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Local conditions drive thermal sensitivity of pencil urchin populations (*Eucidaris galapagensis*) in the Galápagos archipelago
Proyecto de investigación

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**HOJA DE CALIFICACIÓN
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RESUMEN

El archipiélago de Galápagos está influenciado por un sistema complejo de corrientes oceánicas y se encuentra en el centro de acción de los eventos ENSO. La convergencia de corrientes resulta en fluctuaciones de la temperatura superficial del mar, creando una variación térmica espaciotemporal con diferentes regímenes de afloramiento. Las respuestas de organismos ectotérmicos a cambios de temperatura pueden ser modificadas tanto a nivel de individuos como de poblaciones a través de mecanismos de aclimatación o adaptación. Por lo tanto, Galápagos es un sistema ideal para llevar a cabo estudios de aclimatación por su gradiente térmico y porque muchos de los organismos están presentes en el archipiélago durante todo el año. El propósito de este estudio fue entender la sensibilidad térmica de diferentes poblaciones del erizo lapicero (*Eucidaris galapagensis*), a través de la cuantificación de su consumo de oxígeno en un rango determinado de temperaturas. Se realizaron experimentos en cámaras de respirometría con ocho individuos de seis diferentes localidades submareales sujetas a regímenes de afloramientos variables: tres con alto (Cabo Douglas, Punta Espinosa, La Botella) y tres con bajo (Punta Cormorant, Bartolomé, Cabo Ibbetson). Se generaron curvas de rendimiento térmico para caracterizar la sensibilidad térmica de cada población y se compararon las temperaturas óptimas de rendimiento entre localidades. Los resultados concuerdan con la hipótesis de que las poblaciones de especies ectotérmicas están adaptadas y/o aclimatadas a condiciones térmicas locales. Las tasas de respiración calculadas sugieren que las poblaciones de *E. galapagensis* de sitios más cálidos (bajo afloramiento) poseen umbrales térmicos más elevados. Existió un efecto significativo de localidad en la temperatura optima entre Cabo Douglas (sitio más frío) y Bartolomé (sitio más caliente), y entre Cabo Douglas y Punta Cormorant, el segundo sitio más caliente. Las temperaturas óptimas de los erizos colectados en la localidad más caliente y más fría difirieron en aproximadamente 4°C. Este tipo de estudios son una herramienta ideal para modelar las dinámicas poblacionales de distintas comunidades a medida que la temperatura de los océanos aumenta.

Palabras clave: Curva de Rendimiento Térmico, cambio climático, Galápagos, Erizo Lapicero, respiración, afloramiento, sensibilidad térmica.

ABSTRACT

Oceanic conditions of the Galápagos archipelago are highly variable due to its complex ocean current regime and because it sits at the center of action for the ENSO events. The convergence of currents results in fluctuations of the sea surface temperature, creating a spatiotemporal variation of temperature and different upwelling intensities across the Archipelago. The responses of ectothermic organisms to changes in temperature can be modified scaling from individuals to population levels, trough mechanisms of acclimatization or adaptation. Galápagos system is ideal to conduct acclimatization studies, due to its thermal gradient and because most of the organisms are present at all sites throughout the year. The purpose of this study was to quantify the acute thermal sensitivity of different populations of the pencil sea urchin, *Eucidaris galapagensis*, by monitoring individual oxygen consumption in a determined range of temperatures. Respirometry experiments were conducted in acrylic respiration chambers using eight individuals from six different locations with different upwelling regimes: three with high (Cabo Douglas, Punta Espinosa, La Botella) and three with low (Punta Cormorant, Bartolomé, Cabo Ibbetson). Thermal Performance Curves were characterized for each population and the thermal optima of performance was compared among locations. Results agree with the hypothesis that ectothermic species are adapted and/or acclimatized to local thermal conditions. The obtained respiration rates suggest that *E. galapagensis* populations at warmer sites (low upwelling) have higher thermal thresholds. There was a significant effect of site on the thermal optimum between Cabo Douglas (coldest site) and Bartolomé (warmest site), and between Cabo Douglas and Punta Cormorant, the second warmest site. Thermal optimums of urchins collected at the warmest and the coldest sites differed in approximately 4°C. This type of studies is an ideal tool to model the population dynamics of different communities as the temperature of the oceans increases.

Key words: Thermal Performance Curve, climate change, Galápagos, Pencil sea urchin, respiration, upwelling, thermal sensitivity.

TABLA DE CONTENIDO

Title: Local conditions drive thermal sensitivity of pencil urchin populations (*Eucidaris galapagensis*) in the Galápagos archipelago

Running title: Thermal sensitivity of *E. galapagensis* in Galápagos

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Summary statement: A thermal performance curve approach was applied to determine the thermal sensitivity of pencil urchin populations across a temperature gradient to have an insight of future population dynamics of this species as the ocean warms.

