

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

M. D. V. Bodmer<sup>1,2,\*</sup>, P. M. Wheeler<sup>2</sup>, A. M. Hendrix<sup>1</sup>, D. N. Cesarano<sup>3</sup>, A. S. East<sup>4</sup>,  
D. A. Exton<sup>1</sup>

<sup>1</sup>Operation Wallacea, Wallace House, Old Bolingbroke, Spilsby, Lincolnshire PE23 4EX, UK

<sup>2</sup>School of Environment, Earth and Ecosystem Sciences, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK

<sup>3</sup>School of Marine Science and Engineering, Plymouth University, Drake Circus, Plymouth, Devon PL4 8AA, UK

<sup>4</sup>Department of Geography, University of Oxford, Oxford OX1 3QY, UK

**ABSTRACT:** Caribbean long-spined sea urchin *Diadema antillarum* populations crashed following a mass mortality event in 1983–1984 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 2 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; thus, as SST rises, *D. antillarum* may become vulnerable to predation. We compared local current SST (CSST; 29.7°C) with 2 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, so 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-spined phenotypes from Utila's flattened reef maintained higher PAB than black-spined 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.

**KEY WORDS:** Long-spined sea urchin · Climate change · IPCC · Conservation · Future-proof · Honduras · Caribbean

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## INTRODUCTION

As architects of tropical reef ecosystems (Aronson & 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 & Kramer 2000, Aronson et al. 2002, Donner et al. 2005, 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.

The long-spined sea urchin *Diadema antillarum* 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 & Ohlhorst 1986, Maciá et al. 2007). Between 1983 and 1984, a disease epidemic reduced populations by 95–100% (from 1.06–14.38 m<sup>-2</sup> to <0.01 m<sup>-2</sup>) across the 3.5 million km<sup>2</sup> area of the Caribbean (Bak et al. 1984, Lessios et al. 1984a,b, Hughes et al. 1985, Lessios 1988a,b, Levitan 1988, Carpenter 1990, Betchel et al. 2006), and populations remain significantly depressed across the region to this day (Edmunds & Carpenter 2001, Chiappone et al. 2002, Weil et al. 2005, Debrot & 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 & Mumby 2012), which has decreased the availability of refugia (Alvarez-Filip et al. 2009) and has potentially left *D. antillarum* vulnerable to predation. Models produced by Mumby et al. (2006) predict that *D. antillarum* population densities >1 m<sup>-2</sup> 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.

Under natural conditions, it is likely that *D. antillarum* is afforded a degree of environmental protection from predation by the complex structure of the reef (Ogden et al. 1973). However, individuals living on flattened contemporary Caribbean reefs with low percent cover of hard coral are likely to be more heavily reliant on direct predator avoidance behaviour, a role fulfilled by movement of their longest spines which have defensive barbs directed towards the distal end (Randall et al. 1964). Here, *D. antillarum* predator avoidance behaviour (PAB) is defined as the percentage of long predatory spines that move in response to a shadow stimulus. Decreases in light intensity, indicating the potential presence of a predator, evoke an excitatory response in the spines, making the individual hard to capture (Millott & Yoshida 1960a). However, PAB has an energetic cost and should be reduced in the absence of a predation threat (Millott & Yoshida 1960b); therefore, increases in light intensity have an inhibitory effect on spine movement (Millott & Yoshida 1960a).

The underlying physiological mechanism for this behaviour is well understood: a layer of melanin-con-

taining photosensitive melanophores, which give *D. antillarum* its characteristic black colouration, surrounds the test and enables changes in the light environment to be detected (Millott 1954, Millott & Yoshida 1959). This photic response is a direct result of interactions between light and the melanophore, as light stimuli cause expansion of the melanosomes, which in turn induces a nervous signal controlling spine movement (Yoshida 1956). However, melanin loses its structure at high temperature (Millott & Jacobson 1952, Sawhney 1994), suggesting that elevated sea surface temperatures (SSTs) may cause a breakdown in these essential anti-predator light-detecting mechanisms.

