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ORIGINAL PAPER

Local conditions influence thermal sensitivity of pencil urchin populations (*Eucidaris galapagensis*) in the Galápagos Archipelago

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Abstract

The responses of ectothermic organisms to changes in temperature can be modified by acclimatization or adaptation to local thermal conditions. Thus, the effect of global warming and the deleterious effects of extreme heating events (e.g., heatwaves) on the metabolism and fitness of ectotherms can be population specific and reduced at warmer sites. We tested the hypothesis that when environmental temperature is greater, grazer populations in the Galápagos are less thermally sensitive (potentially due to acclimatization or adaptation). We quantified the acute thermal sensitivity of four populations of the pencil sea urchin, *Eucidaris galapagensis*, by measuring individual oxygen consumption across a range of temperatures. Thermal performance curves were estimated for each population and compared to local thermal conditions 2 months prior to collection. Results indicate that *E. galapagensis* populations were adapted and/or acclimatized to short-term local temperature as populations at warmer sites had substantially higher thermal tolerances. The acute thermal optimum (T_{opt}) for the warmest and coolest site populations differed by 3 °C and the T_{opt} was positively correlated with maximum temperature recorded at each site. Additionally, temperature-normalized respiration rate and activation energy (E) were negatively related to the maximum temperature. Understanding the temperature-dependent performance of the pencil urchin (the most significant mesograzer in this system), including its population specificity, provides insight into how herbivores and the functions they perform might be affected by further ocean heating.

Introduction

Scaling between mass-normalized organismal metabolism and temperature (Gillooly et al. 2001; Bruno et al. 2015) has been documented across a wide range of taxa and habitats (Eppley 1972; Houde 1989; Huey and Kingsolver 1989; Clarke and Johnston 1999; López-Urrutia et al. 2006). Through its control of metabolism, temperature indirectly affects the vital rates of organisms and populations as well as the structure of communities and functioning of ecosystems (Sanford 1999, 2002). One temperature-dependent function that underlies such cross-scale linkages is the strength of species interactions, particularly prey consumption rates. Numerous field and laboratory studies have demonstrated the temperature-dependence of *per capita* predation on invertebrate and algal prey (Stickle et al. 1985; Sanford 1999, 2002; O'Connor et al. 2009; Carr and Bruno 2013; Carr et al. 2018). In cases where prey species are habitat forming or are dominant community members, increased predation with warming can lead to wide-ranging changes in community state and functioning. However, adaptation and/or acclimatization to local temperature regimes could decouple temperature from ecological processes across thermal gradients in the sense that phenotypic responses to temperature would be dependent on the local or recent thermal history. This potential for thermal acclimatization is precisely why predictions based on metabolic theory need to be tested

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— although there is usually some effect of temperature on ectotherm performance, the effective magnitude of thermal response and its subsequent ecological relevance is often context- and taxon- dependent (Huey and Kingsolver 1989).

Ectotherms have the ability to alter their thermal tolerance through physiological mechanisms, and in this way, cope with the effects of temperature variation on their performance and fitness (Seebacher et al. 2015; Kern et al. 2015). By different mechanisms, adaptive or non-adaptive, populations can tolerate changes in their local environment: first, by dispersing to a more favorable environment; second, by genetically adapting to the local condition, and third, through acclimatization or phenotypic plasticity (Chevin et al. 2010; Hoffmann and Sgrò 2011). These mechanisms can reduce the extent to which heatwaves and other forms of thermal stress negatively affect fitness, population growth rates, and other aspects of organismal performance (Gunderson and Stillman 2015; Seebacher et al. 2015).

Mechanisms including physiological acclimatization, genetic adaptation, and parental effects have been documented in a wide range of marine invertebrates and fishes (Castillo and Helmuth 2005; Baker et al. 2008; Oliver and Palumbi 2011; Barshis et al. 2013; Palumbi et al. 2014; Putnam and Gates 2015). For example, studies of intertidal porcelain crabs from the genus *Petrolisthes* have shown a clear adaptive variation. Among this group, tropical species possess uniformly higher thermal limits than temperate species and high intertidal zone species present the highest acute lethal temperatures (Stillman 2002). Similar patterns of thermal tolerance are found in subtidal snails (genus *Chlorostoma*) (Tomanek and Somero 1999) and limpets from the genus *Lottia* (Dong and Somero 2009) and *Acmaea* (Wolcott 1973). Measurements of thermal tolerance can show adaptive differences, but only by raising animals through multiple generations to test for a genetically based temperature-adaptive difference among populations. Kuo and Sanford (2009) found, after rearing two generations of the intertidal channeled dogwhelk, *Nucella canaliculata*, that populations that originated from warmer "hot spot" regions were more heat tolerant than conspecifics from cooler sites, suggesting that differences in thermal limits have a genetic basis.

The sensitivity of ectotherms to temperature can be characterized as a Thermal Performance Curve (TPC) (Sinclair et al. 2016). TPCs are quantified experimentally as the shape of the relationship between vital rates such as respiration, growth, or survival, and environmental temperature. TPCs are typically unimodal (Fig. 1), and are characterized by parameters such as the critical thermal minimum (CT_{min}), and maximum (CT_{max}), and by T_{opt}, the optimum performance temperature (Huey and Stevenson 1979; Angilletta Jr and Angilletta 2009; Sinclair et al. 2016). A compensatory response to warming would generally be represented as a rightward shift in the TPC of an individual or population, which would change the CT_{min} and CT_{max} values and should reduce the differences between mean habitat temperature and the T_{opt}. Plasticity or evolution can also cause changes in TPC curves: the total area of the TPC curve can increase or decrease leading to better or worse performance across the same range of temperatures, or, the breadth of the curve can also vary, illustrating thermally specialized individuals (Sinclair et al. 2012). Additionally, TPCs of the most sensitive populations often exhibit steeper slopes pre and post-T_{opt} peak (i.e., high activation E or deactivation energy Eh for enzyme activity) when small changes in temperature around T_{opt} cause large changes in performance (Silbiger et al. 2019).

