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Assessing the Thermal Performance of Galápagos Sessile Invertebrates: Seasonal and Habitat Comparisons

.

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RESUMEN

Se prevee que el cambio climático va a alterar significativamente los patrones estacionales a nivel global. Por lo tanto, las respuestas térmicas de organismos marinos ante cambios en sus regímenes estacionales habituales son cruciales para garantizar su supervivencia y salud poblacional. Nos centramos en investigar las respuestas térmicas estacionales (época fría y época caliente) y específicas de hábitat (intermareal y submareal) de tres invertebrados marinos sésiles (*Budonosoma grande, Megabalanus peninsularis y Tubastraea coccinea*) en las Islas Galápagos, utilizando las diferencias en tasas de respiración como indicadores de aclimatación térmica. Contrario a expectativas, los individuos intermareales no mostraron tasas de respitación más altas, sugiriendo una respuesta sensible a temperaturas elevadas debido a una menor tolerancia al calentamiento del mar en comparación a los individuos submareales. Similarmente, no todas las especies mostraron tasas más altas durante la temporada caliente, desafiando la suposición de plasticidad fenótipica generalizada. Notablemente, solo los individuos intermareales de *T. coccinea,* (especie criptogénica) demostraron una evidencia a aclimatación térmica ocurriendo. Estos resultados destacan la necesidad de realizar más evaluaciones específicas a especies y hábitats para lograr obtener una visión más comprehensiva de las respuestas térmicas de ectotermos marinos ante los efectos del cambio climático.

Palabras clave: respiración, aclimatación térmica, intermareal, estacionalidad, submareal.

ABSTRACT

Climate change is expected to significantly alter seasonality patterns globally. Therefore, the thermal responses of marine organisms to drastic shifts in their usual seasonal regimes are crucial to ensure survival and maintain a heathy population fitness. We focused on investigating the seasonal (cool and warm seasons) and habitat-specific (intertidal and subtidal) thermal responses of three sessile marine invertebrates (*Budonosoma grande, Megabalanus peninsularis*, and *Tubastraea coccinea*) in the Galápagos Islands, using respiration rate differences as indicator for potential thermal acclimatization. Contrary to expectations, intertidal individuals did not exhibit higher respiration rates, suggesting a more sensitive response to high temperatures due to lower warming tolerance compared to their subtidal counterparts. Similarly, not all species showed higher rates during the warm season, challenging the assumption of generalized phenotypic plasticity ocurring. Notably, only intertidal individuals of *T. coccinea,* a cryptogenic species, displayed potential thermal acclimatization. These results highlight the need for species-specific, and habitat-specific assessments in order have a more comprehensive view on marine ectothermic thermal responses to the effects of climate change.

Key words: respiration, thermal acclimatization, intertidal, seasonality, subtidal.

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INTRODUCTION

Climate change has been predicted to dramatically alter seasonality patterns on a global scale. Ocean environments have been particularly susceptible to these alterations, with several examples of unprecedented Sea Surface Temperature (SST) warming events occurring over the last few decades (Alexander et al., 2009; Lima & Wethey, 2012). Anomalous variations in seasonal regimes have gained significant attention in physiology studies focused on marine organism-responses to thermal stress. Ectothermic organisms are exceptionally influenced by temperature, being recognized in various studies as the primary abiotic stressor they encounter in their life history, due to its comprehensive impact on biological processes, ranging from organismal to molecular level (Stillman & Somero, 2000; Stillman & Somero, 1996). Additionally, ectotherms have the capacity to modify their thermal tolerance through physiological acclimatization, also known as phenotypic plasticity. This mechanism can mitigate the effects of thermal stress, which otherwise can have negative impacts on the overall population fitness (Silva-Romero et al., 2021) . Given the exponential impact of climate change on ocean environments and the vital role of the thermal response and acclimatization as a mechanism of adaptation for changing temperature, further research in this field in crucial.

One group that is of particular interest to this subject are intertidal species, that opposed to their subtidal counterparts, usually have greater thermal tolerance limits, and are routinely exposed to wide temporal fluctuations in water and air temperature throughout the tide cycle, as well as many other abiotic stressors such as predation pressure, humidity, desiccation, and changes in salinity (Stillman & Somero, 2000). Moreover, recent studies on these organisms have shown significant intrapopulation differences in their capacity for thermal tolerance acclimatization (Stillman, 2002). These specific characteristics have become relevant on a climate change perspective, because seasonal plasticity can improve survival rates and potentially act as a buffer to the effects thermal stress has on physiological processes (Crickenberger et al., 2015). Sessile intertidal species are particularly impacted by these stressors because contrary to mobile intertidal species, they cannot change their location when intertidal conditions worsen. This features make them great indicator species for evaluating drastic changes in SST, and serving as model organisms to investigate acclimatization to seasonal and habitat-dependant temperature changes.