Abstract

Oceanic conditions of the Galápagos archipelago are highly variable due to its complex ocean current regime and because it sits at the center of action for the ENSO events. The convergence of currents results in fluctuations of the sea surface temperature, creating a spatiotemporal variation of temperature and different upwelling intensities across the Archipelago. The responses of ectothermic organisms to changes in temperature can be modified scaling from individuals to population levels, trough mechanisms of acclimatization or adaptation. Galápagos system is ideal to conduct acclimatization studies, due to its thermal gradient and because most of the organisms are present at all sites throughout the year. The purpose of this study was to quantify the acute thermal sensitivity of different populations of the pencil sea urchin, Eucidaris galapagensis, by monitoring individual oxygen consumption in a determined range of temperatures. Respirometry experiments were conducted in acrylic respiration chambers using eight individuals from six different locations with different upwelling regimes: three with high (Cabo Douglas, Punta Espinosa, La Botella) and three with low (Punta Cormorant, Bartolomé, Cabo Ibbetson). Thermal Performance Curves were characterized for each population and the thermal optima of performance was compared among locations. Results agree with the hypothesis that ectothermic species are adapted and/or acclimatized to local thermal conditions. The obtained respiration rates suggest that E. galapagensis populations at warmer sites (low upwelling) have higher thermal thresholds. There was a significant effect of site on the thermal optimum between Cabo Douglas (coldest site) and Bartolomé (warmest site), and between Cabo Douglas and Punta Cormorant, the second warmest site. Thermal optimums of urchins collected at the warmest and the coldest sites differed in approximately 4°C. This type of studies is an ideal tool to model the population dynamics of different communities as the temperature of the oceans increases.

Introduction

Anthropogenic climate change is increasingly affecting the natural world, intensifying mean environmental temperatures and extreme thermal events (Hansen, Sato and Ruedy, 2012; Diffenbaugh and Field, 2013; Gunderson and Stillman, 2015; Silbiger et al., 2019). To understand how climate change will affect the populations of species is still one of the greatest challenges for ecology (Seebacher, White and Franklin, 2014). Global warming is of substantial concern, because it can decrease genetic diversity, alter ecosystem services and functioning, and cause cascading effects on multiple species (Pinsky et al., 2019). Even though both terrestrial and marine species populations are responding to warming (Pinsky et al., 2019), there is a lack of knowledge of variation in tolerance to temperature of species of different

ecosystems (Gunderson and Stillman, 2015). Aquatic organisms are less able to behaviorally buffer themselves against changing thermal conditions, because aquatic habitats tend to have more spatially constant thermal conditions at an operational scale (Gunderson and Stillman, 2015). In addition, factors such as thermal limits related to geographical range boundaries and oxygen availability suggest that tropical marine species may be the most sensitive group to increasing temperatures (Pinsky et al., 2019).

The Metabolic Theory of Ecology (MTE) states that different biological processes are governed by the rates of the organismal metabolism, which at the same time, are related to the organism mass and temperature. More specifically, metabolism is governed by metabolic enzymes, whose levels of activity increase as a function of temperature (Gillooly et al., 2001, 2002; Brown et al., 2004; Molnár et al., 2017). Many ectothermic species possess the ability to remodel their physiology, adjusting their thermal tolerance in response to changes in their local environment (Gunderson and Stillman, 2015). These abilities reduce the extent to which physiological rates change responding to temperature fluctuations, such as chronic, extemporaneous or recurring changes (Seebacher et al., 2014). Specific mechanisms of ectotherms to resist changes in temperatures and acquire thermal compensation include physiological plasticity, acclimatization (i.e. reversible changes in response to multiple environmental variables under field conditions), thermal acclimation (i.e. in response to a single environmental variable) and/or adaptation (Guderley, 1990; Seebacher et al., 2014; Gunderson and Stillman, 2015). In evolutionary scales, thermal windows shift through adaptation at genomic levels (Pörtner et al., 2009). The whole thermal niche beyond limits of acclimatization capacity would further shift after evolutionary adaptations occur over generations of the population (Pörtner, 2010). These mechanisms involve adjustments through gene expression at the level of energy metabolism capacity (Pörtner, 2010) and can compensate, until a certain point, for the negative consequences of rising habitat temperatures (Gunderson and Stillman, 2015).

Under a climate change context, the importance of studies on organisms' thermal sensitivity arises. Urchins belong to the guild of benthic marine invertebrates that provide crucial services to reef systems, contributing to nutrient cycling, water quality regulation, and most importantly, herbivory (Przeslawski et al., 2008). As key herbivores, they are considered voracious consumers of algae, causing sizeable effects in marine habitats, creating extensive barrens of encrusting coralline algae (Chapman and Johnson, 1990; Andrew, 1993; Irving and Witman, 2009). High densities of urchins are associated with large declines in primary productivity and biodiversity. The absence of factors capable of controlling urchin abundance and/or foraging behavior (e.g. abundance of urchin predators, natural disturbances) lead to