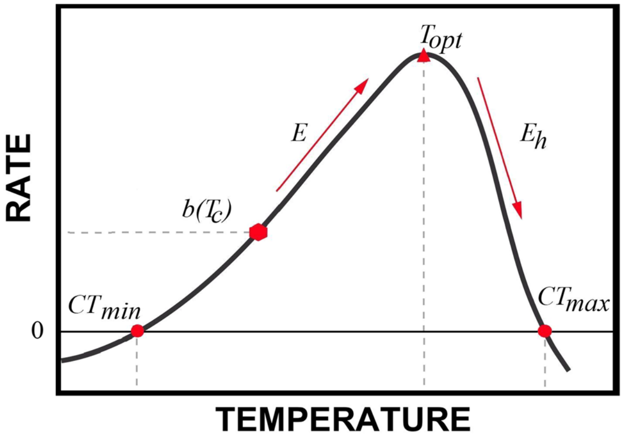

Fig. 1 A thermal performance curve (TPC) model with relevant thermal sensitivity metrics. T_{opt} temperature optimum, E and E_h activation and deactivation rates of energy, respectively, $b(T_c)$ rate at a standardized temperature, CT_{min} and CT_{max} minimal and maximal critical temperatures, respectively

The purpose of this study was to test the hypothesis that the thermal sensitivity of ectotherms varies directionally across a temperature gradient, such that populations from warmer sites have higher thermal optima than cooler sites. To do this we compared TPCs based on temperature-specific individual respiration rates of the conspicuous pencil urchin *Eucidaris galapagensis* at four sites ranging in thermal history in the Galápagos Archipelago.

Materials and methods

Environmental context and study sites

Oceanic conditions of the Galápagos Archipelago are highly variable across space and time due to a complex ocean current regime and the El Niño-Southern Oscillation cycle (ENSO) (Houvenaghel 1984; Ruttenberg 2001; Wellington et al. 2001). The convergence of a number of ocean currents (Panamá current, Perú current and Cromwell or Equatorial Undercurrent) results in variation (14–29 °C) of the sea surface temperature among islands and between seasons (Wellington et al. 2001). Both temperature and upwelling intensity vary across the archipelago: high-upwelling and nutrient-rich zones are usually located in the colder western section of the archipelago, and low-upwelling zones in the warmer, northern sites. Because of this environmental variance and oceanographic conditions, the Galápagos is divided into five distinct bioregions, where the assemblages of fish and macroinvertebrate species vary (Harris 1969; Wellington 1984; Jennings et al. 1994; Edgar et al. 2004). There is also a strong seasonality (resulting from the migration of the Intertropical Convergence Zone Houvenaghel 1978; Wellington et al. 2001)) with a warm and rainy season from December to May and a cooler, dry season from June to November. The maximum average sea surface temperature typically occurs in February/March and the minimum in September/October (Houvenaghel 1978; Schaeffer et al. 2008).

We performed the urchin physiology experiments in August 2018 at four different sites (Fig. 2a), accessed via the RV Queen Mabel. We recorded the temperature at each site by deploying one temperature logger (HOBO Water Temperature Pro v2 Data Logger- U22 001, Onset corporation, USA) during a previous research cruise in March 2018. Temperature was recorded at each site every 30 min at 7–12 m depth from March to August 2018. Punta Espinosa, located in the northeastern point of Fernandina Island in the western bioregion of the archipelago, is within a major upwelling zone (Houvenaghel 1978; Schaeffer et al. 2008). La Botella and Punta Cormorant are located in the western and central–northern sides of Floreana, respectively, a southern island in the central–southeastern bioregion (Fig. 2a). Bartolomé is located in the southeastern side of Santiago Island, in the central bioregion (Edgar et al. 2004). Punta Espinosa and La Botella are considered high-upwelling sites (Houvenagel 1978; Witman et al. 2010); while Bartolomé and Punta Cormorant are low-upwelling sites (Houvenagel 1978).

Study species

Sea urchins are important herbivores in many nearshore benthic marine habitats, often limiting algal biomass and thereby affecting community structure and function (Chapman and Johnson 1990; Andrew 1993; Steneck et al. 2002; Siddon and Witman 2003; Graham 2004; Irving and Witman 2009; Somero 2010). The pencil sea urchin (*E. galapagensis*) (Fig. 2b) is the most abundant echinoid species of the shallow waters of the Galápagos Archipelago (Lessios et al. 1999; Brandt and Guarderas 2002; Lawrence and Sonnenholzner 2004; Alvarado and Solís-Marín 2013). This species is one of the most significant mesograzers and bioeroders in the system (Brandt and Guarderas 2002; Irving and Witman 2009; Brandt et al. 2012; Feingold and Glynn 2014; Manzello et al. 2014; Glynn et al. 2017). Its densities across the Galápagos Archipelago average 3.2 ind m^{-2} (Brandt and Guarderas 2002), however, some sites have densities up to 28 ind m^{-2} (Lawrence and Sonnenholzner 2004; Alvarado and Solís-Marín 2013). At these high densities, *E. galapagensis* can convert macroalgal assemblages to urchin barrens or pavements of encrusting coralline algae (Ruttenberg 2001; Edgar et al. 2010) and reduce hermatypic coral cover (Glynn 1988). Notably, after the 1982–1983 El Niño event that devastated coral reefs around the Galápagos Archipelago (Glynn 1984, 1990; Feingold and Glynn 2014; Glynn et al. 2017), densities of *E. galapagensis* increased sixfold and led to some of the highest reported bioerosion rates in the world (Glynn 1988). Therefore, any changes in *E. galapagensis* behavior, grazing rates, physiology or abundance could have a significant impact on the ecosystem functioning of Galápagos rocky and coral reefs (Steneck et al. 2002; Siddon and Witman 2003; Graham 2004).

