Coral Reefs (2024) 43:1331–1343
https://doi.org/10.1007/s00338-024-02541-5

REPORT

Comparison of juvenile coral assemblages between Australia's Coral Sea and Great Barrier Reef Marine Parks

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Received: 7 December 2023 / Accepted: 1 August 2024 / Published online: 14 August 2024

Abstract Densities of juvenile corals (≤ 50 mm diameter) are expected to vary between geographically isolated and more spatially proximate reefs, and may constrain local recovery potential. This study compared juvenile coral densities and their relationships with local abundance of adult congenerics at geographically isolated reefs within Australia's Coral Sea Marine Park (CSMP) versus highly connected reefs within the Great Barrier Reef Marine Park (GBRMP). Three latitudinal regions and two habitats (reef crest and slope) were examined within both marine parks to test for spatial variation. Densities of juvenile corals in the CSMP (13.99 ± 0.72 juveniles 10 m^{-2}) were significantly lower compared to those in the GBRMP (23.72 ± 1.86 juveniles 10 m^{-2}). Specifically, there were significantly less *Acropora* and *Pocillopora* juveniles on the reef crest in the central CSMP compared to the GBRMP. Relationships between juvenile abundance and percent coral cover were greatest for *Acropora* and *Pocillopora* in the GBRMP. This may be due to the low range of coral cover estimates recorded in the CSMP, especially for *Acropora* (0–15%). Low juvenile coral abundance, and in particular, the lack of fast-growing juvenile corals (e.g., *Acropora*) in the Central CSMP, in combination with low cover of broodstock (particularly *Acropora*) on CSMP reefs, poses a significant constraint on post-disturbance recovery capacity, possibly attributable to isolation and limited connectivity among reefs in this region.

Keywords Juvenile Corals · Replenishment · Reef Recovery · Recruitment · Connectivity

Introduction

The persistence and replenishment of scleractinian coral populations is fundamentally dependent on the supply and settlement of larvae, as well as subsequent growth and survival of juvenile corals (Pearson 1981; Doropoulos et al. 2015; Holbrook et al. 2018). Replenishment of coral populations is particularly important given recent increases in the frequency and diversity of disturbances that are causing elevated rates of coral mortality (Gardner et al. 2003; De'ath et al. 2012; Ortiz et al. 2018; Mellin et al. 2019; Bozec et al. 2022). Interspecific differences in recovery and replenishment capacity will also have a major influence on the structure of coral assemblages (Gilmour et al. 2013; Pratchett et al. 2020). The ability for coral populations to recover and reassemble following extensive coral loss may be constrained by larval supply, which may be extremely limited following loss of broodstock (Chong-Seng et al. 2014; Hughes et al. 2019), and the early post-settlement survival of recruits (Chong-Seng et al. 2014). As such, the density of juvenile corals may be a useful proxy for the recovery potential of coral populations following disturbance (Penin et al. 2010). With disturbances predicted to increase in frequency and severity (Oliver et al. 2018; Walsh et al. 2019), it is becoming increasingly important to understand differential

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-024-02541-5.

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recovery capacity among reefs and species (e.g., Gilmour et al. 2013).

Where coral recovery and replenishment are conditional upon larval supply and recruitment, the spatial arrangement of reefs, as well as the extent and severity of disturbances, are critical determinants of resilience (Gilmour et al 2013). This will further affect which species are likely to recover and predominate in the aftermath of disturbances (e.g., Underwood et al. 2009, 2020). Within more proximal reef systems (where there is limited distance between individual reefs, and/ or continental fringing reefs), coral larvae are likely to be readily exchanged among reefs (Wolanski and Spagnol 2000; Cetina-Heredia and Connolly 2011; Andutta et al. 2012; Golbuu et al. 2012; Figueiredo et al. 2022). In contrast, geographically isolated reefs are likely to be more reliant on self-recruitment at the scale of individual reefs (Jones et al. 2009; Gilmour et al. 2013). Following spatially discrete disturbances, such as cyclones, there is limited risk of compromising all source populations on proximal reefs, whereas comprehensive coral mortality may occur on isolated reefs, leading to recruitment limitation and protracted recovery (Gilmour et al. 2013). However, isolated, oceanic reefs, may also benefit from increased distance from land and corresponding anthropogenic pressures (Box and Mumby 2007; Fabricius et al. 2008; Adjeroud et al. 2010; Thompson et al. 2014). These favourable conditions may play a vital role in facilitating the recovery process, potentially compensating for recruitment limitation.

Coral replenishment is increasingly measured based on the abundance of juvenile corals (corals between 1 and 5 cm diameter; Jonker et al. 2019), which are typically distinguished at the genus or family level. Surveying corals of this size takes into account potentially high levels of early post-settlement mortality experienced by newly settled recruits (Penin et al. 2010) and as such, may be a better proxy of recovery capacity (Graham et al. 2015; Evans et al. 2020). Indeed, the relative abundance of adult corals correlates more with the composition of juvenile corals, rather than recently settled recruits (Penin et al. 2007; Adjeroud et al. 2010; Jonker et al. 2019; Pedersen et al. 2019). Relationships between adult and juvenile corals (hereafter juvenile-adult relationships) have been assessed within or among sites or reefs located hundreds of metres to tens of kilometres apart (Chiappone and Sullivan 1996; Edmunds 2000; Penin et al. 2010; Penin and Adjeroud 2013; Pedersen et al. 2019), where generally positive relationships suggest that recruitment from external sources may be limited. High local retention and self-recruitment is also evident at the reef scale in high-resolution hydrodynamic models (i.e., 100–200 m) (Figueirdo et al. 2022; King et al. 2023; Saint-Amand et al. 2023). This is likely exacerbated on isolated reefs. Apparent differences in connectivity between isolated and more proximal reef systems may lead to stronger juvenile-adult relationships on isolated reefs, owing to the increased reliance on self-recruitment.