scenarios were urchins initiate barrens and maintain low- productivity ecosystems (Steneck et al., 2002; Siddon and Witman, 2003; Graham, 2004). With the highest average densities reported among urchin species in Galápagos, *Eucidaris galapagensis* represents one of the most significant invertebrate meso-grazer in the system (Brandt and Guarderas, 2002; Irving and Witman, 2009). The purpose of this study was to quantify the thermal sensitivity of different populations of the pencil sea urchin, *Eucidaris galapagensis*, by determining individual oxygen consumption in a range of temperatures in locations with different upwelling regimes across the Galápagos archipelago. A Thermal Performance Curve (TPC) can be used to empirically characterize the thermal sensitivity of ectotherms, such as sea urchins. This model quantifies the relationship of a rate of a biological performance (vital and physiological rates such as growth, reproduction and respiration) with a changing temperature (Silbiger et al., 2019), TPCs are typically unimodal, with parameters such as critical maximum (CT_{max}), critical minimum (CT_{min}) and thermal optimum (T_{opt}) that explain the organism's thermal niche (Angilletta, 2009; Molnár et al., 2017; Silbiger et al., 2019). We hypothesized that pencil urchin populations are adapted and/or acclimatized to local thermal conditions: higher thermal optimums will be found in populations of warmer locations, while in colder sties, this metric will be lower. To test this hypothesis, TPCs were generated for each urchin population and then compared among locations.

Materials and Methods

Study site

Oceanic conditions of the Galápagos archipelago are highly variable due to its complex ocean current regimes and because it sits at the center of action for the ENSO events (Houvenaghel, 1984; Ruttenberg, 2001; Wellington, Strong and Merlen, 2001). The convergence of a number of ocean currents (Panama current, Peru 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).

Upwelling intensity varies 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, eastern and northern sites. Because of this, five different bioregions can be identified in the Archipelago, where the assemblages of fish and macroinvertebrate species vary according to the oceanographic conditions (Harris, 1969; Wellington, 1984; Jennings et al., 1994; Edgar et al., 2010). In addition, a strong and marked seasonality exists as a result of the migration of the Intertropical Convergence Zone (Houvenaghel, 1978; Wellington *et al.*, 2001), creating a warm and rainy season from December to May and a cold and dry season

from June to November. As a result, the maximum average sea surface temperature occurs in February/March and the minimum in September/October (Houvenaghel, 1978; Schaeffer et al., 2008).

Study species

The pencil sea urchin (*Eucidaris galapagensis*) is widely distributed in the shallow waters of the Galápagos archipelago (Brandt and Guarderas, 2002; Sonnenholzner et al., 2013). Reaching extremely high densities, *E. galapagensis* is considered the most conspicuous and abundant echinoid species of the islands (Brandt and Guarderas, 2002; Lawrence and Sonnenholzner, 2004), representing one of the most significant meso-grazers in the system (Brandt and Guarderas, 2002; Irving and Witman, 2009; Brandt et al., 2012). Brandt and Guarderas (2002) reported average densities of 3.2 ind·m^{-2} across the Archipelago, however in some sites they can reach up to 28 ind·m^{-2} (Irving and Witman, 2009). At high densities, this urchin species can convert macroalgal assemblages to urchin barrens or pavements of encrusting coralline algae (Ruttenberg, 2001; Edgar et al, 2010).

E. galapagensis is known as an omnivore and bioeroder with a diverse diet. It feeds on encrusting algae (Wellington, 1975; Hickman, 1998), hermatypic corals (*Pocillopora* and *Pavona*) and barnacle plates (Glynn et al., 1979). V. Francisco found in *E. galapagensis* stomachs fragments of other sea urchin species, including the white sea urchin *Tripneustes depressus* and the green sea urchin *Lytechinus semituberculatus*, as well as fragments of cirripedes (taken from Brandt, 2003). After the 1982-1983 El Niño event that devastated coral reefs around the Galápagos archipelago, Glynn (1988) found that the densities of *E. galapagensis* increased six times, from 5 to 30 ind·m^{-2}, evidencing intense and opportunistic predation on both live and dead hermatypic coral polyps.

Data collection and thermal response measurements

Physiology data was collected daily on August 11-17th 2018, during a research cruise around the Galápagos archipelago. Six sites with different upwelling regimes were sampled (Figure 1). By hand and using scuba, eight individuals of *E. galapagensis* per site were collected at depths of 10-15 m in natural subtidal rocky reefs. Urchins were placed in a diving mesh bag during short shallow dives (30-40 min). Once in the boat and before experimentation, individuals were allowed to recover while submerged in a bucket with seawater and air pumps. Sea surface temperature and salinity were recorded for each collection site using a digital thermometer and a refractometer.

