

1 **Expansion of corals on temperate reefs: direct and indirect effects of**
2 **marine heatwaves**

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4 Tuckett CA^{1*}, de Bettignies T^{1,2}, Fromont J³ and Wernberg T¹

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6 ¹ School of Biological Sciences and UWA Oceans Institute, The University of Western
7 Australia, Cnr Fairway and Service Rd 4, Crawley WA 6009, Australia

8 ² UMS 2006 Patrimoine Naturel, Muséum National d'Histoire Naturelle, 36 rue Geoffroy
9 Saint-Hilaire, 75005 Paris, France

10 ³ Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia

11

12 *Corresponding author: chenae.tuckett@research.uwa.edu.au

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16 **Abstract**

17 Globally, many temperate marine communities have experienced significant temperature
18 increases over recent decades in the form of gradual warming and heatwaves. As a result,
19 these communities are shifting towards increasingly subtropical and tropical species
20 compositions. Expanding coral populations have been reported from several temperate reef
21 ecosystems along warming coastlines; these changes have been attributed to direct effects of
22 gradual warming over decades. In contrast, increases in coral populations following shorter-
23 term extreme warming events have rarely been documented. In this study, we compared coral
24 populations on 17 temperate reefs in Western Australia before (2005/06) and after (2013)
25 multiple marine heatwaves (2010–2012) affected the entire coastline. We hypothesised that
26 coral communities would expand and change as a consequence of increasing local
27 populations and recruitment of warm-affinity species. We found differences in coral
28 community structure over time, driven primarily by a four-fold increase of one local species,
29 *Plesiastrea versipora*, rather than recruitment of warm-affinity species. Coral populations
30 became strongly dominated by small size classes, indicative of recent increased recruitment
31 or recruit survival. These changes were likely facilitated by competitive release of corals
32 from dominant temperate seaweeds, which perished during the heatwaves, rather than driven
33 by direct temperature effects. Overall, as corals are inherently warm-water taxa not
34 commonly associated with seaweed-dominated temperate reefs, these findings are consistent
35 with a net tropicalisation. Our study draws attention to processes other than gradual warming
36 that also influence the trajectory of temperate reefs in a changing ocean.

37

38 **Introduction**

39 Temperature is a major driver of the biogeography of species across Earth's biomes
40 and through time. By limiting or enhancing physiological processes and influencing
41 ecological interactions, temperature produces consistent patterns in the distribution and
42 abundance of species. Within the world's oceans these patterns largely follow temperature
43 gradients associated with latitude and depth (Gaston 2000; Tittensor et al. 2010; Wernberg et
44 al. 2013b). Consequently, with the oceans warming on average at rates of $\sim 1.5^{\circ}\text{C } 100 \text{ yr}^{-1}$ or
45 more in global hotspots (Hobday and Pecl 2013), changes in species distributions and
46 abundances are increasingly being documented (Perry et al. 2005; Last et al. 2011; Wernberg
47 et al. 2011; Poloczanska et al. 2013). One particularly prevalent change is the poleward shift
48 of subtropical and tropical species, and the subsequent 'tropicalisation' of temperate reefs
49 (Nakamura et al. 2013; Vergés et al. 2014b; Richards et al. 2016; Wernberg et al. 2016b).

50 Temperate reefs are usually characterised by dense stands of seaweeds that support
51 diverse communities of high social and economic value (Schiel and Foster 1986; Steneck and
52 Johnson 2013; Bennett et al. 2016). However, a decline in cool-water seaweeds and an influx
53 of subtropical and tropical organisms is occurring on many high-latitude reefs. While some
54 tropical species of coral, fish, seaweeds and invertebrates have always been present at high
55 latitudes, recent increases in their diversity and abundance have shifted community structure
56 (Nakamura et al. 2013; Wernberg et al. 2013a, 2016a; Vergés et al. 2014a; Richards et al.
57 2016) with the resulting tropicalisation being most distinct where the dominant benthos has
58 changed towards a distinctive tropical fauna such as corals (e.g., Mezaki and Kubota 2012;
59 Vergés et al. 2014b).

60 Expansion of coral populations has largely occurred in association with gradual
61 temperature increases over decadal time scales. One of the most striking examples comes

62 from Japan (32.75°N) where some reefs were once populated by temperate seaweeds, but are
63 now *Acropora*-dominated coral communities (Yamano et al. 2011; Yara et al. 2011; Mezaki
64 and Kubota 2012, Denis et al. 2013). Similarly, in South Korea (33.41°N) recent high
65 recruitment rates and negatively skewed size-frequency distributions suggest that local coral
66 populations are increasing (Denis et al. 2014; Vieira et al. 2016). Populations of *Acropora*
67 spp. in North America and the introduced species *Oculina patagonica* in the Mediterranean
68 Sea have also expanded poleward in response to gradual warming (Precht and Aronson 2004;
69 Serrano et al. 2013). Likewise, in the southern hemisphere, some corals have undergone
70 poleward range extensions in both eastern and western Australia, increasing the diversity and
71 abundance of corals at temperate latitudes (Thomson 2010; Baird et al. 2012; Richards et al.
72 2016). Such responses to recent warming are consistent with historical fluctuations in coral
73 distributions with periods of cooling and warming (Precht and Aronson 2004; Greenstein and
74 Pandolfi 2008). Thus, gradual warming seems to enable population expansions of these
75 characteristically tropical fauna into temperate communities.