Beyond the influence of stock-recruitment relationships, juvenile coral abundance varies spatially, in response to a variety of biotic and abiotic factors, many of which differ substantially between geographically isolated, oceanic reefs compared with more proximal, coastal reefs (Jonker et al. 2019; Couch et al. 2023). For example, high wave exposure characteristic of oceanic, isolated reefs (particularly on exposed crest habitats) may lead to lower juvenile coral abundance (Cardini et al. 2012; Mumby et al. 2013; Couch et al. 2023) than on coastal, proximal reefs. Conversely, oceanic, isolated reefs are expected to be less exposed to sedimentation and eutrophication which may benefit newly settled corals (Hunte & Wittenberg 1992; Koop et al. 2001). These differences in environmental factors may lead to contrasting recovery capacities between isolated and proximal reefs, although this has never been tested. Variables which influence the abundance and community structure of juvenile corals may also vary with latitude (Jonker et al. 2019; Nozawa et al. 2021), where coral recruitment and juvenile densities may be decreasing at low latitudes owing to climate change related disturbances (Price et al. 2019; Couch et al. 2023).

The purpose of this study was to compare the abundance and composition of juvenile scleractinian corals between geographically isolated reefs in Australia's Coral Sea Marine Park (CSMP) and more proximal reefs of Australia's Great Barrier Reef Marine Park (GBRMP), with the aim of better understanding differences (or similarities) in resilience, and especially recovery capacity within and between these two distinct reef systems. The relative isolation of CSMP reefs from many human- and land-based pressures, combined with oceanic conditions favourable for settlement (such as improved water quality), may result in higher rates of larval recruitment, and high recovery capacity than reefs in the GBRMP. However, following several major bleaching events (Oxley et al. 2005; Harrison et al. 2019; Hoey et al. 2021; Hughes et al. 2021; Burn et al. 2023; Huang et al. 2023) and frequent cyclones (Brewer et al. 2007; Ceccarelli et al. 2013), coral cover on some reefs, especially in the CSMP, remains low. This, combined with anticipated constraints on connectivity among the widely separated reefs in the CSMP (Ceccarelli et al. 2013), may outweigh the positive effects of isolation from coastal processes and anthropogenic pressures, increasing vulnerability to major disturbances. In comparison, the high density and close proximity of individual reefs within the GBRMP may underpin strong population recovery following acute disturbances and localised coral depletion (Hughes et al. 2003; Graham et al. 2006), as there is presumed to be very high levels of inter-reef connectivity in the GBRMP (e.g., Hock et al. 2017; Condie et al. 2021), although this is predicted to decrease under future climate change (Figueiredo et al. 2022). With escalating disturbances, largely driven by emerging effects of global climate change that affect even the most isolated reef systems (Baumann et al. 2022; Gilmour et al. 2022), it is imperative to understand whether isolated reefs might have a higher or lower recovery capacity than more proximal, coastal systems.

Methodology

Study sites

The CSMP lies within Australia's exclusive economic zone, east of the Queensland coast and adjacent to the GBRMP (Fig. 1). The CSMP is Australia's largest marine park, covering 989,836 km^2 and spanning approximately 15° of latitude and 15° of longitude. There are 34 reef systems (containing numerous individual coral reefs) within the CSMP that collectively cover 15,000 km^2 (or 1.5% of the total CSMP area) with individual reefs separated from the mainland by > 160 km and from one another by large expanses of abyssal waters. In comparison, the GBRMP lies between the CSMP and the Queensland coast of Australia, and covers an area of 344,400 km^2, consisting of ~ 3000 individual coral reefs. Prevailing currents run from east to west from the CSMP towards the GBRMP (Choukroun et al. 2010), with some counterflow (e.g., Coral Sea Counter Current at 16°S) moving eastward, although this is much weaker (Qiu et al. 2009). This, combined with the large distances between CSMP reefs, suggests poor connectivity among reefs in the CSMP.

Sampling was undertaken at 17 reefs throughout the CSMP and 17 reefs on the outer shelf of the GBRMP between February 2019 and March 2020 (Fig. 1). Reefs were selected to gain as wide a spatial representation of each marine park as possible, though only 2 reefs were surveyed in the southern section of the GBRMP, which may not be wholly representative of this region. Between two and 10 sites were surveyed at each reef, giving a total of 124 unique sites. Where sites were surveyed in both years (n = 24), results were averaged across years. Sites were generally positioned on the outer edge of reefs, where there was continuous solid reef matrix with a clearly defined reef crest, and a reef slope extending into deeper habitat. An extensive marine heatwave occurred causing mass coral bleaching throughout the CSMP and GBRMP in March 2020, but surveys were conducted before coral mortality exceeded background levels (Burn et al. 2022). Thus, data from 2020 are not confounded by any impacts of bleaching.

Juvenile coral surveys

Juvenile corals were surveyed using three replicate 10 × 1 m belt transects on both the reef slope (8–10 m depth) and the reef crest (2–3 m depth) (hereafter referred to as habitat), at each of 124 sites (n = 885). Transects were separated by ~ 45 m and coincided with the first 10 m of consolidated habitat (i.e., sections of sand or rubble were not surveyed, to ensure consistency of benthic habitat type among surveys)

