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Interacting effects of temperature, habitat and phenotype on predator avoidance behaviour in *Diadema antillarum*: implications for restorative conservation

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Version: Accepted Manuscript

Link(s) to article on publisher's website:
http://dx.doi.org/doi:10.3354/meps12034

oro.open.ac.uk

1   The definitive version of this article is published as:

6

7   **Interacting effects of temperature, habitat and phenotype on predator avoidance**

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23   Running page head: *Diadema antillarum* responses to temperature

24

Abstract

Caribbean *D. antillarum* populations crashed following a mass-mortality event in 1983-4 with cascading effects on reef health. Population restoration efforts may be hampered by unknown effects of short and long-term elevated sea surface temperature (SST). We investigated how a key behavioural trait, predator avoidance behaviour (PAB; percentage of long defensive spines that moved in response to shadow stimuli), was affected by elevated SST in 180 individuals from two contrasting Honduran reefs; Utila (flattened reef structure, dearth of predation refugia), and Banco Capiro (complex reef structure, abundant refugia). Initiation of PAB is mediated by melanin, which breaks down at elevated water temperatures, so, as SST rises, *D. antillarum* may become vulnerable to predation. We compared local current SST (CSST; 29.7°C) with two IPCC predicted long-term climate change scenarios under laboratory conditions. PAB decreased by 13.98-15.37% at CSST +1.4°C and 31.67-42.44% at CSST +3.1°C. Trial temperatures were similar to maxima recorded in the Caribbean during the 2016 El Niño, therefore our results also represent likely responses to worst-case short-term acute temperature anomalies. Juveniles maintained higher PAB than adults, indicating increased reliance on anti-predation behaviours. White phenotypes from Utila's flattened reef maintained higher PAB than black counterparts, likely due to increased conspicuousness to visual predators. Habitat complexity may mitigate temperature-driven losses in natural behavioural defences. *D. antillarum* may be resilient to near-term (<2039) SST increases and periodic temperature stresses but may struggle under long-term, worst-case scenario conditions. Restoration of *D. antillarum* populations must be coupled to augmented reef complexity to improve future resilience.

Introduction

As architects of tropical reef ecosystems (Aronson and Precht 2001; Alvarez-Filip et al. 2009), much global attention is given to the impacts of elevated temperatures in driving the breakdown of symbiosis between scleractinian coral hosts and their photosynthetic zooxanthellae (Hoegh-Guldberg 1999; Kramer and Kramer 2000; Aronson et al. 2002; Sheppard 2003; Donner et al. 2005; De'ath et al. 2009; Cantin et al. 2010). However, acute and long-term temperature increases will also interact with other factors, such as habitat degradation, to affect other reef taxa (Przeslawski et al. 2008), and these effects remain largely unstudied.

Diadema antillarum, the long-spined sea urchin, is an important coral reef herbivore whose prolific grazing ability is essential for the maintenance of scleractinian coral domination throughout the Caribbean (Carpenter 1984; Liddell and Ohlhorst 1986; Macia et al. 2007). Between 1983 and 1984 a disease epidemic reduced populations by 95-100% (from $1.06\text{-}14.38\text{m}^{-2}$ to $<0.01\text{m}^{-2}$) across the 3.5 million km^2 area of the Caribbean (Bak 1984; Lessios et al. 1984a; Lessios et al. 1984b; Hughes et al. 1985; Lessios 1988ab; Levitan 1988; Carpenter 1990; Betchel 2006), and populations remain significantly depressed across the region to this day (Chiappone et al. 2002; Edmunds and Carpenter 2001; Weil et al. 2005; Debrot and Nagelkerken 2006; Bologna et al. 2012; Bodmer et al. 2015). This mass-mortality event is closely associated with macroalgal phase shifts and subsequent habitat flattening (Alvarez-Filip et al. 2009; Roff and Mumby 2012), which has decreased the availability of refugia (Alvarez-Filip et al. 2009) and potentially left *D. antillarum* vulnerable to predation. Models produced by Mumby et al. (2006) predict that *D. antillarum* population densities $>1\text{m}^{-2}$ are required for the maintenance of reef health throughout the Caribbean, therefore, augmentation of their populations, possibly through the deployment of artificial reef structures to replace lost habitat complexity, is a conservation priority throughout the region.

74   Under natural conditions, it is likely that *D. antillarum* is afforded a degree of

75   environmental protection from predation by the complex structure of the reef (Ogden et al.