76 In contrast to gradual warming, discrete spikes in temperature appear to have negative
77 effects on corals at high latitudes. For example, in 2010, Lord Howe Island (~31°S) on the
78 east coast of Australia experienced a heatwave of multiple degree heating weeks, resulting in
79 significant bleaching of the southern-most coral reef in the world (Harrison et al. 2011).
80 Similarly, a 2011 marine heatwave in the southeast Indian Ocean impacted coral
81 communities along the Western Australian coastline with 10–60% coral bleaching between
82 32 and 28°S (Pearce et al. 2011; Abdo et al. 2012; Moore et al. 2012; Smale and Wernberg
83 2012; Lafratta et al. 2016). The high-latitude endemic coral, *Coscinaraea marshae*, also
84 underwent severe bleaching of 95% of colonies in deep waters near Rottneest Island (~32°S)

85 during the 2011 marine heatwave, and at the same latitude reduced coral calcification rates
86 were attributed to the heatwave (Thomson et al. 2011; Foster et al. 2014). In 2003 a
87 Mediterranean heatwave saw partial and complete tissue necrosis and mortality in two
88 endemic coral species (Garrahou et al. 2009; Kersting et al. 2013). However, all these studies
89 focused on immediate, directly adverse responses (bleaching, tissue necrosis and mortality) to
90 discrete warming, and did not consider longer-term effects of changes in demographic
91 processes or ecological interactions.

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

105 Coral establishment and growth is a slow process, and it takes time for changes in
106 recruitment and recruit survival to manifest in visibly expanding populations. Early recruits
107 are microscopic in size and the slow growth rate of corals, particularly at high latitudes (e.g.

108 Lough and Barnes 2000; Carricart-Ganivet 2004; Rodolfo-Metalpa et al. 2006; Burgess et al.
109 2009), implies detection is only possible months after initial recruitment. Consequently,
110 community responses to discrete events cannot be inferred from immediate responses such as
111 mortality alone, but need to also consider demographic processes and indirect ecological
112 effects which play out over relatively long time scales.

113 Here we investigate changes in coral populations on temperate reefs along the mid-
114 west coast of Australia (29–30°S). Coral surveys completed in 2005 and 2006 by the Western
115 Australian Museum (WAM) (Fromont et al. 2006) were repeated in 2013. Within this period
116 the mid-west region experienced significant warming where, between 2010 and 2012,
117 consecutive hot summers were characterised by severe marine heatwaves (Hobday et al.
118 2016; Pearce and Feng 2013). In the aftermath of these heatwaves, temperate communities
119 collapsed at their northern (warm) margin and canopy-forming seaweeds declined by 40% in
120 the mid-west (Pearce et al. 2011; Smale and Wernberg 2013; Wernberg et al. 2013a, 2016a).
121 Although the heatwaves resulted in coral stress and bleaching (Pearce et al. 2011; Thomson
122 et al. 2011; Abdo et al. 2012; Moore et al. 2012; Smale and Wernberg 2012; Foster et al.
123 2014), the decline in temperate seaweeds could have provided increased habitat availability
124 and new ecological niches for corals on mid-west reefs. As a result, we hypothesised that
125 coral communities would have expanded from local population increases and range shifts of
126 warm-affinity species.

127

128 **Methods**

129 **Study area**

130 This study focused on the mid-west of Western Australia, a biogeographical overlap
131 zone of temperate and tropical biota (Fromont et al. 2006; Wernberg et al. 2013a). Study sites
132 (reefs) were nested within four regions: Dongara (29°016'S, 114°055'E) (3 sites); Green Head
133 (30°004' S, 114°058'E) (3 sites); Jurien Bay (30°018'S, 115°002'E) (6 sites); and Cervantes
134 (30°030'S, 115°004'E) (5 sites) (Fig. 1).

135

136 **Coral surveys**

137 This study contrasted two datasets collected ~8 years apart at the same sites using
138 identical methods. The first data set was collected in 2005/2006 (before heatwaves) and the
139 second one in 2013 (after heatwaves). The 'before heatwaves' data were collected as part of a
140 comprehensive biodiversity study of multiple habitat types by the WAM and the Australian
141 Commonwealth Scientific and Industrial Research Organisation (CSIRO) (Fromont et al.
142 2006). Of the initial 30 sites surveyed by WAM, 17 sites were re-sampled in 2013 and used
143 in this comparison. The sites were selected based on the presence of habitats conducive for
144 coral presence (rocky reefs) or habitats where corals were previously found. The 17 sites
145 encompassed a variety of environmental conditions with different distances from the shore
146 (inshore, midshore, offshore) and wave exposure (sheltered, exposed) within each region
147 (Dongara, Green Head, Jurien Bay and Cervantes) (Electronic supplementary material, ESM
148 Table S1). At each site, all corals >1 cm diameter (corresponding to an area of 1.6–4.6 cm²)
149 were counted, identified and measured within three haphazardly placed 5-m² (1 x 5 m)
150 transects by divers using SCUBA. Transects were five contiguous 1-m² quadrats placed at
151 least 10 m apart within 20–30 m of the site marker. Approximately 10–15 min were spent
152 searching for corals in each transect. The haphazard placement of transects in both before and

153 after surveys ensured transects included rocky reef habitat and incorporated representative
154 sampling across seaweed types where seaweeds were a significant constituent of the reef-
155 scape (e.g. areas of *Ecklonia radiata*, *Sargassum* spp. or turfs; see ESM Table S1 for list of
156 dominant seaweeds at each site). Areas visibly dominated by corals were not targeted
157 specifically. All coral colonies were photographed with a scale to assist with species
158 identifications and to allow subsequent size measurements. Species identity was assigned
159 based on morphological features following Veron and Marsh (1988) and Veron (1993, 2000).

