1   **Title**: Contrasting patterns of changes in abundance following a bleaching event

2   between juvenile and adult scleractinian corals

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20   **Key words**

21   coral reefs, climate change, ecology, thermal stress, juvenile corals

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23   **Conflict of interest statement**

24   On behalf of all authors, the corresponding author states that there is no conflict of

25   interest.

Abstract

Coral bleaching events have caused extensive mortality on reefs around the world. Juvenile corals are generally less affected by bleaching than their conspecific adults, and therefore have the potential to buffer population declines and seed recovery. Here, we use juvenile and adult abundance data at 20 sites encircling Lizard Island, Great Barrier Reef, before and after the 2016 bleaching event to quantify: 1) correlates of changes in juvenile abundance following a bleaching event; 2) differences in susceptibility to extreme thermal stress between juveniles and adults. Declines in juvenile abundance were lower at sites closer to the 20m depth contour and higher for *Acropora* and *Pocillopora* juveniles than for other taxa. Juveniles of *Acropora* and *Goniastrea* were less susceptible to bleaching than adults, but the opposite was true for *Pocillopora* spp. and taxa in the family Merulinidae. Our results indicate that the potential of the juvenile life-stage to act as a buffer during bleaching events is taxon-dependent.

Introduction

Coral reefs have been facing numerous anthropogenic stressors for decades, leading to a severe decline in the abundance of corals and associated organisms on reefs (Jackson et al. 2001). Among those stressors, increasing atmospheric carbon dioxide concentrations have had a strong negative effect on coral health by causing rapid and prolonged increases in sea surface temperatures that, in combination with high solar radiation, disrupt the relationship between the coral host and photosynthetic endosymbiotic algae (Lesser et al. 1990). Thermal bleaching often results in partial colony mortality or death (Harriott 1985), but the severity of bleaching depends on many factors. Importantly, juvenile corals tend to bleach less and survive better than adults (Mumby 1999; Shenkar

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51 et al. 2005; Loya et al. 2001), and therefore have the potential to facilitate post-

52 bleaching recovery.

53   A few explanations for the difference in bleaching susceptibility between

54 juveniles and adults have been proposed. First, mass transfer to eliminate toxic by-

55 products occurs more rapidly in small organisms than in large ones (Nakamura and van

56 Woesik 2001) and in flat rather than branching organisms (Patterson 1992). Juvenile

57 corals are both small and relatively flat, and mass transfer dynamics might at least partly

58 explain their lower susceptibility to bleaching. Additionally, differences between

59 juvenile and adult susceptibilities to bleaching might be partially driven by higher

60 concentrations of fluorescent proteins in juveniles (Papina et al. 2002), which enhance

61 resistance to coral bleaching by dissipating excess light energy (Salih et al. 2000).

62 Moreover, being non-reproductive might allow juveniles to invest more energy into

63 maintenance to survive thermal stress when compared to adults.

64   Responses to thermal stress can differ widely between corals and environments.

65 Some coral taxa are more susceptible to bleaching than others (Marshall and Baird

66 2000; Loya et al. 2001). Structural complexity can also be important because it

67 increases variation in irradiance (Brakel 1979). High irradiance worsens the effects of

68 high water temperatures on coral health (Lesser et al. 1990), and therefore colonies in

69 shaded microhabitats typically bleach less (Hoogenboom et al. 2017; Muir et al. 2017).

70 High water flow facilitates the removal of toxins produced at high water temperatures

71 and high irradiance, reducing bleaching-induced mortality (Nakamura and van Woesik

72 2001) and facilitating post-bleaching recovery (Nakamura et al. 2003). This

73 experimental work is supported by field work indicating that sites close to deeper water

74 were more resistant to bleaching on the Great Barrier Reef (GBR) in 2002, presumably

75 due to proximity to cooler water and a greater capacity for water mixing (Done et al.

76 2003).

77   Warm water temperatures in the austral summer of 2016 led to the most severe

78 bleaching event on record on the GBR and caused widespread mortality, particularly in

79 the northern section of the GBR (Hughes et al. 2017). We use environmental data and

80 juvenile and adult abundance before and after the 2016 bleaching event to answer the

81 following questions: 1) What are the best environmental predictors of changes in

82 juvenile abundance after a bleaching event? 2) Per taxon, are adult or juvenile colonies

83 more resistant to extreme thermal disturbance?