Significant increases in SST are expected to occur on a decadal timescale and may reach values >3.5°C higher than current averages by 2100 (Collins et al. 2013). Additionally, the often catastrophic thermal anomalies of El Niño Southern Oscillation (ENSO) are also predicted to become biennial events of increasing severity by 2050 (Donner et al. 2005). With a lifespan of up to 8 yr (Randall et al. 1964), *D. antillarum* have relatively long generation times, and their capacity to adapt to both long-term gradual, and short-term acute, SST increases is likely to be limited. However, there is well documented phenotypic plasticity associated with *D. antillarum* melanin production (Millott 1954), and numerous ecological factors, such as wave exposure and water clarity, can alter melanin distribution and concentration within an individual's test and spines (Kristensen 1964). This phenotypic plasticity may afford individuals with a degree of resilience to rising SST via upregulation of melanin to counter breakdown associated with thermal stress.

We used laboratory manipulations on natural populations to investigate how *D. antillarum* PAB is affected by increases in water temperature, and how this subsequently interacts with habitat and phenotype. We compared 2 separate populations from contrasting reef systems, representing both structurally complex and structurally simple 'flattened' habitat types, in order to address whether habitat complexity influences PAB. Given that *D. antillarum* colouration and light-detecting mechanisms are both controlled by phenotypically plastic melanin regulation, we also explored whether PAB varies between phenotype (black- and white-spined) and life-history stage (juvenile or adult) in relation to the individual's site of origin. White-spined individuals are defined as adult urchins whose complete complement of predatory defence spines is white in colour. Theoretically, restoration of *D. antillarum* is an obvious conservation

target; however, to date, no studies have investigated how they will respond to predicted environmental change. The results of this study will allow conservation managers to gain better understanding of the interactions between PAB and temperature, and make decisions on population restoration initiatives based on their future survival potential.

## MATERIALS AND METHODS

### Study sites

Data were collected on the Honduran island of Utila and the 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 *Diadema 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 2 sites (Bodmer et al. 2015).

### Future climate change predictions

The Intergovernmental Panel on Climate Change (IPCC) has recently described 4 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  $W\ m^{-2}$  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 4 RCPs are modelled on assumptions of socio-economic activity that are used to predict the extent of GHG accumulation in 2100, and they have been designed to represent a range of possible future climate change scenarios. Table 1

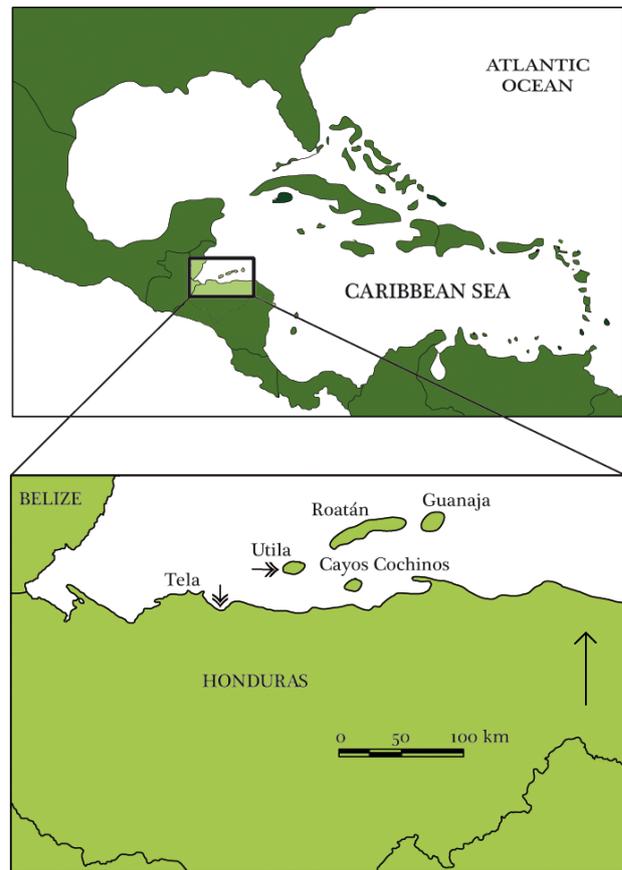


Fig. 1. Locations of the study sites at Utila and Banco Capiro (in Tela Bay), Honduras



