | 122 | 1.59   | 3.27            | 0.29 | 0.2 | −0.26 | BC          |
|                | South      | 2010 | 655 | 7.28   | 2.98            | 0.63 | 0.3 | 1.17 | C           |
|                |            | 2016a| 772 | 8.62   | 3.64            | 0.37 | 0.06 | 0.57 | A           |
|                |            | 2016b| 371 | 4.14   | 3.58            | 0.31 | −0.15 | 0.37 | AB          |
|                |            | 2018 | 453 | 5.04   | 3.39            | 0.44 | −0.07 | 0.89 | B           |
|                |            | 2019 | 248 | 3.07   | 3.59            | 0.32 | 0.48 | −0.61 | AB          |
| Mid-shelf      | Northwest  | 2010 | 124 | 1.38   | 3.18            | 0.58 | −0.22 | 0.76 | A           |
|                |            | 2012 | 196 | 2.28   | 3.17            | 0.42 | 0.25 | 0.35 | A           |
|                |            | 2016a| 125 | 1.4    | 3.68            | 0.4 | −0.04 | 0.45 | AB          |
|                |            | 2016b| 85  | 0.95   | 3.8             | 0.39 | 0.11 | 0.04 | AB          |
|                |            | 2018 | 79  | 0.89   | 3.65            | 0.38 | −0.07 | 0.52 | AB          |
|                |            | 2019 | 15  | 1      | 4.12            | 0.34 | 0.23 | 0.71 | B           |
|                | Southwest  | 2010 | 158 | 1.76   | 3.27            | 0.48 | 0.01 | 0.66 | AC          |
|                |            | 2012 | 267 | 2.97   | 2.89            | 0.49 | 0.04 | 0.49 | A           |
|                |            | 2016a| 211 | 2.35   | 3.41            | 0.48 | −0.01 | 0.52 | BC          |
|                |            | 2016b| 121 | 1.36   | 3.7             | 0.36 | −0.07 | 0.05 | BCD         |
|                |            | 2018 | 155 | 1.74   | 3.82            | 0.37 | 0.02 | 0.73 | BD          |
|                |            | 2019 | 138 | 1.75   | 4.18            | 0.34 | 0.09 | 1.07 | D           |

Fig. 5 Effects of maximum juvenile thermal stress (DHW1C-max) on: a juvenile coral density and b adult coral density based on GLMMs, for offshore (red shading) and mid-shelf (blue shading) regions. Fitted values (line ± 95% bootstrapped CI) are based on photo-level counts, while points show transect-level mean coral density ± 95% CI and site-level DHW1C-max values.
However, we observed no evidence for early recovery of *P. aliciae* populations in the Solitary Islands to pre-bleaching levels (2010–2016a) within the short post-bleaching timeframe of our study (3 yr). Even in 2019, juvenile and adult coral densities remained at the same levels recorded directly after the mass bleaching event in 2016. *Pocillopora* spp. are predominantly weedy species (Ward 1992; Darling et al. 2012; Edmunds 2017) and effective colonisers after disturbance, but *P. aliciae* in the Solitary Islands have not yet responded in this way. However, 3 yr of post-disturbance sampling is insufficient to comprehensively assess recovery patterns. The data presented here suggest that the persistence of *P. aliciae* coral populations is likely hampered by sporadic recruitment and recruitment failure even under moderate thermal stress.

This study highlights the importance of sporadic recruitment pulses in sustaining subtropical coral populations. While typically there are stable patterns in coral demographic processes during disturbance-free periods (Babcock 1991; Gilmour 2004; Crabbe 2009; Leray et al. 2012), this study recorded highly variable recruitment and growth during such periods. Successful recruitment was indicated by strong positive-skewed size-frequency distributions in 2010 followed by concurrent cohort growth (Fig. 3). However, a lack of cohort growth in mid-shelf sites suggests recruitment failure that may have been influenced by colony breakage and mortality due to severe storms and wave heights in 2013. As partial mortality was so rare in this study, it is likely that the observed population size-structure trends were in part influenced by sporadic recruitment pulses. Notably, only one such pulse was observed over the 10 yr timeframe of this study (in 2010, Fig. 3), suggesting a strong reliance of high-latitude *P. aliciae* populations on such processes. This mirrors findings from other high-latitude coral populations that also are recruitment limited (e.g. *Plesiastrea versipora*, Precoda et al. 2018). The recruitment pulse was much larger at North Solitary Island than at South Solitary Island. Given similar thermal extremes (95th percentile temperatures) at both sites during the 2009–2011 period, the differences in recruitment may have been attributable to other factors, such as substrate availability, other physical oceanographic drivers, or localised self-recruitment typical of brooding corals (Ward 1992; Figueiredo et al. 2014).

