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Do Tropical Specialist Sea Urchins Have Higher Thermal Tolerances and Optimal Temperatures
Than Their More Widely Distributed Relatives?

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27 **Abstract**

28 Warming tolerance (WT), thermal safety margins (TSM), and thermal performance curves have
29 been documented empirically for few tropical marine invertebrates, although calculations of
30 realized niches from biogeographic data suggest that WT is smaller for tropical organisms than
31 for temperate organisms. To determine these characteristics for 8 species of Caribbean sea
32 urchins, we documented the effects of acute heat stress and cold stress on righting time (a
33 measure of performance) and survival. The upper lethal limit occurred between 35.1 and 37.1 °C
34 for all of the species, and the upper limit for righting occurred very close to this between 34.0 °C
35 and 36.9 °C. The lower lethal limit occurred between 4.8 °C and 7.6 °C for all species except for
36 *Tripneustes ventricosus* where it was 14.6 °C. The lower limit for righting was significantly
37 warmer than the lower lethal limit and occurred between 13.4 °C and 14.6 °C for all species
38 except for *T. ventricosus* where it was 19.1°C. Within these critical limits, the thermal
39 performance curves are broad and optimal performance windows range from 24°C and 32°C.
40 Environmental data shows that in Bocas del Toro, Panama have warming tolerances of 6°C to
41 8°C for 2-hour exposures but that thermal safety margins range from -4°C to 2°C, highlighting
42 the vulnerability of these species are to moderate environmental warming. Species with
43 exclusively tropical ranges did not show higher optimal temperatures than species with ranges
44 that extend into the subtropics or temperate regions.

45

46 **Introduction**

47 Caribbean sea surface temperatures (SST) are predicted to warm by 1.5-2°C before the
48 end of the century (Nurse & Charlery 2016). It is fairly well documented how this might impact
49 the distributions of corals and reef fishes (e.g., Bruns 1985, Precht & Aronson 2004, Carilli et al.
50 2010, Clauson-Kaas et al. 2017), but little information is available on how ocean warming may
51 alter the distribution of other organisms from the region. Our goal was to compare the warming
52 tolerance and thermal safety margins (Deutsch et al. 2008) of Caribbean sea urchins to determine
53 if the species with exclusively tropical ranges are more heat tolerant or thermally specialized
54 than are those species with ranges that extend through the subtropics.

55 To understand and predict organisms' responses to changing environmental conditions
56 and their biogeographic ranges it is necessary to document the breadth and shape of organism's
57 thermal niches or performance curves (Bozinovic & Naya 2014, Jablonski et al. 2013, Ling et al.
58 2009, Andersen et al. 2015, Hoffman et al. 2013; but see caveats in Sinclair et al. 2016). Thermal
59 breadth, the range between the critical temperature limits (i.e., CT_{max} and CT_{min}) at which the
60 organisms fail to maintain the ability to perform or to survive (Dowd et al. 2015) is a coarse
61 measure often assessed with short exposures to extreme temperatures (e.g., Walther et al. 2013).
62 These are useful standard assays for comparing multiple species, and are particularly effective
63 for species where it is logistically difficult to make more nuanced measurements (e.g., Nguyen et
64 al. 2011, Compton et al. 2007). Critical temperatures may be good predictors of range limits for
65 some species (e.g., Sunday et al. 2011; Andersen et al. 2015). In terrestrial organisms, critical
66 temperatures vary among species with latitude, with upper limits often showing little variation
67 with latitude, while lower limits change considerably with latitude producing wider thermal
68 niches at higher latitudes (Addo Bediako et al. 2000). A similar pattern has been documented for
69 fishes and other marine organisms (Sunday et al. 2012, Comte & Olden 2017, Stuart-Smith et al.
70 2017). Many of these data are based on realized thermal niches calculated from distribution data
71 and not from empirical measurements as direct measures of CT_{max} and CT_{min} are both available
72 for few species.

73 Direct measures of CT_{max} may also be useful as predictors of which sudden extreme
74 events could cause mortality in the field. For example, intertidal or shallow-water organisms may
75 naturally experience short-term extreme changes in temperatures during low tides either during
76 hot, midday exposures in the summer, or extreme cold exposures in the winter (Glynn 1968,

77 Anthony & Kerswell 2007, Beddingfield & McClintock 1994, Helmuth et al. 2002). Finally,
78 warming tolerance (WT), the difference between the average temperatures experienced in the
79 environment and the maximum critical temperature (Deutsch et al. 2008), is generally lower in
80 the tropics than at higher latitudes (Comte & Olden 2017).

81 Within the thermal range of thermal tolerance, the relationship between performance and
82 temperature is described by the thermal performance curve (Angilletta 2009). These curves are
83 generated using easily quantified aspects of performance (sprint speed, consumption rate, etc.)
84 measured across a range of temperatures, although in many cases too few temperatures are
85 assayed to determine the shape of the entire curve (discussed in Dowd et al. 2015). Among
86 marine invertebrates such curves have been used to compare: the effects of temperature on aerial
87 and underwater performance among species (Tagliarolo & McQuaid 2015); swimming speeds
88 and respiration rates among populations from locations with different thermal conditions
89 (Walther et al. 2013); and developmental success among species from different latitudes
90 (Karelitz et al. 2016). The optimal temperature T_{opt} can be determined from the performance
91 curves, and the thermal safety margin is calculated as the difference between the T_{opt} and the
92 environmental temperature (Deutsch et al. 2008). Thermal tolerance curves also provide
93 important context to help select relevant temperature treatments for experimental work.