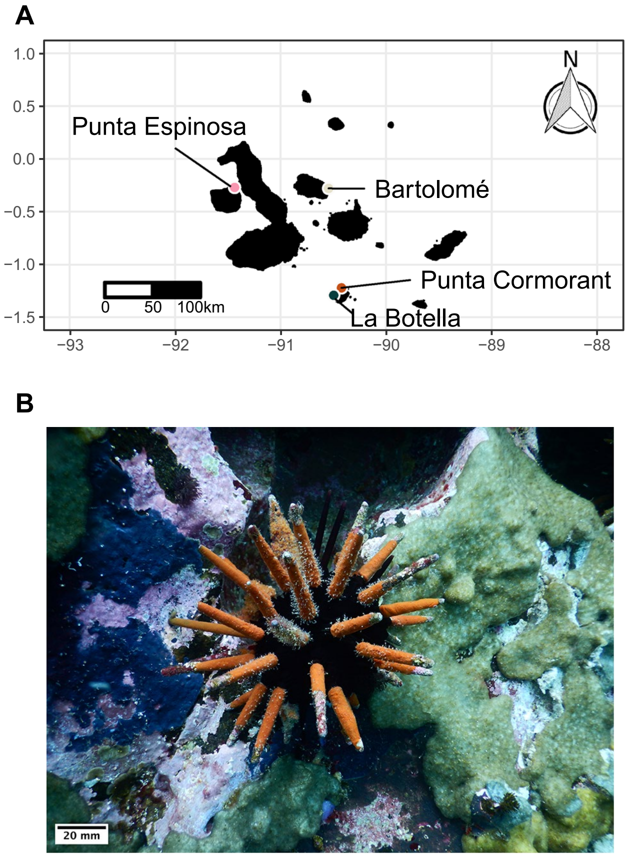

Fig. 2 **a** Map of the four study sites in the Galápagos Archipelago. Punta Espinosa and La Botella represent colder sites with high upwelling. Bartolomé and Punta Cormorant represent warmer sites with low upwelling. **b** Pencil sea urchin (*Eucidaris galapagensis*)

Using SCUBA at rocky reefs of depths of 7–12 m, eight individuals of *E. galapagensis* were hand-collected from each of the four sites during the August 2018 cruise. Selected sites displayed average urchin densities ranging from 2.5 to 5.0 ind m^{-2} (Brandt and Guarderas 2002). After collections, urchins were allowed to stabilize in a bucket on the ship with seawater and an aerator at ambient temperature for 30 min. Sea surface temperature was recorded for each collection site using a calibrated digital thermometer (Traceable High Accuracy ± 0.2 °C Digital Thermometer S/N 170718701).

Thermal response measurements

The thermal sensitivity of each urchin ($n = 8$ per site) was measured in a closed system of ten 620-ml acrylic respiration chambers with magnetic stir bars. In this respirometry setup, there were eight replicate chambers that contained sea urchins and two chambers with only seawater as controls (Fig. S1). Oxygen consumption and temperature were monitored in each individual chamber with a fiber-optic oxygen probe (Presens dipping probes [DP-PSt7-10-L2.5-ST10-YOP], Germany) and a temperature probe (Pt1000), respectively. Measurements were taken using a Presens Oxygen Meter System (OXY-10 SMA (G2) Regensburg, Germany) with temperature correction made for each probe independently. Oxygen concentration in the urchin and control chambers was measured every 1 s during trials, that lasted 6–10 min for a given temperature. Temperature was controlled [± 0.2 °C] using a thermostat system (Apex Aquacontroller, Neptune Systems), bucket heaters (King Work Bucket Heater 05-742G 1000 W), and a chiller (AquaEuroUSA Max Chill-1/13 HP). At each site, the initial (and lowest) temperature was the local ambient. After each trial, the temperature was increased by 1–3 °C, depending on the temperature. We decreased the range between treatment temperatures around the expected respiration peak (based on pilot data) because increased resolution improves curve fitting. We tested sequential temperatures to avoid artifacts in respiration reading due to excessive stress imposed on the organisms. We used the following temperatures (in °C) for urchins tested from each of the four sites: La Botella (20, 23, 26, 28, 30, 31, 32, 33, 34, 36, 38, 42), Punta Espinosa (19, 23, 26, 28, 30, 31, 32, 33, 34, 36, 38, 42), Punta Cormorant (22, 26, 28, 30, 31, 32, 33, 34, 36, 38, 42) and Bartolomé (23, 26, 28, 30, 31, 32, 33, 34, 36, 38, 41), with temperatures truncated past mortality as needed. It took 10 to 20 min to warm the water bath between treatment levels (temperature ramping rates did not differ between sites). Once stabilized at the new temperature treatment level, the water inside the chambers was replaced with new seawater to ensure that it matched the temperature of the water bath, and to reset O_2 and CO_2 levels. After all measurements had been made, urchins were frozen on the ship and brought to the Marine Ecology Laboratory of the Galápagos Science Center (GSC) on San Cristóbal Island. Respiration rates were normalized to urchin Ash-Free Dry Weight, which was determined by first drying each sample in a drying oven for 24 h at 60 °C and then burning it in a muffle furnace (Optic Ivymen System Laboratory Furnace 8.2/1100) for 4 h at 500 °C.

TPC characterization

TPCs were used to characterize the relationship between urchin organic-biomass-normalized respiration rates and temperature for every individual. A TPC approach is a widely used model in climate change research to predict if organisms will be able to cope with increasing environment temperatures (Schulte et al. 2011; Vasseur et al. 2014) and to compare performance metrics across organisms, populations, species, localities and time (Sinclair et al. 2016; Silbiger et al. 2019). Acute TPCs were modelled with a modified Sharpe–Schoolfield equation for high-temperature inactivation (Schoolfield et al. 1981; Padfield et al. 2017), using a non-linear least squares regression (Elzhov et al. 2013; Padfield et al. 2016) in the *nls.multsart* R package (Padfield and Matheson 2018):

$$\log\,(\text{rate}) = b\left(T_\text{c}\right) + E\left(\frac{1}{T_\text{c}} - \frac{1}{k \times T_\text{i}}\right) - \log\left(1 + e^{E_\text{h}^{\left(\frac{1}{k\times T_\text{h}} - \frac{1}{k\times T_i}\right)}}\right),$$

where $b(T_\text{c})$ is the log rate at a constant temperature (for respiration μmol g^{-1} h^{-1}), E is the activation energy (electron volts, eV) referring to enzyme activity, E_h is the deactivation energy (eV), T_c is the reference temperature at which no temperature inactivation is experienced (Kelvin, K; we used 299.15 K), k is Boltzmann constant (8.62×10^{-5} eV K^{-1}), T_h is the Temperature in Kelvin (K), where half the enzymes are inactivated, or the temperature after the optimum, where the rate is half of the maximal rate, and T_i is the Temperature in K.

In addition, to calculate the acute thermal optimum (T_opt) of each urchin population, the following equation was used:

$$T_{opt} = \left(\frac{E_h \times T_h}{E_h + \left(k \times T_h \times \log\left(\frac{E_h}{E} - 1\right)\right)}\right).$$

Statistical analysis

We used simple linear models to compare the relationship between thermal history and site-level means and variances ($n = 4$ sites) of three TPC metrics (T_opt, E, and $b(T_\text{c})$). We compared five thermal history metrics from the two months preceding collections using AICs (Akaike Information

Criterion), including maximum, mean, minimum, range, and upper 95th percentile temperature. The upper 95th percentile temperature always had the lowest AIC scores and, thus, was used as the independent variable in all models reported in the results. Normality of residuals was visually inspected using quantile–quantile plots. All data were analyzed using R, and data and code are publicly available at https://github.com/njsilbiger/GalapagosUrchins.