Fig. 2. Landscape photograph of Banco Capiro showing the high percent cover of hard coral and resultant architectural complexity. Photo credit: Dan Exton



Fig. 3. Landscape photograph of Utila showing 'typically' low hard coral cover and associated lack of habitat structure. Photo credit: Adam Laverty

outlines the 4 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).

### Specimen collection and acclimatisation

Trials were run between March and August 2015. We collected 30 individuals in each of 3 categories (black-spined adult, white-spined adult, juvenile; Fig. 4) from each site giving a total sample size of 180 urchins over the 6 mo sampling period. Juveniles were identified by their distinctive black and white banded spines and a test diameter <20 mm (Randall et al. 1964). Four *D. antillarum* individuals were collected each day by a combination of snorkelling and SCUBA, and trials were conducted on the same day. All individuals were returned alive to the reef within 24 h of collection. Pseudoreplication was avoided by collecting from a different sub-site each day. When removing individuals from the reef, care was taken to ensure that minimal damage was caused to the spines and test. Once an individual was located, a 50 cm length of PVC pipe (outside diameter = 2.6 cm) was used to coerce it into the open. The PVC pipe was then used to lift the individual off the reef and into a container for safe storage.

Table 1. Data extracted from Table SM30-4, Section 7 'Coral Reef Provinces', Row 1 'Caribbean Sea/Gulf of Mexico' in Hoegh-Guldberg et al. (2014). RCP: representative concentration pathway, SST: sea surface temperature, GHG: greenhouse gas

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	<ul style="list-style-type: none"> <li>• Mid-century peak at 3.1 W m<sup>-2</sup></li> <li>• Decrease to 2.6 W m<sup>-2</sup> by 2100</li> </ul>	<ul style="list-style-type: none"> <li>• Unlikely</li> <li>• Requires immediate GHG emission reduction on a global scale</li> </ul>
RCP 4.5 (stabilising)	0.64	1.43	<ul style="list-style-type: none"> <li>• Rise to 4.5 W m<sup>-2</sup> by 2100</li> <li>• No further increases</li> </ul>	<ul style="list-style-type: none"> <li>• Moderately likely; radiative forcing peaks in 2040 and then plateaus</li> <li>• Would require immediate cooperation and coordination between the world's governments</li> </ul>
RCP 6.0 (stabilising)	0.61	1.87	<ul style="list-style-type: none"> <li>• Rise to 6.0 W m<sup>-2</sup> by 2100</li> <li>• No further increases</li> </ul>	<ul style="list-style-type: none"> <li>• Most likely; radiative forcing peaks in 2080 and then plateaus</li> <li>• Pressure put on governments to address climate change issues will likely cause GHG emission reductions, but time is required to coordinate the effort</li> </ul>
RCP 8.5 (worst case)	0.83	3.14	<ul style="list-style-type: none"> <li>• Rise to 8.5 W m<sup>-2</sup> by 2100</li> <li>• Continue unabated into 22nd century</li> </ul>	<ul style="list-style-type: none"> <li>• Unlikely</li> <li>• Requires GHG emissions to continue at current rates; concerted efforts are already being made to reduce them</li> </ul>

