

# Expansion of corals on temperate reefs: direct and indirect effects of marine heatwaves

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**Abstract** Globally, many temperate marine communities have experienced significant temperature increases over recent decades in the form of gradual warming and heatwaves. As a result, these communities are shifting towards increasingly subtropical and tropical species compositions. Expanding coral populations have been reported from several temperate reef ecosystems along warming coastlines; these changes have been attributed to direct effects of gradual warming over decades. In contrast, increases in coral populations following shorter-term extreme warming events have rarely been documented. In this study, we compared coral populations on 17 temperate reefs in Western Australia before (2005/06) and after (2013) multiple marine heatwaves (2010–2012) affected the entire coastline. We hypothesised that coral communities would expand and change as a consequence of increasing local populations and recruitment of warm-affinity species. We found differences in coral community structure over time, driven primarily by a fourfold increase of one local species, *Plesiastrea versipora*, rather than recruitment of warm-

affinity species. Coral populations became strongly dominated by small size classes, indicative of recent increased recruitment or recruit survival. These changes were likely facilitated by competitive release of corals from dominant temperate seaweeds, which perished during the heatwaves, rather than driven by direct temperature effects. Overall, as corals are inherently warm-water taxa not commonly associated with seaweed-dominated temperate reefs, these findings are consistent with a net tropicalisation. Our study draws attention to processes other than gradual warming that also influence the trajectory of temperate reefs in a changing ocean.

**Keywords** Tropicalisation · Kelp forests · Seaweed decline · High-latitude corals · *Plesiastrea versipora*

## Introduction

Temperature is a major driver of the biogeography of species across Earth's biomes and through time. By limiting or enhancing physiological processes and influencing ecological interactions, temperature produces consistent patterns in the distribution and abundance of species. Within the world's oceans, these patterns largely follow temperature gradients associated with latitude and depth (Gaston 2000; Tittensor et al. 2010; Wernberg et al. 2013b). Consequently, with the oceans warming on average at rates of  $\sim 1.5$  °C 100 yr<sup>-1</sup> or more in global hotspots (Hobday and Pecl 2013), changes in species distributions and abundances are increasingly being documented (Perry et al. 2005; Last et al. 2011; Wernberg et al. 2011; Poloczanska et al. 2013). One particularly prevalent change is the poleward shift of subtropical and tropical species, and the subsequent 'tropicalisation' of temperate

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reefs (Nakamura et al. 2013; Vergés et al. 2014b; Richards et al. 2016; Wernberg et al. 2016b).

Temperate reefs are usually characterised by dense stands of seaweeds that support diverse communities of high social and economic value (Schiel and Foster 1986; Steneck and Johnson 2013; Bennett et al. 2016). However, a decline in cool-water seaweeds and an influx of subtropical and tropical organisms is occurring on many high-latitude reefs. While some tropical species of coral, fish, seaweeds and invertebrates have always been present at high latitudes, recent increases in their diversity and abundance have shifted community structure (Nakamura et al. 2013; Wernberg et al. 2013a, 2016a; Vergés et al. 2014a; Richards et al. 2016) with the resulting tropicalisation being most distinct where the dominant benthos has changed towards a distinctive tropical fauna such as corals (e.g. Mezaki and Kubota 2012; Vergés et al. 2014b).

Expansion of coral populations has largely occurred in association with gradual temperature increases over decadal time scales. One of the most striking examples comes from Japan (32.75°N) where some reefs were once populated by temperate seaweeds, but are now *Acropora*-dominated coral communities (Yamano et al. 2011; Yara et al. 2011; Mezaki and Kubota 2012; Denis et al. 2013). Similarly, in South Korea (33.41°N) recent high recruitment rates and negatively skewed size-frequency distributions suggest that local coral populations are increasing (Denis et al. 2014; Vieira et al. 2016). Populations of *Acropora* spp. in North America and the introduced species *Oculina patagonica* in the Mediterranean Sea have also expanded poleward in response to gradual warming (Precht and Aronson 2004; Serrano et al. 2013). Likewise, in the southern hemisphere, some corals have undergone poleward range extensions in both eastern and western Australia, increasing the diversity and abundance of corals at temperate latitudes (Thomson 2010; Baird et al. 2012; Richards et al. 2016). Such responses to recent warming are consistent with historical fluctuations in coral distributions with periods of cooling and warming (Precht and Aronson 2004; Greenstein and Pandolfi 2008). Thus, gradual warming seems to enable population expansions of these characteristically tropical fauna into temperate communities.