Results

Temperature regimes varied substantially among the four sites during the two months prior to the experiment (Table 1, Fig. 3). Specifically, the coolest site over the 2-month period, La Botella, had a mean and upper 95th percentile temperature of 20.6 and 22.3 °C, respectively, while the warmest site over the 2-month period, Bartolomé, had a mean and 95th percentile temperature of 22.4 and 24.0 °C. Measured respiration rates for all individuals and populations displayed typical unimodal responses to temperature (Fig. 4). The thermal performance curves varied substantially both within (i.e., among-population replicates) and among sites (Fig. 4). The mean acute thermal optimum (T_{opt}) ranged from 30.3 °C at the site with the coolest 95th percentile temperature (La Botella) to 33.3 °C at the site with the warmest 95th percentile temperature (Bartolomé) during the experimental period. For all populations there was a strong positive linear relationship between upper 95th percentile temperature and mean population T_{opt} ($P=0.016$, $F(2,2)=62.1$, $R^2=0.97$, Fig. 5), where the T_{opt} increased by 1.6 ± 0.2 °C for every degree increase in the 95th percentile temperature. The mean population rate at a constant temperature, $b(T_c)$, decreased by 0.2 ± 0.04 μmol g^{-1} h^{-1} for every degree increase in the 95th percentile temperature ($P=0.04$, $F(2,2)=22.4$, $R^2=0.92$). Although E also decreased with the

Table 1 Thermal characteristics of the four sites (°C) from which urchin population TPCs were measured for the 2 months preceding collections

Site	Lat, Long	Mean	Var	Min	Max	95th Max
La Botella	1.2914° S, 90.4965° W	20.6	2.1	16.1	22.7	22.3
Punta Cormorant	1.2206° S, 90.4226° W	21.8	1.6	16.2	23.9	23.4
Punta Espinosa	0.2703° S, 91.4358° W	20.6	3.4	15.9	24.9	23.5
Bartolomé	0.2797° S, 90.5448° W	22.4	1.0	18.1	24.9	24.0

95th Max = upper 95th percentile temperature (the metric used in the statistical analysis, testing for a correlation between thermal history and the mean and variance for three TPC parameters in Fig. 5)

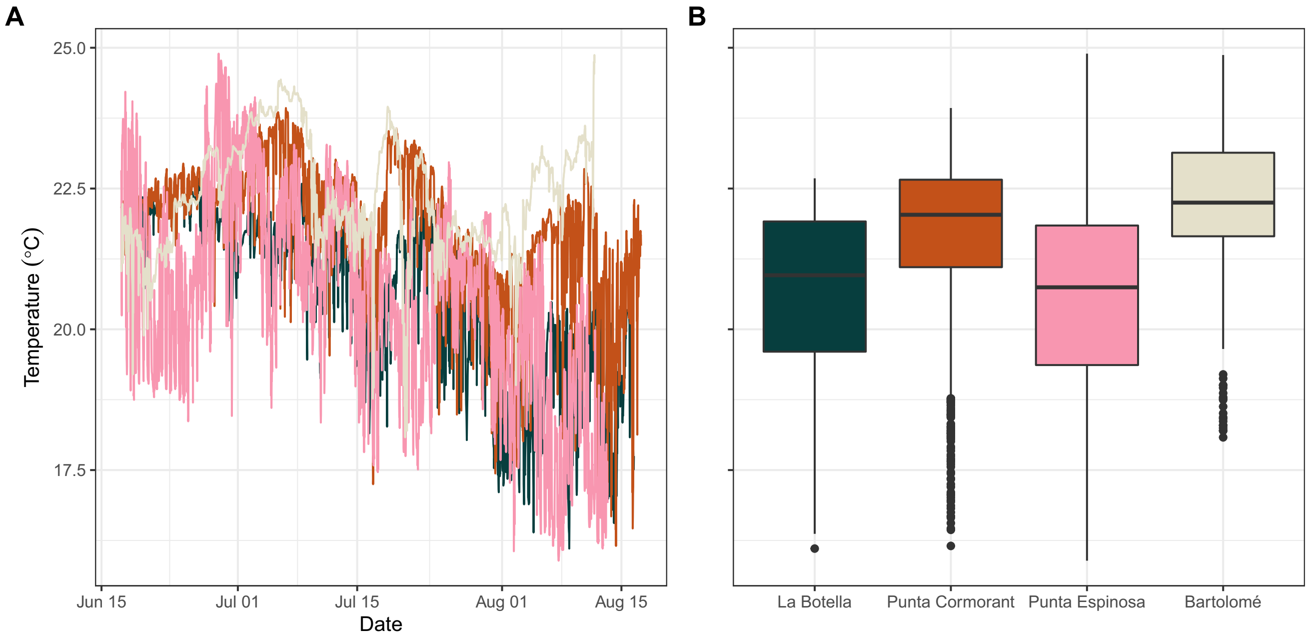

Fig. 3 In situ temperature at the collection sites for the two months preceding the experiment. Subset **a** shows the raw temperature data. Notice the rapid and extreme subtidal temperature fluctuations commonly observed in the Galápagos. Subset **b** are boxplots of the upper 95th percentile temperature from each site