76   1973). However, individuals living on flattened contemporary Caribbean reefs with low

77   percent cover of hard coral are likely to be more heavily reliant on direct predator avoidance

78   behaviours; a role fulfilled by movement of their longest spines which have defensive barbs

79   directed towards the distal end (Randall et al. 1964). Here, *D. antillarum* predator avoidance

80   behaviour (PAB) is defined as the percentage of long predatory spines that move in response

81   to a shadow stimulus. Decreases in light intensity, indicating the potential presence of a

82   predator, evoke an excitatory response in the spines, making the individual hard to capture

83   (Millott and Yoshida 1960a). However, PAB has an energetic cost and should be reduced in

84   the absence of a predation threat (Millott and Yoshida 1960b), therefore increases in light

85   intensity have an inhibitory effect on spine movement (Millott and Yoshida 1960a).

86   The underlying physiological mechanism for this behaviour is well understood: a

87   layer of melanin-containing photosensitive melanophores, which give *D. antillarum* its

88   characteristic black colouration, surrounds the test and enables changes in the light

89   environment to be detected (Millott 1954; Millott and Yoshida 1959). This photic response is

90   a direct result of interactions between light and the melanophore, as light stimuli cause

91   expansion of the melanosomes, which in turn induces a nervous signal controlling spine

92   movement (Yoshida 1956). However, melanin loses its structure at high temperature (Millott

93   and Jacobson 1952; Sawhney 1994), suggesting elevated sea surface temperatures (SSTs)

94   may cause a breakdown in these essential anti-predator light-detecting mechanisms.

95   Significant increases in SST are expected to occur on a decadal timescale and may

96   reach values >3.5°C higher than current averages by 2100 (Collins et al. 2013). Additionally,

97   the often catastrophic thermal anomalies of El Niño Southern Oscillation (ENSO) are also

98   predicted to become biennial events of increasing severity by 2050 (Donner et al. 2005).

99   With a lifespan of up to 8 years (Randall et al. 1964*), D. antillarum* has relatively long

100   generation times, and their capacity to adapt to both long-term gradual, and short-term acute,

101   SST increases is likely to be limited. However, there is well documented phenotypic

102   plasticity associated with *D. antillarum* melanin production (Millott 1954), and numerous

103   ecological factors, such as wave exposure and water clarity, have been found to alter melanin

104   distribution and concentration within an individual's test and spines (Kristensen 1964). This

105   phenotypic plasticity may afford individuals with a degree of resilience to rising SST via

106   upregulation of melanin to counter breakdown associated with thermal stress.

107   We use laboratory manipulations on natural populations to investigate how *D.*

108   *antillarum* PAB is affected by increases in water temperature, and how this subsequently

109   interacts with habitat and phenotype. We compare two separate populations from contrasting

110   reef systems, representing both structurally complex and structurally simple 'flattened'

111   habitat types, in order to address whether habitat complexity influences PAB. Given that *D.*

112   *antillarum* colouration and light-detecting mechanisms are both controlled by phenotypically

113   plastic melanin regulation, we also explore whether PAB varies between phenotype (black-

114   and white-spined) and life-history stage (juvenile or adult) in relation to the individual's site

115   of origin. White-spined individuals are defined as adult urchins whose complete complement

116   of predatory defence spines are white in colouration. Theoretically, restoration of *D.*

117   *antillarum* is an obvious conservation target, however, to date, no studies have investigated

118   how they will respond to predicted environmental change. The results of this study will allow

119   conservation managers to gain better understanding of the interactions between PAB and

120   temperature, and make decisions on population restoration initiatives based on their future

121   survival potential.

122

Materials and Methods

Study sites

Data were collected on the Honduran island of Utila and nearby mainland reef system of Banco Capiro located within Tela Bay (fig 1). Full details of study sites can be found in Bodmer et al 2015. Banco Capiro (fig 2) has a mean scleractinian coral cover of 62%, which creates a structurally complex habitat that supports one of the highest contemporary *D. antillarum* population densities ever recorded. Utila (fig 3), by contrast, is a typical 'flattened' Caribbean reef system with low percentage scleractinian coral cover (15-20%) and consequently structural complexity is 25% less than at Banco Capiro (Bodmer et al 2015). Crucially, the abundance of key *D. antillarum* predators is similar between these two sites (Bodmer et al. 2015).

Future climate change predictions

The Intergovernmental Panel on Climate Change (IPCC) has recently described four new climate change scenarios, known as Representative Concentration Pathways (RCPs). Each RCP uses a different value of radiative forcing, dictated by the specific greenhouse gas (GHG) accumulation scenario being modelled, to predict the climatic changes that might occur by 2100 (Arora et al. 2011). Radiative forcing is measured in Wm^{-2} and is determined by the proportion of solar insolation that is trapped in the atmosphere relative to the energy radiated back into space and is, therefore, influenced by rates of GHG emission and accumulation (Van Vuuren et al. 2011). The four Representative Concentration Pathways (RCPs) are modelled on assumptions of socio-economic activity that are used to predict the

145 extent of GHG accumulation in 2100, and they have been designed to represent a range of

146 possible future climate change scenarios (table 1).