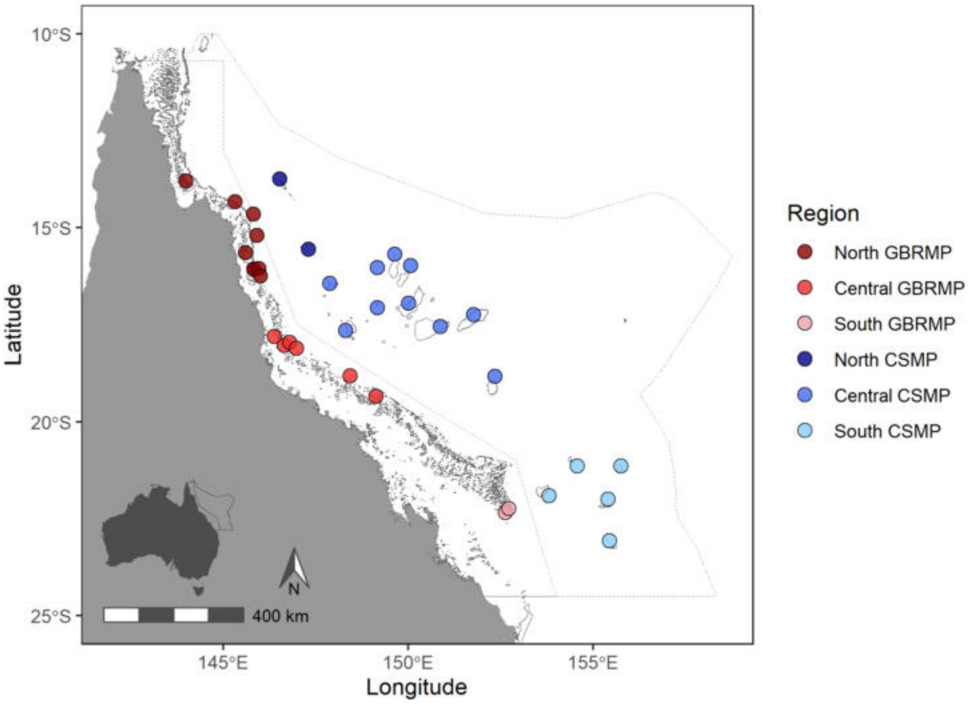

Fig. 1 Reefs (n = 34) in the CSMP (blue) and GBRMP (red) surveyed in 2019–2020. Shades of colour represent latitudinal regions for each marine park. Dashed lines represent marine park boundaries, with the GBRMP adjacent to the Queensland coast and the CSMP directly to the East

of 50 m point-intercept transects used to determine benthic cover (see below). All juvenile corals 1–5 cm maximum diameter falling wholly or mostly (i.e., > 50% of the colony) within the belt were counted and identified to genus. Where possible, surveys were restricted to juvenile corals that directly resulted from larval recruitment, excluding small remnant corals resulting from extensive partial mortality and fragmentation of formerly large colonies; however, it is not easy to distinguish between larval recruits versus remnants for some taxa (e.g., massive *Porites*). Therefore, it may be possible that some of the juveniles reported here are artefacts of partial mortality and fragmentation.

Per cent cover of common coral taxa

To determine per cent cover of different coral taxa, three replicate 50 m point-intercept transects were undertaken at each habitat within each site (n = 6 per site), following the depth contour and separated by ~ 5 m. Benthic substrate and organisms occurring directly below the tape at 50 cm intervals were placed into categories (Sand, Rubble, Pavement, Hard Coral, Soft Coral, Macroalgae, Sponge, and other). Organisms were identified to the lowest taxonomic unit possible, with corals and macroalgae identified to genus (n = 100 points per transect). Per cent coral cover was calculated by dividing the number of points falling on hard coral by the total number of points, minus the number of points falling on sand. This provides a measure of hard coral cover as a function of available hard substrate. This estimate of per cent coral cover was calculated for each of the major genera, *Porites*, *Acropora*, and *Pocillopora*.

Statistical analyses

Spatial variation in juvenile abundance across the GBRMP and CSMP

Spatial variation in the abundance of juvenile corals was analysed using generalised linear mixed effects models (GLMMs), comparing between marine parks (GBRMP and CSMP), among latitudinal regions (three levels), and between habitats (crest and slope). Separate analyses were undertaken for *Porites*, *Acropora*, *Pocillopora*, and 'other juvenile taxa', which were pooled across the remaining taxa. For *Porites*, *Acropora* and *Pocillopora*, models were fit with a three-way interaction between marine park, region and habitat, with nested random effects of site within reef. For 'other juvenile taxa' the interaction between marine park and region was not included as it did not improve the fit of the model according to the corrected Akaike information criterion (AICc) (Table 1). Abundance of juvenile corals was modelled against a negative binomial distribution with a log link function to account for the overdispersion in the data.

For each model, combinations of fixed and random effects were tested using maximum likelihood (REML = FALSE) and retained only if they improved the fit of the model, based on the AICc (Table 1). Each model was validated, and goodness of fit was checked visually and statistically, including checks of simulated residuals and dispersion, using the 'DHARMa' package (Hartig 2021), and tested for zero-inflation using the 'performance' package (Lüdecke et al. 2021). Post hoc Tukey's pairwise comparisons were calculated using estimated marginal means in the 'emmeans'

Table 1 Corrected Akaike Information Criterion (AICc) scores and degrees of freedom (df) for combinations of fixed effects tested within each model.