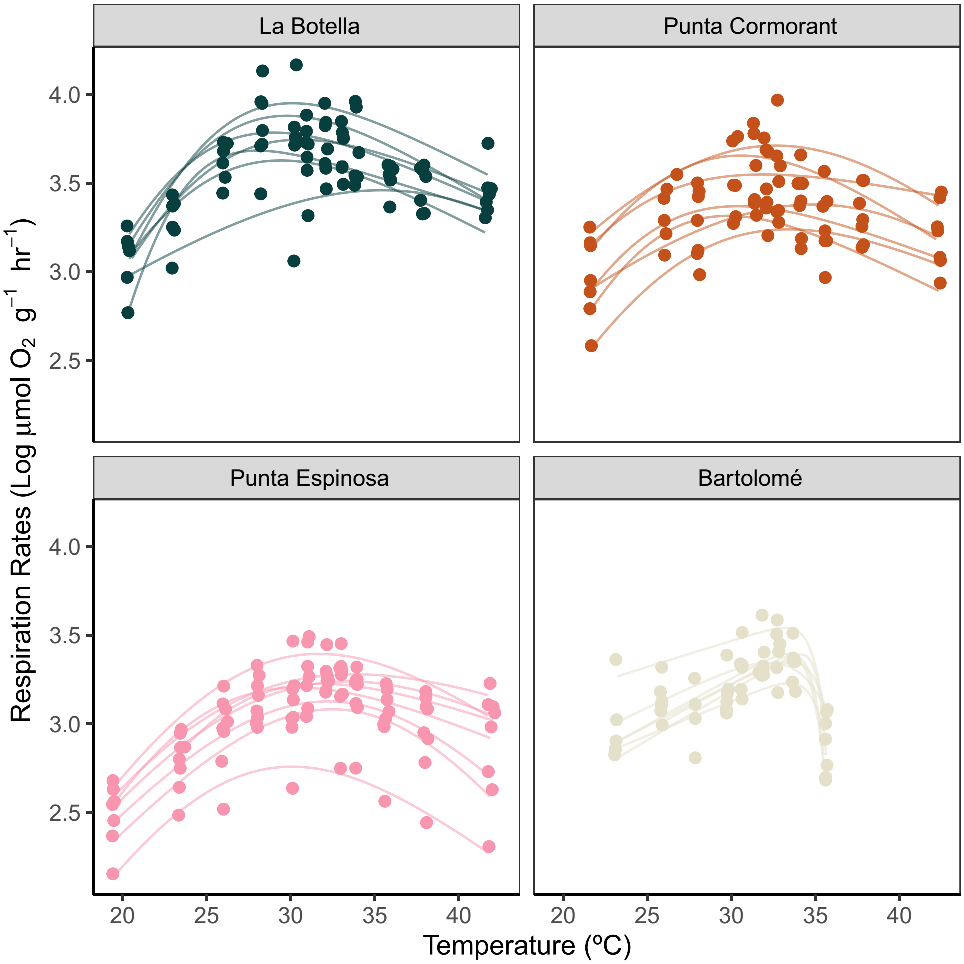

Fig. 4 Thermal performance curves of log $(x+1)$ respiration rates (µmol O_2 g^{-2} h^{-1}) from urchin populations at different locations. Top panel shows cooler sites and the bottom panel warmer sites (based on the 95th percentile temperatures measured at each site for two months prior to the experiment). Each dot represents a data point and the lines represent the estimated TPC for each individual of *E. galapagensis*. Each graph shows the changes in the respiration rates at different temperatures. Colored-line regions indicate the temperature range where respiration data was collected. Peaks in the graphs show the temperature at which oxygen consumption was the highest

95th percentile temperature, this effect was not statistically significant ($P = 0.07$, $F(2,2) = 13.0$, $R^2 = 0.80$). Finally, for all three parameters, variance was considerably greater at the sites with cooler maximum temperatures and decreased significantly with increased temperature (T_{opt}: $P = 0.04$, $F(2,2) = 26.1$, $R^2 = 0.93$; $b(T_c)$: $P = 0.03$, $F(2,2) = 34.6$, $R^2 = 0.95$; E: $P = 0.02$, $F(2,2) = 58.6$, $R^2 = 0.97$; Fig. 5).

Discussion

Our results indicate that local conditions could influence the thermal sensitivity of pencil urchin populations in the Galápagos Archipelago. Populations at warmer sites were more tolerant of high temperatures than cooler site populations. The T_{opt} for the population was 3 °C greater at the site with the highest short-term 95th percentile temperature than for the site with the lowest 95th percentile temperature. There were strong linear relationships between upper 95th percentile temperature and two TPC parameters [T_{opt} and $b(T_c)$, and a non-significant linear trend between temperature and E (Fig. 5)]. Moreover, the range of the observed T_{opt} values is similar to the range of upper 95th percentile temperatures among sites (2.2 °C). The population mean of temperature-normalized respiration and activation energy were negatively related to upper 95th percentile temperature, while the relationship with mean T_{opt} was positive. These results indicate both a shift to the right and a change in the shape of TPCs at warmer sites.

The urchins in our study were exposed to each temperature treatment for approximately 10 min with only a short time to acclimatize. Thus, we assessed physiological responses to acute thermal stress (in the absence of adaptation or acclimatization). Individual and population-level responses to longer term warming (including the sensitivity rankings) could be very different. However, rapid temperature changes are common in the near-surface marine environments of the Galápagos. Based on the widely perceived thermal gradients of the region, we expected the thermal ranking to be (from coolest to warmest): La Botella > Punta Espinosa > Punta Cormorant > Bartolomé. However, our 2-month measurements suggested a slightly different ranking than predicted: La Botella > Punta Cormorant > Punta Espinosa > Bartolomé. This was unsurprising as temperature