160

161 **Colony counts and species presence**

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

165 Colony counts were used as a measure of abundance of each species. Due to a high
166 proportion of zeros at the transect level, abundances were pooled (summed) for each site. Site
167 counts were then transformed ($\text{Log } x + 1$) to down-weight very abundant taxa and allow
168 representation of patterns within the whole coral community (Anderson et al. 2008).
169 Transformed site counts were then used as replicates to test for differences in coral
170 communities with permutational analysis of variance (PERMANOVA) between years (fixed)
171 and regions (fixed). The PERMANOVA test was based on a zero-adjusted Bray–Curtis
172 similarity matrix and followed by pairwise tests when significance ($P < 0.05$) was met
173 (Anderson et al. 2008). Differences in the multivariate structure of the coral communities
174 between sampling times and among regions were visualised with a principal coordinates
175 ordination based on the same matrix used for PERMANOVA. Non-parametric Spearman

176 rank correlations (> 0.7) overlaid the ordination plot to show coral species likely contributing
177 most to dissimilarities. The contribution of species to differences between years was also
178 investigated with a similarity percentage (SIMPER) analysis on transformed ($\text{Log } x+1$) site
179 counts.

180

181 **Demographic measurements**

182 Most high-latitude corals have flat, encrusting or laminar forms (Sommer et al. 2014),
183 and many of the corals encountered were small individuals with minimal thickening of
184 skeletal structures. Consequently, area was considered a good proxy for age and performance,
185 and was estimated for each colony based on measurements of minimum and maximum
186 diameter and the formula for an ellipse ($\text{area} = \pi \times r_{\min} \times r_{\max}$, where r is the radius). Size
187 frequencies were constructed from pooled area measurements per species for before and after
188 periods. The number of bins used in the frequency distributions was based on the rounded
189 result from Sturges' formula ($1 + 3.322 \text{ Log } [N]$, where N is the sample size), effective for
190 sample sizes < 200 (Sturges 1926). Bin size was then calculated from the range (minus
191 outliers) divided by the number of bins. A two-sample Kolmogorov–Smirnov test was used to
192 determine whether size frequencies were significantly different between pooled before and
193 after data, and a two-sample t-test was used to test whether the mean number of small (1.6–
194 11.8 cm^2) and large (12.4–27.5 cm^2) colonies differed between times.

195

196 **Results**

197 The number of coral species recorded at the 17 mid-west sites increased from nine
198 before the heatwaves to eleven after the heatwaves. Also, the total number of coral colonies
199 recorded increased more than two-fold (76 before, 163 after) across the 17 sites, with the
200 increase largely being corals smaller than 12 cm² (Table 1; ESM Table S2). Of the 17 sites
201 re-surveyed in 2013, three sites had new coral species not recorded in the surveys before the
202 heatwaves. PERMANOVA confirmed that these increases constituted a significant change in
203 multivariate community structure between the before and after surveys (Table 1; Fig. 2).
204 There were also significant differences between regions but the pairwise comparisons did not
205 reveal any systematic latitudinal differences between regions (Table 1; Fig. 2). Separation of
206 sampling times in the midwest regions was predominantly along PCO1, which was highly
207 correlated with changes in *Plesiastrea versipora*. Changes in *Coelastrea aspera*, *Pocillopora*
208 *damicornis* and species of *Montipora* were strongly associated with both PCO1 and PCO2.
209 Specifically within the regions of Dongara and Cervantes time differences showed alignment
210 with changes in *Turbinaria mesenterina* and *P. damicornis*. At Green Head changes over
211 time showed association with PCO2 and with changes in *Montipora* species.

212 There were few colonies (<40) of all species except *P. versipora*, even in pooled
213 samples. Thus, size frequencies were only constructed for *P. versipora*; even within this
214 species the sample size for Dongara ($N = 5$ colonies) was limiting and thus this region was
215 not included in this analysis. The size-frequency distributions were significantly different
216 before and after the heatwaves (two-sample Kolmogorov–Smirnov test, $P < 0.05$). After the
217 heatwaves size distributions were clearly negatively skewed due to an increase in the
218 smaller size classes, with 70% of all colonies sampled in 2013 smaller than 12 cm² (Fig. 3).