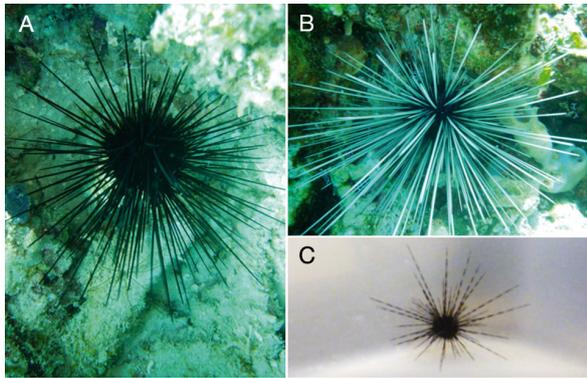


Fig. 4. *Diadema antillarum* adult and juvenile phenotypes. (A) black-spined adult, (B) white-spined adult, (C) juvenile

On returning to the laboratory, individuals were placed into a 200 l plastic holding tank where they were allowed to acclimatise for a minimum of 8 h before trials were conducted. This short acclimatisation period was chosen to minimise stress and maximise survivorship to reduce adverse effects on populations of this key reef herbivore. Thus our trials tested the shock responses of *D. antillarum* to increased water temperature, and did not account for the possibility of potential short- or long-term adaptation/phenotypic plasticity; therefore, our results must be interpreted in that light.

#### Experimental setup and climate change scenarios

Experimental manipulations were conducted in 3 transparent 64 l 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 150 W) 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 the IPCC climate change scenarios. 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, i.e. the current annual mean peak SST (CSST) recorded off the Caribbean coast of Honduras ([www.seatemperature.org](http://www.seatemperature.org)). Experimental temperatures were then cal-

culated 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 may be affected by the structural complexity of the population's site of origin. It is possible that temperature and site interact to affect PAB, which has major implications for *D. antillarum* restoration initiatives aiming to provide artificial reef structure to stimulate recovery.

#### Trial protocol

Trials were conducted at night in a laboratory setting under artificial lighting maintained at an intensity of ca. 20 lm. The phenotype of each individual urchin was recorded and the total number of long defensive spines counted, along with individual weight (to the nearest mg) and test diameter (to the nearest mm) using long-jaw callipers. These measurements were recorded immediately after collection before individuals were placed in the holding tank to avoid inducing stress immediately prior to the trials. The PAB of each individual was then tested under each temperature scenario. Individuals were acclimated to each temperature for at least 30 min before trials began, or until they had settled in a corner of the tank for a period of at least 10 min. This was done to ensure that urchins were adjusted to the heat shock and were therefore responding to the shadow stimulus and not to the change in temperature.

At the start of each trial, a GoPro Hero 3 underwater video camera was placed in the trial tank facing the urchin and set to record for the duration of the trial. Urchins were initially exposed to ambient light conditions for 30 s. A shadow was then created over the urchin using an opaque wooden board to simulate the presence of a predator, and maintained for 30 s before returning the urchin to ambient light. This was repeated 3 times for each urchin under each temperature scenario. The order in which individuals were exposed to the different temperature treatments was randomised ahead of each trial.

#### Quantifying PAB

PAB was defined here as the percentage of an individual's total spines that moved in response to a

shadow stimulus, and quantified visually. Test diameter was measured in order to account for any confounding effect of body size on PAB. Only the movements of the longest spines were counted because the main function of these is known to be predatory defence, whereas the shorter spines are used predominantly for feeding and locomotion (Randall et al. 1964).

Prior to their analysis, all 540 videos were renamed using RandomNames software. The video analyst was therefore unaware of the site of origin and climate change scenario of the urchin they were processing, thus removing any potential observer bias from the data. Video recordings were replayed in slow motion, allowing accurate counts of the number of long defensive spines that moved in response to the shadow stimulus. The PAB for each simulated 'attack' was calculated, and the means of these PAB values were used for statistical analysis.

### Statistical methods

PAB data were normally distributed, and their relationships with climate change scenario, site and phenotype were analysed using a 3-way repeated measures ANOVA with urchin number nested within climate change scenario. PAB was the continuous dependent variable, site and phenotype were nominal, fixed-effects between subjects variables, and climate change scenario was a nominal, fixed-effect within subject variable.