In contrast to gradual warming, discrete spikes in temperature appear to have negative effects on corals at high latitudes. For example, in 2010, Lord Howe Island (~31°S) on the east coast of Australia experienced a heatwave of multiple degree heating weeks, resulting in significant bleaching of the southern-most coral reef in the world (Harrison et al. 2011). Similarly, a 2011 marine heatwave in the southeast Indian Ocean impacted coral communities along the Western Australian coastline with 10–60% coral bleaching between 32° and 28°S (Pearce

et al. 2011; Abdo et al. 2012; Moore et al. 2012; Smale and Wernberg 2012; Lafratta et al. 2016). The high-latitude endemic coral, *Coscinaraea marshae*, also underwent severe bleaching of 95% of colonies in deep waters near Rottneest Island (~32°S) during the 2011 marine heatwave, and at the same latitude reduced coral calcification rates were attributed to the heatwave (Thomson et al. 2011; Foster et al. 2014). In 2003, a Mediterranean heatwave saw partial and complete tissue necrosis and mortality in two endemic coral species (Garrahou et al. 2009; Kersting et al. 2013). However, all these studies focused on immediate, directly adverse responses (bleaching, tissue necrosis and mortality) to discrete warming and did not consider longer-term effects of changes in demographic processes or ecological interactions.

The indirect effects of ecological interactions mediated by temperature, such as competition with cool-water seaweeds, are also likely to shift after a thermal event. Seaweeds dominate temperate reefs (Steneck and Johnson 2013), where they likely contribute to suppressing coral populations through physical interference (e.g. shading and abrasion) and superior resource utilisation (e.g. light and space) (Coyer et al. 1993; Miller and Hay 1996; Thomson et al. 2012). Temperate seaweeds are vulnerable to marine heatwaves which can lead to a decline in performance and abundance (e.g. Serrano et al. 2012; Vergés et al. 2014b; Wernberg et al. 2016a). Declines in seaweed cover are likely to alleviate competitive stress on coral communities through reduced physical interference and increased resource availability, potentially increasing successful recruitment and recruit survival. This, in turn, provides an opportunity for coral populations to expand through local population increase and recruitment of new species, especially when the seaweeds cannot recover, for example due to increases in herbivores (Bennett et al. 2015).

Coral establishment and growth is a slow process, and it takes time for changes in recruitment and recruit survival to manifest in visibly expanding populations. Early recruits are microscopic in size and the slow growth rate of corals, particularly at high latitudes (e.g. Lough and Barnes 2000; Carricart-Ganivet 2004; Rodolfo-Metalpa et al. 2006; Burgess et al. 2009), implies detection is only possible months after initial recruitment. Consequently, community responses to discrete events cannot be inferred from immediate responses such as mortality alone, but need to also consider demographic processes and indirect ecological effects which play out over relatively long time scales.

Here we investigate changes in coral populations on temperate reefs along the mid-west coast of Australia (29°–30°S). Coral surveys completed in 2005 and 2006 by the Western Australian Museum (WAM) (Fromont et al. 2006) were repeated in 2013. Within this period, the mid-west region experienced significant warming, when between

2010 and 2012, consecutive hot summers were characterised by severe marine heatwaves (Hobday et al. 2016; Pearce and Feng 2013). In the aftermath of these heatwaves, temperate communities collapsed at their northern (warm) margin and canopy-forming seaweeds declined by 40% in the mid-west (Pearce et al. 2011; Smale and Wernberg 2013; Wernberg et al. 2013a, 2016a). Although the heatwaves resulted in coral stress and bleaching (Pearce et al. 2011; Thomson et al. 2011; Abdo et al. 2012; Moore et al. 2012; Smale and Wernberg 2012; Foster et al. 2014), the decline in temperate seaweeds could have provided increased habitat availability and new ecological niches for corals on mid-west reefs. As a result, we hypothesised that coral communities would have expanded from local population increases and range shifts of warm-affinity species.

## Methods

### Study area

This study focused on the mid-west of Western Australia, a biogeographical overlap zone of temperate and tropical biota (Fromont et al. 2006; Wernberg et al. 2013a). Study sites (reefs) were nested within four regions: Dongara (29°016'S, 114°055'E) (3 sites); Green Head (30°004'S, 114°058'E) (3 sites); Jurien Bay (30°018'S, 115°002'E) (6 sites); and Cervantes (30°030'S, 115°004'E) (5 sites) (Fig. 1).

