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1    **Expansion of a colonial ascidian following consecutive mass coral**  
2                    **bleaching at Lizard Island, Australia**

3

4    **Short Title:**

5    Expansion of a colonial ascidian

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## 21 **Abstract**

22           Mass coral bleaching is challenging today's coral reefs. However, our understanding  
23 of dynamics in benthic space holders, following such disturbances, is limited. To address this,  
24 we quantified successional dynamics of the ascidian, *Didemnum cf. molle* using a series of  
25 temporally and spatially matched photoquadrats across both the 2016 and 2017 mass coral  
26 bleaching events on the Great Barrier Reef. Unlike corals, *D. cf. molle* appeared to flourish in  
27 the warm temperatures and rapidly expanded. Indeed, colony density increased nearly 6-fold  
28 over two years with one quadrat experiencing an increase of over 1000 ind. m<sup>-2</sup>. However,  
29 this increase did not simply track the increase in space due to coral mortality, but may have  
30 benefitted from reduced predation or increased nutrient availability following mass coral  
31 mortality. This study highlights the potential of *D. cf. molle* to expand under bleaching  
32 conditions and to become a more prominent component of future reef configurations.

## 33 **Keywords:**

34 Benthos; Coral Reef; *Didemnum molle*; Ecosystem Change; Great Barrier Reef; Marine  
35 Ecology; Reefs

## 36 **1. Introduction**

37           Coral reefs are amongst the most biodiverse ecosystems on Earth, with intense  
38 competition for benthic space (Jackson, 1977) and disturbances causing shifts in species  
39 composition (Hughes et al., 2018). Unfortunately, large-scale disturbances are becoming  
40 more prevalent on coral reefs (Hughes et al., 2019). In the wake of these events, new reef  
41 configurations are emerging with fewer coral species and lower coral cover (Hughes et al.,  
42 2018; Norström et al., 2009). Indeed, during the austral summers of 2016 and 2017  
43 Australia's Great Barrier Reef (GBR) experienced unprecedented back-to-back mass coral

44 bleaching and coral mortality (Hughes et al., 2019). Such mortality provides free space which  
45 is often rapidly colonised by algae, especially turfing forms (Diaz-Pulido and McCook,  
46 2002). However, while post-bleaching dynamics of corals (e.g. Hughes et al., 2018; Torda et  
47 al., 2018; Wismer et al., 2019) and to a lesser extent algae (e.g. Diaz-Pulido and McCook,  
48 2002) have received attention in the literature, our understanding for other benthic space  
49 holders is relatively limited (reviewed in Norström et al., 2009).

50         One common, yet often overlooked group of benthic organisms on coral reefs are  
51 ascidians. Ascidians are a unique group of basal chordates, which have tadpole-like larvae  
52 with a notochord which is lost once the larvae settle (Lambert, 2005). This life history allows  
53 them to actively disperse over short distances, with the potential to colonize suitable down-  
54 stream sites (Olson, 1985). This expansion is facilitated by the ability of some ascidians to  
55 move short distances over the benthos and reproduce asexually through division (Cowan,  
56 1981). Indeed, expansions of ascidians on coral reefs have been noted previously (e.g. Bak et  
57 al., 1996; Oren and Benayahu, 1998; Roth et al., 2018; Shenkar et al., 2008), yet their  
58 successional dynamics following coral mortality on such unprecedented scales is currently  
59 unclear. The aim of this study, therefore, was to utilise a series of temporally and spatially  
60 matched photoquadrats to examine the successional dynamics of a widespread ascidian  
61 across both the 2016 and 2017 mass coral bleaching events on the GBR.