We investigated the relationship between *D. antillarum* body size (test diameter) and PAB in order to control for this as a confounding variable, since smaller individuals are more vulnerable to predation, and predation threats are generally considered more relevant to juveniles than adults (Clemente et al. 2007, Jennings & Hunt 2010). All data were analysed using R.

## RESULTS

### Establishing a baseline PAB

The mean PAB of black-spined adult urchins at CSST on Banco Capiro ( $17.39 \pm 0.68$ [SE]%) was used as a baseline for comparisons of different combinations of climate change sce-

nario (CSST, RCP 4.5 or RCP 8.5), site (Utila or Banco Capiro) and phenotype (black- or white-spined adults, and juveniles). 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 ( $>2 \text{ m}^{-2}$ ) 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 & 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

We found 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 2 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; juve-

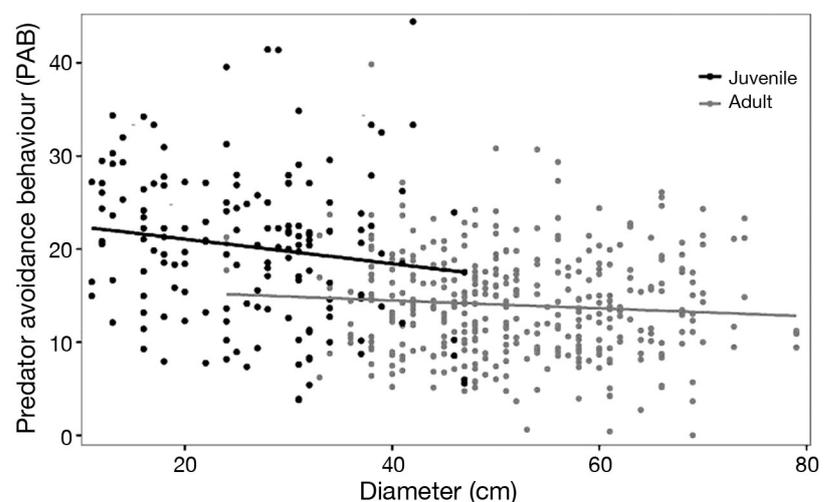
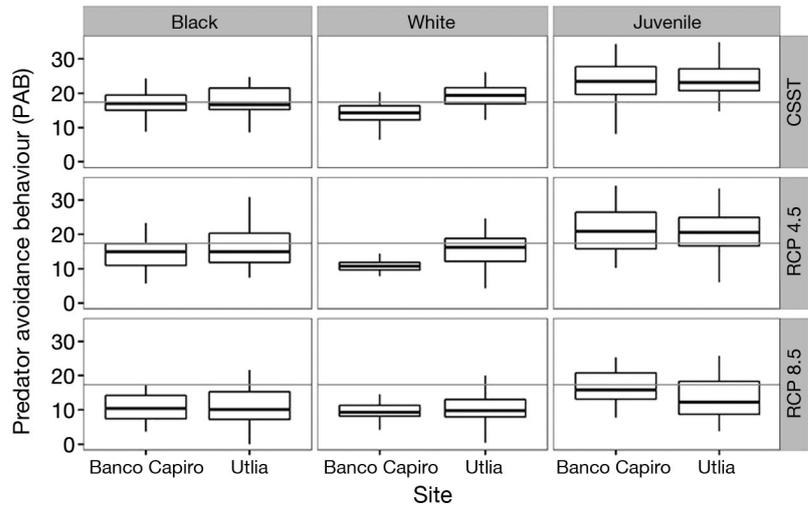


Fig. 5. Relationship between body (test) size and predator avoidance behaviour (PAB) in juvenile (black points) and adult (grey points) long-spined urchins *Diadema antillarum*. Plotted lines are least-squares regression lines. PAB was defined as the percentage of an individual's total spines that moved in response to a shadow stimulus