### Coral surveys

This study contrasted two datasets collected ~8 yr apart at the same sites using identical methods. The first data set was collected in 2005/2006 (before heatwaves) and the second one in 2013 (after heatwaves). The 'before heatwaves' data were collected as part of a comprehensive biodiversity study of multiple habitat types by the WAM and the Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) (Fromont et al. 2006). Of the initial 30 sites surveyed by WAM, 17 sites were re-sampled in 2013 and used in this comparison. The sites were selected based on the presence of habitats conducive for coral presence (rocky reefs) or habitats where corals were previously found. The 17 sites encompassed a variety of environmental conditions with different distances from the shore (inshore, midshore, offshore) and wave exposure (sheltered, exposed) within each region (Dongara, Green Head, Jurien Bay and Cervantes) (Electronic supplementary material, ESM Table S1). At each site, all corals >1 cm diameter (corresponding to an area of 1.6–4.6 cm<sup>2</sup>) were counted, identified and measured within three haphazardly placed 5-m<sup>2</sup> (1 × 5 m) transects by divers using

SCUBA. Transects were five contiguous 1-m<sup>2</sup> quadrats placed at least 10 m apart within 20–30 m of the site marker. Approximately 10–15 min was spent searching for corals in each transect. The haphazard placement of transects in both before and after surveys ensured transects included rocky reef habitat and incorporated representative sampling across seaweed types where seaweeds were a significant constituent of the reef-scape (e.g. areas of *Ecklonia radiata*, *Sargassum* spp. or turfs; see ESM Table S1 for list of dominant seaweeds at each site). Areas visibly dominated by corals were not targeted specifically. All coral colonies were photographed with a scale to assist with species identifications and to allow subsequent size measurements. Species identity was assigned based on morphological features following Veron and Marsh (1988) and Veron (1993, 2000).

### Colony counts and species presence

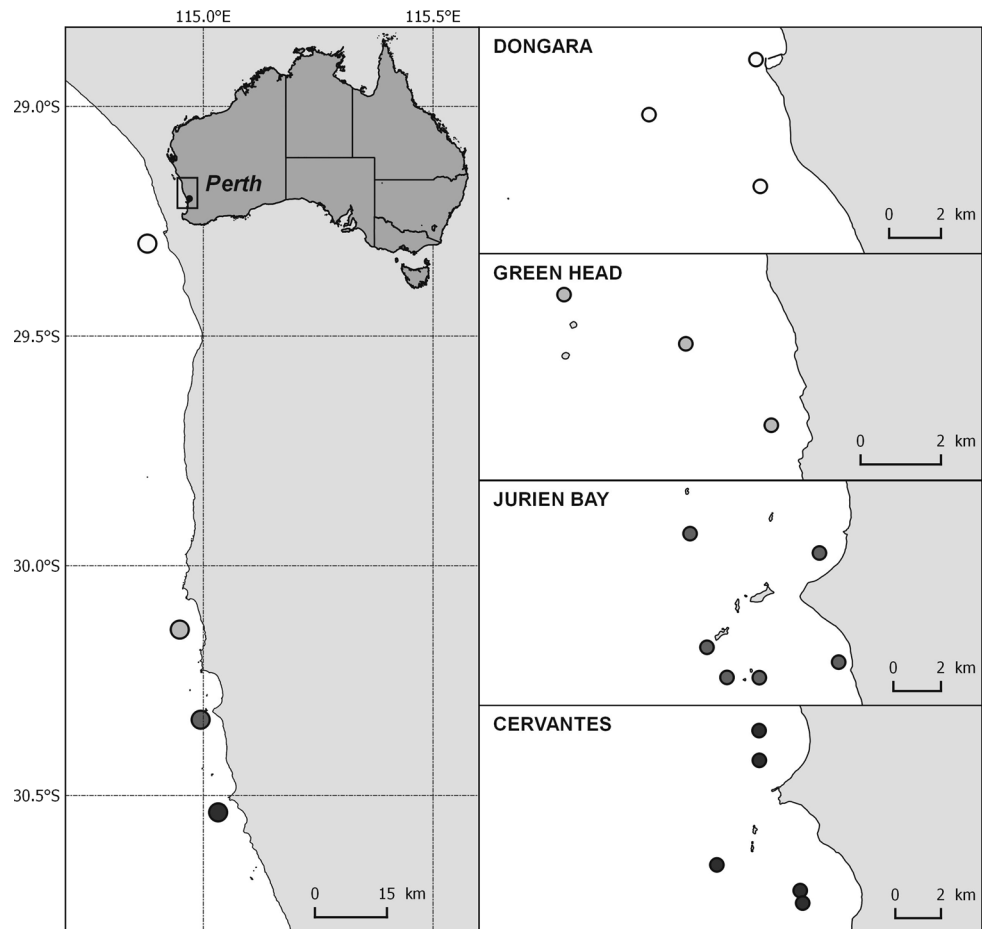
Species of the genus *Montipora* were pooled to genus as species identity could not be confidently assigned from photographs (distinguishing features can be <1 mm). All other corals were identified to species.