94 Tropical sea urchins play an important role as ecosystem engineers (Birkeland 1989;
95 Steneck 2013). On reefs, grazing by herbivorous urchins suppresses macroalgal growth and helps
96 to maintain healthy coral populations (Steneck 2013). Herbivory by urchins can be particularly
97 important in the absence of herbivorous fishes and may help prevent phase shifts from coral
98 dominated to algal dominated habitats (Jackson et al. 2014, Sangil & Guzman 2016). The
99 activity of *Echinometra* species, which excavate depressions can contribute significantly to
100 bioerosion on reefs (Asgaard & Bromley 2008, Bak 1994, Griffin et al. 2003, McClanahan and
101 Muthiga 2013) and may also provide microhabitats and increase diversity of other invertebrates
102 (Schoppe & Werding 1996). In seagrass meadows, *Lytechinus variegatus* may regulate seagrass
103 biomass and meadow size, and overgrazing may permanently eliminate vegetation (Heck &
104 Valentine 1995, Valentine & Heck 1991, Watts et al. 2013). Finally, irregular sea urchins can be
105 important bioturbators and bioeroders, with *Clypeaster rosaceus* playing an important role in
106 sand production (Telford et al. 1987). Their ecological importance suggests that changes in sea
107 urchin distributions could significantly impact ecosystem function.

108 Our overarching goal is to understand the thermal tolerances of these species in the
109 context of environmental conditions and species' geographic ranges. Specifically, we test the
110 following hypotheses: (1) Exclusively tropical species show higher warming tolerance and
111 thermal safety margins than do species that also occur in the subtropics. (2) Species that occur in
112 the subtropics have lower lethal limits under cooling than the exclusively tropical species. To
113 address these questions, we documented the thermal breadth of each species by determining both
114 the upper and lower critical temperatures (i.e., CT_{max} and CT_{min}) for righting, a measure of
115 performance, and for survival. To determine the shape of the performance curve we documented
116 righting performance every 2°C between the thermal tolerance limits.

117

118 **Materials and Methods**

119 *Study Species* - We selected 6 species (*Echinometra lucunter*, *E. viridis*, *Lytechinus variegatus*,
120 *L. williamsi*, *Tripneustes ventricosus*, and *Eucidaris tribuloides*) of common, ecologically
121 important, shallow-water regular sea urchins to study righting time in detail and 2 species
122 (*Clypeaster rosaceus* and *C. subdepressus*) of irregular sea urchins for which we tested thermal
123 tolerance, but which can never turn themselves over due to their shape and lack of adhesive tube
124 feet. These species all occur throughout the Caribbean but the extent of their ranges outside the
125 Caribbean varies considerably (Table 1). Two of the species, *E. viridis* and *L. williamsi* are
126 exclusively tropical, while their sister species *E. lucunter* and *L. variegatus* have ranges that
127 extend significantly further south and north. Long-term monthly average sea surface
128 temperature maps obtained from optimum interpolation (Reynolds et al. 2007) for the warmest
129 and coolest months (August and February; Figure 1) show that the range limits for these species
130 tend to occur where winter temperatures drop below 20°C. But that *E. viridis* and *L. williamsi*
131 inhabit ranges where the water temperatures are unlikely to fall below 25°C (Figure 1).

132 All of the study species occur in shallow water in Bocas del Toro, and were collected by
133 hand while snorkeling at less than 5 meters depth. In this area, the *Echinometra* species live on
134 rocks and coral rubble in very shallow water, and may occur in only a few centimeters of water.
135 *Lytechinus variegatus* lives in shallow *Thalassia* meadows while its sister species *L. williamsi*
136 lives in crevices in shallow reefs. *Eucidaris tribuloides* lives under coral rubble and in crevices
137 on reefs and *Tripneustes ventricosus* lives in seagrass meadows, among rubble and on shallow
138 rocky reefs, but we collected them primarily from seagrass habitats. Animals were kept

139 submerged in buckets while they were transported to the Smithsonian Tropical Research
140 Institute's Bocas del Toro Research Station. They were maintained in 300-liter aquaria with
141 flow-through seawater for no longer than 7 days before thermal performance trials.

142
143 *Tolerance and Performance Trials* – Our chosen measure of performance is the speed of the
144 righting response (Brothers & McClintock 2015, Sherman 2015, Challenger & McClintock 2017).
145 The righting response, the speed at which the animals can turn over from an inverted position,
146 has been used for 80 years to assess the impacts of temperature on performance in echinoderms
147 (Kleitman 1941, Farmanfarmaian & Giese 1963, Lawrence 1973, Lawrence & Cowell 1996,
148 Brothers & McClintock 2015). Rapid righting is clearly important for fitness in animals that are
149 dislodged. Righting involves the strong adhesion of tube feet and coordinated movement of tube
150 feet and spines, which are also key components of other fitness related functions like movement,
151 attachment to the substrate and covering (a behavior where the animal holds algae, seagrass or
152 other debris over the dorsal surface) (Brothers & McClintock 2015, Sherman 2015, Challenger &
153 McClintock 2017). At extreme temperatures, animals lose the ability to right and eventually
154 enter heat/cold-coma and ultimately die.