84

85 **Methods**

86 **Study location and data collection**

87 Data were collected at 20 sites around Lizard Island in the northern GBR (14.6688° S,

88 145.4594° E) in November in each of 2015 and 2016 (Fig. 1). At each site, five quadrats

89 of 1m^2 or 0.81m^2 (in 2015 and 2016, respectively) were haphazardly placed and all

90 juvenile corals within them were counted and identified to genus following Veron

91 (2000) but updating genus and family following the World Register of Marine Species.

92 Colonies with a maximum diameter <5cm were considered to be juveniles (*sensu* Bak

93 and Engel 1979). Fragments were not considered juveniles. Five or six 10m line

94 intercept transects were laid at each site to record abundances of adult corals (≥5cm

95 diameter). Abundance was the number of individual colonies that were intercepted by

96 the transect tape.

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Predictor variables

We tested the extent to which bleaching susceptibility measured by changes in abundance was predicted by five factors: thermal stress, rugosity, aspect, distance to the 20m depth contour, and taxon (Table A1). We used site-level maximum water temperature recorded by temperature loggers at the sites from November 2015 to November 2016 as a proxy for thermal stress (Done et al. 2003). Rugosity was used as a proxy for structural complexity and was estimated from 3D reconstructions of $130m^2$ areas within each site in 2015 (Pizarro et al. 2017). Rugosity was defined as the ratio of the site's 3-D surface area to the 2-D area of the plane of best fit (Friedman et al. 2012). Sites differ in water currents and wind exposure depending on their location around the island, therefore aspect (NW, NE, SW, SE) was included as a variable to capture these differences. Sites close to the 20m depth contour (m, log scale) are expected to have a greater proximity to deep and presumably cooler water and a greater capacity for water mixing than sites farther away (Done et al. 2003). Finally, taxonomic category was also included as a variable (Marshall and Baird 2000).

Analysis

To test whether juvenile abundance per m^2 decreased in 2016 relative to 2015, we fitted a linear mixed effects model with year as a fixed effect and site as a random effect ('lme4' R package; Bates et al. 2015). To examine the best predictors of change in juvenile abundance (number of juveniles), we calculated the yearly mean abundance (m^{-2}) for each taxonomic category at each site. Genera with fewer than 20 juveniles were grouped with other genera with fewer than 20 individuals belonging to the same family. Family groups with fewer than 20 juveniles were eliminated to ensure estimates for juvenile change were not strongly influenced by rare taxa. We fitted a series of linear

125 models predicting proportional change in juvenile abundance between years for

126 taxonomic category i at site j ($\log_{10}$(abundance 2016_{ij} / abundance 2015_{ij})) as a function

127 of each combination of predictor variables. Our sample size allowed for a maximum of

128 two predictor variables to be included in each model. We included models with site as a

129 random effect and without random effects and we calculated the R^2 value for each

130 model ('r2glmm'; Jaeger et al. 2016).

131 To examine the similarity of changes in abundance post bleaching between

132 juveniles and adults, we plotted mean proportional change in adults vs. mean

133 proportional change in juveniles for each taxon, using changes in proportional

134 abundance as a proxy for mortality. All analyses were performed in R version 3.2 (R

135 Core Team 2016).

136

137 **Results and discussion**

138 Total mean juvenile abundance from did not vary significantly between 2015 and 2016

139 at the island scale (Table A2) and changes among sites were highly variable (Fig. A1).

140 Proportional change in juvenile abundance was best explained by distance to the 20m

141 depth contour and taxonomic category (Table A3; site as a random effect was not

142 significant: p-value=1).