**Thermal stress and bleaching**

In 2016, severe bleaching of *P. aliciae* occurred during an intense heat stress event. Although there was a heat stress event in 2015, the magnitude and rate of onset were lower (Fig. 2), and only low levels of bleaching were noted (Malcolm personal comms). Moreover, maximum juvenile thermal stress (DHW$_{1C\text{-max}}$) was correlated with temporal variation in successful recruitment processes (exponential decay of juvenile coral density, Fig. 5). Slight increases in juvenile coral density at offshore sites post-bleaching (2018) were associated with reduced DHW$_{1C\text{-max}}$ (Fig. 2); however, further reductions in recruitment were observed in 2019 (Fig. 5), associated with increased thermal stress (Fig. 2). Comparable thermal stress associations between adult colony density and DHW$_{1C\text{-max}}$ were not evident, probably because adult corals likely experienced higher DHWs before the 2-yr pre-survey window used to calculate the DHW$_{1C\text{-max}}$ metric. Non-bleaching physiological responses to low-magnitude thermal stress (i.e. calcification, photosynthesis, or respiration) are similar for adult and juvenile corals, as determined from tank experiments (Edmunds and Burgess 2018). However, the effects of low-magnitude thermal stress are rarely reported from the field, in part due to the lack of an easily measurable response (i.e. bleached corals) (Edmunds 2005). Our study suggests that recruitment processes may be closely linked to thermal stress, providing important field observations of stage-specific coral associations to low-magnitude thermal stress. However, recruitment failure in the aftermath of major disturbances has also been attributed to declines in both the reproductive output of remaining adult corals and the size of the remaining population’s reproductive stock (Hughes et al. 2019). Given that we observed declines in both adult and juvenile density post-bleaching, such processes may also be influencing post-disturbance recruitment failure at the Solitary Islands.

**Future outlook**

Future thermal regimes for the Solitary Islands paint an uncertain picture for the persistence of the subtropical endemic *P. aliciae*, with likely future declines given its demographic responses to thermal stress (Cant et al. 2020). This uncertainty is driven by both acute thermal stress events and long-term climatological trends. In eastern Australia, the intensity, frequency, and duration of acute thermal stress events have been increasing over the past century (Oliver et al. 2018; Holbrook et al. 2019), with such trends predicted to continue into the coming century (Hughes et al. 2017b). Such marine heatwaves have already severely damaged local and regional endemic coral populations (Beger et al. 2014; Kim et al. 2019) and will continue to supress recovery processes (Hughes et al. 2019). Our demographic study is consistent with the finding that subtropical endemics and specialists were the hardest hit taxa from recent bleaching events in subtropical eastern Australia (Harrison et al. 2011; Kim et al. 2019; Dalton et al. 2020). For instance, *Acropora* spp., the dominant reef builders in the tropics, were not affected in
the Solitary Islands (Kim et al. 2019). Thus, species will likely respond unevenly to acute thermal stress in this region (Kim et al. 2019). Assessing whether the demographic responses of other genera and species mirror our findings for *P. alicae* is a next step for this research, though it is likely that demographic responses will differ among taxa, much like the taxa-specific nature of bleaching responses (Kim et al. 2019). This single-species study highlights the urgent need to investigate the complex dynamics of high-latitude marine communities for multiple taxa, to assess the vulnerability of these ecosystems to climate change and future warming.

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Declarations

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

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