155 We tested the response of adult urchins from each species to a single 2-hour temperature
156 exposure ranging from 6°C to 36°C. Each animal was only tested once. Prior to the test, they
157 were maintained at ambient temperature (27-29°C) in the running seawater system. For each
158 species, 3 sea urchins were tested in each trial and we conducted 3-6 independent trials per
159 temperature for each species for a total of 9-18 urchins tested at each temperature. Prior to the
160 exposure to the test temperature, the righting time of the urchin was recorded at the holding
161 temperature. Animals were gently removed from the substrate, placed on their aboral side on a
162 flat surface, and the time for them to turn over to the normal resting position was recorded.
163 Animals with unusually long initial righting times were excluded from the trials.

164 The temperature was then raised or lowered gradually over 15 minutes to attain the
165 desired temperature. After 2 hours at the test temperature the animal was overturned and the
166 righting time was recorded again. If the urchin failed to right in an hour it was scored as being
167 unresponsive. Unresponsive urchins could be in torpor (cold treatments), heat coma (hot
168 treatments), or potentially dead. Urchins from temperatures where any animal failed to right,
169 were allowed to slowly return to ambient temperature and given a day to recover in flow-through

170 holding tanks, and then scored as alive or dead. All trials were conducted in clean aquaria
171 without materials that could be used for covering and with a smooth substrate, as these factors
172 have been shown to influence righting times (Challener & McClintock 2017). We aimed to
173 standardize the size of the sea urchins across trials for each species by collecting only animals in
174 size range most typical for our collecting sites. Unusually large or small animals were excluded
175 for the study. Because heating rate and exposure duration are not independent and because we
176 wanted to standardize the static temperature exposure we used different heating rates to attain the
177 experimental temperatures, which were then experienced for 2 hours regardless of treatment.
178 This ensured that individuals in the more extreme treatments were not exposed to elevated
179 temperatures for longer periods than those in more moderate treatments. Thermal tolerance
180 studies use a variety of methods including ramping experiments, where the temperature increases
181 gradually until the organisms die, to more static experiments where the test temperature is
182 reached quickly and subsequently maintained. It should be noted that ramping experiments with
183 low ramping rates often find lower thermal tolerance, most likely due to extended exposures
184 (Peck et al. 2009, Vinagre et al. 2013, Nguyen et al. 2014, Faulkner et al. 2014). Studies that
185 employ such vastly different methods cannot strictly be compared, however comparisons can be
186 made between organisms that have been exposed to the same protocol in a single study.

187 To identify the CT_{max} urchins were initially tested at 28 (ambient), 30, 32, 34, and 36°C.
188 Once a temperature with 100% mortality was identified, we conducted an additional trial at 1°C
189 below this temperature, in order to identify more precisely the CT_{max} . To identify CT_{min} and to
190 obtain the complete performance curve, urchins were tested at temperatures every 2°C from
191 28°C down to 6°C.

192

193 *Environmental Conditions* - Environmental temperature was monitored at a depth of
194 approximately 5m (2m off the bottom) on the instrument platform at the Bocas del Toro
195 Research Station (BRS). Data were logged at 15-min intervals by data-loggers attached to a
196 Campbell Model 107 electronic temperature sensor. The platform is located over the seagrass
197 bed where adult *L. variegatus* were collected for this study. Temperatures from this site are
198 generally representative of other monitoring locations at similar depths in the region (Collin et al.
199 2009). To determine if extremely shallow water inhabited by *Echinometra* species is
200 significantly warmer than the more open water over the seagrass we also recorded temperatures

201 at 0.25 m in a rubble patch at the base of the BRS dock, and at 0.5m depth on a shallow part of a
202 *Porites* fringing reef at the small point across from the BRS. *Echinometra viridis* live in the
203 rubble at the base of the dock and *E. viridis*, *L. variegatus* and *L. williamsi* all live in the *Porites*
204 reef. Temperatures were recorded using a HOBO Stow-Away TidbiT and HOBO Water
205 Temperature Pro V2 (Onset Computer Corporation, Bourne, MA) with an accuracy of 0.25 °C
206 (Kaufmann & Thompson 2005) between October 15, 2015 and June 30, 2016.

207 To understand how temperatures measured in Bocas del Toro compare to temperatures in
208 similar habitats throughout the Caribbean, we used temperatures measured weekly over coral,
209 seagrass and mangrove habitats as part of the Caribbean wide CARICOMP project (Chollett et
210 al. 2017; data available online at <https://doi.org/10.1371/journal.pone.0188564.s002>). These sites
211 span much of the ranges of each species in the northern hemisphere. The maximum and
212 minimum temperatures reported were compared to the critical temperatures of the urchins
213 measured in this study.