143 Proportional change in juvenile abundance decreased in 2016 relative to 2015

144 with increasing distance to the 20m depth contour (Fig. 2-a; Table A4). Sites closer to

145 the 20m depth contour are closer to deeper and potentially cooler water, as well as

146 having a higher capacity for these waters to mix due to the greater angle of the reef

147 slope (Done et al. 2003). On Lizard Island, sites closer to the 20m contour are on the

148 eastern side of the island and therefore are also more exposed to the south-easterly trade

149 winds that will stimulate water mixing and movement (Fig. A2). Moreover, high water

150 flow facilitates the mass transfer of toxic by-products of bleaching (Nakamura and van

151 Woesik 2001), ameliorating the effects of bleaching. In contrast, Hoogenboom et al.

152 (2017) attributed their finding that bleaching severity was higher in adults at sites that

153 were closer to open water on Lizard Island to the fact that these sites experience less

154 temperature variability, a factor known to promote thermal tolerance in adults (Oliver

155 and Palumbi 2011). These contrasting results between adult and juveniles suggest that

156 factors associated with bleaching susceptibility differ among life-history stages.

157   Some previous studies have suggested that juveniles are 'immune' to the effects

158 of bleaching (e.g. Mumby 1999; Depczynski et al. 2013). In contrast, our results reveal

159 an order of magnitude decline in the abundance of *Pocillopora* and *Acropora* (Fig. 2-b)

160 and lesser, but still significant, declines in *Dipsastraea, Favites* and other Merulinidae

161 (Fig. 2-b). Mumby (1999) conducted his research in Belize, were there are no

162 *Pocillopora,* and *Acropora* colonies are rare: juveniles of these genera were the most

163 susceptible to bleaching at Lizard Island. Therefore, the contrasting results are most

164 likely driven by differences in species composition. Depczynski et al. (2013) used a

165 different size cut-off for juveniles (less than 10 cm vs. our 5 cm). In addition, their

166 estimates of mortality were based on the proportion of individual in different categories

167 a few months post-bleaching (i.e. dead vs. alive). In fact, it is often difficult to detect

168 dead coral colonies, particularly when they are small; therefore it is possible they

169 underestimated mortality in the juvenile size class.

170   Overall, the percentage of variation in the proportional change of juvenile

171 abundance explained by any combination of two or fewer variables was low (Table A2).

172 More than one cohort of corals corresponds to the juvenile size class in this study.

173 Juvenile abundance is ultimately increased by recruitment and decreased by juveniles

174 dying or growing larger than 5cm. While bleaching can affect juvenile survival, many

175 other factors, such as the strength of yearly recruitment and the bleaching-independent

176 mortality, will also contribute to changes in juvenile abundance.

177   Differences in susceptibility to the 2016 bleaching event between juveniles and

178 adults differed among taxa (Fig. 3). Total mean abundance of *Cyphastrea, Porites,*

179 *Montipora*, *Favites*, and *Dipsastraea* spp. remained stable in both life-stages. Overall,

180 adults of *Acropora* and *Goniastrea* spp. were more affected than juveniles (mean

181 abundance of *Goniastrea* juveniles actually increased; Fig. A3), a finding consistent

182 with previous studies (Mumby 1999; Loya et al. 2001; Bena and van Woesik 2005;

183 Depczynski et al. 2013). However, juveniles of *Pocillopora* spp. and the family

184 Merulinidae had a stronger decline in abundance post-bleaching than adults, indicating

185 that the decrease in susceptibility as a function of size is taxon-dependent.

186   Demographic processes of juvenile corals have important effects on population

187 dynamics and are key to population persistence after disturbance (Connell et al. 1997).

188 Our results show that differences in bleaching susceptibility between juveniles and

189 adults among taxa need to be considered when predicting changes to reef communities

190 following episodes of thermal stress.

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292 **Figure Legends**

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294   Figure 1. Map of Lizard Island showing the sites that were surveyed. Dotted lines show

295   the 20m depth contour.

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297   Figure 2. Panel a- proportional change in juvenile abundance

298   ($\log_{10}[\text{abundance}_{2016}/\text{abundance}_{2015}]$) as a function of distance to the 20m depth contour

299   (m). The black line shows the predicted proportional change in juvenile abundance, and

300   the grey ribbon shows 95% confidence intervals. Panel b- proportional change in

301   juvenile abundance ($\log_{10}[\text{abundance}_{2016}/\text{abundance}_{2015}]$) for each taxonomic category.