## 62 **2. Materials and methods**

### 63 *2.1 Study site and species*

64         The abundance and coverage of the ascidian *Didemnum cf. molle* was studied in the  
65 Lagoon and on Loomis Reef at Lizard Island (14°40'8.04"S, 145°27'33.84"E; ESM Fig. S1),  
66 in the northern Great Barrier Reef, Australia. These sheltered reefs at Lizard Island were  
67 some of the worst affected by the 2016 bleaching event (Wismer et al., 2019), but were

68 largely protected from two cyclones which struck the exposed side of the island in the years  
69 prior (2014/2015) to the bleaching (Brandl et al., 2016; Khan et al., 2017). Coral bleaching  
70 was particularly pronounced at Lizard Island during the 2016 event as a result of >8 degree  
71 heating weeks by April 2016 (Hughes et al., 2019; Wismer et al., 2019). From January 2016  
72 – April 2016 average water temperature at 0.6 m depth regularly exceeded 30°C and  
73 maximum photosynthetically active radiation often exceeded 2000  $\mu$  moles  $s^{-1} m^{-2}$  (ESM Fig.  
74 S2). It must be noted that DNA barcoding is recommended for the correct identification of  
75 ascidians (Jaffarali et al., 2018), and without this certainty the conservative nomenclature *D.*  
76 *cf. molle* is used herein. Indeed, *Atriolum robustum* is often misidentified as *D. molle* (see  
77 ESM Text S1 and Fig. S3 for details).

## 78 2.2 Sampling

79 Along the reef edge (1-3 m depth), in both the Lagoon and on Loomis Reef (ESM Fig.  
80 S1), 27 and 36 quadrats, respectively, were examined to assess changes in *D. cf. molle*  
81 abundance. Quadrats (1 m<sup>2</sup>) were initially placed haphazardly (~5 m apart) along the reef  
82 edge in February 2016, prior to major bleaching, and photographed from above using a Nikon  
83 Coolpix W300 digital camera. The same quadrat areas were re-photographed in April 2016  
84 (during peak bleaching), October 2016 (approximately six months post-bleaching) and  
85 January 2018 (approximately 21 months post 2016 bleaching and 10 months post 2017  
86 bleaching). Quadrats were not left fixed in place. They were placed in the same locations on  
87 each trip using previous photographs loaded onto an additional digital camera (Nikon  
88 Coolpix W300) as a guide (see Wismer et al., (2019) for full details and a sensitivity analysis  
89 of methods). It should be noted that the present study represents a focused examination of *D.*  
90 *cf. molle* dynamics on these two specific reef locations. These locations were selected as both  
91 had *D. cf. molle* populations prior to the bleaching events. Other sites around Lizard Island,  
92 especially exposed locations, generally lacked *D. cf. molle*. This lack of *D. cf. molle* at other

93 sites is likely to be a consequence of the previous cyclones that scoured the benthos in  
94 exposed localities (details above). In addition, limited connectivity among sites is likely to be  
95 due to the influence of water currents on the dispersal abilities of *D. cf. molle* larvae (see  
96 Olson, (1985) for a detailed study of *D. molle* dispersal at Lizard Island).

### 97 *2.3 Image processing*

98 To assess the abundance and benthic coverage of *D. cf. molle* photographs were  
99 examined in two ways. Firstly, quadrats in the photographs were systematically searched for  
100 *D. cf. molle* and the number of individual *D. cf. molle* were recorded. Due to the propensity  
101 of *D. cf. molle* to form dense, clustered colonies, and their ability to reproduce asexually via  
102 fission, this method may overestimate *D. cf. molle* abundance as it was not always clear if  
103 two *D. cf. molle* were completely separated or were in the process of dividing. Secondly,  
104 therefore, the proportion of benthic space occupied by *D. cf. molle*, as well as other benthic  
105 organisms, was calculated by generating 50 random points in each quadrat using the software  
106 photoQuad V1.4 (Trygonis and Sini, 2012). Each point was categorised as either *D. cf. molle*,  
107 crustose coralline algae (CCA)/algal turfs, hard corals, soft corals, sand/small rubble,  
108 macroalgae (algae > 2cm high), cyanobacterial mat, and other (predominantly *Tridacna*  
109 clams). As this method of quadrat examination can undercount rare benthic cover categories,  
110 the coverage of *D. cf. molle* is likely to be a conservative estimate.