Individual-specific thermal sensitivity was measured in a closed system of ten 620 ml acrylic respiration chambers with magnetic stir bars (Figure 2). Each specimen was individually placed in a chamber. The two other chambers remained empty and served as controls. Each chamber maintained independent-controllable temperatures. For each individual, oxygen consumption was monitored with a fiber-optic oxygen probe (Presens dipping probes). In addition, ambient temperature inside each chamber was measured with an individual temperature probe (Pt1000). Oxygen consumption by the urchins and in the control chambers was measured every 1 s during 10 min trials, while urchins were exposed to different temperatures. In order to control for the temperature, the respirometry setup included a thermostat system (Apex Aquacontroller, Neptune Systems), bucket heaters and a chiller. The temperature at which each trial started matched the ambient temperature of the site where the specimens were collected. Eleven temperatures were used for the populations of low upwelling sites and 12 for high upwelling sites, ranging from 22-42°C and 19-42°C, respectively. The highest temperature tested led to the deceased of the specimens at each site. After finishing all trials, the volume of each urchin was recorded by placing each urchin in a 1000 mL beaker and reading the volume of water that it displaced. Finally, each urchin was preserved individually in a labeled ziploc bag and then placed in a freezer. Frozen urchin samples were brought back to the Marine Ecology Laboratory of the Galápagos Science Center (GSC) at San Cristóbal Island. In order to estimate their Ash-Free Dry Weight (AFDW) based on organic carbon contents. Samples were placed in a drying oven for 24 hrs at 60°C (Preburn weight) and then burned in a muffle furnace for 4 hrs at 500°C (Postburn weight).

Data Analyses, Model Construction and Fitting

TPCs were used to characterize the relationship between urchin respiration and temperature. The TPCs approach is a widely used model in climate change research to predict if organisms will be able to cope with increasing environment temperatures. A conscious TPC approach (Schulte et al., 2011) can provide useful metrics to compare performance between organisms, populations, species, localities and across time (Sinclair et al., 2016; Silbiger et al., 2019). Respiration data was normalized to the urchin individual organic carbon content. TPCs were modelled using a modified log-transformed Sharpe-Schoolfield equation (Schoolfield et al., 1981, Padfield et al., 2017; Silbiger et al., 2019):

$$log(rate) = b(T_c) + E\left(\frac{1}{T_c} - \frac{1}{k \cdot T_i}\right) - log\left(1 + e^{Eh\left(\frac{1}{K \cdot Th} - \frac{1}{K \cdot T_i}\right)}\right)$$

,

where:

$b(T_c)$ is the log rate at a constant temperature (for respiration μmol cm^{-2} hr^{-1}),

E is the activation energy,

E_h is the deactivation energy,

T_c is the reference temperature at which no temperature inactivation is experienced,

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 obtain the thermal optima of each urchin population, the following equation was used:

$$Topt = \left(\frac{Eh \cdot Th}{Eh + (K \cdot Th_k \cdot log(\frac{Eh}{E} - 1))}\right)$$

In order compare T_{opt} across sites, an ANOVA test was ran. A Tukey post hoc test for multiple comparisons of means of 95% family-wise confidence level was used to test the differences among sites. Finally, a quality control was carried out with the respirometry files: noisy files that used less than 30 points to calculate the slope were deleted. Six hundred and forty-nine respirometry files were used: 533 of urchin-chambers and 116 of blank-chambers.

Results

Thermal optimums of urchins collected at the warmest and the coldest sites differed in approximately 4°C: 29.5°C for Cabo Douglas vs. 33°C for Bartolomé (Figure 3). The descendent order of thermal optimum values, being higher at warmest sites and lower in colder sites, roughly matches the order of the mean temperatures of each site. Urchin populations from different parts of the Galápagos archipelago had notably distinct respiration responses to changes in seawater temperature (Figure 4). In addition, the TPCs of each urchin varied within the population. Each urchin presented a different oxygen consumption rate in accordance to its organic mass content. All TPCs together, showed the thermal sensitivity of respiration at a population level, with a peak signaling the temperature were oxygen consumption was the highest (Figure 4). There was a significant effect of site on the thermal optimum ($F_{5,38}=4.57$, $p=0.0023$) between Cabo Douglas (coldest site) and Bartolomé (warmest site) ($p<0.001$), and between Cabo Douglas and Punta Cormorant, the second warmest site ($F_{5,38}=4.57$, $p=0.02$).

Discussion

For this study we hypothesized that *E. galapagensis* populations in the Galápagos archipelago are adapted and/or acclimatized to local thermal conditions; modeling the thermal sensitivity of each population using a Thermal Performance Curve approach tested this. The results indicate that pencil urchin populations from different locations around the Archipelago have different responses to acute warming. Each population, depending on its site, presented a different local thermal optimum. Statistical analysis proved an effect of location in the T_{opt}. It was expected to have obtained significant differences between the most different sites (Bartolomé- Cabo Douglas, Punta Cormorant- Cabo Douglas), because these sites present the most different thermal histories and mean temperatures (4°C of difference, approximately). These results corroborate that differences in the thermal regimes of each site can affect urchin metabolism. Cabo Douglas in Fernandina Island is the westernmost site that can be sampled in the Galápagos archipelago, with nutrient-rich waters and high upwelling mainly brought by the Cromwell current. For Bartolomé in Santiago Island (northern bioregion of the Archipelago) and Punta Cormorant in Floreana Island (southern-eastern bioregion) have conditions were ocean water is warmer and upwelling regimes are lower. These sites are mostly linked to the warmer and nutrient-poor Panama Current (Houvenaghel, 1984; Ruttenberg, 2001; Wellington et al., 2001).