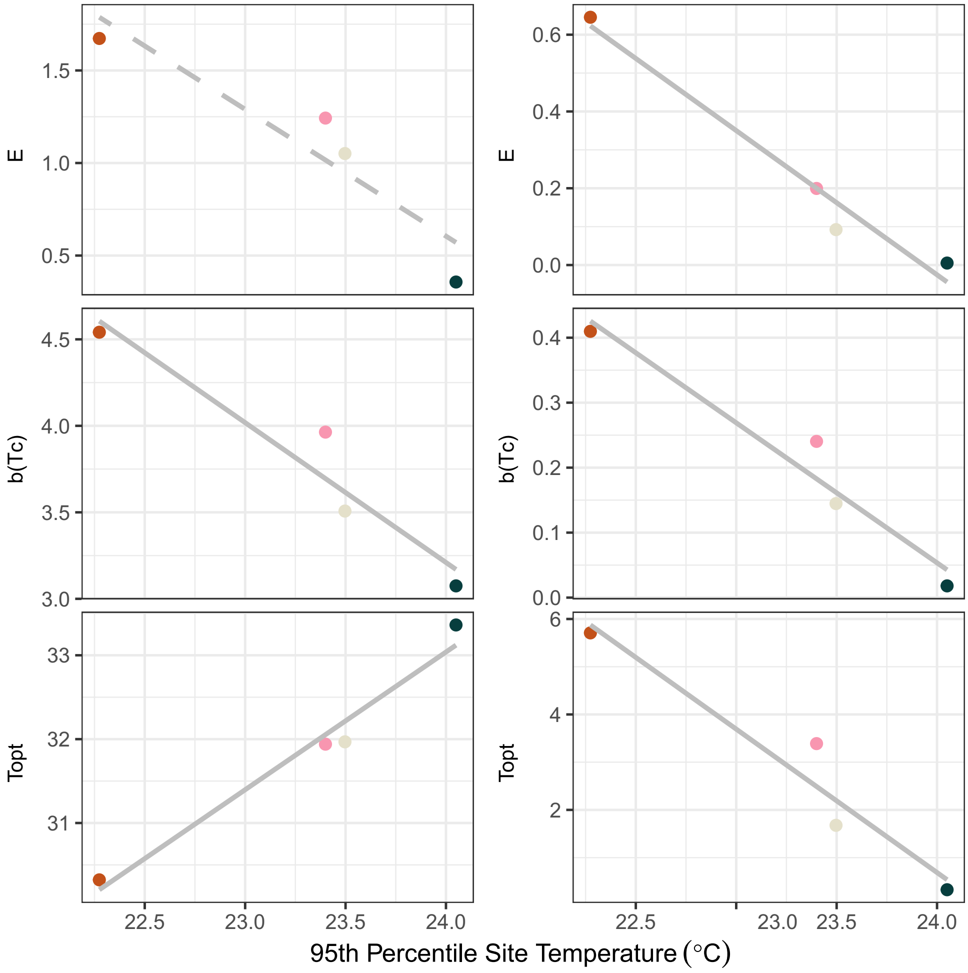

Fig. 5 Relationship between the upper 95th percentile site temperature and the mean (left panel) and variance (right panel) for three TPC parameters, estimated from values in Fig. 4, and measured with the physiology system (Fig. S1) at each of the four sites (Fig. 2a) across the thermal gradient. Each point is a population mean value. Solid lines represent statistically significant ($\alpha < 0.05$) linear regressions, dashed lines insignificant ($\alpha > 0.05$)

patterns in the archipelago are very dynamic and can greatly change within short periods, even if a classification according to the temperature gradients and seasonality of locations across the islands is generally known and established. Localized upwelling, tidal bores, and local currents can cause changes of several degrees Celsius in hours to days (Fig. 3, Witman et al. 2010). Thus, populations in this environment naturally experience harsh daily fluctuations in water temperatures with little or no time to acclimatize. Our AIC analysis indicated that the short-term thermal history (the 95th percentile used for analysis is based on 2 months prior to the experiment) was a better fit than the longer term temperature ranking (based on mean temperature). The results suggest that relatively short-term exposure to local temperature extremes can influence the thermal sensitivity of this species, even overriding adaptation to the longer term conditions.

A better understanding of population responses to warming of the temperature-dependence of other vital rates (such as reproduction, larvae mortality, dispersal and growth) is needed; these other rates could be influenced differently by temperature than respiration (Pinsky et al. 2019). For example, Sewell and Young (1999) found that thermal optima for fertilization and early development of the tropical sea urchin species *Echinometra lucunter* can occur at temperatures outside those seen in natural conditions in any part of the geographical range of the species. This indicates high thermal resilience of gametes and larvae in comparison with the thermal limits of adults. The distribution and abundance of the pencil urchin *E. galapagensis* could also be limited by thermal sensitivity of different rates, such as growth, spawning, larval settlement, and juvenile survival.

Based on our study design, we were not able to assess the relative contribution of genetic adaptation (via natural selection), acclimatization, epigenetic or other mechanisms in the observed among-population differences in thermal sensitivity (yet note, this was not the purpose of the study). We also cannot estimate how long it took for these population-specific traits to develop or how flexible they are. *E. galapagensis* have planktonic larvae and the regional occurrence (Lessios et al. 1999) of the species (including Cocos Island, Clipperton Island, and all the islands in the Galápagos) suggests the potential for long-distance dispersal and thus, at least some connectivity among populations.

Nothing is known about the population genetic structure of the study species, such as how much genetic connectivity there is among our study sites or at smaller or larger spatial scales across the Galápagos Archipelago. Clearly, information about these and other related attributes of this functionally important species would enable us to better predict its near-future response to the warming of the region via anthropogenic climate change. That said, the observed among-population variation in thermal sensitivity (i.e., a range of 3 °C for T_{opt}) does suggest the urchins may be resistant to higher temperatures, to a point. The ability to acclimatize to localized, natural variability is believed to predict the resilience of a species to anthropogenic heating (Somero 2010; Gunderson and Stillman 2015). And yet, the reduction in within-population variance for all three TPC characteristics at the warmest site suggests a reduction in genetic variance and adaptive potential. In fact, the observed rapid post-T_{opt} decline in performance (i.e., Bartolomé's TPC graph in Fig. 4) could mean that those populations are vulnerable to temperatures above these values, and therefore more sensitive to high temperatures post-T_{opt} (i.e., in the absence of further adaptation and/or acclimatization) (Schulte et al. 2011). Deutsch et al. (2008) emphasize that the expected warming in the tropics will likely have the most detrimental effects for the most warmth-adapted species living close to their upper thermal limits. The fate of the most heat-tolerant ectotherm species relies on the proximity of the acute lethal temperature of their performance and their maximal habitat temperature (Somero 2010).

Other indirect effects of heating could negatively affect this functionally important species. For example, reductions in its prey species (primarily *Ulva* spp.) due to warming, reduced upwelling and nutrient flux, or other physico–chemical changes. Echinoderm species are generally susceptible to disease outbreaks, including warming-induced epizootics (Staehli et al. 2009; Burge et al. 2014; Sweet et al. 2016; Harvell et al. 2019). Finally, ocean heating could increase pencil urchin metabolism (and metabolic demand) to the point where its prey base becomes so depleted that urchin populations become food limited and decline in density. Pencil urchin populations and many other species in this complex marine system are vulnerable to sea-level rise, shifts in ENSO amplitude and frequency, changes in mass transport of surface waters, acidification, and other aspects of climate change affecting the archipelago (Banks et al. 2011). Estimating TPCs for multiple species including representatives from other functional groups would provide a more complete assessment of the Galápagos marine ecosystem's sensitivity to anthropogenic heating.

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Author contributions JFB and MB designed the experiment. JFB provided the materials and funding. MB, JFB, and ISR collected the data. ISR processed the data. NJS statistically analyzed the data. ISR, JFB, NJS, and MB wrote the manuscript.