214
215 *Statistical Analysis* - The CT_{max} and CT_{min} for righting and for survival were estimated as the
216 LT_{50} . That is, survival CT is the temperature at which 50% of the animals failed to survive and
217 the righting CT is the temperature at which 50% of the animals failed to right. Each CT was
218 estimated using logistic regression in JMP12 using the Fit Model menu and the inverse
219 prediction option. In some cases where every temperature produced either 100% success or
220 100% failure the exact LT_{50} with confidence limits could not be estimated in this way, and was
221 therefore estimated using linear interpolation. Logistic regression with species and temperature
222 as factors was used to determine if thermal tolerances of the species differed significantly. To
223 find the optimal temperatures (T_{opt}), performance curves were generated by fitting quadratic and
224 biexponential curves to the time to right for each species using the nonlinear models
225 implemented in JMP12. The inflection point, at the minimum time to right (i.e., optimal
226 performance) was calculated using the first derivative of the function that provided the best fit to
227 the data based on comparisons of AICc values. Finally, one-way ANOVA with post-hoc Tukey
228 HSD tests was used to determine at which temperatures performance was statistically
229 significantly reduced compared to the optimal temperature.

230 CT_{max} and T_{opt} were combined with environmental data to calculate the WT and TSM
231 following Deutsch et al. (2008). We used 29°C, the grand average of the temperatures at the 2

reefs reported in Collin & Chan 2016), as the average environmental temperature to calculate WT and TSM. We calculated WT as the difference between the average habitat temperature and the lowest assayed temperature at which sea urchins experienced 50% failure to survive or to right. We calculated the TSM as the difference between the T_{opt} identified by biexponential and quadratic curve fitting and the habitat temperature.

237

238 **Results**

239 ***Thermal Tolerance***

240 *Thermal limits* – Survival CT_{max} (temperature at which half of the animals died) and righting
241 CT_{max} (temperature at which half of the animals failed to right) were assayed between August 20
242 and October 17, 2016, when average daily water temperatures averaged 29.6°C (28.3°C -
243 31.0°C). Logistic regression showed that trial temperature and species both had a significant
244 effect on the probability that the animal righted and survived (Tables 2 & 3). The survival CT_{max}
245 was 0.3-1.5°C higher than the righting CT_{max} (Table 2; Figure 1). Post-hoc pair-wise
246 comparisons among species showed that the two *Echinometra* species had significantly higher
247 survival CT_{max} (37.5°C for *E. lucunter* and 37.0°C for *E. viridis*) than any of the other species.
248 *Eucidaris tribuloides* (36.5°C) had a survival CT_{max} significantly higher than the remaining
249 species and survival CT_{max} for *Clypeaster rosaceus* (36.0°C) was higher than the last four
250 species, which did not differ from each other (Table 2). Likewise, the righting CT_{max} was
251 significantly higher for the two *Echinometra* species than for the others, and it was significantly
252 lower for *Tripneustes ventricosus* than for the remaining species (Table 2).

253 The lower thermal limits were assayed between February 18, 2016 and April 28, 2016,
254 when the average daily water temperature was 29.2°C (27.8°C - 30.5°C). The range of low
255 temperatures tested included the temperatures at which all urchins failed to right regardless of
256 species. In only one species, *Tripneustes ventricosus*, did all of the animals fail to survive
257 exposures at the coldest temperatures. Logistic regression analysis showed that trial temperature
258 and species had a significant effect on the probability that the animal righted (Table 3). Post-hoc
259 tests showed that the 2 species of *Lytechinus*, the 2 species of *Echinometra*, and *Eucidaris*
260 *tribuloides* did not differ in the temperature at which they failed to right (righting CT_{min} = 13.4-
261 14.6°C; Table 2; Figure 2), while *T. ventricosus* fails to right at a significantly warmer
262 temperature (LTL_{R50} = 19.1°C; Table 2; Figure 2). *T. ventricosus* also showed a significantly

263 higher survival CT_{min} , at 14.1°C, while survival CT_{min} , for the two *Echinometra* species was 6.5-
264 8 °C. It was estimated to be 4.5-6.5°C for the other species. Overall the righting CT_{min} is about
265 5°C warmer than the survival CT_{min} (Table 2).

266

267 ***Thermal Optima***

268 Thermal performance curves were determined for temperatures from 18°C to the upper
269 thermal limit of each species. In three species (*E. lucunter*, *L. variegatus* and *L. williamsi*) both
270 the quadratic and biexponential curves fit the data with a clear minimum righting time (Figure 4;
271 Table 4). In *E. lucunter* and *L. variegatus* the two methods identified optimal temperatures
272 within 1°C of each other, around 30°C and 27°C respectively. In *L. williamsi* the two methods
273 produced quite different curves, but comparisons of AICc showed that the biexponential curve is
274 a significant better fit and gives an T_{opt} of 28°C (Figure 4; Table 4). In the other three species (*E.*
275 *viridis*, *T. ventricosus*, and *E. tribuloides*) the biexponential curve was also the best fit, but
276 minimum righting times could not be identified with confidence. Data from *E. viridis* and *E.*
277 *tribuloides* both show very flat biexponential curves between 25 and 34°C (Figure 4; Table 4).
278 Above 34°C *E. tribuloides* completely failed to right. For *E. viridis* those few that did right at
279 34°C did not take much longer than those that righted at cooler temperatures. Optimal
280 temperatures estimated from the quadratic curves (which did not fit the data as well as the
281 biexponential curves), gave optimal temperatures for righting as 28.5 and 29.5°C respectively.
282 Finally, righting times in *T. ventricosus* were much slower than in the other species, probably
283 due to their large size, and decreased consistently with decreasing temperature over the range
284 where righting occurred. This suggests that the T_{opt} is around 32°C, very close to the righting
285 CT_{max} . As predicted based on other organisms (Dowd et al. 2015) all of the species had
286 performance curves with T_{opt} much closer to the CT_{max} than to the CT_{min} .