The differences observed between T_{opt} values of the pencil urchin populations roughly match differences in the average temperatures of each location, suggesting an adaptation to local thermal conditions of this ectotherm species. The fairly large differences in environmental temperatures of each site is a likely explanation for the observed thermal sensitivities in the urchin populations. Because of short thermal acclimation periods and since short- duration extreme hot temperatures often drive the strongest responses (Pinsky et al., 2019), acute thermal sensitivity measurements in this study could also be explained. Acute TPCs can be the result of an instantaneous thermal stress test (Silbiger et al., 2019) because sharp increments in temperature are the ones tested without a proper acclimatization time for the organisms. However, the Galápagos system also subject species populations to short acclimation times due to its highly variable thermal settings and harsh daily fluctuations in water temperatures. To better represent the population, more replicates with different individuals could be assessed per location. With a higher number of urchin replicates, TPCs can present a more homogeneous shape, giving a better representation of how temperature affects the whole urchin population at each location. For each site, we used eight individuals to estimate the TPCs for that population. This quantity of urchins could explain the variability at the individual level. The

decision of sampling this number of urchins per site was made following time and money restrictions.

Sewell and Young (1999) found that temperature 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, showing a high heat resistance of gametes and larvae in comparison with the thermal limits of adults. This type of studies shows that for a direct estimate of population responses to warming a full knowledge of other rates of performance (such as reproduction, larvae mortality, dispersal and growth) as a function of sublethal temperature is needed; since these other rates may be compromised differently to temperature than respiration (Pinsky et al., 2019). As it happens for *E. lucunter*, the distribution and abundance of pencil urchins *E. galapagensis* should be limited by thermal sensitivity of different factors, such as adult temperature tolerances, temperatures needed for growth, spawning, larval settlement and juvenile survival. This study gives an insight in adult pencil urchins temperature tolerance. Regarding respiration rates, thermal optima of urchin populations in Galápagos are considerably higher than the average local temperature in which they are settled. This suggests that *E. galapagensis* could still cope with increasing temperatures; maintaining a high prevalence in the Galápagos ecosystems. In a scenario were ocean temperature increases in the Galápagos archipelago (Solomon et al., 2007 states a rise by 1-3°C during the 21st century), it would be expected a shift in primary productivity of the ecosystems in the different bioregions, triggering changes in fish and benthic fauna assemblages. Ecosystems of cold sites would start to resemble the ones at warmer sites, and warmer sites could turn unbearable for the current Galápagos fauna. The high thermal optimums of pencil urchin populations can make them one of the fewer species that would still be present in the Archipelago. Demographic explosion of urchins can alter the shallow subtidal ecosystem (Ruttenberg, 2001; Edgar et al., 2010) strengthening the top-down effect of urchins on macroalgal assemblages, resulting in increased urchin barrens (Brandt and Guarderas, 2002; Carr and Bruno, 2013) and possibly in loss of existing algae beds (Przeslawski et al., 2008).

Ectothermic individuals and populations can acclimate to new local thermal conditions through different mechanisms. Changes in thermal regime trigger these mechanisms for urchins to be in constant acclimatization to cope with their local thermal conditions, suggesting a highly adaptive physiology through high plasticity of individuals. Seeking thermal refugia may represent a challenge for marine species, increasing their vulnerability to higher ocean temperatures (Pinsky et al., 2019). However, the high mobility of this urchin species allows for them to have a behavioral thermoregulation: it eases access to different microclimates by

moving to deeper parts of the ocean or to protected-shaded regions. To individual levels, marine organisms' thermal studies at harsh environments have shown a strong selection pressure for a high thermal tolerance in the population (Edney, 1961; Wolcott, 1973; Newel and Branch, 1980). Even though our results suggest that populations are adapted to thermal conditions and that the ability to acclimatize is a primary factor to dictate vulnerability of the species to the rising temperatures (Stillman, 2003; Somero, 2010; Tomanek, 2010; Huey et al., 2012; Botero et al., 2015; Gunderson and Stillman, 2015), TPCs showed that Galápagos urchin populations are vulnerable to the increasing temperature: populations whose graphs have steeper slopes at each side of the Top peak are considered as most sensitive because a small change in temperature causes them to quickly move from optimal to suboptimal conditions (Silbiger et al., 2019). Bartolomé population experienced a steep drop in respiration rates short after reaching its thermal optimum (Figure 4). Similarly, this was found for the Cabo Douglas population, were respiration quickly increased after a small change in temperature, showing the close proximity of this population's thermal optimum to the ambient temperature of the site.

As many studies of thermal sensitivity have been conducted in organisms comparing its performance in a latitudinal range (review of Gunderson and Stillman, 2015; Pinsky et al., 2019), this is one of the few doing it in the same geographical position but across a highly variable temperature gradient, such as the one provided by the Galápagos archipelago. Modelling TPCs for a multiple species and representatives from functional groups can help to better predict responses to temperature at an ecosystem level (Silbiger et al., 2019). Understanding rates of performance as a function of temperature and thermal sensitivity of not only the pencil urchin but of multiple species of Galápagos is essential for projecting the future of its ecosystems and for giving an insight of population dynamics of different communities as the ocean critically warms.