### 111 *2.4 Statistical analysis*

112 Initially, changes in the entire benthic assemblage over time were examined using a  
113 permutational multivariate analysis of variance (PERMANOVA) based on a Euclidean  
114 distance matrix of standardised data. In the PERMANOVA sampling trip was treated as a  
115 fixed factor, while site and individual quadrat identity nested within site were treated as  
116 random factors to account for the repeated measures design of the study, any variability

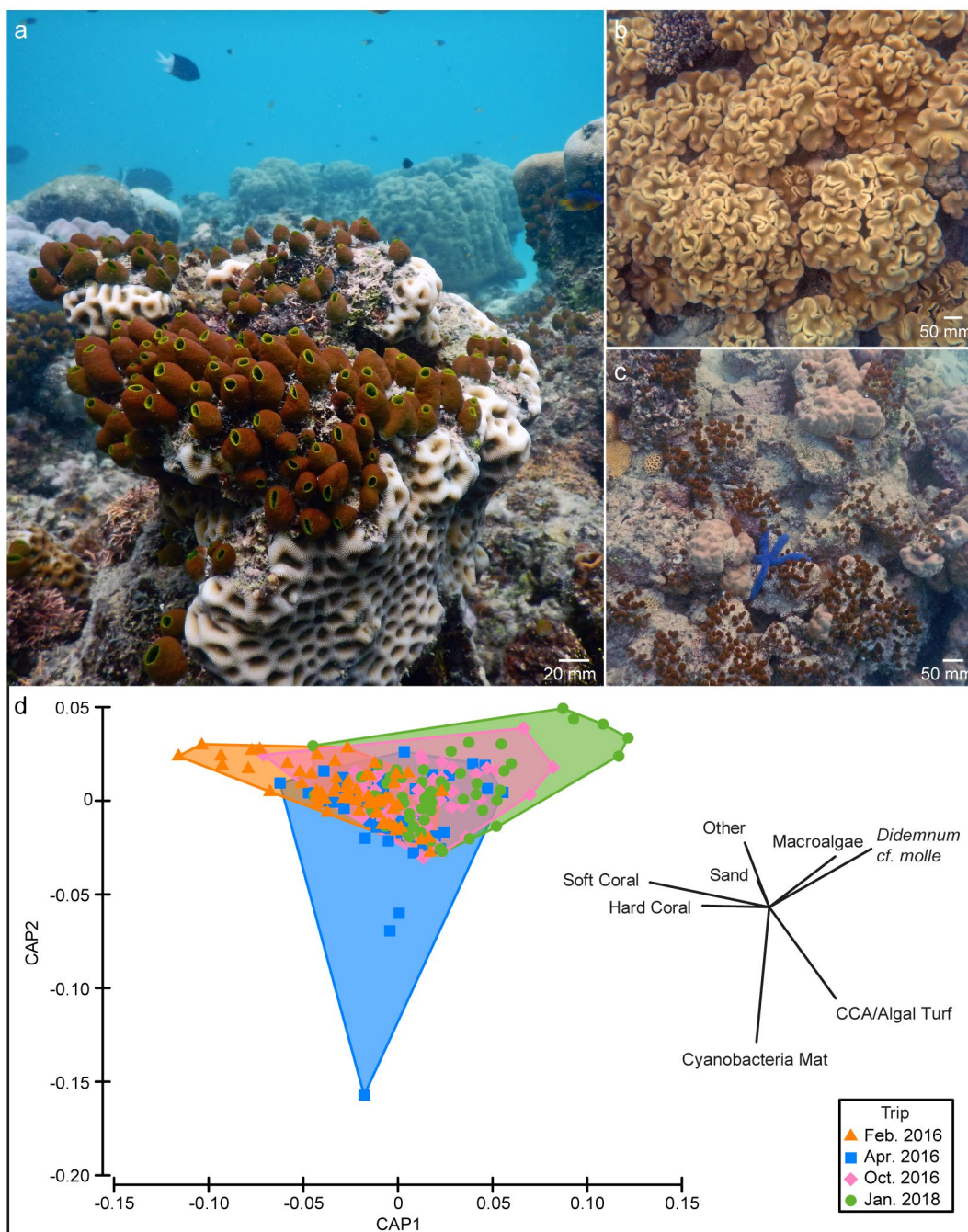
117 between sites, and the lack of spatial independence among replicate quadrats. Following the  
118 PERMANOVA, pair-wise tests were performed to determine within-factor differences. The  
119 assumption of homogeneity of dispersions in the PERMANOVA was assessed using a  
120 permutational analysis of multivariate dispersions (PERMDISP), which revealed  
121 homogeneity. A canonical analysis of principle co-ordinates (CAP) was used to  
122 explore/visualise specific differences among sampling periods. All multivariate analysis was  
123 performed in Primer 6.0 PERMANOVA+.