Colony counts were used as a measure of abundance of each species. Due to a high proportion of zeros at the transect level, abundances were pooled (summed) for each site. Site counts were then transformed ( $\log x + 1$ ) to down-weight very abundant taxa and allow representation of patterns within the whole coral community (Anderson et al. 2008). Transformed site counts were then used as replicates to test for differences in coral communities with permutational analysis of variance (PERMANOVA) between years (fixed) and regions (fixed). The PERMANOVA test was based on a zero-adjusted Bray–Curtis similarity matrix and followed by pairwise tests when significance ( $p < 0.05$ ) was met (Anderson et al. 2008). Differences in the multivariate structure of the coral communities between sampling times and among regions were visualised with a principal coordinates ordination based on the same matrix used for PERMANOVA. Non-parametric Spearman rank correlations (>0.7) overlaid the ordination plot to show coral species likely contributing most to dissimilarities. The contribution of species to differences between years was also investigated with a similarity percentage (SIMPER) analysis on transformed ( $\log x + 1$ ) site counts.

### Demographic measurements

Most high-latitude corals have flat, encrusting or laminar forms (Sommer et al. 2014), and many of the corals encountered were small individuals with minimal thickening of skeletal structures. Consequently, area was

**Fig. 1** Sample regions and sites within the mid-west of Western Australia. The grey scale for the dots on the left panel matches the four regions (Dongara, Green Head, Jurien Bay and Cervantes) on the right panels



considered a good proxy for age and performance and was estimated for each colony based on measurements of minimum and maximum diameter and the formula for an ellipse ( $\text{area} = \pi \times r_{\min} \times r_{\max}$ , where  $r$  is the radius). Size frequencies were constructed from pooled area measurements per species for before and after periods. The number of bins used in the frequency distributions was based on the rounded result from Sturges' formula ( $1 + 3.322 \log [N]$ , where  $N$  is the sample size), effective for sample sizes  $<200$  (Sturges 1926). Bin size was then calculated from the range (minus outliers) divided by the number of bins. A two-sample Kolmogorov–Smirnov test was used to determine whether size frequencies were significantly different between pooled before and after data, and a two-sample  $t$  test was used to test whether the mean number of small ( $1.6\text{--}11.8 \text{ cm}^2$ ) and large ( $12.4\text{--}27.5 \text{ cm}^2$ ) colonies differed between times.

## Results

The number of coral species recorded at the 17 mid-west sites increased from nine before the heatwaves to eleven after the heatwaves. Also, the total number of coral

colonies recorded increased more than twofold (76 before, 163 after) across the 17 sites, with the increase largely being corals smaller than  $12 \text{ cm}^2$  (Table 1; ESM Table S2). Of the 17 sites re-surveyed in 2013, three sites had new coral species not recorded in the surveys before the heatwaves. PERMANOVA confirmed that these increases constituted a significant change in multivariate community structure between the before and after surveys (Table 1; Fig. 2). There were also significant differences between regions, but the pairwise comparisons did not reveal any systematic latitudinal differences between regions (Table 1; Fig. 2). Separation of sampling times in the mid-west regions was predominantly along PCO1, which was highly correlated with changes in *Plesiastrea versipora*. Changes in *Coelastrea aspera*, *Pocillopora damicornis* and species of *Montipora* were strongly associated with both PCO1 and PCO2. Specifically, within the regions of Dongara and Cervantes, time differences aligned with changes in *Turbinaria mesenterina* and *P. damicornis*. At Green Head changes over time were associated with PCO2 and with changes in *Montipora* species.

There were few colonies ( $<40$ ) of all species except *P. versipora*, even in pooled samples. Thus, size frequencies were only constructed for *P. versipora*; even within this

**Table 1** Comparison of coral communities before (2005–2006) and after (2013) multiple heatwaves in the mid-west of Western Australia