287 Finally, one-way ANOVA showed that righting time at the optimal temperature did not
288 differ significantly from righting time at several other temperatures in each of the species (Table
289 5; Figure 4). This suggests that for short exposures there is a functionally optimal window that
290 ranges from around 26°C to 32°C in these species. However longer exposures or more
291 challenging performance criteria may amplify differences and result in a narrower functional
292 window.

293

294 ***Environmental temperatures, WT and TSM***

295 The highest temperatures reported for seawater at the BRS and over a shallow reef in
296 Bocas del Toro during 2006-2015 are around 31°C and seldom exceed 32°C, with 10 year
297 average temperatures of 28.8°C and 29.3°C at the 2 sites studied (Collin & Chan 2016). Daily
298 average temperatures registered at the BRS instrument platform during the present study in
299 2015-2016 ranged from 27.4-31.8°C. Comparisons of the 3 sites (platform, dock and *Porites*
300 reef) between October 15, 2015 and June 30, 2016 showed little difference among sites (26.7-
301 31.3°C and 26.7- 32.3°C daily at the shallow sites; 27.7-31.3°C at the instrument platform)
302 suggesting that microhabitat does not greatly alter thermal conditions. The CARICOMP
303 monitoring data (Chollett et al 2017) show that Bocas del Toro is not unusually warm when
304 compared to other Caribbean sites. Average temperature in Bocas del Toro measured weekly
305 over coral, seagrass, and mangrove habitats with the CARICOMP protocol gives average
306 temperatures of 28.5°C in all 3 habitats. Average temperatures at 13 of the 45 other sites were
307 greater than or equal to those reported for Bocas del Toro.

308

309 **Discussion**

310 ***Are exclusively tropical species thermal specialists?***

311 Two of the species studied here, *E. viridis* and *L. williamsi* are restricted entirely to the
312 tropics. We wanted to test the hypothesis that their restricted ranges are due to limited cold
313 tolerance, and that as warm-water specialists they have higher CT_{max} and T_{opt} than their sister
314 species and the other species in the Caribbean fauna. However, our data do not support such a
315 scenario for *Echinometra*. *E. viridis* does not differ significantly from *E. lucunter* in survival
316 CT_{max} or righting CT_{max} (Table 2). In addition, T_{opt} is virtually the same when estimated with a
317 quadratic equation and higher in *E. lucunter* when estimated with a biexponential equation
318 (Table 4). Finally, CT_{min} is higher but not significantly higher in *E. lucunter* than in *E. viridis*.
319 Similar results were obtained for *Lytechinus*. Neither CT_{max} or CT_{min} differed between *L.*
320 *williamsi* and *L. variegatus* when either survival or righting were assessed. *L. williamsi* does
321 have a higher T_{opt} than *L. variegatus* with the preferred biexponential fit, but the pattern is
322 reversed with the slightly less robust fit generated by the quadratic fit (Table 4). Overall there is
323 little evidence that the two species with the most limited tropical distributions have warmer
324 thermal niches or performance curves, as their thermal optima and critical temperatures are not

325 substantively different from the other 6 species (Table 4) whose distributions extend into
326 significantly cooler waters.

327

328 ***How does adult thermal performance relate to species ranges?***

329 Distributions of the 8 species studied here overlap broadly. However, there are large
330 differences in the species range endpoints. Many ranges end around North Carolina and Santa
331 Catarina Island, Brazil, both of which experience average winter water temperatures around
332 20°C (Figure 1). For example, *L. variegatus* ranges from North Carolina to Southern São Paulo
333 State in Brazil, consistent with the idea that winter temperatures limit the geographic range of
334 this species. However, in several species one end of the range seems to be limited by winter
335 temperatures, while the other end of the range occurs in a significantly warmer region. For
336 example, the range of *Clypeaster rosaceus* ends in North Carolina in the north, but extends only
337 as far south as Venezuela, although this species has been observed once in Brazil (Table 1;
338 Hendler 1995, C. Cordeiro pers. com, 2016). The one species with a significantly warmer CT_{min}
339 and high T_{opt} , *Tripneustes ventricosus*, does not have a particularly restricted range compared to
340 the other species.

341 Recent meta-analyses have shown that, in general, marine species fill their thermal niches
342 more completely than terrestrial species and that their range boundaries are close to those
343 predicted by climatic data (Sunday et al. 2012). In addition, data suggest that species with large
344 ranges the distribution is limited by temperature or climatic conditions, while those with more
345 restricted ranges are more likely to have ranges limited by other factors (Sunday et al. 2015).
346 Our data for Caribbean sea urchins supports this idea, as the species with restricted ranges do not
347 show different thermal tolerances. The causes of the smaller ranges of *E. viridis* and *L. williamsi*
348 remain unknown. However, some potential causes can be ruled out. These two species have
349 similar larvae and larval durations to their sister species, suggesting that their dispersal abilities
350 are roughly similar. Large river plumes have been suggested to influence sea urchin distributions
351 in South America (Lessios et al. 2003), but depressed salinity from river outflows combined with
352 different salinity tolerances cannot account for the differences in northern range end points of
353 species with similar thermal tolerances.