124 To examine specific variation in *D. cf. molle* numbers and benthic coverage  
125 generalised linear mixed effects models (GLMMs) were used. GLMMs were based on the  
126 same fixed and random factors as above. *D. cf. molle* abundance was examined using a  
127 negative binomial distribution to account for the overdispersed nature of the count data. The  
128 proportion of benthic space occupied by *D. cf. molle* was examined using a binomial  
129 distribution. The fits and relevant assumptions of all models were assessed using residual  
130 plots, all of which were satisfactory. All statistical modelling was performed in the software  
131 R (R Core Team, 2017) using the *lme4* (Bates et al., 2015) package.

### 132 **3. Results and discussion**

133 Following the bleaching events the average cover of hard and soft corals at the two  
134 study sites declined by 36% and 90%, respectively (Fig. 1, Table S1). Concomitantly, there  
135 was a 1.4-fold increase in the coverage of CCA/algal turfs (Table S1). Overall significant  
136 changes in the composition of the benthic community were detected between all sampling  
137 trips apart from between April 2016 and October 2016 (Fig. 1d, Tables S2, S3). While these  
138 changes align with general expectations following a bleaching event, especially a decrease in  
139 living corals (e.g. Diaz-Pulido and McCook, 2002; Hughes et al., 2018; Torda et al., 2018),

140 there was also a particularly marked increase in the ascidian *D. cf. molle* on these two reefs  
141 (Fig. 1).



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143 **Fig. 1** a) A dense cluster of the ascidian *Didemnum cf. molle* growing on top of a coral  
144 outcrop at Lizard Island on the Great Barrier Reef, b) the soft coral *Sarcophyton* sp.  
145 covering the benthos at Lizard Island prior to mass bleaching (February 2016), c) the  
146 same site approximately two years later (January 2018) revealing a marked increase in



147 the cover of *D. cf. molle*. d) Canonical analysis of principle (CAP) coordinates  
148 ordination based on a Euclidean distance matrix of standardised benthic cover data for  
149 each trip. Vectors show the relationship among benthic components and how they  
150 influence the position of data points in the CAP. Vectors were calculated using a  
151 multiple correlation model. Coloured polygons are to aid visual interpretation and do not  
152 denote significant groupings (April 2016 and October 2016 do not differ significantly).