Time	Total colony count	Small colony count	Large colony count		
Before	76	11	60		
After	163	89	74		
	Average density (colonies/region)	se	Average density (colonies m <sup>-2</sup> )	se	
Before	19.5	1.68	0.557	0.158	
After	40.8	2.26	0.259	0.107	
PERMANOVA summary					
Sources of variation	df	MS	F	p	
Time	1	3220	3.732	0.009*	
Region	3	3218	3.729	0.001*	
Time × region	3	1157	1.341	0.210	
Residual	26	863			
Region (pairwise test)	t	p			
Dongara, Green Head	2.624	0.005*			
Dongara, Jurien Bay	1.958	0.014*			
Dongara, Cervantes	1.674	0.051			
Green Head, Jurien Bay	1.066	0.349			
Green Head, Cervantes	2.497	0.003*			
Jurien Bay, Cervantes	1.948	0.011*			

Total colony counts are for all regions ( $n = 4$ ), small colonies are  $<12 \text{ cm}^2$ , large colonies  $>12 \text{ cm}^2$ , and mean colony density is given per region and  $\text{m}^{-2}$ . Small and large colony counts do not equal the total for ‘before’ as five colonies were not measured. Permutational analysis of variance (PERMANOVA) tested for differences in community structure between years (fixed) and regions (fixed). PERMANOVA is based on a zero-adjusted Bray–Curtis similarity matrix

\* Significant differences at  $p < 0.05$

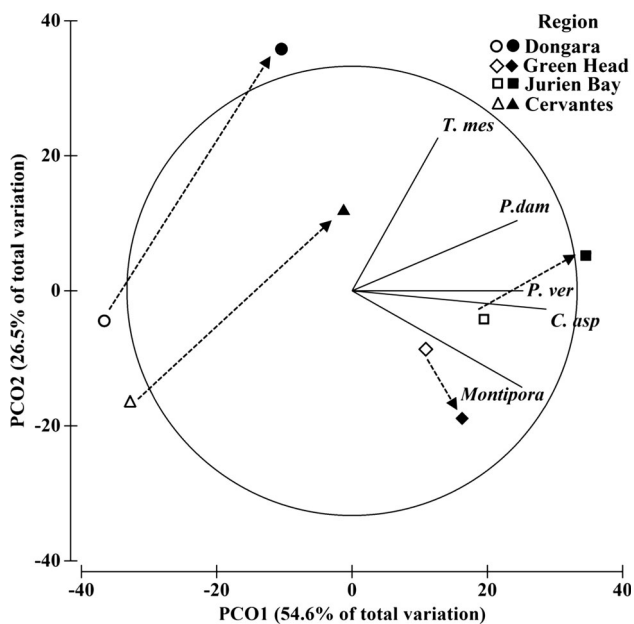
species the sample size for Dongara ( $N = 5$  colonies) was limiting, and thus, this region was not included in this analysis. The size-frequency distributions were significantly different before and after the heatwaves (two-sample Kolmogorov–Smirnov test,  $p < 0.05$ ). After the heatwaves, size distributions were clearly negatively skewed due to an increase in the smaller size classes, with 70% of all colonies sampled in 2013 smaller than  $12 \text{ cm}^2$  (Fig. 3). In contrast, 63% of all *P. versipora* colonies sampled before the heatwaves were larger than  $12 \text{ cm}^2$ .

The species with the greatest change in mean abundance over time was, by far, *P. versipora* (Fig. 4; ESM Table S2). Smaller *P. versipora* colonies ( $<12 \text{ cm}^2$ ) from Green Head, Jurien Bay and Cervantes increased significantly from a mean of  $2.5 (\pm 1.7 \text{ SD})$  colonies before the heatwaves to a mean of  $25 (\pm 8.7)$  colonies after the heatwaves (two-sample  $t$  test,  $p < 0.05$ ). The mean number of larger colonies ( $>12 \text{ cm}^2$ ) did not increase from before ( $3.0 \pm 2.6$ ) to after ( $6.0 \pm 3.0$ ) the heatwaves (two-sample  $t$  test,  $p > 0.05$ ). Coral species of warmer affinity increased, but this was limited to one *Acropora millepora*

and six *Alveopora fenestrata* colonies; this increase did not affect the overall community changes between datasets.

## Discussion

In this study, we found significant increases in coral abundances on temperate reefs over an  $\sim 8$ -yr period associated with gradual warming and heatwaves. This change was driven by increases in species common to both sampling periods. New, more tropically affiliated species were recorded but in very low abundances insufficient to drive a shift in the community structure relative to the substantial increase in other species. The most pronounced abundance change was found for *P. versipora*. The strongly skewed size-frequency distributions of *P. versipora* colonies demonstrated a large increase in small colonies, suggesting an increase in recruitment or recruit survival after the heatwaves. Age estimates for small *P. versipora* colonies ( $<12 \text{ cm}^2$ ) reinforce the idea of recent juvenile success. Based on a conservative growth rate of  $4 \text{ mm yr}^{-1}$