Fig. 6. Predator avoidance behaviour (PAB) of long-spined urchins *Diadema antillarum* of 3 categories (black-spined adult phenotype, white-spined adult phenotype and juvenile), across 2 sites (Utila: flattened reef; Banco Capiro: complex reef), under conditions simulating 3 different IPCC climate change scenarios (see Table 1; current mean sea surface temperature [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 adults on Banco Capiro under CSST. PAB was defined as the percentage of an individual's total spines that moved in response to a shadow stimulus. Vertical lines represent  $\pm 1$  SE; lower and upper boundaries of boxes represent interquartile range



niles,  $F_2 = 4.86$ ,  $p = 0.0091$ ; adults  $F_2 = 15.37$ ,  $p < 0.0001$ ), and juvenile urchins had higher PAB than adults in all temperatures. Mean  $\pm$  SE juvenile PAB declined from  $24.54 \pm 1.28\%$  at CSST to  $21.1 \pm 1.45\%$  under RCP 4.5 and  $15.19 \pm 1.22\%$  under RCP 8.5. Repeated measures ANOVA revealed that there was no difference in PAB of juveniles between sites overall ( $F_1 = 0.303$ ,  $p = 0.58$ ) but the data for RCP 8.5 suggested lower PAB at Utila than Banco Capiro (Fig. 6). PAB of black-spined adults declined similarly to juveniles, from  $17.66 \pm 0.76\%$  at CSST to  $15.09 \pm 0.9\%$  at RCP 4.5 to  $10.80 \pm 0.87\%$  at RCP 8.5. The percentage declines in PAB from CSST to RCP 8.5 were proportionately similar: 38.1% for juveniles and 38.8% for black-spined adults. Interestingly, PAB of juveniles under RCP 4.5 was still 21.33% higher than that of black-spined adults under CSST.

There was no evidence of between-site differences in PAB or its response to temperature for black-spined adult urchins, but the pattern differed for white-spined adults, reflected by a significant interaction between phenotype and site ( $F_1 = 8.96$ ,  $p = 0.003$ ). White urchins from Banco Capiro ( $14.35 \pm 0.58\%$ ) displayed lower PAB than those from Utila ( $19.50 \pm 1.34\%$ ), and mean white urchin PAB on Banco Capiro ( $14.35 \pm 0.58\%$ ) was lower than that of their black counterparts ( $17.39 \pm 0.68\%$ ). However, the inverse was true on Utila, where mean white-spined adult *D. antillarum* PAB ( $19.50 \pm 1.34\%$ ) was higher than that of the black population ( $17.93 \pm 0.84\%$ ). However, these differences were less apparent at RCP 8.5 (Fig. 6). At CSST, mean PAB of white-spined adults was almost 36% higher on Utila ( $19.50 \pm 1.34\%$ ) than on Banco Capiro ( $14.35 \pm 0.58\%$ ). This difference was maintained at

RCP 4.5 ( $15.49 \pm 0.91\%$  and  $11.20 \pm 0.47\%$ , respectively) but was roughly halved at RCP 8.5 ( $11.44 \pm 0.92\%$  and  $9.70 \pm 0.49\%$ ). See Table 2 for complete breakdown of results.

## DISCUSSION

### Demographic influences on PAB

At CSST, mean PAB of juveniles was 41.12% greater than that of black-spined adults on Banco Capiro, and the higher PAB value was maintained even under moderate thermal stress (RCP 4.5). This is not surprising, as juvenile test diameters are typically smaller than the 40 mm predator escape threshold above which vulnerability is believed to decrease (Clemente et al. 2007, Jennings & 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 & 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 *Diadema antillarum* individuals had 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, Grown 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 urchins are likely to be nutrient-limited and may therefore be unable to invest in metabolically expensive melanin production. Whilst white-spined adults appear to be less sensitive to predation stimuli, their overall vulnerability may be unaffected by this decreased PAB ability because they favour shaded, and presumably more complex, habitats.