354

355 ***Do environmental conditions expose sea urchins to stressful or lethal temperatures?***

356 Extreme thermal events, either heating or cooling, can result in significant mortality of
357 marine invertebrates, including sea urchins (Glynn 1968, Lawrence 1996, Beddingfield &
358 McClintock 1994, Helmuth et al. 2002, Anthony & Kerswell 2007, Canning-Clode et al. 2011).
359 It is therefore useful to know how the critical thermal tolerance limits of marine organisms relate
360 to expected environmental temperature extremes. Our data show that tropical Caribbean sea
361 urchins have CT_{max} for righting between 34-37°C under short-term exposures, and similar CT_{max}
362 for survival. When available, assays of CT_{max} for these species in other parts of the Caribbean are
363 similar (Glynn 1968; Sherman 2015). This suggests that acclimation to local conditions does not
364 drastically alter thermal limits, but few sites have been studied.

365 Likewise, detailed temperature information from sea urchin habitats are not widely
366 available. Nevertheless, environmental monitoring data from Panama and the CARICOMP
367 comparative dataset indicate that, as expected for locations with healthy sea urchin populations,
368 environmental temperatures seldom exceed CT_{max} . However, it is likely that some shallow
369 microhabitats with particularly low water exchange may reach or exceed these critical
370 temperatures. For example, pools on reef flats in Puerto Rico experience temperatures >34°C and
371 invertebrate mortality has been observed when even higher temperatures are caused by mid-day
372 low tides coincident with sunny weather (Glynn 1968). The same can be said for CT_{min} , which
373 ranges from 5-15°C for survival and 13-19°C for righting. Such low temperatures are unlikely to
374 be experienced in the Caribbean, but cold winter weather combined with low tides can drive
375 water temperature to critical limits as far south as Florida (Beddingfield & McClintock 1994).

376 Understanding chronic exposures to suboptimal conditions that reduce performance may
377 be more useful to predict population decline and/or geographic range shifts under gradual
378 environmental warming scenarios than are critical temperatures. This idea is reflected in the
379 thermal safety margin. Our performance curves give TSMs of -3°C to 2°C, evidence that these
380 species are already experiencing suboptimal conditions. However, these results should be
381 viewed with some caution. Primarily, the calculation of the TSM focuses heavily on the optimal
382 temperature, but does not very well reflect the rate of change of performance around the
383 optimum (Dowd et al. 2015). Since the performance curves recovered for Caribbean sea urchins
384 are very flat the difference in righting performance over 2-3°C is not always large, making it
385 unclear if such differences would result in notable changes in fitness, especially in light of the
386 other environmental factors that can influence righting performance (Challener & McClintock

387 2017). However, it is clear that in many parts of the Caribbean water temperatures routinely
388 exceed the optimal temperatures.

389 Both the heating (or cooling) rate and the duration of the exposures used in this
390 experiment may adequately model extreme events during low tides, but may not adequately
391 model slower seasonal changes. Nevertheless, experiments with longer exposure durations show
392 results consistent with our performance curves. For example, ten-day exposures of *L. variegatus*
393 to 32°C reduce righting performance and reduce Aristotle's lantern reflex compared to 28°C
394 (Brothers & McClintock 2015). One-day exposures of *L. variegatus* to 31°C reduce ingestion
395 efficiency and consumption rate compared to 29°C (Lemoine & Burkepile 2012) and one-day
396 exposures to 34°C reduced righting compared to 28°C (Lawrence 1975). *Eucidaris tribuloides*
397 exposed to different temperatures for 2 months showed reduced spermatogenesis at 30°C while
398 other measures of performance were maintained at this temperature (Lares & McClintock 1991).
399 Finally, *E. lucunter* acclimated for 7 days to 30°C showed little change in immunological
400 function compared to those acclimated to 25°C (Branco et al. 2013). These results support our
401 results that performance declines above 29-31°C and suggest that experiments based on short-
402 term exposures may be fairly accurate at predicting temperatures at which longer-term studies
403 will also detect reduced performance.

404

405 ***Future Scenarios***

406 As Caribbean sea urchins are already living at temperatures above T_{opt} , it becomes important to
407 assess WT in terms of future predicted warming scenarios. Tropical oceans have been predicted
408 to warm by 2–3°C by the end of this century (IPCC 2007, Poloczanska et al. 2007, Ganachaud et
409 al. 2011) and models of the Caribbean predict region-wide SST warming of 1.5-2°C (Nurse and
410 Charlery 2016). In addition, models of sea surface temperatures for Bocas del Toro predict that
411 average water temperatures will increase significantly with nighttime temperatures around 32-
412 33°C in much of the shallow-water fringe of Bahia Almirante by 2080 (Li & Reidenbach 2013).
413 This is an increase of 3-4°C over current average water temperatures. With our estimates of WT
414 ranging from 5-8°C in Bocas del Toro, the warming predicted by Li & Reidenbach is likely to
415 bring these species perilously close to their CT_{max} and to put them far enough above T_{opt} to show
416 ecologically significant reductions in performance. Because acclimation or natural selection
417 occurring over the course of the next few decades may be important in shaping how these

418 urchins respond to environmental warming (Díaz et al. 2017), more long-term studies focused on
419 temperatures between the thermal optimum and the upper lethal limit could help us better predict
420 if and/or when these key ecosystem engineers are likely to be extirpated from the warmest parts
421 of their ranges.