**Fig. 2** Principal coordinates analysis of variation in coral community structure on mid-west temperate reefs. The first two axes (PCO1 and PCO2) explain 81.1% of the variability in multivariate space. *White shapes* denote before heatwave centroids, and *black shapes* are centroids for after the heatwaves. *T. mes*, *Turbinaria mesenterina*; *P. dam*, *Pocillopora damicornis*; *P. ver*, *Plesiastrea versipora*; *C. asp*, *Coelastrea aspera*

(average rate calculated from South Australia, where water temperatures were cooler than the mid-west; Burgess et al. 2009) the age of small colonies recorded after the heatwave could be 1.3–7.3 yr (radius range of colonies <12 cm<sup>2</sup> colonies was ~0.5–2.9 cm). The magnitude of this population expansion indicates that our findings are not due to sampling artefacts and the increase seen here is unlikely due to cyclical variation as size-frequency distributions were clearly unimodal and negatively skewed in 2013. If this was a cyclical change, we would expect to see a multimodal distribution of progressive cohorts, but this was not the case. Overall, these results are consistent with our hypotheses, indicating that there has been a change in coral communities driven by substantial local population expansion and, to a lesser extent, a possible increase in warm-affinity species (see below).

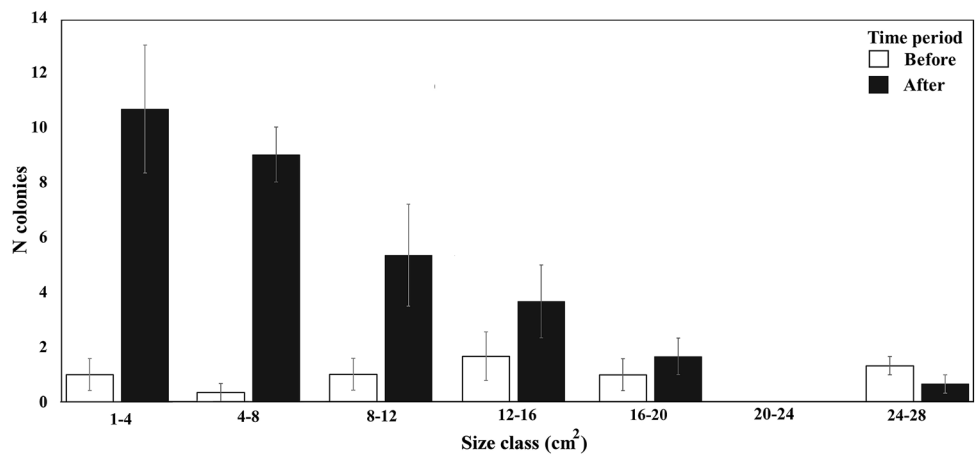
Extreme temperatures during the marine heatwaves are unlikely to have directly driven the observed changes in coral communities and the success of recruitment or survival of small *P. versipora*. Coral larvae and microscopic recruits are heat sensitive, with temperature stress prompting reduced pre-competency periods, increased mortality during metamorphosis, and increased mortality post-settlement (Edmunds et al. 2001; Bassim and Sammarco 2003; Nozawa and Harrison 2007; Randall and Szmant 2009; Yakovleva et al. 2009; Ross et al. 2013). While negative effects do not always result from heat stress

(e.g. Edmunds et al. 2001), it is likely the long duration and high intensity of the 2011 heatwave would have had deleterious effects on reproduction and early life stages. Specifically, coral recruitment (likely due to reduced reproductive output) at the Houtman Abrolhos Islands (approximately 70 km northwest of the study region) in 2011 and 2012 was significantly reduced compared to subsequent cooler years, (Markey et al. 2016). Further, adult coral colonies, which are generally more resilient to temperature stress than early life stages (larvae and microscopic recruits), experienced bleaching and reduced growth during the heatwave periods (Pearce et al. 2011; Thomson et al. 2011; Abdo et al. 2012; Moore et al. 2012; Smale and Wernberg 2012; Foster et al. 2014). Thus, direct effects of high temperature during the heatwaves would most likely have had a net negative effect on the mid-west coral communities and would not have benefitted the juvenile coral population.