Conversely, juveniles develop black spines when reared in high-light environments (Kristensen 1964), typically when individuals settle on more exposed areas rather than within the complex coral framework. It is therefore likely that black-spined adult *D. antillarum* are grazing algae from light-exposed reefs that have greater energy availability per unit area (Ogden & Lobel 1978) than darker reefs where their white-spined counterparts live. Black-spined individuals may therefore be able to invest more heavily in melanin production. This investment in their light-detecting sensory systems is further justified in black-spined adults because their more exposed lifestyle leaves them vulnerable to predation.

For black-spined adults and juveniles, the magnitude of PAB does not differ between sites, but for white-spined adults, PAB is significantly greater on Utila. Unlike on Banco Capiro, white urchins on Utila are living in a flattened habitat and therefore lack abundant predation refugia. The major fish predators of *D. antillarum* (Ballistidae, Haemulidae and Labridae) all possess typical vertebrate visual systems comprised of image-forming eyes (Lamb et al. 2007), which rely, at least partially, on contrast for prey detection (Schuster et al. 2011). Against the darker backdrop of the reef, white individuals are likely to be more conspicuous to predators in a habitat where they are less able to hide. Therefore, while black individuals on Utila are less conspicuous to predation, and both adult phenotypes on Banco Capiro are afforded environmental protection by the reef structure, white-spined adults on Utila must invest more heavily in the maintenance of their innate behavioural PAB.

### 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 1983–1984 mass mortality event, and potentially hamper current conservation initiatives as seas warm. We found 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 this 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 & 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 & Bennett (2009), Eme et al. (2011) and Dabruzzi et al. (2013), and thus our results do not account for phenotypic plasticity associated with the *D. antillarum* melanin-regulatory system (Millott 1954). This may serve to mitigate the negative effects of rising SST on PAB, meaning this study represents a worst-case scenario and not the end of the road for conservation efforts throughout the Caribbean.

It is also important to consider the temporal scale over which ocean warming will actually occur. We show that under the long-term water temperatures predicted by RCP 4.5 (CSST +1.43°C), *D. antillarum* will likely be partially resilient with respect to the

tection of, and reaction to, predators. With long-term temperature increases under RCP 4.5 greater than short-term increases under RCP 8.5 (CSST +0.83°C), we can assume that *D. antillarum* will be resilient to near-term SST increases across the severity range. This suggests that, at least until 2039, incremental ocean warming is unlikely to negatively impact the success of *D. antillarum* restoration initiatives.

However, increases in the frequency and severity of El Niño anomalies means that long-term warming is not the only thermal threat to be faced. In winter 2016, average Caribbean SST was 0.5–1.5°C higher than the 1981–2010 average (NOAA, [www.ncdc.noaa.gov/cag/](http://www.ncdc.noaa.gov/cag/)). Fortunately, our focus on acute temperature increases, similar to those experienced during El Niño, indicate that *D. antillarum* will be able to maintain PAB provided that sudden increases do not exceed ~3°C. In general, the severity of El Niño in the Caribbean is less than other global coral reef hotspots, and this ~3°C threshold falls outside the temperature anomalies previously experienced in the region (NOAA, [www.ncdc.noaa.gov/cag/](http://www.ncdc.noaa.gov/cag/)).

It has been suggested that *D. antillarum* conservation efforts should focus on reintroduction coupled with artificially augmented structural complexity (Bodmer et al. 2015). Our results suggest that conservation interventions seeking to increase structural complexity will reduce the reliance of *D. antillarum* on innate behavioural PAB, and increase survivorship even in the face of worst-case scenario increases in SST. In essence, structural complexity may provide a buffer against the increased threat of predation caused by reduced PAB via melanin breakdown. Stakeholders can use this information to make informed decisions about strategies to increase the health of Caribbean coral reef ecosystems by focusing on this important species. This is in line with the IPCC's goal of 'working with scenarios...in order to consider how robust decisions or options may be under a wide range of possible futures' (Moss et al. 2010, p. 747). Our results indicate that if *D. antillarum* populations are going to recover and aid the reversal of ubiquitous macroalgal phase-shifts, they require urgent conservation attention to be buffered from climate change-induced thermal stressors.

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