Author Contributions

JFB and MB chose the experimental design. JFB provided the materials and funding. MB, JFB and ISR collected the data. ISR processed the data. NJS statistically analyzed the data. ISR, JFB and MB wrote the manuscript.

Acknowledgements

Competing Interests

The author has no competing interest

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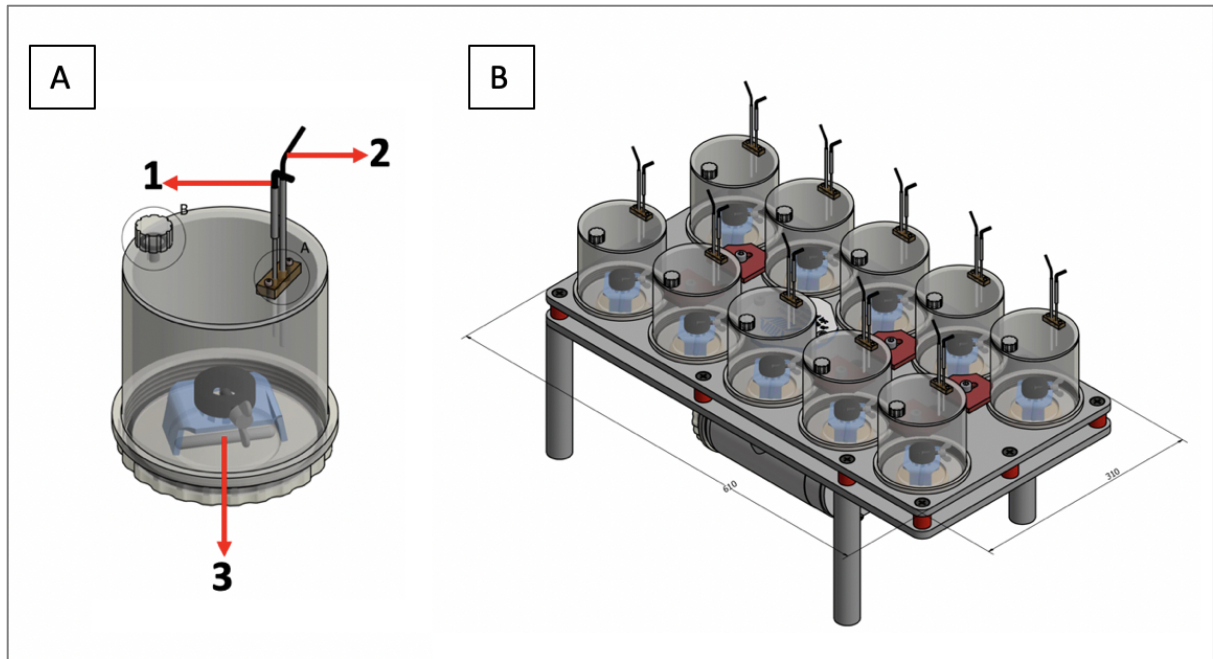
Data Availability