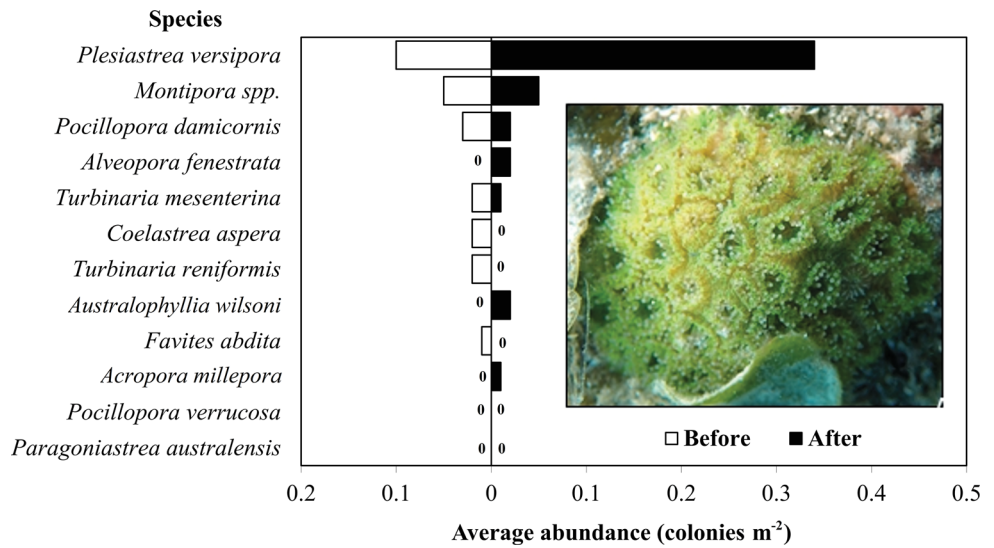
The recent success of small (juvenile) corals is likely the consequence of competitive release mediated by temperature through the reduction in canopy-forming temperate seaweeds and increases in herbivorous fishes. Seaweeds often limit corals in temperate environments through competitive stress, abrasion and dislodgement (Miller and Hay 1996). Seaweed removal experiments and natural canopy-free patches have shown a relaxation of these processes, leading to greater coral persistence, increased recruitment success and growth (Coyer et al. 1993; Miller and Hay 1996; Thomson et al. 2012). The heatwaves caused a substantial loss of seaweed canopy cover, which declined from 80–90 to 50% or less across the study region (Fig. 5a, b) (Smale and Wernberg 2013; Wernberg et al. 2013a, 2016b), a loss that has been maintained and reinforced over time by increasing herbivory by tropical fishes (Bennett et al. 2015). The loss of seaweed canopies would have facilitated the growth and survival of juvenile corals that recruited prior to the heatwave (Fig. 5c–e), presumably outweighing the direct negative effects of the heatwave on these animals. This could explain why high frequencies were found across several small size classes for *P. versipora* rather than within a single size class (which would have suggested a single recruitment pulse). We expect this recruitment facilitation to continue where the heatwave has caused a persistent shift to low canopy abundance (Wernberg et al. 2016b).

Other species within the coral community showed smaller changes than *P. versipora* and were found in abundances too low for size-frequency analyses. In some instances, species recorded before the heatwave did not increase or were not recorded after the heatwave. It remains unclear why other local species did not show stronger positive responses to the direct and indirect effects of the heatwaves. Lower initial abundances compared to *P.*

**Fig. 3** Size-class distributions of *Plesiastrea versipora* in the mid-west regions before multiple heatwaves (2005/2006, white) and after the heatwaves (2013, grey). Graphs are based on pooled data for the mid-west (excluding Dongara), and estimates of coral area, assuming corals are elliptical



**Fig. 4** SIMPER analysis showing the change in the average abundance of the 12 species recorded before and after heatwaves. Inset photo shows a small *Plesiastrea versipora* colony. Photo: C. Tuckett