219 In contrast, 63% of all *P. versipora* colonies sampled before the heatwaves were larger than
220 12 cm².

221 The species with the greatest change in mean abundance over time was, by far, *P.*
222 *versipora* (Fig. 4; ESM Table S2). Smaller *P. versipora* colonies (<12 cm²) from Green
223 Head, Jurien Bay and Cervantes increased significantly from a mean of 2.5 (\pm 1.7 SD)
224 colonies before the heatwaves to a mean of 25 (\pm 8.7) colonies after the heatwaves (two-
225 sample t-test, $P < 0.05$). The mean number of larger colonies (>12 cm²) did not increase from
226 before (3.0 \pm 2.6) to after (6.0 \pm 3.0) the heatwaves (two-sample t-test, $P > 0.05$). Coral
227 species of warmer affinity increased but this was limited to one *Acropora millepora* and six
228 *Alveopora fenestrata* colonies; this increase did not affect the overall community changes
229 between datasets.

230

231 **Discussion**

232 In this study, we found significant increases in coral abundances on temperate reefs
233 over an ~8-yr period associated with gradual warming and heatwaves. This change was
234 driven by increases in species common to both sampling periods. New, more tropically
235 affiliated species were recorded but in very low abundances insufficient to drive a shift in the
236 community structure relative to the substantial increase in other species. The most
237 pronounced abundance change was found for *P. versipora*. The strongly skewed size-
238 frequency distributions of *P. versipora* colonies demonstrated a large increase in small
239 colonies, suggesting an increase in recruitment or recruit survival after the heatwaves. Age
240 estimates for small *P. versipora* colonies (<12 cm²) reinforce the idea of recent juvenile

241 success. Based on a conservative growth rate of 4 mm yr⁻¹ (average rate calculated from
242 South Australia, where water temperatures were cooler than the mid-west; Burgess et al.
243 2009) the age of small colonies recorded after the heatwave could be 1.3 to 7.3 yr (radius
244 range of colonies <12 cm² colonies was ~0.5–2.9 cm). The magnitude of this population
245 expansion indicates that our findings are not due to sampling artefacts and the increase seen
246 here is unlikely due to cyclical variation as size-frequency distributions were clearly
247 unimodal and negatively skewed in 2013. If this was a cyclical change, we would expect to
248 see a multimodal distribution of progressive cohorts but this was not the case. Overall, these
249 results are consistent with our hypotheses, indicating that there has been a change in coral
250 communities driven by substantial local population expansion and, to a lesser extent, a
251 possible increase in warm-affinity species (see below).

252 Extreme temperatures during the marine heatwaves are unlikely to have directly
253 driven the observed changes in coral communities and the success of recruitment or survival
254 of small *P. versipora*. Coral larvae and microscopic recruits are heat sensitive, with
255 temperature stress prompting reduced pre-competency periods, increased mortality during
256 metamorphosis, and increased mortality post settlement (Edmunds et al. 2001; Bassim and
257 Sammarco 2003; Nozawa and Harrison 2007; Randall and Szmant 2009; Yakovleva et al.
258 2009; Ross et al. 2013). While negative effects do not always result from heat stress (e.g.
259 Edmunds et al. 2001), it is likely the long duration and high intensity of the 2011 heatwave
260 would have had deleterious effects on reproduction and early life stages. Specifically, coral
261 recruitment (likely due to reduced reproductive output) at the Houtman Abrolhos Islands
262 (approximately 70 km northwest of the study region) in 2011 and 2012 was significantly
263 reduced compared to subsequent cooler years, (Markey et al. 2016). Further, adult coral

264 colonies, which are generally more resilient to temperature stress than early life stages (larvae
265 and microscopic recruits), experienced bleaching and reduced growth during the heatwave
266 periods (Pearce et al. 2011; Thomson et al. 2011; Abdo et al. 2012; Moore et al. 2012; Smale
267 and Wernberg 2012; Foster et al. 2014). Thus, direct effects of high temperature during the
268 heatwaves would most likely have had a net negative effect on the mid-west coral
269 communities and would not have benefitted the juvenile coral population.

270 The recent success of small (juvenile) corals is likely the consequence of competitive
271 release mediated by temperature through the reduction in canopy-forming temperate
272 seaweeds and increases in herbivorous fishes. Seaweeds often limit corals in temperate
273 environments through competitive stress, abrasion and dislodgement (Miller and Hay 1996).
274 Seaweed removal experiments and natural canopy-free patches have shown a relaxation of
275 these processes, leading to greater coral persistence, increased recruitment success and
276 growth (Coyer et al. 1993; Miller and Hay 1996; Thomson et al. 2012). The heatwaves
277 caused a substantial loss of seaweed canopy cover, which declined from 80–90% to 50% or
278 less across the study region (Fig. 5a, b) (Smale and Wernberg 2013; Wernberg et al. 2013a,
279 2016b), a loss that has been maintained and reinforced over time by increasing herbivory by
280 tropical fishes (Bennett et al. 2015). The loss of seaweed canopies would have facilitated the
281 growth and survival of juvenile corals that recruited prior to the heatwave (Fig. 5c–e),
282 presumably outweighing the direct negative effects of the heatwave on these animals. This
283 could explain why high frequencies were found across several small size classes for *P.*
284 *versipora* rather than within a single size class (which would have suggested a single
285 recruitment pulse). We expect this recruitment facilitation to continue where the heatwave
286 has caused a persistent shift to low canopy abundance (Wernberg et al. 2016b).