422

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429

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735

736 **Table 1:** Study species, collection sites and range information

737

Species	Collection Sites	Habitat	Northern Limit*	Southern Limit
Echinometridae				
<i>Echinometra viridis</i>	BRS Signpost (9.351N, 82.259W) Cristobal Point (9.299N, 82.291W) Hospital Point (9.334N, 82.218W)	reef	Florida 29°N	Panama 9°N
<i>Echinometra lucunter</i>	Hospital Point	reef/rubble	North Carolina 35°N	Brazil 28°S §
Toxopneustidae				
<i>Lytechinus variegatus</i>	Cristobal Point Macca Point (9.256N, 82.156W)	seagrass	North Carolina 35°N	Brazil 27°S §
<i>Lytechinus williamsi</i>	BRS Signpost	reef	Florida 25° N	Panama 9°N
<i>Tripneustes ventricosus</i>	Hospital Point Macca Point	seagrass	Florida, ~25°N Bermuda 32°N	Brazil 27°S §
Clypeasteridae				
<i>Clypeaster subdepressus</i>	Cristobal Point	sand	North Carolina 35°N	Brazil 23°S §
<i>Clypeaster rosaceus</i>	STRI Point (9.347N, -82.262W)	sparse seagrass	South Carolina 33°N	Brazil 20°S
Cideroidea				
<i>Eucidaris tribuloides</i>	Hospital Point	reef/rubble	Cape Hatteras 34° N	Brazil 27°S §

738

739 * From compilations by Hendler 1995; Rodríguez-Barreras, R. (2014)

740 § From ecological surveys in Netto et al. 2005; Labbé-Bella et al. (2016); C. Cordeiro, pers. com. (2016)

741

742 **Table 2:** Thermal tolerance window for the 8 Caribbean sea urchin species studied.

743

Species	LTL ₅₀ (95% ci)*		UTL ₅₀ (95% ci)*	
	survival	righting	survival	righting
<i>Echinometra viridis</i>	6.7°C (5.7-7.6)	13.4°C (12.5-14.4)	37.0°C (36.7-37.2)	37.0°C (33.6-40.3)
<i>Echinometra lucunter</i>	7.6°C (6.7-8.6)	14.3°C (13.3-15.3)	37.5°C (37-38)#	36.0°C (34.1-37.8)
<i>Lytechinus variegatus</i>	6.1°C (5.1-7.1)	14.6 °C (13.6-15.6)	34.9°C (34.7-35.3)	34.5°C (34-36)#
<i>Lytechinus williamsi</i>	5.9°C (4.7-6.9)	14.3 °C (13.3-15.3)	35.0°C (33.6-36.3)	34.5°C (34-36)#
<i>Tripneustes ventricosus</i>	14.6°C (13.7-15.6)	19.1°C (18.1-20.2)	34.9°C (32.7-37.2)	34.0°C (30.5-37.4)
<i>Clypeaster subdepressus</i>	4.8°C (3.1-6.1)	NA	35.1°C (32.8-37.3)	NA
<i>Clypeaster rosaceus</i>	4.8°C (3.1-6.1)	NA	36.0 (35.3-36.8)	NA
<i>Eucidaris tribuloides</i>	4.8°C (3.1-6.1)	13.7 °C (12.7-14.6)	36.6°C (36-37)#	34.7°C (34-36)#

744

745

746 *LT₅₀ and 95% confidence intervals generated by the inverse prediction function from the logistic regression model for all of the
747 species (Table 3) generated by JMP.

748

749 # In cases where no temperature generated a mix of success and failure, the confident interval cannot be estimated and the Likelihood
750 models produce unrealistically wide estimates. The confident interval is therefore given as the range between the temperatures with
751 100% success and 100% failure.

752 **Table 3:** Logistic regression results for lower thermal limit (LTL) and upper thermal limit (UTL) of righting and survival.
 753 Bold highlights results with $p < 0.05$.

754

Factor	df	likelihood ratio chi-Square	p
LTL - righting			
Temperature	1	152.33	<0.0001
Species	5	69.99	<0.0001
N=243; generalized $r^2 = 0.66$			
LTL - survival			
Temperature	1	95.61	<0.0001
Species	7	154.83	<0.0001
N=306; generalized $r^2 = 0.66$			
UTL - righting			
Temperature	1	820.28	<0.0001
Species	5	121.46	<0.0001
N=351; generalized $r^2 = 0.97$			
UTL - survival			
Temperature	1	439.19	<0.0001
Species	7	178.15	<0.0001
N=459; generalized $r^2 = 0.93$			

755

756

757 **Table 4:** Thermal performance curves over temperatures from 18°C to 34°C for righting time for
 758 sea urchins that righted within an hour after a 2-hour exposure. The model preferred by the AICc
 759 is highlighted in bold for each species.
 760