153 CCA = crustose coralline algae.

154

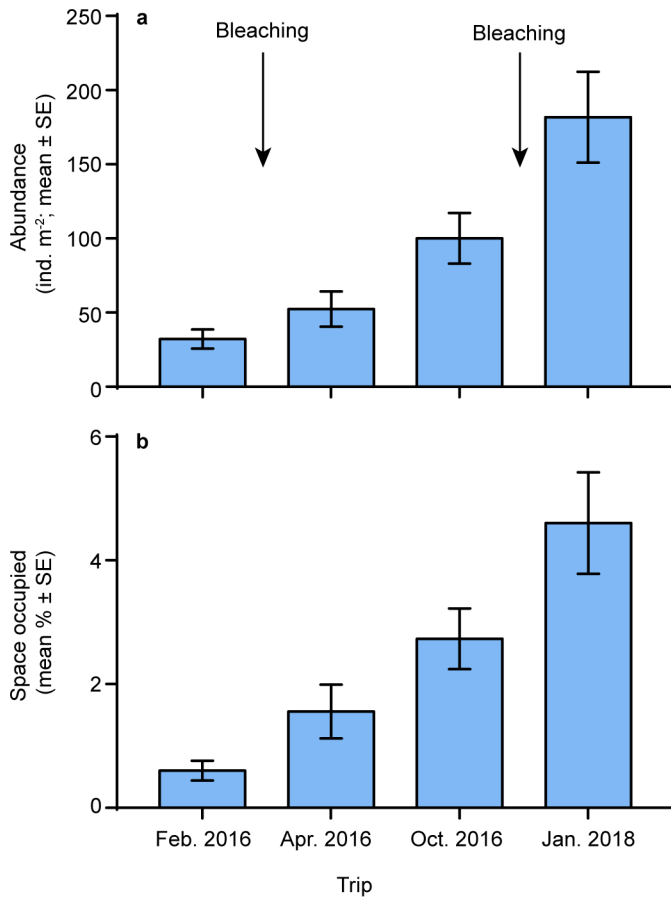
155

156 Unlike corals, *D. cf. molle* appeared to be unaffected by the warm temperatures, and  
157 instead flourished, rapidly expanding and occupying space (Fig. 1). Over two years the mean  
158 abundance of *D. cf. molle* increased nearly 6-fold on average from  $32.1 \pm 6.6$  to  $181.9 \pm 30.6$   
159 individuals  $m^{-2}$  ( $\pm$  SE) (Fig. 2a). This was statistically significant (GLMM;  $p < 0.001$ ; Table  
160 S4). Indeed, in one of the quadrats an increase of over 1000 ind.  $m^{-2}$  was recorded. Similarly,  
161 the percentage of benthic space occupied by *D. cf. molle* increased 7.7-fold, from  $0.6 \pm 0.2\%$   
162 to  $4.6 \pm 0.8\%$  (Fig. 2b) (GLMM;  $p < 0.001$ ; Table S4). Thus the increase in *D. cf. molle* was  
163 not merely tracking the increase in ‘empty’ benthic space (i.e. a 1.4-fold increase in  
164 CCA/algal turf cover) following coral mortality, but showed a disproportional 7.7-fold  
165 increase.

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170 **Fig. 2** Change in a) the abundance of, and b) the benthic coverage by, *Didemnum cf. molle* at  
 171 Lizard Island on the Great Barrier Reef, Australia over a two year period.  $n = 63$   
 172 quadrats in each sampling period.

173

174 The rapid increase in *D. cf. molle* cover was not due to the ‘canopy effect’ whereby  
 175 the loss of coral cover suddenly exposes hidden components of the benthos underneath (sensu  
 176 Goatley and Bellwood, 2011). Instead, we found a steady increase in *D. cf. molle* over the 21  
 177 month period, following loss of coral cover (Fig. 2). Indeed, *D. molle* predominantly live in  
 178 locations exposed to sunlight, rather than under coral canopies (Olson, 1985). The preference  
 179 for *D. molle* to live in sunlit locations is due to their symbiosis with the prokaryotic alga,  
 180 *Prochloron* sp. (Kott, 2001; Olson, 1986), which appears to enhance growth (Olson, 1986).

181 The symbiosis between some ascidians and *Prochloron* sp. is unique in that it is the only  
182 known example of an obligate photosymbiont in the Chordata (Hirose and Fukuda, 2006).  
183 Unlike the symbiosis between corals and their photosynthetic symbionts (zooxanthellae,  
184 *Symbiodinium* spp.) that breaks down with heating leading to coral bleaching (Hughes et al.,  
185 2018), the symbiosis between *D. molle* and *Prochloron* sp. appears to be more resilient to  
186 heat stress (Figs. 1, 2). Indeed, adult *D. molle* colonies even utilise mycosporine-like amino  
187 acids as UV-absorbing substances to protect *Prochloron* sp. from UV radiation (Hirose et al.,  
188 2006). The resilience of this *D. molle/Prochloron* symbiosis appears to allow *D. molle*  
189 colonies to persist through heat stress and expand.