147

148 **Specimen collection and acclimatisation**

149   Trials were run between March and August 2015. 30 individuals in each of three

150 categories (black-spined adult, white-spined adult, juvenile; Fig 4) were collected from each

151 site giving a total sample size of 180 urchins over the six-month sampling period. Juveniles

152 were identified by their distinctive black and white banded spines, and their possession of a

153 test diameter <20mm (Randall et al. 1964). Four *D. antillarum* individuals were collected

154 each day by a combination of snorkelling and SCUBA, and trials conducted on the same day.

155 All individuals were returned alive to the reef within 24 hours of collection.

156 Pseudoreplication was avoided by collecting from a different sub-site each day. When

157 removing individuals from the reef, care was taken to ensure that minimal damage was

158 caused to the spines and test. Once an individual was located, a 50cm length of PVC pipe

159 (outside diameter = 2.6cm) was used to coerce them into the open. The PVC pipe was then

160 used to lift the individual off the reef and into a container for safe storage.

161   On returning to the laboratory, individuals were placed in to a 200L plastic holding

162 tank where they were allowed to acclimatise for a minimum of 8 hours before trials were

163 conducted. This short acclimatisation period was chosen to minimise stress and maximise

164 survivorship to reduce adverse effects on populations of this key reef herbivore. Thus our

165 trials tested the shock responses of *D. antillarum* to increased water temperature, and did not

166 account for the possibility of potential short or long-term adaptation/phenotypic plasticity and

167 our results must be interpreted in that light.

168

Experimental setup and climate change scenarios

Experimental manipulations were conducted in three transparent 64L plastic trial tanks. All tanks underwent 100% water changes daily with fresh seawater collected from the specimen collection sites. Aquarium filters (Eheim Pick Up) were installed in the holding tanks to maintain water quality overnight, but were not included in trial tanks due to the short time urchins were housed within them, and to ensure no external stimuli were present which may have influenced urchin responses. Aquarium heaters (Aquael Easy Submersible Aquarium Heater 150w) and digital thermometers (Aqua One ST-3 Electronic Thermometer) were used to achieve and maintain the required water temperature in each trial tank.

Trial temperatures were based on recently described climate change scenarios from the Intergovernmental Panel on Climate Change (IPCC). They described four new scenarios, (Representative Concentration Pathways, RCPs), to predict the climatic changes that might occur by 2100 (Arora et al. 2011). Table 1 outlines the four RCPs, which range from a best-case scenario (RCP 2.6) to a worst-case scenario (RCP 8.5). SST increases are subsequently expected to range from 1°C (under RCP 2.6) to >3°C (under RCP 8.5) (Collins et al. 2013).

We used predicted SST increases for the Caribbean Sea/Gulf of Mexico under each RCP (Table 1; Hoegh-Guldberg et al. 2014), with one trial tank maintained as a control at 29.7°C; the current annual mean peak SST (CSST) recorded off the Caribbean coast of Honduras (http://www.seatemperature.org). Experimental temperatures were then calculated by adding predicted SST increases to this CSST. The second trial tank was used to represent an intermediate/stabilising pathway (RCP 4.5; 31.1°C), while the final tank was used to represent a worst case pathway (RCP 8.5; 32.8°C).

Having access to *D. antillarum* from both Utila and Banco Capiro also enabled us to evaluate whether the effects of rising SST are likely to be universal, or affected by the structural complexity of the population's site of origin. It is possible that temperature and site

194   interact to affect PAB, which has major implications for *D. antillarum* restoration initiatives

195   aiming to provide artificial reef structure to stimulate recovery.

196

197   **Trial protocol**

198   Trials were conducted at night in a laboratory setting under artificial lighting

199   maintained at an intensity of ca. 20 lm. The phenotype of each individual urchin was

200   recorded and the total number of long defensive spines counted, along with individual weight

201   (to the nearest mg) and test diameter (to the nearest mm) using long-jaw callipers. These

202   measurements were recorded immediately after collection before individuals were placed in

203   the holding tank to avoid inducing stress immediately prior to the trials. The predation

204   avoidance behaviour (PAB) of each individual was then tested under each temperature

205   scenario. Individuals were acclimated to each temperature for at least 30 mins before trials

206   began, or until they had settled in a corner of the tank for a period of at least 10 minutes. This

207   was done to ensure that urchins were adjusted to the heat shock and were therefore

208   responding to the shadow stimulus and not the change in temperature.