The respirometry data used to support the findings of this study is available from the corresponding author upon request.
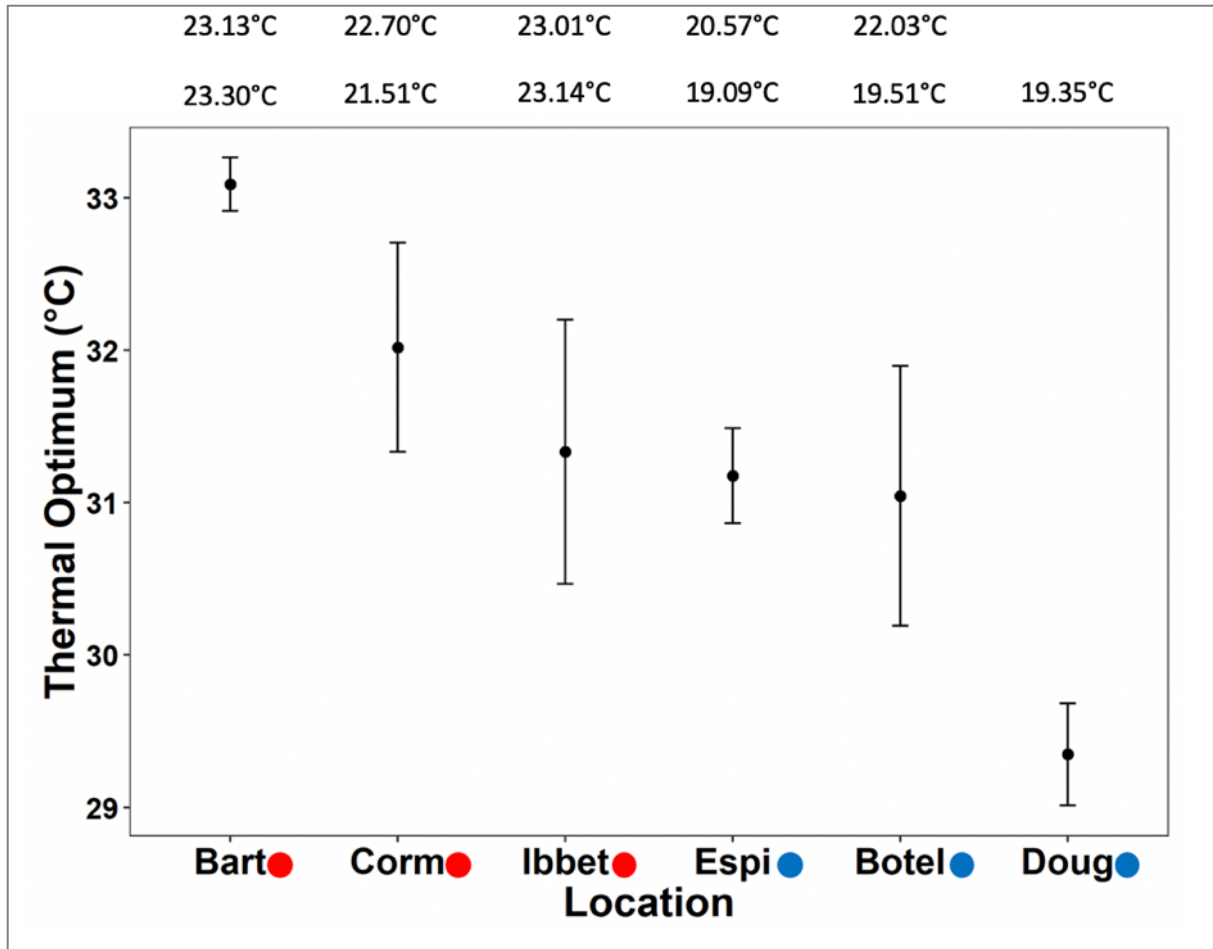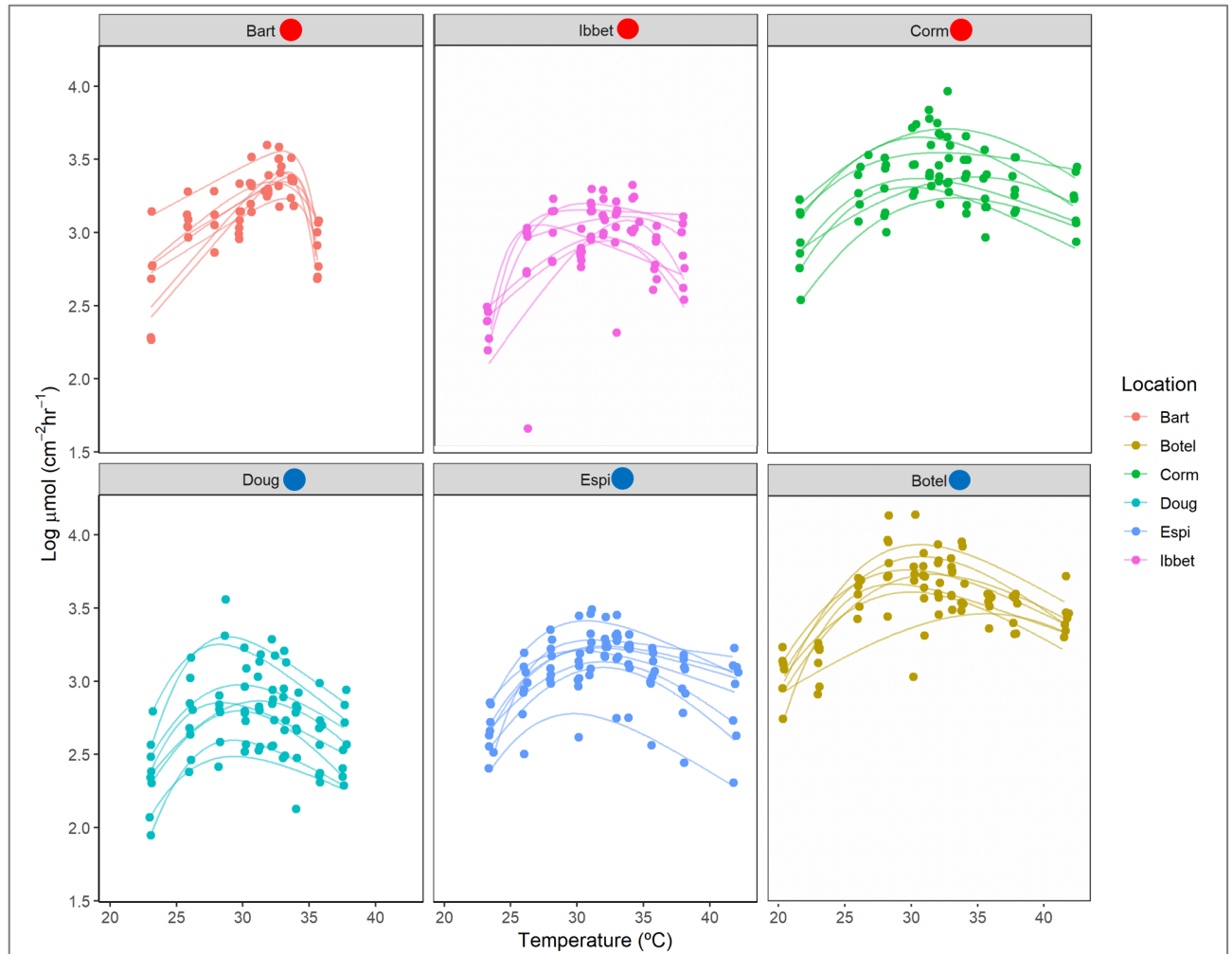
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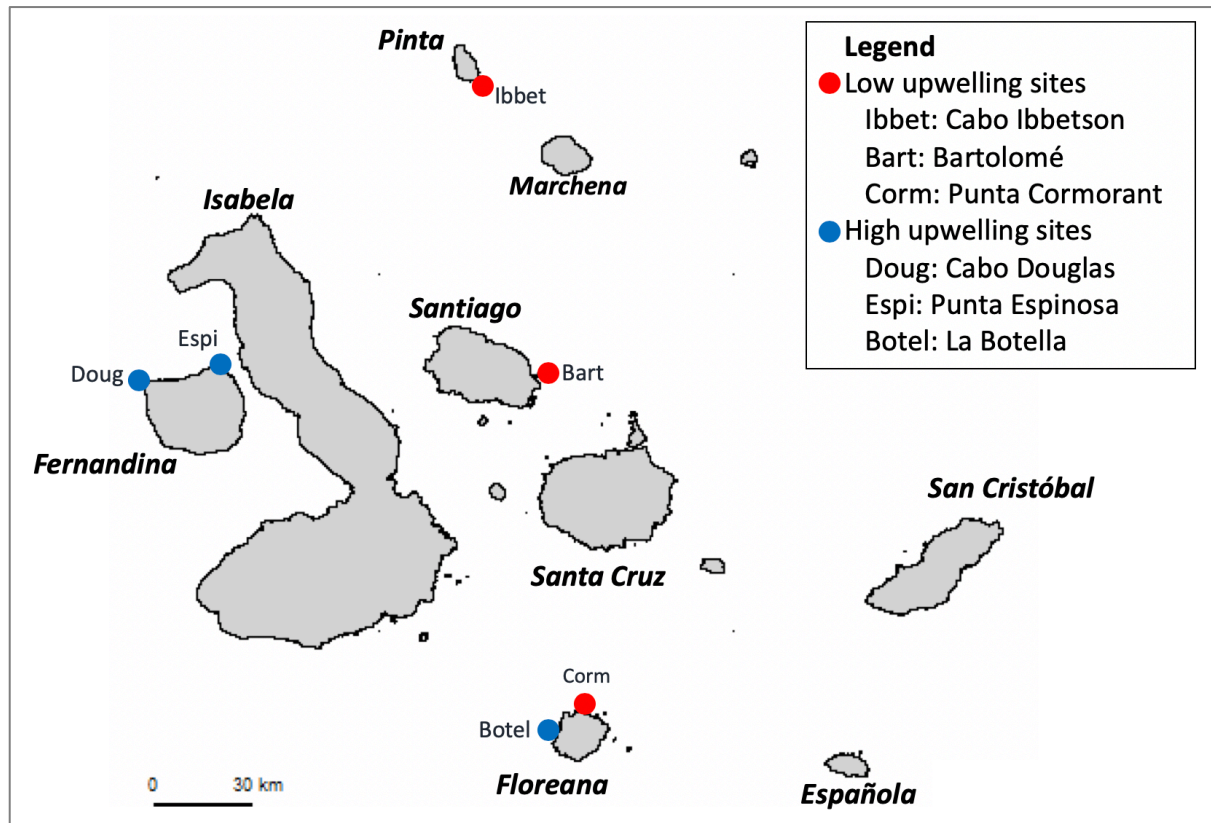
Figure 1. Map of study sites in the Galápagos archipelago. Blue dots indicate high upwelling sites and red dots indicate low upwelling sites.

Figure 2. (A) Acrylic respirometry chamber of 620 ml capacity. 1. Temperature probe; 2. Fiber-optic oxygen probe; 3. Magnetic stir bar. **(B)** Respirometry setup for individual-specific thermal sensitivity measurements. *Diagram source: Australian Institute for Marine Science.*

Figure 3. Thermal optima for each urchin population, according to their location with different upwelling regimes: sites marked with red dots are low upwelling sites, those with blue, high upwelling sites. First row of temperature values (top) above each plot represent the means of temperatures from each site measured from March to August 2018 with a HOBO temperature logger. Because logistical reasons, a logger was not deployed at Cabo Douglas, making temperature data unavailable for this site. Second row of values (down) are the SSTs recorded at each site the day of urchin collection.

Figure 4. Thermal performance curves of log (x+1) respiration rates (μmol O_2 cm^{-2}hr^{-1}) from urchin populations at different locations. Top panel: sites with low upwelling, bottom panel: sites with high upwelling. Each dot represents one individual of *Eucidaris galapagensis*. Each graph shows the changes of 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.

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