Model	df	AICc
Acropora ~ 1 + (1|Reef/Site)	4	4004.3
Acropora ~ MarinePark + (1|Reef/Site)	5	3996.6
Acropora ~ MarinePark * Region + (1|Reef/Site)	9	3997.5
***Acropora* ~ MarinePark * Region * Habitat + (1|Reef/Site)**	**15**	**3931.7**
Porites ~ 1 + (1|Reef/Site)	4	4509.1
Porites ~ MarinePark + (1|Reef/Site)	5	4509.2
Porites ~ MarinePark * Region + (1|Reef/Site)	9	4495.7
***Porites* ~ MarinePark * Region * Habitat + (1|Reef/Site)**	**15**	**4482.7**
Pocillopora ~ 1 + (1|Reef/Site)	4	2905.6
Pocillopora ~ MarinePark + (1|Reef/Site)	5	2904.1
Pocillopora ~ MarinePark * Region + (1|Reef/Site)	9	2901.6
***Pocillopora* ~ MarinePark * Region * Habitat + (1|Reef/Site)**	**15**	**2850.7**
OtherTaxa ~ 1 + (1|Reef/Site)	4	4177.9
OtherTaxa ~ MarinePark + (1|Reef/Site)	5	4177.5
OtherTaxa ~ MarinePark + Region + (1|Reef/Site)	7	4162.9
OtherTaxa ~ MarinePark * Region + (1|Reef/Site)	9	4162
OtherTaxa ~ MarinePark + Region * Zone + (1|Reef/Site)	**10**	**4096.1**

Models used for analyses are highlighted in bold package (Lenth 2021) to test for significant differences in juvenile coral abundances among fixed effects.

Juvenile-adult relationships between common taxa within marine parks.

The relationship between per cent coral cover and juvenile abundance was assessed for each of three most abundant taxa (*Porites*, *Acropora*, and *Pocillopora*), using Spearman's rank correlation coefficients. Separate analyses were undertaken for each marine park; GRBMP (n = 17 reefs) and CSMP (n = 17 reefs), to test whether relationships were stronger or weaker among more isolated reef systems. Per cent cover of each taxon from point-intercept transects and juvenile abundance of each taxon from belt transects were averaged across transects, habitats, and sites, to gain a reef-wide per cent cover and average juvenile abundance for each taxon.

All statistical analyses were performed in the R statistical and graphical environment version 4.1.1 (R Core Team, 2021), with models built using the 'glmmTMB' package (Brooks et al. 2017). Data wrangling was completed in the 'TidyVerse' (Wickham et al. 2019), with plots created using 'ggplot2' (Wickham 2016). GLMMs were not fit for the juvenile-adult relationships due to the models not converging.

Results

Spatial variation in juvenile coral assemblages

A total of 14,711 juvenile corals from 42 distinct genera were surveyed across 34 reefs (5,265 juvenile corals in the GBRMP and 9,446 in the CSMP) in 2019 and 2020. This equated to an average of 23.72 (± 1.86 SE) and 13.99 (± 0.72 SE) juvenile corals 10 m^{-2} in the GBRMP and CSMP, respectively. Juvenile coral assemblages were dominated by *Porites* (5,376 juveniles; 36.5%), *Acropora* (4,399; 29.9%) and *Pocillopora* (1,555; 10.6%). The remaining 39 taxa were pooled and are hereafter referred to as 'other juvenile taxa', together comprising 23% of the juvenile community.

Whilst densities of juvenile corals were higher in the GBRMP compared with the CSMP for all 4 taxa (*Porites*, *Pocillopora*, *Acropora*, and others), this pattern was not consistent across all latitudinal regions or habitats, as evidenced by the interactions in each model (Fig. 2; Table 1; Supplementary Material Table 1). Notably, there was a significantly higher density of juvenile *Porites* colonies in the GBRMP, compared to the CSMP, but only in the northern region (Fig. 2a; Table 2). Significantly more *Acropora* and *Pocillopora* juveniles were also found in the GBRMP, but only in the central regions and only on the reef crest (Fig. 2b, c; Table 2). For the other juvenile taxa, there were significantly more juveniles in the GBRMP compared to the CSMP across all latitudinal regions and both habitats (Fig. 2d; Table 2).

Despite high variability in the density of juvenile corals within regions (at the site and reef level), there were broad latitudinal patterns, especially in the CSMP (Fig. 2). In the CSMP, *Porites* was significantly less abundant in the north compared to the south for both habitats (Fig. 2a). However, there was no difference among latitudinal regions in the GBRMP. In contrast, *Pocillopora* juveniles appeared to increase in abundance in the north; however, this increase was only statistically significant between the south and central regions on the reef slopes of the CSMP (Fig. 2c). On average, there were less juvenile *Acropora* in the central CSMP than other regions; however, this was not statistically significant for either habitat (Fig. 2b). In contrast, the central region of the GBRMP harboured the highest average density of juvenile *Acropora* for both habitats, although this was also not statistically significant (Fig. 2b). Similar to *Porites*, other juvenile taxa were significantly less abundant in the north compared to the south for both habitats; however, this was the case in both marine parks (Fig. 2d).

On average, total juvenile density was highest on the reef crest (18.84 juveniles 10 m^{-2} ± 1.27 SE) compared to the reef slope (13.98 ± 0.68 SE); however, this varied among taxa and latitudinal region (Fig. 2). Two regions (central and north) in the GBRMP had a significantly higher density of juvenile *Acropora* on the reef crest compared to the reef slope (Fig. 2b), and three regions (central and north GBRMP and south CSMP) had significantly higher densities of juvenile *Pocillopora* on the reef crest compared with the slope (Fig. 2c). For other juvenile taxa, the opposite trend was observed, with significantly more juveniles recorded on the reef slope as opposed to the reef crest for each region of both marine parks (Fig. 2d). Juvenile *Porites* were significantly more abundant on the reef crest in the northern GBRMP, but significantly more abundant on the slope in the central region of the CSMP (Fig. 2a).