287 Other species within the coral community showed smaller changes than *P. versipora*
288 and were found in abundances too low for size-frequency analyses. In some instances,
289 species recorded before the heatwave did not increase or were not recorded after the
290 heatwave. It remains unclear why other local species did not show stronger positive responses
291 to the direct and indirect effects of the heatwaves. Lower initial abundances compared to *P.*
292 *versipora* could have limited propagule supply such that abundance changes would take
293 longer to manifest, especially if these species also have less opportunistic life histories.
294 Similarly, the increase in new warm-water species was very small. Warm-water, low-latitude
295 species could have been limited by their lower environmental tolerances, not only to
296 temperature but also depth, water clarity and light levels (Sommer et al. 2014; Keith et al.
297 2015; Mizerek et al. 2016).

298 Dispersal and recruitment could also be a factor limiting the response of warm-water
299 species in this study. Long-distance dispersal from upstream sources would be required for an
300 increase in warm-water species as the nearest coral reefs are ~70 km offshore at the Houtman
301 Abrolhos Islands (28°S). Under normal conditions, larval longevity could favour connectivity
302 between the Houtman Abrolhos Islands and the mid-west as after ~100 d (the last stage of
303 coral mortality) patterns show increasing mortality (Graham et al. 2008; Markey et al. 2016).
304 However, coral larvae show reduced pre-competency periods under thermal stress, which
305 could promote settlement on natal reefs and reduce dispersal duration within the pelagic
306 period (Nozawa and Harrison 2000; Heyward and Negri 2010). In addition, the timing of
307 arrival of new warm-water species relative to the loss of seaweed canopies might have
308 limited successful settlement and recruitment. Thus, the probability of successful dispersal to
309 the coastal reefs in the study area seems very low, and the likelihood of recruit limitation

310 high. Thermal stress to early life stages during the heatwaves and dispersal limitation may be
311 at least partially responsible for warm-water species not increasing.

312 The species predominantly responsible for the increase in coral abundance, *P.*
313 *versipora*, is often considered a temperate species. However, it has been recorded in many
314 more tropical than temperate locations (~80% of 283 records north of 30.3°S; Atlas of Living
315 Australia, www.ala.org.au) and is perhaps more correctly classified as a tropical species with
316 broad environmental tolerances. As temperate reefs are generally characterised by abundant
317 seaweeds and not corals, the substantial expansion of coral populations observed in this study
318 is consistent with the ongoing tropicalisation of temperate reefs seen in Western Australia
319 and globally (Yamano et al. 2011; Wernberg et al. 2013a, 2016a; Vergés et al. 2014b). It is
320 likely that greater juvenile recruitment and/or survival of newly recruited corals was largely
321 the indirect result of competitive release from seaweeds rather than a response to consecutive
322 marine heatwaves. However further investigation is needed to determine whether coral
323 increases will be moderated by changing community interactions, such as the increase in turf
324 algae (Wernberg et al. 2013a, 2016a) and herbivory (Bennett et al. 2015). Regardless, we
325 expect to see coral populations increase in these high-latitude reef communities with future
326 warming, heatwaves and seaweed declines.

327

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335

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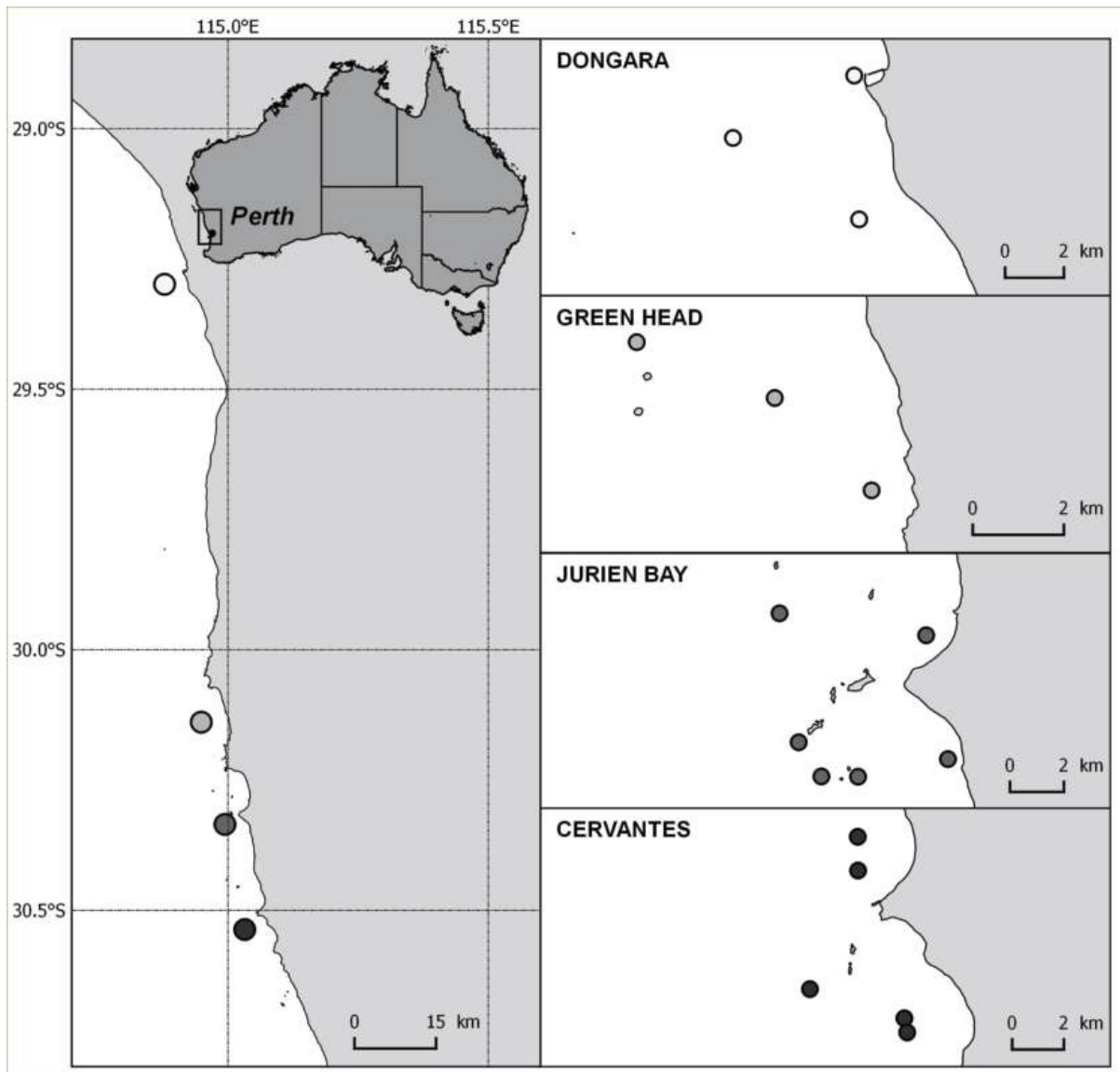
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531 **Figures**