Currently, one of the most common ways of studying the effects of thermal sensitivity on marine life is through Thermal Performance Curves (TPCs) (Schulte et al., 2011; Sinclair et al., 2016). TPCs graphically represent the relationship between temperature and physiological processes such as photosynthesis, respiration, survival, growth, among others, illustrating how organisms respond to the thermal variations of their environment. TPCs are characterized by their unimodal shape which describes various key parameters, for example activation energy (E) , deactivation energy (Eh, i.e., metabolic sensitivity), and thermal optimum (Topt). The Topt is the parameter mostly used in these studies and it describes the temperature point at which fitness of a specific organism is maximized (Silbiger et al., 2019a).

Generally, sessile intertidal species are found on either the intertidal zone or the subtidal zone, however some organisms can live on both habitats. This is the case for our study species, the sea anemone *Budonosoma grande*, the giant barnacle *Megabalanus peninsularis*, and the cup coral *Tubastraea coccinea*, which all have the ecological role of being filter feeders in their respective habitats and some have been considered ecosystem health indicators for the Galápagos. For instance, barnacles were chosen as indicators for the archipelago due to their potential as keystone species and high sensitivity to environmental change (Adsersen et al., 2002).

In this project, we collected oxygen consumption (respiration) measurements of the above-mentioned species, from both the intertidal and subtidal zones during the cold and warm season of the Galápagos, subjecting them to a range of temperatures. The Galápagos Islands have a long history of significant seasonal events (El Niño Southern Oscillation-ENSO), which have continuously shaped its marine diversity (Dueñas et al., 2021; Glynn et al., 2018; Manzello et al., 2014; Wolff, 2010; Edgar et al., 2010), and are key to understand the physiological responses of organisms to these periodic changes in temperature.

Our aim through this study was to test the acclimatization potential of these sessile species, both seasonally and habitat-specifically. For which, we formulated the following research question: Does seasonality and habitat of origin have an effect on the thermal performance of our study species? We predict that 1) the respiration rates of the three study species will be higher during the warm season compared to the cool season, and 2) the respiration rates of intertidal individuals will be higher than that of subtidals during both the warm and cool seasons, as a reflection of higher thermal tolerance acquired because of the extreme abiotic pressures present in the intertidal zones.

While there are numerous studies studies globally that have explored the thermal sensitivity of intertidal organisms or the effects of seasonality on acclimatization (Crickenberger et al., 2015; Diederich & Pechenik, 2013; Hopkin et al., 2006; Roberts et al., 1997; J. H. Stillman, 2002), typically, these investigations do not account for both aspects (seasonality and habitat of origin). Furthermore, intertidal studies tend to only focus on comparisons between different intertidal elevations. There is an important gap in research focused on the acclimatization capabilities of marine invertebrates that inhabit both intertidal and subtidal habitats. Finally, to the best of our knowledge, the present study is first to delve into the seasonality effects within distinct marine habitats of the Galápagos Islands; it will allow us to shed light on how some of the most common sessile species of Galápagos might deal with the extreme thermal events climate change will bring, whilst also highlighting the importance of acclimatization as mechanism to buffer the effects of thermal stress in marine invertebrates.

METHODS

Study Area

The study was carried out on San Cristóbal, the easternmost island of the Galápagos Archipelago. In Galápagos there is maximum tide level difference of 2.5m and this can vary depending on ENSO conditions (INOCAR, 2023). Field samples were taken at two different sites of the southwestern section of the island, Tijeretas, a small gently sloped rocky bay close to the town of Puerto Baquerizo Moreno (0°53'15.71"S, 89°36'24.21"O) and León Dormido, a vertical tuff cone outcrop 18 km from port (0°46'42.05"S, 89°31'5.61"O). Both sites have a generally similar species composition in regards to to fish diversity, however sessile organisms such as macroalgae, gorgonians, sponges, and ascidians are more common in León Dormido due its vertical nature. These sites were selected due to their advantageous proximity to the Galapagos Science Center marine laboratories and also because of the abundant presence of the species of interest, on both subtidal and intertidal habitats. *B. grande* and *T. coccinea* were collected from Tijeretas and only *M. peninsularis* was collected from León Dormido.