190 As ascidians can overgrow most benthic organisms, including corals and macroalgae  
191 (Bak et al., 1996; Littler and Litter, 1995; Roth et al., 2018), this suggests ‘available space’ is  
192 not a limiting factor and, as such, the expansion of *D. cf. molle* may not be directly due to  
193 coral mortality opening up new space to occupy. While the direct increase in *D. cf. molle*  
194 following the bleaching event is unlikely to be coincidental, the mechanistic basis  
195 underpinning this increase is currently unclear. One influential factor could be altered  
196 predation rates due to a decrease in the abundance of particular fishes following the bleaching  
197 event at Lizard Island (for details on the fish assemblage see Wismer et al., 2019). For  
198 example, some planktivorous damselfishes declined by nearly 40% between February 2016  
199 and October 2016 (Wismer et al., 2019) and these fishes have been shown to prey heavily on  
200 dispersing ascidian larvae with the potential to limit recruitment rates (Olson and McPherson,  
201 1987; Stoner, 1990). Furthermore, predation on settled ascidians by larger fishes can limit  
202 their establishment (Kremer and da Roch, 2016; Roth et al., 2017; Russ 1980) and this may  
203 have been altered as a result of the changing fish assemblage, although such changes are  
204 unlikely to be as marked as for the planktivorous damselfishes (Wismer et al., 2019).

205 In addition to predation, another factor may lie in the flux of nutrients and particulate  
206 organic matter released into the water following the mass-mortality of corals. When corals  
207 bleach and/or die, excess nutrients and organic matter are released (Niggel et al., 2009), which  
208 may be utilised by a range of organisms. Indeed, during and shortly after the 2016 mass-  
209 bleaching event, cyanobacterial mats, which are known to benefit from nutrient fluxes (Ford  
210 et al., 2018), were a widespread feature at Lizard Island (Wismer et al., 2019). As filter-  
211 feeders, the growth and expansion of *D. cf. molle* is also likely to be enhanced under these  
212 conditions, with several studies revealing enhanced growth of ascidians, including *Didemnum*  
213 sp., under eutrophic conditions (Muñoz et al., 2015; Roth et al., 2017; Shenkar et al., 2008).  
214 While nutrient fluxes may have had some effect (unfortunately these were not quantified in  
215 the current study) any fluxes are likely to be temporally limited to the weeks immediately  
216 following coral mortality. Although the mechanistic basis was not assessed in the current  
217 study, our data revealed a clear and progressive increase in *D. cf. molle* on bleaching-  
218 impacted reefs.

219 The bleaching events and subsequent expansion of *D. cf. molle* could have a two-fold  
220 impact on coral recovery. With reduced adult coral populations, coral recruit densities could  
221 be suppressed, limiting recruits available for recolonization. Furthermore, coral recruitment is  
222 dependent on the availability of suitable settlement locations and cues (Hughes et al., 2018).  
223 Evidence suggests the availability of microtopographic refuges that are not grazed heavily  
224 (Brandl and Bellwood, 2016), contain low sediment loads (Ricardo et al., 2017), and are not  
225 shaded by algae (Brandl and Bellwood, 2016) are critical for the establishment of  
226 scleractinian corals. Therefore, by rapidly expanding post-bleaching, the proliferation of *D.*  
227 *cf. molle* could affect future recovery trajectories, with microtopographic refuges becoming  
228 occupied or shaded, limiting the ability of corals to exploit such refugia.

229           The extent of any spatial competition between *D. cf. molle* and corals will depend on  
230 how long the expansion of *D. cf. molle* persists. While expansion of *D. cf. molle* appears to  
231 be previously unreported, expansion of other ascidian species on coral reefs has been noted  
232 (e.g. Littler and Littler, 1995; Roth et al., 2018; Vargas-Ángel et al., 2009). For example,  
233 *Trididemnum solidum* in the Caribbean (Bak et al., 1996) and *Botryllus eilatensis* in the Red  
234 Sea (Shenkar et al., 2008). These expansions range in temporal persistence from seasonal e.g.  
235 *B. eilatensis* (Shenkar et al., 2008), to over 15 years e.g. *T. solidum* (Bak et al., 1996). Herein,  
236 abundances of *D. cf. molle* have increased continuously over two years (Fig. 2). This  
237 expansion could be ephemeral and reversed by direct ascidian removal through physical  
238 disturbance (Olson, 1985), colony senescence (Olson, 1985), or by predation by fishes,  
239 nudibranchs, or other molluscs (Lambert, 2005; Paul et al., 1990). However, for now, it  
240 appears that in some locations *D. cf. molle* will be a more prominent component of changing  
241 reef environments. Further understanding of the organisms, such as *D. cf. molle*, which  
242 succeed in these changing ecosystems, will be a rich area for future investigation.

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