209   At the start of each trial a GoPro Hero 3 underwater video camera was placed in the

210   trial tank facing the urchin and set to record for the duration of the trial. Urchins were

211   initially exposed to ambient light conditions for 30s. A shadow was then created over the

212   urchin using an opaque wooden board to simulate the presence of a predator, and maintained

213   for 30s before returning the urchin to ambient light. This was repeated three times for each

214   urchin under each temperature scenario. The order in which individuals were exposed to the

215   different temperature treatments was randomised ahead of each trial.

216

217   **Quantifying predator avoidance behaviour (PAB)**

218   Predator avoidance behaviour (PAB) was defined here as the percentage of an

219   individual's total spines that move in response to a shadow stimulus, and quantified visually.

220   Test diameter was measured in order to account for any confounding effect of body size on

221   PAB. Only the movements of the longest spines were counted because the main function of

222   these is known to be predatory defence whereas the shorter spines are used predominantly for

223   feeding and locomotion (Randall et al. 1964).

224   Prior to their analysis, all 540 videos were renamed using RandomNames software.

225   The video analyst was therefore unaware of the site of origin and climate change scenario of

226   the urchin they were processing, thus removing any potential observer bias from the data.

227   Video recordings were replayed in slow motion allowing accurate counts of the number of

228   long defensive spines that moved in response to the shadow stimulus. The PAB for each

229   simulated 'attack' was calculated and the means of these PAB values were used for statistical

230   analysis.

231

232   **Statistical Methods**

233   PAB data were normally distributed and its relationships with climate change

234   scenario, site and phenotype were analysed using a three-way repeated measures ANOVA

235   with urchin number nested within climate change scenario. PAB was the continuous

236   dependent variable, site and phenotype were nominal, fixed-effect between subject variables,

237   and climate change scenario was a nominal, fixed-effect within subject variable.

238   We investigated the relationship between *D. antillarum* body size (test diameter) and

239   PAB in order to control for this as a confounding variable, since smaller individuals are more

240   vulnerable to predation, and predation threats are generally considered more relevant to

241   juveniles than adults (Clemente et al. 2007; Jennings and Hunt 2010). All data were analysed

242   using R.

Results

Establishing a baseline PAB

The mean PAB of black-spined adult urchins at CSST on Banco Capiro (17.39 ±0.68%) is used as a baseline for comparisons of different combinations of climate change scenario (CSST, RCP 4.5, or RCP 8.5), site (Utila, or Banco Capiro), and phenotype (black, or white). This is because black individuals on Banco Capiro are living in conditions that are most similar to those under which *D. antillarum* existed prior to the mass-mortality event, i.e. they are the most common phenotype, living within a dense population ($>2m^{-2}$) on a reef system with a high percentage cover of hard coral (>60%). There is debate in the literature about the population densities under which *D. antillarum* evolved, and their relative importance as macroalgal herbivores over evolutionary timescales has been called into question (Jackson and Kaufmann 1987). However, countless studies conducted throughout the 20th century clearly document high *D. antillarum* population densities, and demonstrate the importance of this species for maintaining reef health on the overharvested Caribbean coral reefs of the Anthropocene.

Effects of temperature, site and phenotype on PAB

There was a significant negative relationship between PAB and urchin test diameter for juveniles ($F_1 = 4.993$, $p = 0.027$) but not for adults ($F_1 = 1.808$, $p = 0.18$) (Fig 5); therefore, all subsequent analyses dealt with these two groups separately. Juvenile analysis included test diameter as an independent variable while the analysis of adults did not.

Increasing water temperature caused a decline in PAB in both age categories of urchins (Fig 6; Juveniles $F_2 = 4.86$, $p = 0.0091$; Adults $F_2 = 15.37$, $p = 3.9 \times 10^{-7}$) and

266 juvenile urchins had higher PAB than adults in all temperatures. Mean juvenile PAB declined

267 from 24.54% (SE = 1.28) at CSST to 21.1% (SE = 1.45) under RCP 4.5 and 15.19% (SE =

268 1.22) under RCP 8.5. Repeated measures ANOVA revealed that there was no difference in

269 PAB of juveniles between sites overall (F_1 = 0.303, p = 0.58) but the data for RCP 8.5

270 suggested lower PAB at Utila than Banco Capiro (Fig 6). Black-spined adult PAB declined

271 similarly to juveniles from 17.66% (SE = 0.76) at CSST to 15.09% (SE = 0.9) at RCP 4.5 to

272 10.80% (SE = 0.87) at RCP 8.5. The percentage declines in PAB from CSST to RCP 8.5

273 were proportionately similar: 38.1% for juveniles and 38.8% for black-spined adults.

274 Interestingly, PAB of juveniles under RCP 4.5 was still 21.33% higher than that of black-

275 spined adults under CSST.