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Data availability All R data and code will be made publicly available at https://github.com/njsilbiger/GalapagosUrchins.

Compliance with ethical standards

Conflict of interest The authors have no conflict of interests.

Ethical approval All applicable national and institutional guidelines for sampling, care and experimental use of organisms for the study have been followed. We obtained all necessary approvals and performed all the fieldwork and data collection under the permit PC 25–18 granted by the Galápagos National Park Directorate.

References

Alvarado JJ, Solís-Marín FA (2013) Echinoderms of Ecuador. Echinoderm research and diversity in Latin America. Springer, Berlin, pp 191–202

Andrew N (1993) Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. Ecology 74:292–302

Angilletta MJ Jr, Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80:435–471

Banks S, Edgar G, Glynn P, Kuhn A, Moreno J, Ruiz D, Schuhbauer A, Tiernan JP, Tirado N, Vera M (2011) A review of Galápagos marine habitats and ecological processes under climate change scenarios. Clim Change Vulnerability Assess Galápagos Isl 47

Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR (2013) Genomic basis for coral resilience to climate change. Proc Natl Acad Sci 110:1387–1392

Brandt M, Guarderas P (2002) Erizos de mar. In: Reserva Marina de Galápagos. Línea Base de la Biodiversidad. Fundación Charles Darwin/Servicio Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador. Fundación Charles Darwin/Servicio Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador, pp 396–418

Brandt M, Witman JD, Chiriboga AI (2012) Influence of a dominant consumer species reverses at increased diversity. Ecology 93:868–878

Bruno JF, Carr LA, O'Connor MI (2015) Exploring the role of temperature in the ocean through metabolic scaling. Ecology 96:3126–3140. https://doi.org/10.1890/14-1954.1

Burge CA, Mark Eakin C, Friedman CS, Froelich B, Hershberger PK, Hofmann EE, Petes LE, Prager KC, Weil E, Willis BL (2014) Climate change influences on marine infectious diseases: implications for management and society. Annu Rev Mar Sci 6:249–277

Carr LA, Bruno JF (2013) Warming increases the top-down effects and metabolism of a subtidal herbivore. PeerJ 1:e109

Castillo K, Helmuth B (2005) Influence of thermal history on the response of *Montastraea annularis* to short-term temperature exposure. Mar Biol 148:261–270

Chapman A, Johnson C (1990) Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. Hydrobiologia 192:77–121

Chevin L-M, Lande R, Mace GM (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLOS Biol 8:e1000357. https://doi.org/10.1371/journal.pbio.1000357

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68:893–905

Carr LA, Gittman RK, Bruno JF (2018) Temperature influences herbivory and algal biomass in the Galápagos Islands. Front Mar Sci. https://doi.org/10.3389/fmars.2018.00279

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci 105:6668–6672. https://doi.org/10.1073/pnas.0709472105

Dong Y, Somero GN (2009) Temperature adaptation of cytosolic malate dehydrogenases of limpets (genus *Lottia*): differences in stability and function due to minor changes in sequence correlate with biogeographic and vertical distributions. J Exp Biol 212:169–177. https://doi.org/10.1242/jeb.024505

Edgar G, Banks S, Fariña J, Calvopiña M, Martínez C (2004) Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. J Biogeogr 31:1107–1124

Edgar GJ, Banks SA, Brandt M, Bustamante RH, Chiriboga A, Earle SA, Garske LE, Glynn PW, Grove JS, Henderson S (2010) El Niño, grazers and fisheries interact to greatly elevate extinction risk for Galapagos marine species. Glob Change Biol 16:2876–2890

Elzhov TV, Mullen KM, Spiess A-N, Bolker B (2013) minpack. lm: R interface to the Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds. R package version 1.1–8

Eppley RW (1972) Temperature and phytoplankton growth in the sea. In: Fishery Bulletin. U.S. Department of Commerce/National Oceanic and Atmospheric Administration/National Marine Fisheries Services, Seattle, pp 1063–1085

Feingold JS, Glynn PW (2014) Coral research in the Galápagos Islands, Ecuador. The Galapagos marine reserve: a dynamic social–ecological system. Springer, New York, pp 3–22

Glynn PW (1984) Widespread coral mortality and the 1982–83 El Niño warming event. Environ Conserv 11:133–146

Glynn PW (1988) El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. Galaxea 7:129–160

Glynn PW (1990) Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. In: Global Ecological Consequences of the 1982–1983 El Nino—Southern Oscillation. Elsevier Oceanography Series, pp 55–126

Glynn PJ, Glynn PW, Riegl B (2017) El Niño, echinoid bioerosion and recovery potential of an isolated Galápagos coral reef: a modeling perspective. Mar Biol 164:146

Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems 7:341–357

Gunderson AR, Stillman JH (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. Proc R Soc B Biol Sci 282:20150401

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. Science 293:2248–2251. https://doi.org/10.1126/science.1061967

Harris M (1969) Breeding seasons of sea-birds in the Galapagos Islands. J Zool 159:145–165

Houde ED (1989) Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish Bull 87:471–495

Harvell C, Montecino-Latorre D, Caldwell J, Burt J, Bosley K, Keller A, Heron S, Salomon A, Lee L, Pontier O (2019) Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). Sci Adv 5:eaau7042

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. Nature 470:479–485. https://doi.org/10.1038/nature09670

Houvenaghel G (1978) Oceanographic conditions in the Galapagos Archipelago and their relationships with life on the Islands. Upwelling ecosystems. Springer Berlin, Heidelberg, New York, pp 181–200

Houvenaghel G (1984) Oceanographic setting of the Galapagos Islands. Key environments: Galapagos. Pergamon Press, Oxford, pp 43–54

Huey RB, Kingsolver JG (1989) Evolution of thermal sensitivity of ectotherm performance. Trends Ecol Evol 4:131–135

Huey RB, Stevenson R (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Integr Comp Biol 19:357–366. https://doi.org/10.1093/icb/19.1.357

Irving AD, Witman JD (2009) Positive effects of damselfish override negative effects of urchins to prevent an algal habitat switch. J Ecol 97:337–347

Jennings S, Brierley A, Walker J (1994) The inshore fish assemblages of the Galápagos Archipelago. Biol Conserv 70:49–57

Kern P, Cramp RL, Franklin CE (2015) Physiological responses of ectotherms to daily temperature variation. J Exp Biol 218:3068–3076. https://doi.org/10.1242/jeb.123166