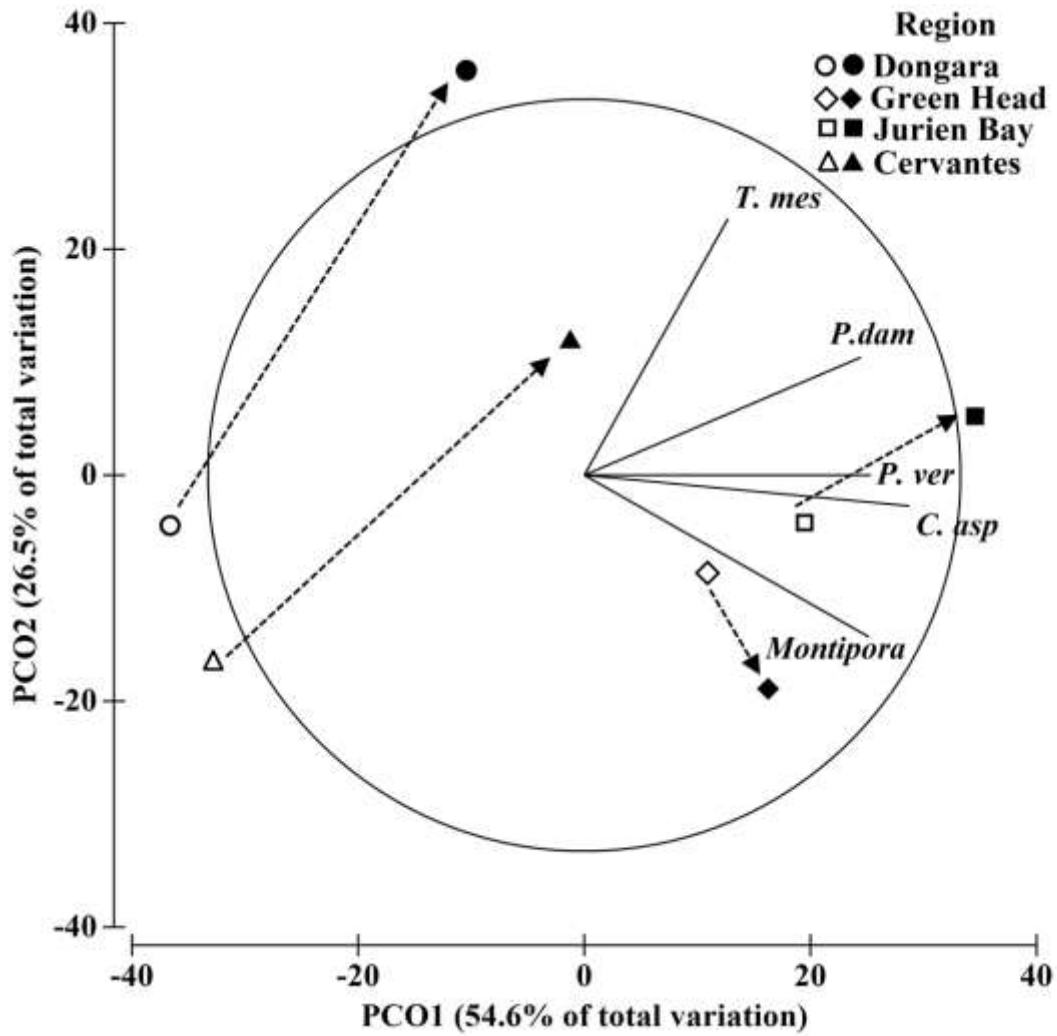


532

533 **Fig. 1** Sample regions and sites within the mid-west of Western Australia. The grey scale for