276   There was no evidence of between-site differences in PAB or its response to

277 temperature for black-spined adult urchins but the pattern differed for white-spined adults,

278 reflected by a significant interaction between phenotype and site (F_1 = 8.96, p = 0.003).

279 White urchins from Banco Capiro (14.35 ±0.58%) displayed lower PAB than those from

280 Utila (19.50 ±1.34%), and mean white urchin PAB on Banco Capiro (14.35 ±0.58%) was

281 lower than that of their black counterparts (17.39 ±0.68%). However, the inverse was true on

282 Utila where mean white-spined adult *D. antillarum* PAB (19.50 ±1.34%) was higher than that

283 of the black population (17.93 ±0.84%). However, these differences were less apparent at

284 RCP 8.5 (Fig 6). At CSST mean PAB of white-spined adults on Utila (19.50%, SE = 1.34)

285 was almost 36% higher than those on Banco Capiro (14.35%, SE = 0.58). This difference

286 was maintained at RCP 4.5 (15.49%, SE = 0.91, and 11.20%, SE = 0.47 respectively) but was

287 roughly halved at RCP 8.5 (11.44%, SE = 0.92, and 9.70%, SE = 0.49). See table 2 for

288 complete breakdown of results.

289

Discussion

Demographic influences on PAB

At CSST, mean juvenile PAB is 41.12% greater than black-spined adults on Banco Capiro, and the higher PAB value is maintained even under moderate thermal stress (RCP 4.5). This is not surprising, as juvenile test diameters are typically smaller than the 40mm predator escape threshold above which vulnerability is believed to decrease (Clemente et al. 2007; Jennings and Hunt 2010). The need for juveniles to maintain high PAB, even under physiological stress, is far greater than for their adult counterparts. This is supported by the negative relationship observed between juvenile body size and PAB magnitude; larger juveniles can partially relax PAB in favour of the energetic benefits associated with reduced spine movement (Millott and Yoshida 1960b). However, juveniles living within the complex structure of Banco Capiro still maintain similar PAB to those on the flattened reefs of Utila, despite potentially being able to gain energetic benefits from reducing PAB on a reef that provides individuals with environmental protection. The risk of death under any given attack is much higher for juveniles than adults, and thus the energetic benefits of reducing PAB on Banco Capiro are likely to be outweighed by the ultimate price of failing to respond to a potential predation threat.

On Banco Capiro, white-spined adult *D. antillarum* individuals have a significantly lower PAB than black-spined adults. One possible explanation relates to the developmental and environmental processes driving these phenotypic differences. Experimental manipulations have shown that adult *D. antillarum* will develop white spines if reared in low-light environments, while also favouring shaded areas of reef during adulthood (Kristensen 1964; Growns 1989). Due to reduced energy content in algae growing on shaded compared to light-exposed reef areas (Carpenter 1985; McCook et al. 2001), white-spined adult sea

314   urchins are likely to be nutrient-limited and may therefore be unable to invest in

315   metabolically expensive melanin production. Whilst white-spined adults appear to be less

316   sensitive to predation stimuli, their overall vulnerability may be unaffected by this decreased

317   PAB ability because they favour shaded, and presumably more complex, habitats.

318   Conversely, juveniles develop black spines when reared in high-light environments

319   (Kristensen 1964), typically when individuals settle on more exposed areas rather than within

320   the complex coral framework. It is therefore likely that black-spined adult *D. antillarum* are

321   grazing algae from light exposed reefs that have greater energy availability per unit area

322   (Ogden and Lobel 1978) than their white-spined counterparts. Black-spined individuals may

323   therefore be able to invest more heavily in melanin production. This investment in their light-

324   detecting sensory systems is further justified in black-spined adults because their more

325   exposed lifestyle leaves them vulnerable to predation.

326   For black-spined adults and juveniles the magnitude of PAB does not differ between

327   sites, but for white-spined adults PAB is significantly greater on Utila. Unlike on Banco

328   Capiro, white urchins on Utila are living in a flattened habitat and therefore lack abundant

329   predation refugia. The major fish predators of *D. antillarum* (Ballistidae, Haemulidae and

330   Labridae) all possess typical vertebrate visual systems comprised of image-forming eyes

331   (Lamb et al. 2007), which rely, at least partially, on contrast for prey detection (Schuster et al.