Juvenile-adult relationships for common coral taxa

In both marine parks, there was evidence of a positive relationship among reefs between per cent coral cover and average density of juveniles for *Acropora* and *Pocillopora*, with the relationship being stronger for *Pocillopora* than *Acropora* (Fig. 3b, c). However, juvenile *Porites* showed no significant juvenile-adult relationship in both parks (Fig. 3a). Coral cover for each of the three taxa varied between parks, with higher mean cover of *Acropora* in the GBRMP (10.4% ± 0.75 SE) compared with the CSMP (5.7% ± 0.26 SE), but marginally lower cover of *Porites* and *Pocillopora* in the GBRMP (*Porites*: 3.6% ± 0.22 SE;

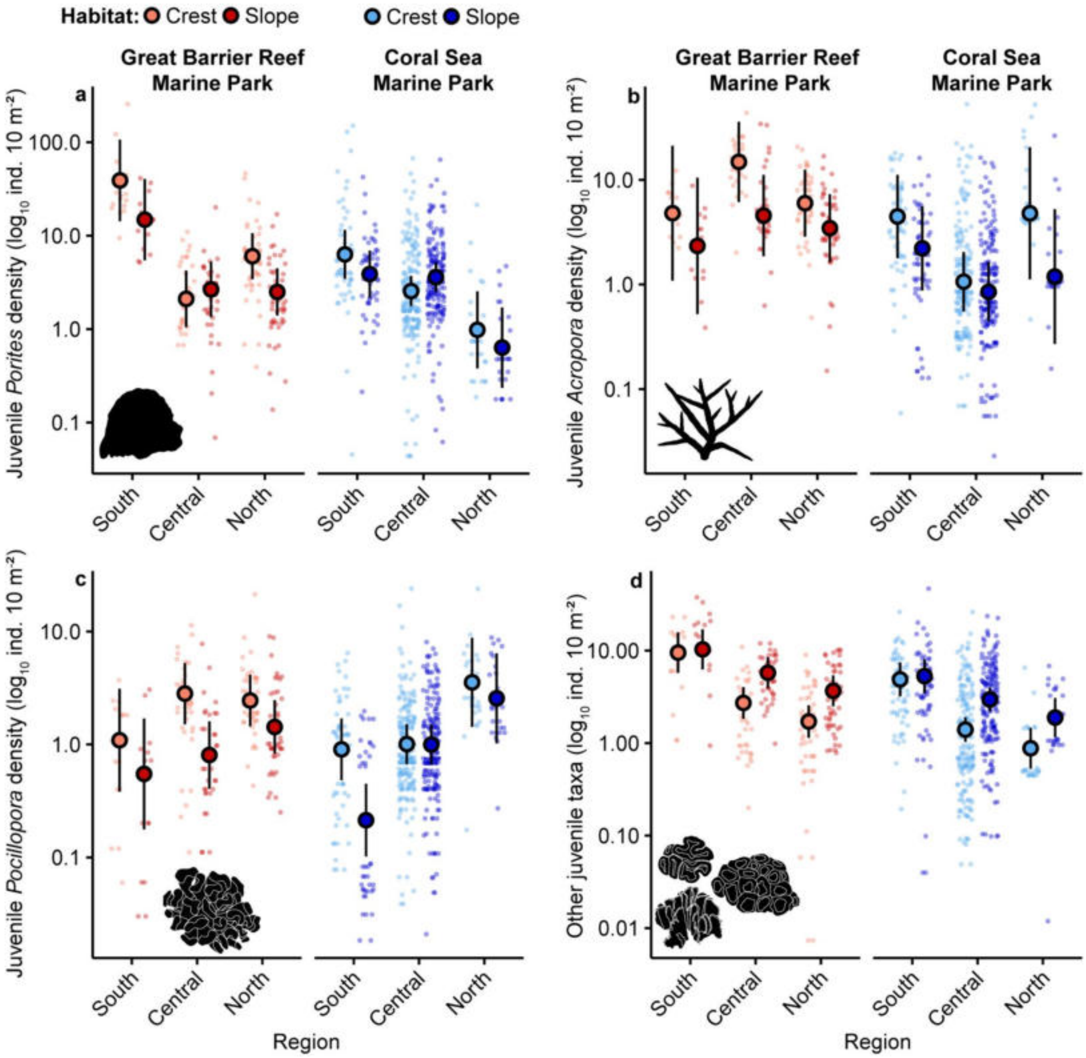

Fig. 2 Marginal effects plots showing the interactive effects of marine park, habitat and latitudinal region on the density of juvenile **a** *Porites*, **b** *Acropora*, **c** *Pocillopora*, and **d** other juvenile taxa. Bold circles represent estimated marginal means with error bars indicating 95% confidence intervals. Faded points represent model fitted predictions with overlaid residuals. Colours represent marine park (red = GBRMP, blue = CSMP) and shades represent habitat (dark = slope; light = crest). Estimated marginal means and predicted residuals account for the fixed and random effects included in the GLMMs

Pocillopora: 3.3% ± 0.27 SE), compared with the CSMP (*Porites*: 4.8% ± 0.27 SE; *Pocillopora*: 4.7% ± 0.2 SE).

Discussion

This study revealed that juvenile corals were much less (42% less) abundant on isolated reefs in Australia's CSMP, compared with more spatially proximal outer shelf reefs of Australia's GBRMP. Comparatively low abundance of juvenile corals in the CSMP is likely a result of a combination of factors, but low adult coral cover found at many reefs is likely limiting local larval production and supply (Gilmour et al. 2013). This may be further compounded by limited connectivity among the widely separated reefs in the CSMP, constraining larval supply from external sources (Ceccarelli et al. 2013; Gilmour et al. 2013; Payet et al. 2023). It is also possible that, despite the relatively high distance from many localised anthropogenic pressures and expected favourable oceanic conditions, there are some factors negatively affecting the settlement and survival of coral recruits in the CSMP (e.g., high abundance of excavating parrotfish *Bolbometapon muricatum*; Penin et al. 2010; Trapon et al. 2013b). Regardless of the cause, low abundances of juvenile corals likely constrain recovery capacity for CSMP reefs, making them particularly vulnerable to sustained and ongoing disturbances.