534 the dots on the left panel match the four regions (Dongara, Green Head, Jurien Bay and

535 Cervantes) on the right panels



536

537 **Fig. 2** Principal coordinates analysis of variation in coral community structure on mid-west

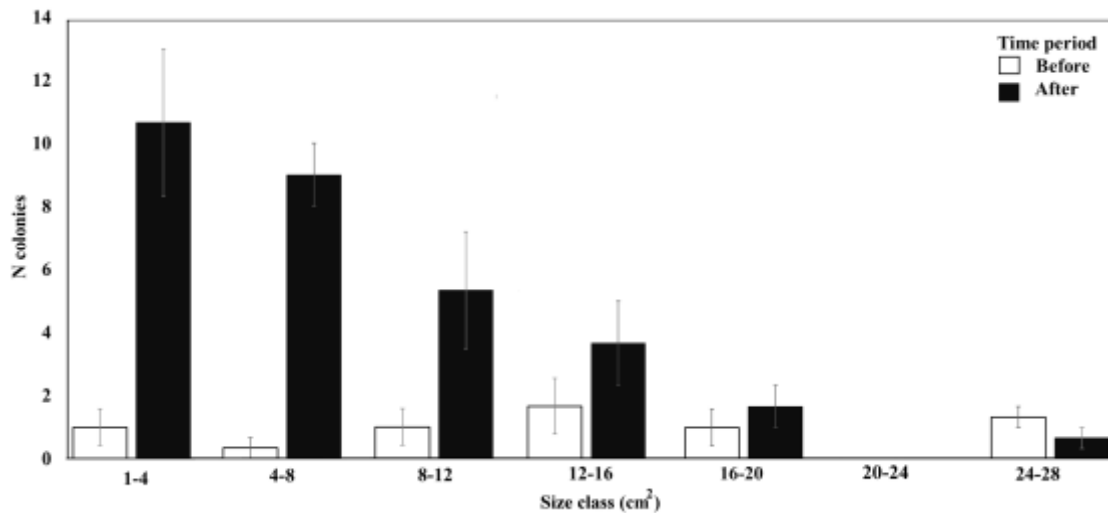
538 temperate reefs. The first two axes (PCO1 and PCO2) explain 81.1% of the variability in

539 multivariate space. *White shapes* denote before heatwave centroids and *black shapes* are

540 centroids for after the heatwaves. *T. mes* = *Turbinaria mesenterina*, *P. dam* = *Pocillopora*

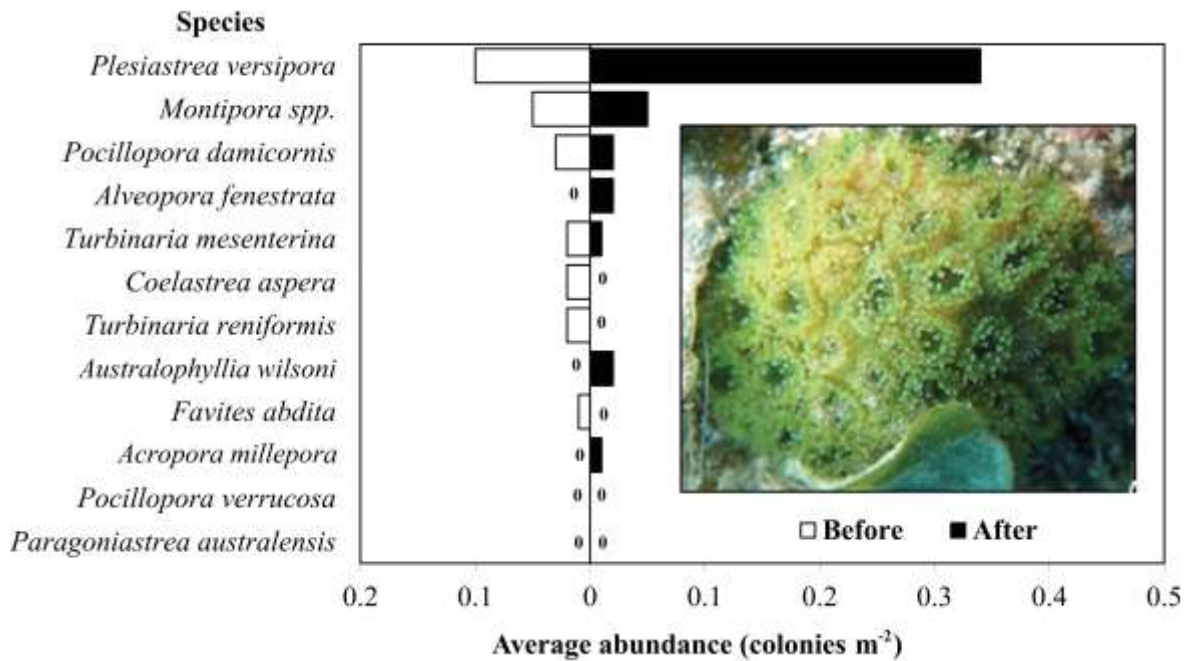
541 *damicornis*, *P. ver* = *Plesiastrea versipora*, *C. asp* = *Coelastrea aspera*