332   2011). Against the darker backdrop of the reef, white individuals are likely to be more

333   conspicuous to predators in a habitat where they are less able to hide. Therefore, while black

334   individuals on Utila are less conspicuous to predation, and both adult phenotypes on Banco

335   Capiro are afforded environmental protection by the reef structure, white-spined adults on

336   Utila must invest more heavily in the maintenance of their innate behavioural PAB.

337

Elevated SSTs and their implications for restoration

Across all combinations of site and phenotype, mean *D. antillarum* PAB was

negatively affected by increases in water temperature, with the greatest reductions under the

most extreme temperature trials (RCP 8.5). This suggests that *D. antillarum* is likely to

become increasingly vulnerable to predation as climate change progresses, especially if

'worst case' temperature models arise. Subsequent increased predation vulnerability will

further hinder population recovery from the 1983-84 mass mortality event, and potentially

hamper current conservation initiatives as seas warm. We find that, under RCP 8.5

conditions, *D. antillarum* PAB will be reduced by between 32.44% and 41.33% relative to

CSST. However, it is generally accepted that RCP 4.5 is a much more likely future

temperature scenario (Masui et al. 2011; Thomson et al. 2011). According to our results,

under RCP 4.5, smaller PAB decreases of between 14.55% and 21.95% will be seen;

although this still represents a significant loss of anti-predation capability in such a threatened

species.

Unfortunately, our results indicate that juvenile urchins will be similarly affected by

rising SST as black-spined adults. Given that juveniles are more vulnerable to predation due

to their small size below the predation threshold (Clemente et al. 2007; Jennings and Hunt

2010), it is likely that this decrease in PAB will translate into elevated mortality rates among

younger cohorts. Previous research has already identified maturation as the key life history

bottleneck to *D. antillarum* recovery (Williams et al. 2010 & 2011; Bodmer et al. 2015),

meaning any further reduction in juvenile survival will ultimately drive Allee effects and

eventual extinction. However, it is important to remember that this study has tested responses

to sudden and acute thermal stress, using similar approaches to much other ecophysiology

research, e.g. Eme and Bennett (2009), Eme et al. (2001) and Dabruzzi et al. (2012), and thus

our results do not account for phenotypic plasticity associated with the *D. antillarum*

363   melanin-regulatory system (Millott 1954). This may serve to mitigate the negative effects of

364   rising SST on PAB, meaning this study represents a worst-case scenario and not the end of

365   the road for conservation efforts throughout the Caribbean.

366   It is also important to consider the temporal scale over which ocean warming will

367   actually occur. We show that under the long-term water temperatures predicted by RCP 4.5

368   (CSST +1.43°C), *D. antillarum* will likely be partially resilient with respect to the detection

369   of, and reaction to, predators. With long-term temperature increases under RCP 4.5 greater

370   than short-term increases under RCP 8.5 (CSST +0.83°C), we can assume that *D. antillarum*

371   will be resilient to near-term SST increases across the severity range. This suggests that, at

372   least until 2039, incremental ocean warming is unlikely to negatively impact the success of

373   *D. antillarum* restoration initiatives.

374   However, increases in the frequency and severity of El Niño anomalies means that

375   long-term warming is not the only thermal threat to be faced. In winter 2016, average

376   Caribbean SST was 0.5-1.5°C higher than the 1981-2010 average (NOAA). Fortunately, our

377   focus on acute temperature increases, similar to those experienced during El Niño, indicate

378   that *D. antillarum* will be able to maintain PAB provided that sudden increases do not exceed

379   ~3°C. In general, the severity of El Niño in the Caribbean is less than other global coral reef

380   hotspots, and this ~3°C threshold falls outside the temperature anomalies previously

381   experienced in the region (NOAA).

382   It has been suggested that *D. antillarum* conservation efforts should focus on

383   reintroduction coupled with artificially augmented structural complexity (Bodmer et al.

384   2015). Our results suggest that conservation interventions seeking to increase structural

385   complexity will reduce the reliance of *D. antillarum* on innate behavioural PAB, and increase

386   survivorship even in the face of worst-case scenario increases in SST. In essence, structural

387 complexity may provide a buffer against the increased threat of predation caused by reduced

388 PAB via melanin breakdown. Stakeholders can use this information to make informed

389 decisions about strategies to increase the health of Caribbean coral reef ecosystems by

390 focusing on this important species. This is in line with the IPCC's goal of "working with

391 scenarios…in order to consider how robust decisions or options may be under a wide range

392 of possible futures" (Moss et al. 2010). Our results indicate that, if *D. antillarum* is going to

393 recover and aid the reversal of ubiquitous macroalgal phase-shifts, they require urgent

394 conservation attention to be buffered from climate change induced thermal stressors.

395

Acknowledgements

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558   Table 1. Data extracted from table SM30-4, section 7 "Coral Reef Provinces", row 1

559   "Caribbean Sea/Gulf of Mexico" (Hoegh-Guldberg et al. 2014).