Species	AICc	r ²	Optimum	N
<i>Echinometra viridis</i>				
Biexponential	2015.06	0.51	27.4*	186
Quadratic	2071.07	0.42	29.5	186
<i>Echinometra lucunter</i>				
Biexponential	1890.21	0.31	30.1	183
Quadratic	1887.24	0.32	29.4	183
<i>Lytechinus variegatus</i>				
Biexponential	1908.09	0.41	27.2	162
Quadratic	1915.10	0.37	27.4	162
<i>Lytechinus williamsi</i>				
Biexponential	1985.78	0.13	28.1	162
Quadratic	1989.34	0.10	25.4	162
<i>Tripneustes ventricosus</i>				
Biexponential	1253.58	0.47	NA*	129
Quadratic	1259.81	0.41	30.7	129
<i>Eucidaris tribuloides</i>				
Biexponential	1600.68	0.35	NA*	171
Quadratic	1615.04	0.27	28.6	171

761
 762 * Flat or virtually flat shape makes this a poor fit to the data.

763 NA = no inflection point present.

764
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 766

767 **Table 5:** One-way analysis of variance of the effect of temperature on log (righting time) for sea
 768 urchins that righted successfully during the test period.
 769

Species	DF	F-Ratio	p	Lower bound*%	Upper bound#%
<i>Echinometra viridis</i>					
Temperature	10	6.04	<0.0001	30°C > 24°C	30°C > 36°C
<i>Echinometra lucunter</i>					
Temperature	9	9.35	<0.0001	26-34°C > 22°C	26-34°C > 36°C
<i>Lytechinus variegatus</i>					
Temperature	8	11.04	<0.0001	24-32°C > 22°C	24-32°C > 34°C
<i>Lytechinus williamsi</i>					
Temperature	8	11.04	<0.0001	28°C > 26°C	28°C > 32°C
<i>Tripneustes ventricosus</i>					
Temperature	8	10.65	<0.0001	28-32°C > 26°C	28-32°C > 34°C
<i>Eucidaris tribuloides</i>					
Temperature	8	4.64	<0.0001	24-34°C > 20°C	24-34°C > 36°C

770
 771 * The lower limit of the optimal temperature range was evaluated by comparing down from the
 772 optimal temperature until a temperature at which the Tukey HSD post-hoc test showed a
 773 significant difference; all comparisons are shown in Figure 4.

774
 775 # The upper limit of the optimal temperature range was evaluated by comparing up from the
 776 optimal temperature until a temperature at which the Tukey HSD post-hoc test showed a
 777 significant difference; all comparisons are shown in Figure 4.

778
 779 % If the next temperature tested was one at which all urchins failed to right or at which so few
 780 failed to right that the confidence limits were unrealistically large, that temperature was
 781 considered to be significantly worse. The > indicates that performance is better (i.e., righting
 782 time is significantly faster).

783

784 **Table 6:** Calculation of Warming Tolerance (WT) and Thermal Safety Margin (TSM) for each
 785 species.

786

Species	Warming Tolerance (CT_{max} – T_{hab}) survival	Warming Tolerance (CT_{max} – T_{hab}) righting	TSM (T_{opt}-T_{hab}) biexponential	TSM (T_{opt}-T_{hab}) quadratic
<i>Echinometra viridis</i>	8°C	8°C	-1.6°C	0.5°C
<i>Echinometra lucunter</i>	7.5°C	7°C	1.1°C	0.4°C
<i>Lytechinus variegatus</i>	5.9°C	5.5°C	-1.8°C	-1.6°C
<i>Lytechinus williamsi</i>	6°C	5.5°C	-0.9°C	-3.6°C
<i>Eucidaris tribuloides</i>	7.6°C	5.7°C	NA	-0.4°C
<i>Tripneustes ventricosus</i>	5.9°C	5°C	NA	1.7°C
<i>Clypeaster rosaceus</i>	7°C	NA	NA	NA
<i>Clypeaster subdepressus</i>	6.1°C	NA	NA	NA

787

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790

791 **Figure Legends**

792

793 **Figure 1:** Average sea surface temperature map for the western Atlantic for February and
794 August. Image provided by Physical Sciences Division, Earth System Research Laboratory,
795 NOAA, Boulder, Colorado, from their Web site at <http://www.esrl.noaa.gov/psd/>. Arrows
796 indicate the areas where most of the ranges end points occur for the species in this study and
797 stars indicate where the ranges of the tropical specialists, *E. viridis* and *L. williamsi* end along the
798 continental coastlines (although the southernmost point in the ranges occurs in Panama).

799

800 **Figure 2:** CT_{max} of 8 species of sea urchins. Squares and diamonds show the percentage of the 9
801 urchins tested at each temperature that survived (white diamonds) or were able to right (black
802 squares).

803

804 **Figure 3:** CT_{max} of 8 species of sea urchins. Squares and diamonds show the percentage of the 9
805 urchins tested at each temperature that survived (white diamonds) or were able to right (blue
806 squares).

807

808 **Figure 4:** Performance curves for the righting of 6 species of sea urchins between 18°C and
809 34°C or 36°C. The blue line shows the biexponential curve fit through the data and the green line
810 shows the quadratic curve fit through the data. Letters below each cluster of points shows the
811 results of the Tukey HSD test, where temperatures not linked by the same letter differ
812 significantly. Between 12 and 18 individuals were tested at each temperature.

813