542



543

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

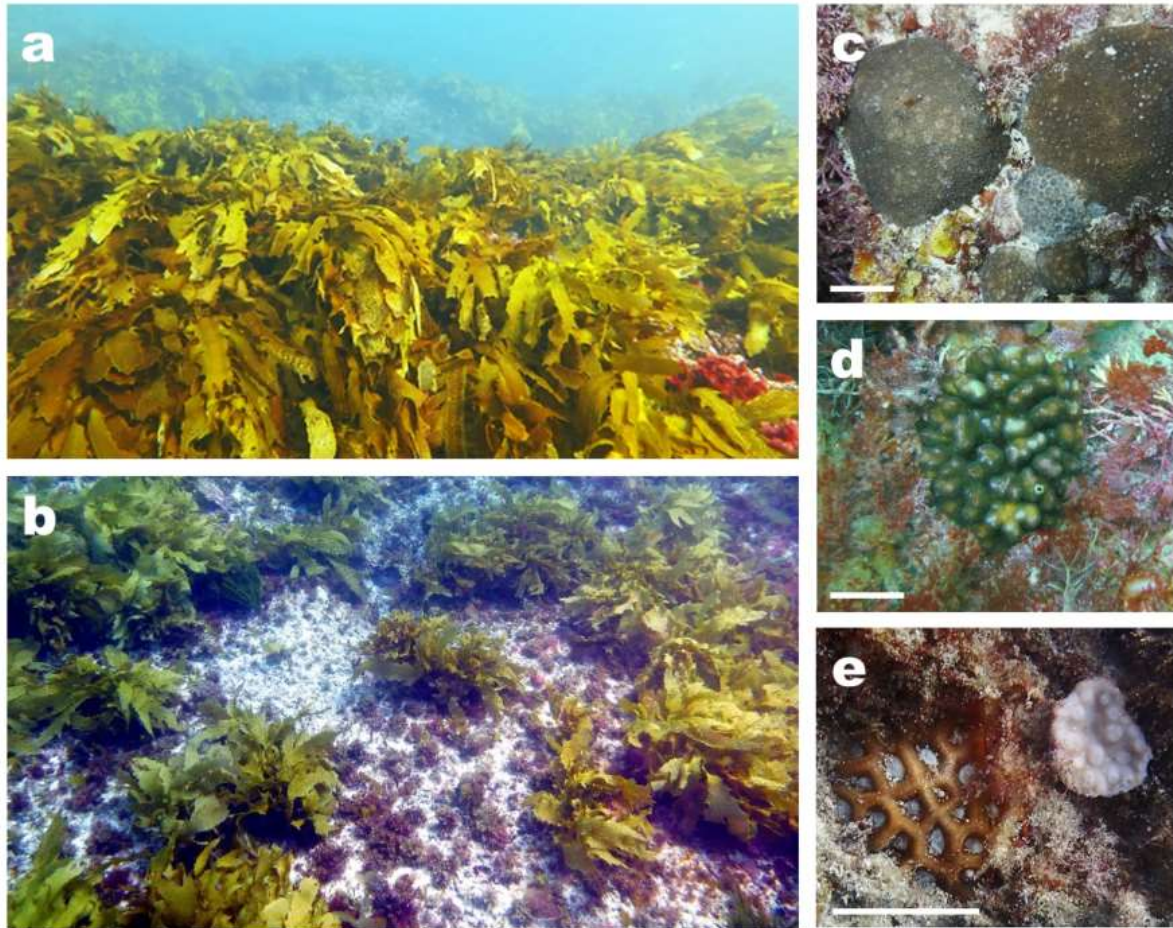


548

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

551 Photo: C. Tuckett

552



553

554 **Fig. 5** Underwater photographs from mid-west Western Australia showing **a** benthos
555 dominated by the seaweed canopy prior to the marine heatwaves; **b** benthos with significantly
556 reduced canopy and large open patches post heatwaves; **c** juvenile *Plesiastrea versipora*
557 colonies found post heatwaves; **d** juvenile *Pocillopora damicornis* colony found post

558 heatwaves; **e** juvenile Merulinidae and Turbinaria post heatwaves. **c–e** Scale bars = 2.5 cm.

559 Photo credits: **a, b** T. Wernberg; **c, d** T. de Bettignies; **e** C. Tuckett

560

561 **Table 1.** Comparison of coral communities before (2005-2006) and after (2013) multiple
562 heatwaves in the midwest of Western Australia.

Data Summary				
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 ⁻²)	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	<i>F</i>	<i>p</i>
Time	1	3220	3.732	0.009*
Region	3	3218	3.729	0.001*
Time x Region	3	1157	1.341	0.210
Residual	26	863		
Region (pairwise test)		<i>t</i>	<i>p</i>	
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*	

563 *significant difference <0.05

564 Total colony counts are for all regions (n=4), small colonies are <12cm², large colonies >12cm², mean colony
565 density is given per region and per m⁻². Small and large colony counts do not equal the total for 'before' as five
566 colonies were not measured. Permutational analysis of variance (PERMANOVA) tested for differences in

567 community structure between years (fixed) and regions (fixed). PERMANOVA is based on a zero adjusted Bray
568 Curtis similarity matrix. Pairwise testing showing the variability between regions.