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Climate Change Scenario	Predicted near-term (2010-2039) increases in SST (°C)	Predicted long-term (2010-2099) increases in SST (°C)	Pattern of radiative forcing value increase	Likelihood of occurrence
RCP 2.6 (best-case)	0.48	0.68	• Mid-century peak at $3.1 Wm^{-2}$ • Decrease to $2.6\ Wm^{-2}$ by 2100	• Unlikely • Requires immediate GHG emission reduction on a global scale
RCP 4.5 (stabilising)	0.64	1.43	• Rise to $4.5 Wm^{-2}$ by 2100 • No further increases	• Moderately likely; radiative forcing peaks in 2040 and then plateaus • Would require immediate cooperation and coordination between the world's governments
RCP 6.0 (stabilising)	0.61	1.87	• Rise to $6.0 Wm^{-2}$ by 2100 • No further increases	• Most likely; radiative forcing peaks in 2080 and then plateaus • Pressure put on governments to address climate change issues will likely cause GHG emission reductions, but time is required to coordinate the effort
RCP 8.5 (worst-case)	0.83	3.14	• Rise to $8.5 Wm^{-2}$ by 2100 • Continue unabated into 22nd century	• Unlikely • Requires GHG emissions to continue at current rates; concerted efforts are already being made to reduce them

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574   Figure 1. Site map showing the locations of Utila and Tela Bay, Honduras.

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576   Figure 2. Landscape photograph of Utila showing 'typically' low hard coral cover and

577   associated lack of habitat structure. Photo credit: Adam Laverty.
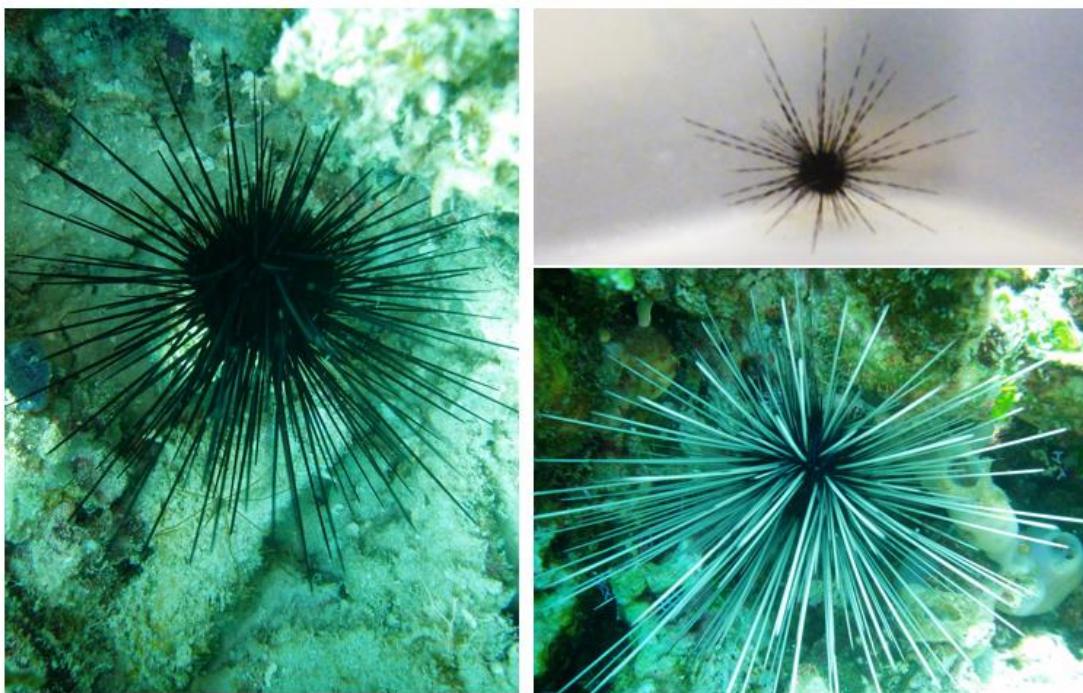

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579   Figure 3. Landscape photograph of Banco Capiro showing the high percent cover of hard

580   coral and resultant architectural complexity. Photo credit: Dan Exton.


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582   Figure 4. Panel photograph of *D. antillarum* adult and juvenile phenotypes. Far-left = black-