Kuo ESL, Sanford E (2009) Geographic variation in the upper thermal limits of an intertidal snail: implications for climate envelope models. Mar Ecol Prog Ser 388:137–146. https://doi.org/10.3354/meps08102

Lawrence J, Sonnenholzner J (2004) Distribution and abundance of asteroids, echinoids, and holothuroids in Galápagos. Echinoderms: München. A.A. Balkema Publishers, New York, pp 239–244

Lessios HA, Kessing BD, Robertson DR, Paulay G (1999) Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. Evolution 53:806–817

López-Urrutia Á, San Martin E, Harris RP, Irigoien X (2006) Scaling the metabolic balance of the oceans. Proc Natl Acad Sci 103:8739–8744. https://doi.org/10.1073/pnas.0601137103

Manzello DP, Enochs IC, Bruckner A, Renaud PG, Kolodziej G, Budd DA, Carlton R, Glynn PW (2014) Galápagos coral reef persistence after ENSO warming across an acidification gradient. Geophys Res Lett 41:9001–9008

Oliver T, Palumbi S (2011) Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30:429–440

O'Connor MI, Piehler MF, Leech DM, Anton A, Bruno JF (2009) Warming and resource availability shift food web structure and metabolism. PLoS Biol 7:e1000178. https://doi.org/10.1371/journal.pbio.1000178

Padfield D, Matheson G (2018) nls. multstart: robust non-linear regression using AIC scores.

Padfield D, Yvon-Durocher G, Buckling A, Jennings S, Yvon-Durocher G (2016) Rapid evolution of metabolic traits explains thermal adaptation in phytoplankton. Ecol Lett 19:133–142

Padfield D, Lowe C, Buckling A, Ffrench-Constant R, Student Research Team, Jennings S, Shelley F, Ólafsson JS, Yvon-Durocher G (2017) Metabolic compensation constrains the temperature dependence of gross primary production. Ecol Lett 20:1250–1260

Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future climate change. Science 344:895–898

Pinsky ML, Eikeset AM, McCauley DJ, Payne JL, Sunday JM (2019) Greater vulnerability to warming of marine versus terrestrial ectotherms. Nature 569:108

Putnam HM, Gates RD (2015) Preconditioning in the reef-building coral *Pocillopora damicornis* and the potential for trans-generational acclimatization in coral larvae under future climate change conditions. J Exp Biol 218:2365–2372

Ruttenberg BI (2001) Effects of artisanal fishing on marine communities in the Galapagos Islands. Conserv Biol 15:1691–1699

Sanford E (1999) Regulation of keystone predation by small changes in ocean temperature. Science 283:2095–2097

Sanford E (2002) The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. J Exp Mar Biol Ecol 273:199–218

Schaeffer BA, Morrison JM, Kamykowski D, Feldman GC, Xie L, Liu Y, Sweet W, McCulloch A, Banks S (2008) Phytoplankton biomass distribution and identification of productive habitats within the Galapagos Marine Reserve by MODIS, a surface acquisition system, and in-situ measurements. Remote Sens Environ 112:3044–3054

Schoolfield R, Sharpe PJ, Magnuson C (1981) Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. J Theor Biol 88:719–731

Schulte PM, Healy TM, Fangue NA (2011) Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integr Comp Biol 51:691–702

Seebacher F, White CR, Franklin CE (2015) Physiological plasticity increases resilience of ectothermic animals to climate change. Nat Clim Change 5:61

Sewell MA, Young CM (1999) Temperature limits to fertilization and early development in the tropical sea urchin *Echinometra lucunter*. J Exp Mar Biol Ecol 236:291–305

Siddon CE, Witman JD (2003) Influence of chronic, low-level hydrodynamic forces on subtidal community structure. Mar Ecol Prog Ser 261:99–110

Silbiger NJ, Goodbody-Gringley G, Bruno JF, Putnam HM (2019) Comparative thermal performance of the reef-building coral *Orbicella franksi* at its latitudinal range limits. Mar Biol 166:126

Sinclair B, Williams C, Terblanche J (2012) Variation in thermal performance among insect populations. Physiol Biochem Zool 85:594–606. https://doi.org/10.1086/665388

Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS, Slotsbo S, Dong Y, Harley CD, Marshall DJ, Helmuth BS (2016) Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecol Lett 19:1372–1385

Somero G (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers.' J Exp Biol 213:912–920

Staehli A, Schaerer R, Hoelzle K, Ribi G (2009) Temperature induced disease in the starfish *Astropecten jonstoni*. Mar Biodivers Rec 2:e78. https://doi.org/10.1017/S1755267209000633

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436–459

Stillman JH (2002) Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, genus *Petrolisthes*. Integr Comp Biol 42:790–796. https://doi.org/10.1093/icb/42.4.790

Stickle W, Moore M, Bayne B (1985) Effects of temperature, salinity and aerial exposure on predation and lysosomal stability of the dogwhelk *Thais* (*Nucella*) *lapillus* (L.). J Exp Mar Biol Ecol 93:235–258. https://doi.org/10.1016/0022-0981(85)90242-4

Sweet M, Bulling M, Williamson JE (2016) New disease outbreak affects two dominant sea urchin species associated with Australian temperate reefs. Mar Ecol Prog Ser 551:171–183

Tomanek L, Somero GN (1999) Evolutionary and acclimation-induced variation in the heat-shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats: implications for limits of thermotolerance and biogeography. J Exp Biol 202:2925–2936

Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CD, McCann KS, Savage V, Tunney TD, O'Connor MI (2014) Increased temperature variation poses a greater risk to species than climate warming. Proc R Soc B Biol Sci 281:20132612

Wellington GM (1984) Marine environment and protection. Key environments: Galapagos. Pergamon Press, Oxford, pp 247–264

Wellington GM, Strong AE, Merlen G (2001) Sea surface temperature variation in the Galapagos Archipelago: a comparison between AVHRR nighttime satellite data and in situ instrumentation (1982–1998). Bulletin of marine science. University of Miami—Rosenstiel School of Marine and Atmospheric Science, Miami, pp 27–42

Witman JD, Brandt M, Smith F (2010) Coupling between subtidal prey and consumers along a mesoscale upwelling gradient in the Galapagos Islands. Ecol Monogr 80:153–177

Wolcott TG (1973) Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at" limiting factors". Biol Bull 145:389–422