Table 2 Estimated marginal mean density (10 m^{-2}) of juvenile corals in each marine park. Pairwise contrasts and p values are provided for the comparison between marine parks for each region and habitat for each of four GLMMs. * denotes statistically significant differences

GLMM	Estimated marginal means (juveniles 10 m^{-2})					
	Region	Habitat	GBRMP	CSMP	Contrast estimate	p value
Porites	Northern	Crest	6.035	0.982	5.053	0.0053*
		Slope	2.502	0.634	1.868	0.0209*
	Central	Crest	2.106	2.555	−0.448	0.6148
		Slope	2.661	3.599	−0.938	0.4142
	Southern	Crest	39.051	6.309	32.742	0.1034
		Slope	14.848	3.882	10.966	0.1525
Acropora	Northern	Crest	5.996	4.796	1.2	0.7759
		Slope	3.461	1.191	2.271	0.1545
	Central	Crest	14.875	1.065	13.81	0.0398*
		Slope	4.563	0.851	3.712	0.0779
	Southern	Crest	4.803	4.469	0.33	0.9365
		Slope	2.339	2.216	0.124	0.9524
Pocillopora	Northern	Crest	2.449	3.549	−1.1	0.5342
		Slope	1.428	2.563	−1.135	0.3681
	Central	Crest	2.82	1.008	1.813	0.0494*
		Slope	0.807	0.997	−0.191	0.5852
	Southern	Crest	1.09	0.905	0.185	0.776
		Slope	0.548	0.214	0.335	0.3044
Other juvenile taxa	Northern	Crest	1.71	0.88	0.832	0.0025*
		Slope	3.67	1.89	1.785	0.0021*
	Central	Crest	2.72	1.4	1.323	0.0098*
		Slope	5.77	2.96	2.801	0.0094*
	Southern	Crest	9.52	4.89	4.624	0.0176*
		Slope	10.33	5.31	5.017	0.0172*

Reefs in the central CSMP were particularly depauperate of juvenile *Acropora;* a taxon likely to contribute to fast growth and recovery of coral cover in the aftermath of disturbances (Linares et al. 2011; Morais et al. 2021). This likely reflects the suppressed adult stock of *Acropora* in this region, which is attributable to the disproportionate vulnerability of these corals to recurrent cyclones and mass coral bleaching (Loya et al. 2001; Madin and Connolly 2006; Hughes et al. 2018), which have impacted this area (Oxley et al. 2005; Brewer et al. 2007; Harrison et al. 2019; Burn et al. 2023). While many *Acropora* corals produce larvae that are capable of extensive dispersal (Connolly and Baird 2010; Miller et al. 2020; Figueiredo et al. 2022), the large scale of stock depletion in the central CSMP, combined with inherent constraints to larval exchange among reefs, suggest that there is unlikely to be significant larval recruitment and recovery of *Acropora* corals in this region.

The most common juvenile genus recorded on CSMP reefs was *Porites* (37%), which is among the slowest growing taxa (Pratchett et al. 2015) and will contribute little to increasing coral cover following disturbances (Pratchett et al. 2020). We report relatively high abundances of juvenile *Porites* colonies, combined with low per cent cover of *Porites*. This may be partly due to the difficulty in differentiating between true juveniles and fission of larger colonies due to partial mortality. Partial mortality is particularly prevalent in *Porites* (Pisapia and Pratchett 2014), which can result in many small remnant colonies, potentially mistaken here as juveniles. Naturally slow growth rates in this taxon (Pratchett et al. 2015) combined with possible physiological constraints following injury (Henry and Hart 2005; but see Graham and van Woesik 2013) may explain low per cent cover reported herein. The community composition of juvenile corals in the central CSMP reinforces the notion that this region has poor recovery capacity, which is supported by the persistently low ($<20\%$) records of coral cover since the 1980’s (Ayling and Ayling 1985; Oxley et al. 2003, 2004; Ceccarelli et al. 2008, 2009; Hoey et al. 2020, 2021).

Whilst abundance of juvenile corals was higher on the GBRMP compared with the CSMP, recorded densities (~2.4 juvenile corals m^{-2}) are low compared to many published studies. Previously in the GBRMP, 6.9 juvenile corals m^{-2} were recorded on the mid-continental shelf in 2009 (Trapon et al. 2013a, 2013b), with substantially more recorded on the outer- continental shelf in 2008 (11.2 juvenile corals m^{-2}; Jonker et al. 2019) and 2019 (6.3–26.9 juvenile corals m^{-2}; Emslie et al. 2019). However, the methods employed in the