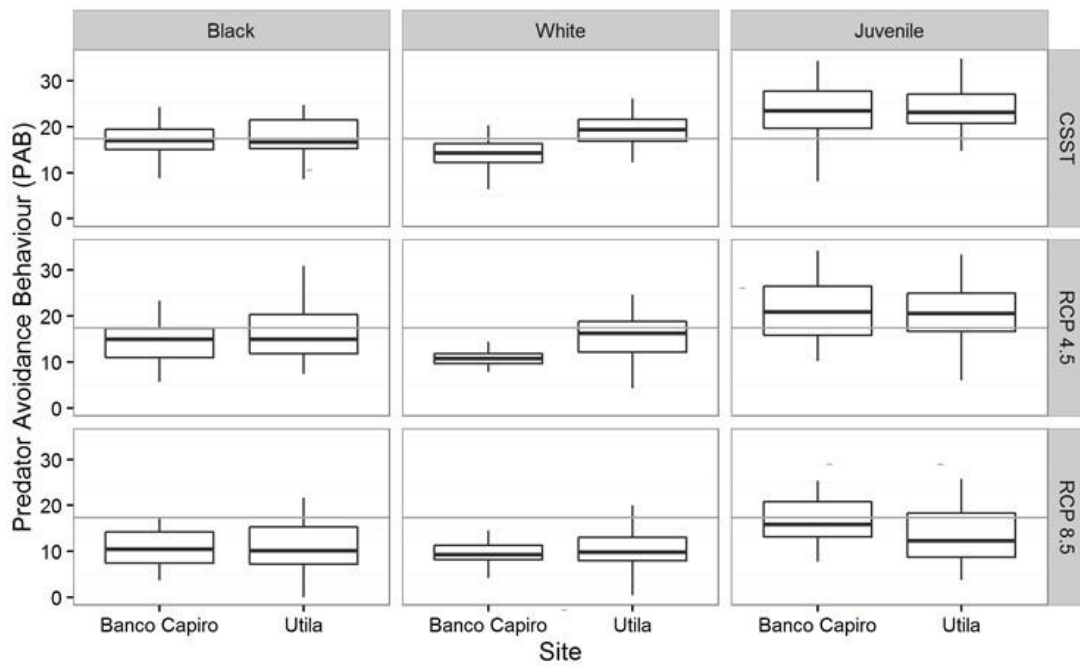583   spined adult, bottom-right = white spined adult, top-left = juvenile.

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585   Figure 5. Relationship between urchin body (test) size and predator avoidance behaviour

586   (PAB) in juvenile (black points) and adult (grey points) urchins. Plotted lines are least-

587   squares regression lines.
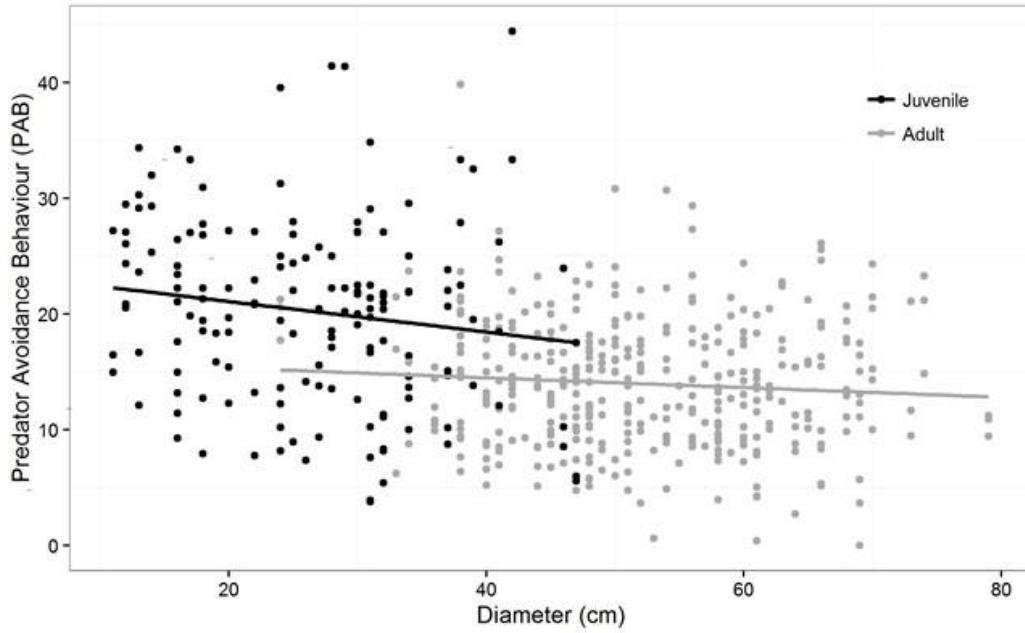
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Figure 6. Predator avoidance behaviour (PAB) of *Diadema antillarum* of three categories (black-spined adult phenotype, white-spined adult phenotype and juvenile), across two sites (Utila: flattened reef and Banco Capiro: complex reef), under conditions simulating three different IPCC climate change scenarios (CSST = 29.7°C, RCP 4.5 = 31.13°C, and RCP 8.5 = 32.84°C). Grey horizontal lines represent a baseline for comparison set as the mean PAB of black-spined adult *D. antillarum* on Banco Capiro under CSST. Vertical lines represent ±1SE.