302   Error bars show standard errors. Grey dots represent observed data, with the dot size

303   showing the number of observations.

304

305

306   Figure 3. Proportional change in adult abundance versus proportional change in juvenile

307   abundance (log-log scale) between 2015 and 2016 for each taxonomic category. Line-

308   ranges indicate standard errors. The dotted vertical and horizontal lines indicate no

309   proportional change in adult and juvenile abundance, respectively, between years. The

310   dashed line indicates values for which the proportional change in adult abundance is

311   equal to the proportional change in juvenile abundance.
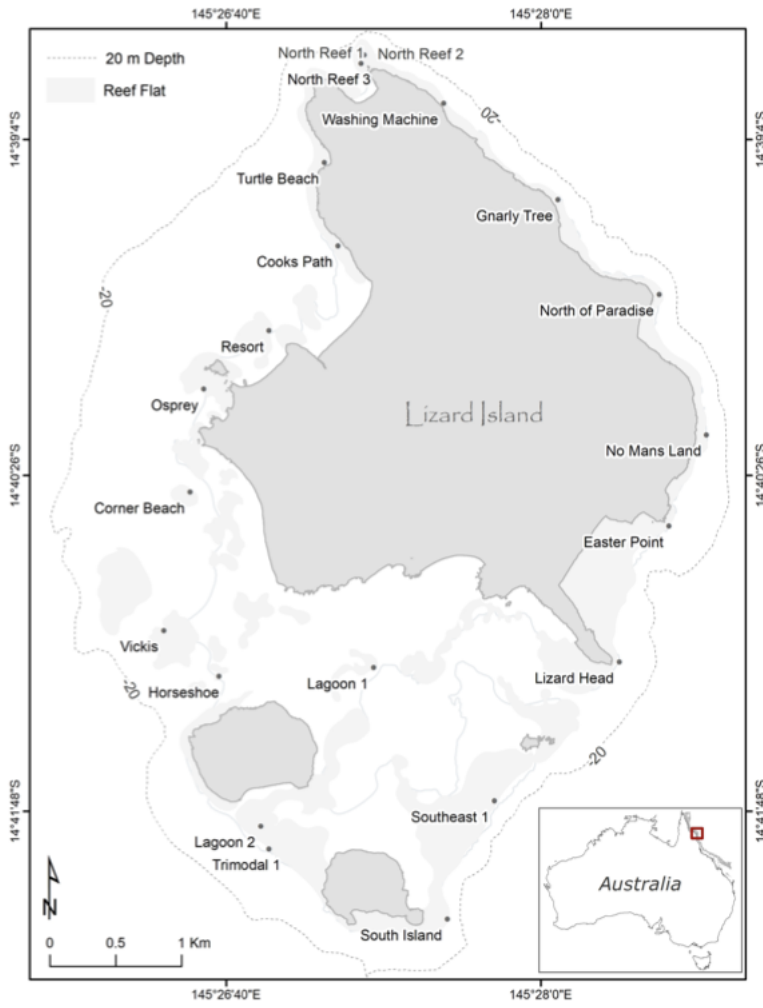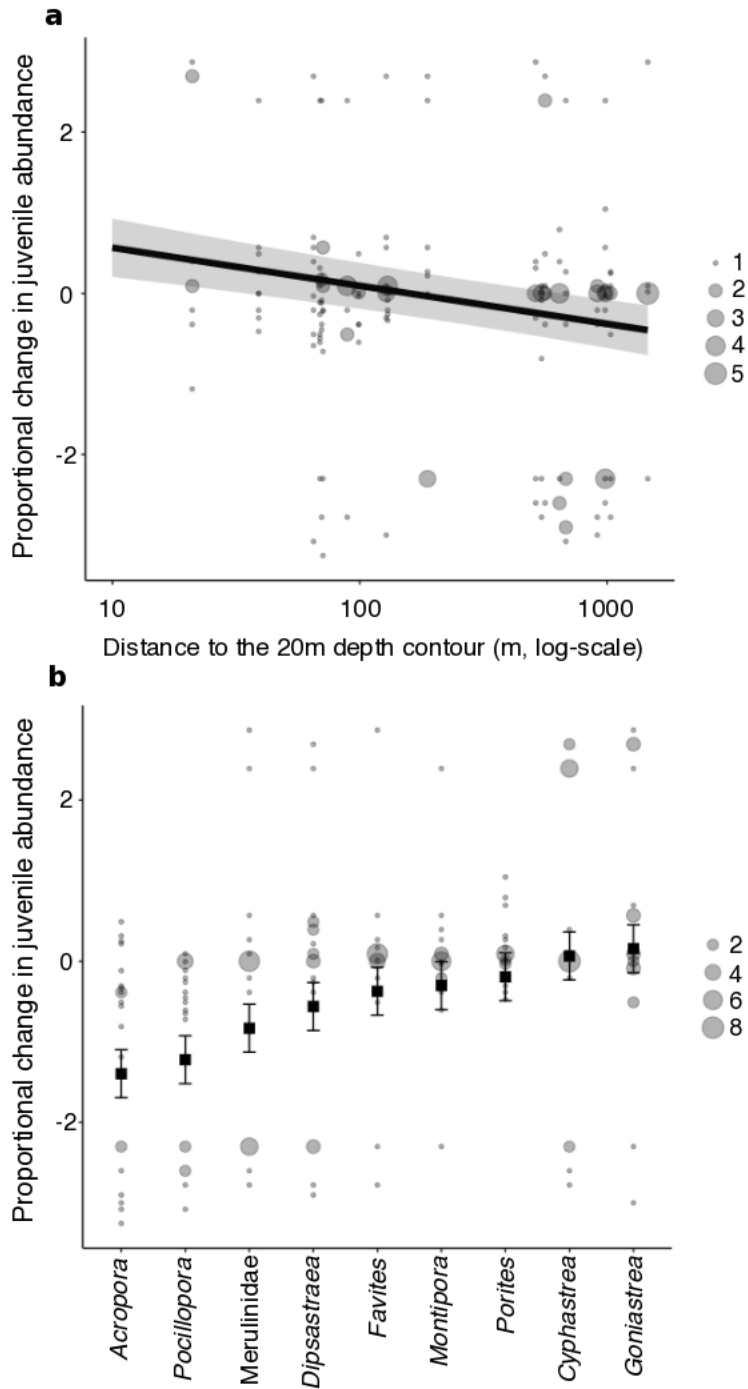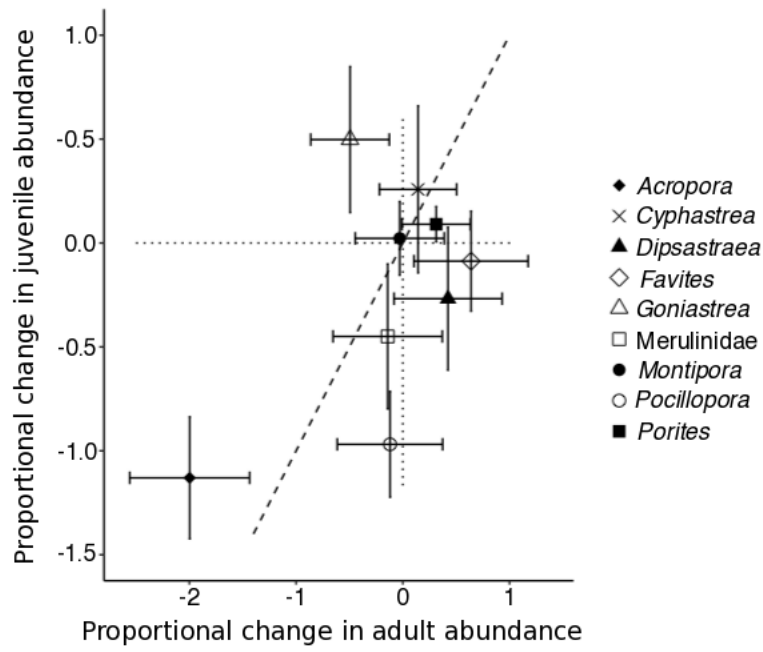
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319   Figure 1

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