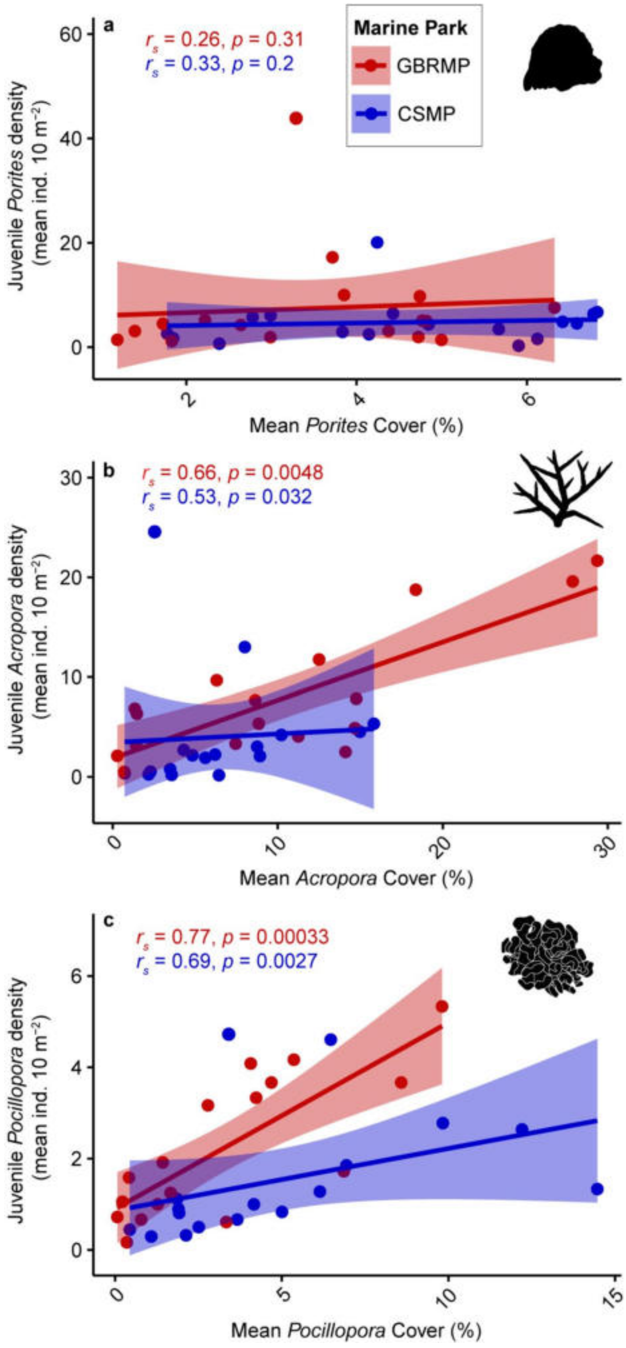

Fig. 3 The relationship between reef-wide per cent cover and mean density of juveniles (10 m^{-2}) for **a** *Porites*; **b** *Acropora*; and **c** *Pocillopora*. Colours represent marine parks (red = GBRMP, blue = CSMP). Ribbons represent 95% confidence intervals. Text refers to the r_s (Spearman's rank correlation coefficient), with corresponding p-values

latter two studies account for available substrate (excluding substrate not covered with crustose coralline algae or turf algae), which may inflate juvenile abundances when compared with those reported here. Nevertheless, our estimates of juvenile abundance are among the lowest reported, particularly when compared with other Indo-Pacific reefs (Table 3). Juvenile abundance was comparatively low at several Caribbean locations (Table 3), as well as the Maldives and Seychelles archipelagos in the aftermath of the 2016 bleaching event, and Wake Atoll and the Phoenix Islands; two other remote, isolated Pacific locations (Table 3). The low densities of juvenile corals reported herein may reflect the impact of recent cumulative disturbances occurring in the GBRMP and CSMP (De'ath et al. 2012; Mellin et al. 2019), and may be reflective of subsequent loss of recovery capacity, even on well-connected reefs (Graham et al. 2015; Ortiz et al. 2018; Hughes et al. 2019).

Positive relationships between juvenile and adult corals were found for *Acropora* and *Pocillopora*, but not for *Porites* for both the GBRMP and CSMP, with the relationships being stronger in the GBRMP compared to the CSMP. This finding contradicts our initial hypothesis that the isolation of CSMP reefs might lead to a greater reliance on self-recruitment and local retention, thus strengthening the relationship. Stock-recruitment relationships for corals are expected to be strong at the reef scale regardless of isolation as genetic evidence suggests most larvae are of local origin (Ayre and Hughes 2000; Hughes et al. 2000; Underwood et al. 2020). Whilst self-recruitment (the proportion of recruits that originated from larvae produced by the same reef) may be high on isolated reefs of the CSMP, it is likely that local retention (the proportion of larvae produced by a reef that settles on the same reef) is low, weakening stock-recruitment relationships (Burgess et al. 2014). Local retention may be greater for GBRMP reefs due to the ebb and flood of tides that might bring larvae back to natal reefs (Andutta et al. 2012), whereas larval dispersal in the CSMP may be driven by predominant unidirectional oceanic currents (Ceccarelli et al. 2013), which tend to be fast on isolated reefs (Black et al. 1990). The weaker juvenile-adult relationship for *Acropora* in the CSMP compared with the GBRMP may also be related to the limited range and low level of *Acropora* cover. At lower cover, the supply of larvae may be more variable and dependent on local hydrodynamics. If *Acropora* cover increases, larval supply may become more predictable, resulting in a stronger (likely nonlinear) relationship (Gilmour et al. 2013). However, *Acropora* take at least 5 days to develop into larvae and become competent to settle, resulting in a relatively long pelagic period (i.e., in comparison with *Pocillopora*), and a higher likelihood of being flushed away from the reef of origin (Figueiredo et al. 2013). Moreover, differences in demographic or physiological traits important for reproduction, not accounted for in coral cover estimates, might account for the weaker relationships in the CSMP, such as colony size (Hughes 1984).

Remote, oceanic coral reefs are expected to be isolated from most local anthropogenic stressors (e.g., poor water quality, coastal development), and limited connectivity

Table 3 Juvenile coral densities reported in the literature. All densities have been standardised to abundance 1 m^{-2}. Means provided are taken from the text or extracted from figures. The sampling unit for each dataset is provided to clarify when means were extrapolated up or down