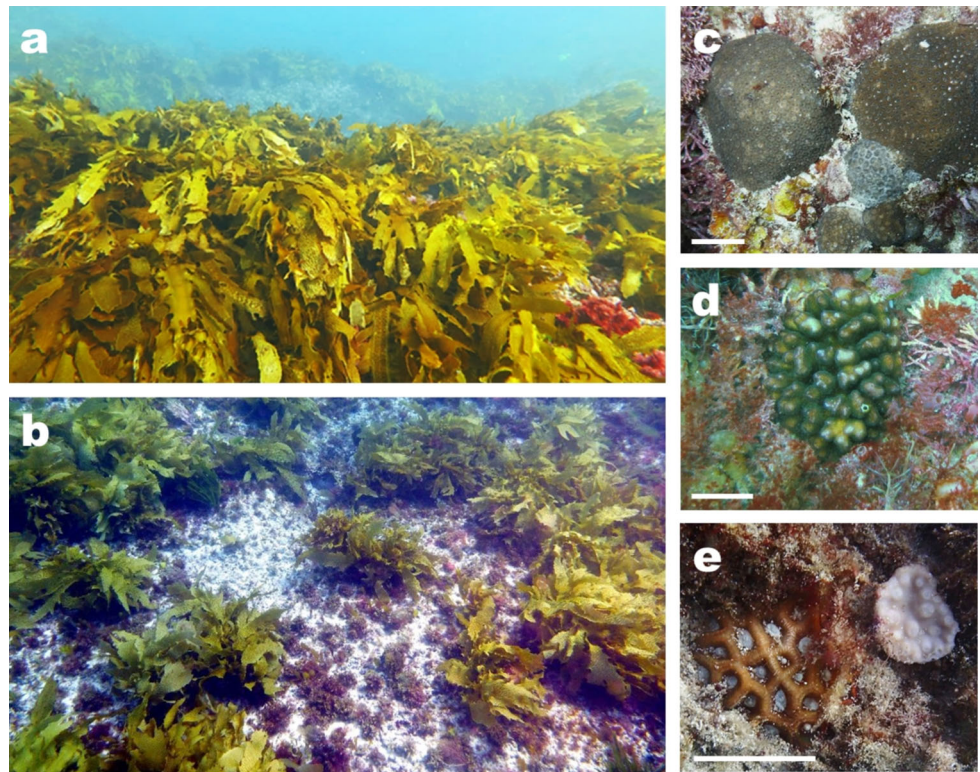
*versipora* could have limited propagule supply such that abundance changes would take longer to manifest, especially if these species also have less opportunistic life histories. Similarly, the increase in new warm-water species was very small. Warm-water, low-latitude species could have been limited by their lower environmental tolerances, not only to temperature but also depth, water clarity and light levels (Sommer et al. 2014; Keith et al. 2015; Mizerek et al. 2016).

Dispersal and recruitment could also be a factor limiting the response of warm-water species in this study. Long-distance dispersal from upstream sources would be required for an increase in warm-water species as the nearest coral reefs are ~70 km offshore at the Houtman Abrolhos Islands (28°S). Under normal conditions, larval longevity could favour connectivity between the Houtman Abrolhos Islands and the mid-west as after ~100 d (the last stage of coral mortality) patterns show increasing mortality (Graham et al. 2008; Markey et al. 2016). However, coral larvae show reduced pre-competency periods under thermal stress, which could promote settlement on natal reefs and reduce dispersal duration within the pelagic

period (Nozawa and Harrison 2000; Heyward and Negri 2010). In addition, the timing of arrival of new warm-water species relative to the loss of seaweed canopies might have limited successful settlement and recruitment. Thus, the probability of successful dispersal to the coastal reefs in the study area seems very low, and the likelihood of recruit limitation high. Thermal stress on early life stages during the heatwaves and dispersal limitation may be at least partially responsible for warm-water species not increasing.

The species predominantly responsible for the increase in coral abundance, *P. versipora*, is often considered a temperate species. However, it has been recorded in many more tropical than in temperate locations (~80% of 283 records north of 30.3°S; Atlas of Living Australia, [www.ala.org.au](http://www.ala.org.au)) and is perhaps more correctly classified as a tropical species with broad environmental tolerances. As temperate reefs are generally characterised by abundant seaweeds and not corals, the substantial expansion of coral populations observed in this study is consistent with the ongoing tropicalisation of temperate reefs seen in Western Australia and globally (Yamano et al. 2011; Wernberg et al. 2013a, 2016a; Vergés

**Fig. 5** Underwater photographs from mid-west Western Australia showing **a** benthos dominated by the seaweed canopy prior to the marine heatwaves; **b** benthos with significantly reduced canopy and large open patches post heatwaves; **c** juvenile *Plesiastrea versipora* colonies found post heatwaves; **d** juvenile *Pocillopora damicornis* colony found post heatwaves; **e** juvenile Merulinidae and Turbinaria post heatwaves. **c–e** Scale bars 2.5 cm. Photo credits: **a, b** T. Wernberg; **c, d** T. de Bettignies; **e** C. Tuckett



et al. 2014b). It is likely that greater juvenile recruitment and/or survival of newly recruited corals was largely the indirect result of competitive release from seaweeds rather than a response to consecutive marine heatwaves. However, further investigation is needed to determine whether coral increases will be moderated by changing community interactions, such as the increase in turf algae (Wernberg et al. 2013a, 2016a) and herbivory (Bennett et al. 2015). Regardless, we expect to see coral populations increase in these high-latitude reef communities with future warming, heatwaves and seaweed declines.

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