Region	Location	Year	Mean Juvenile density (m^{-2})	Unit displayed	Sampling unit	Citation
Caribbean	Curacao,	1974–1975	15	Curacao mean	1 m^2 quadrats	Bak and Engel (1979)
	Bonaire		18	Bonaire mean		
Caribbean	Florida	1994	< 1–4	Range of site level means	1 m^2 quadrats	Miller et al. (2000)
Caribbean	Florida	1993–1994	1.18–3.74	Range of site level means	1 m^2 quadrats	Chiappone and Sullivan (1996)
Caribbean	Florida	1995	7.6–8.4	Range of depth level means	0.25 m^2 quadrats	Edmunds et al. (2004)
Caribbean	Jamaica, USVI	1994–1995	5.2–18.1	Range of site level means	0.25 m^2 and 1 m^2 quadrats	Edmunds and Bruno (1996)
Caribbean	USVI	1994–2001	13.84–21.6	Range of year level means	0.25 m^2 quadrats	Edmunds (2004)
Caribbean	Various countries (no sea urchins present)	2003–2004	2.5–12.9	Range of site level means in algal zones	1 m^2 quadrats	Carpenter and Edmunds (2006)
Caribbean	Various countries (sea urchins present)	2003–2004	4.5–32.3	Range of site level means in urchin zones	1 m^2 quadrats	Carpenter and Edmunds (2006)
Indo-Pacific	American Samoa	2015	4.8 (± 0.41)	Mean (± s.e)	1 m^2 quadrats	Couch et al. (2023)
		2018	5.7 (± 0.56)			
Indo-Pacific	CSMP	2019–2020	1.39(± 0.07)	Mean (± s.e)	10 m × 1 m belt transect	Present study
Indo-Pacific	French Polynesia	2003	7.9	Mean	10 m × 1 m belt transect	Penin et al. (2007)
Indo-Pacific	French Polynesia	2004	6.4	Mean	10 m × 1 m belt transect	Penin and Adjeroud (2013)
Indo-Pacific	GBRMP	2019–2020	2.4(± 0.18)	Mean (± s.e)	10 m × 1 m belt transect	Present study
Indo-Pacific	Line Islands	2015	4.2 (± 0.52)	Mean (± s.e)	1 m^2 quadrats	Couch et al. (2023)
		2018	8.6 (± 0.81)			
Indo-Pacific	Maldives	1999	29	Mean	0.09 m^2 quadrats	McClanahan (2000)
Indo-Pacific	Maldives	2000–2002	~ 3.32–7.96	Range of means	1 m^2 quadrats	Bianchi et al. (2006)
Indo-Pacific	Maldives	2006–2007	17.4–38.2	Range of depth and reef type means	0.72 m^2 quadrats	Cardini et al. (2012)
Indo-Pacific	Maldives	2017	2.88 (± 0.97)	Mean (± s.e)	10 m × 1 m belt transect	Pisapia et al. (2019)
Indo-Pacific	Main Hawaiian Islands	2013	7.3 (± 0.75)	Mean (± s.e)	1 m^2 quadrats	Couch et al. (2023)
		2016	5.8 (± 0.81)			
		2019	10.9 (± 1.20)			
Indo-Pacific	New Caledonia	2007	5.6	Mean	10 m × 1 m belt transect	Adjeroud et al. (2010)
Indo-Pacific	North Marianas Islands	2014	8.2 (± 0.68)	Mean (± s.e)	1 m^2 quadrats	Couch et al. (2023)
		2017	13.2 (± 1.23)			
Indo-Pacific	Phoenix Islands	2015	3 (± 0.85)	Mean (± s.e)	1 m^2 quadrats	Couch et al. (2023)
		2018	1.4 (± 0.61)			
Indo-Pacific	Seychelles	2008–2017	12.3	Mean in 2008	0.25 m^2 quadrats	Dajka et al. (2019)
			12.8	Mean in 2011		
			4.2	Mean in 2017		
Indo-Pacific	South Marianas Island	2014	9.2 (± 0.96)	Mean (± s.e)	1 m^2 quadrats	Couch et al.(2023)
		2017	10.3 (± 0.82)			
Indo- Pacific	Wake Atoll	2014	1.5 (± 0.33)	Mean (± s.e)	1 m^2 quadrats	Couch et al. (2023)
		2017	1.4 (± 0.26)			

Table 3 (continued)

Region	Location	Year	Mean Juvenile density (m^{-2})	Unit displayed	Sampling unit	Citation
Red Sea	Eilat, Israel	2000–2001	42.09–172.92	Range of site level means	3 m × 0.2 m belt transect	Glassom and Chadwick (2006)

among coral assemblages on isolated reefs may also promote localised adaptation to changing environmental conditions (Marzonie et al. 2023). However, isolation can also reduce connectivity to viable sources of larval supply, constraining capacity for recovery from disturbances that are independent of coastal/human proximity (Smith et al. 2008; Gilmour et al. 2013; Bruno and Valdivia 2016). As disturbances increase in frequency and severity (McWhorter et al. 2022), the benefits afforded by isolation may be outweighed by constraints to connectivity and resilience. Our study has revealed low abundances of juvenile corals on isolated reefs in the CSMP, in combination with low abundance of broodstock (particularly fast-growing *Acropora*), posing a significant constraint on post-disturbance recovery capacity of isolated coral assemblages. Work on specific constraints to larval recruitment and recovery in isolated reef systems is still warranted, noting that constraints to larval supply may be further compounded (or moderated) by early post-settlement growth and survival.

Acknowledgements Authors are grateful to the crew and Captain Rob Benn of the MV Iron Joy, as well as to Russell Kelley for sharing his extensive knowledge and assistance in the field. We thank J. Woerner and T. Saxby from the Integration and Application Network for coral images. Thanks also go to the relevant staff at Parks Australia, particularly Martin Russell and Mitchell Baskys. The findings and views expressed are those of the authors and do not necessarily represent the views of Parks Australia, the Director of National Parks, or the Australian Government.

Author Contributions DB, ASH, and MSP contributed to the study conception and design. DB, MSP, CT, and JFC collected the data. Analyses were performed by DB. The first draft of the manuscript was written by DB, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. This research was jointly funded by the Director of National Parks, Australia (ASH, MSP), and the ARC Centre of Excellence for Coral Reef Studies (MSP). Centre of Excellence for Coral Reef Studies, Australian Research Council, CE140100020, Morgan S. Pratchett,D irector of Parks, Australia, DNP-MPA-1718-006, Andrew S. Hoey, DNP-MPA-1718-006, Morgan S. Pratchett

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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