San Cristóbal Island and Galápagos as a whole, experience two seasons annually, a warm season from January to May, and a cool season from July to November, with June and December considered transition months (Trueman & D'Ozouville, 2010). However, in addition to this seasonality pattern, the occurrence of ENSO events can significantly exacerbate SST trends on the islands (Dueñas et al., 2021). The SST regime for San Cristóbal during the time of sample collection (2022-2023) reflected the increased cold influence of a prolonged La Niña event that had started in 2020 (Shi et al., 2023), as well as the warming effects of a developing El Niño event on early 2023 (NOAA, 2023). The average ocean temperature in the area for the time of collection during August 2022 was 21°C, in contrast the to April 2023 average of 27°C.

Sample Collection

Samples were collected during August 2022 and April 2023, coinciding with the cool and warm seasons of Galápagos respectively. For each season, we collected 18 individuals per species from both intertidal and subtidal habitats, with nine from each habitat. Depending on the site, the organisms were collected through either scuba diving or snorkeling. Due to the calcareous life forms of *M. peninsularis* and *T. coccinea*, collection was carried out using a hammer and chisel, whilst only *B. grande* was collected by bare hand. All intertidal individuals were collected during low tide, and as a means to avoid overlapping habitat collection, subtidal individuals were collected at least 3 m below sea level. The organisms were placed inside water buckets and the transportation period from the Tijeretas site to GSC was approximately 30 min, whilst León Dormido to GSC took close to 1 hr so a water change was done before arriving to the laboratories. Once at the GSC, the species were placed in mesocosms with water temperature set to the ocean temperature recorded at the sample site.

Thermal Response (respirometry) measurements

All experiments began the morning after collection to avoid overstressing the organisms before the trials. Respirometry measurements were taken first on the intertidal individuals and subtidal individuals were measured the day after (no individuals stayed in the mesocosms longer than 2 d); this was done sequentially during a total of 6 d (2 d per species) to cover all three species.

For the thermal tolerance measurements, we used a closed respirometry set-up, consisting of 10 620-cm3 acrylic chambers, each with a magnetic stir bar to provide water circulation inside the chambers and to also prevent oxygen saturation (**[Figure 1](#page-16-0)**) . This set-up was placed inside a cooler with sea water which had passed through a filtration system. Of the 10 chambers, nine contained the live organisms, leaving 1 chamber as a blank (control) with only seawater inside. These control readings were necessary to account for the oxygen

consumption of any potential microorganisms that could be present in the water. Salinity tests were also performed each day before the trials to ensure the seawater matched the collection site levels.

Oxygen consumption and temperature was measured in each individual chamber using a temperature probe (Pt1000) and a fiber optic probe (respiration). For each species trial, we used 10 different temperature exposures, chosen to aim at a better TPC resolution: 16°C, 20°C, 24°C, 26°C, 28°C, 30°C, 32°C, 34°C, 38°C, and 41°C. The temperature inside the cooler was initially lowered to 16°C using a chiller, and then it was sequentially increased with heaters. The organisms were exposed to each temperature for an average of 10 min and the transition time between one temperature and the next never exceeded 30 min, as to avoid acclimatization or heat stress. All measurements were simultaneously visualized and recorded with the PreSens Measurement Studio 2 Software as the trials were performed, with oxygen concentration being measured every 1s. Each measurement was automatically downloaded as a CSV file into a computer, for further analyses.

At the end of the experiments, all individuals were measured with a volumetric cylinder in order to record the water displacement volume inside each chamber. Subsequentially, the organisms were labeled and wrapped in aluminum foil to be frozen at -17° C. In the next stage, the individuals were dried in an oven for 24 hrs at 60°C and then weighed in a scale to record their dry weight. Afterwards, the organisms were burned in a muffle furnace for 4 hrs at 500°C and were then weighed once more. This process was carried out in order to calculate their Ash Free Dry Weight (AFDW) to normalize respiration rates.

Figure 1. Respirometry system. Ten acrylic chambers (nine for species' individuals, one as control) measuring O2 consumption rates and water temperatue by using two probes. These probes were connected to a computer in order to record and visualize the measurements in real time.

Data Analysis

The data analyses were performed using an R code methodology created by (Silbiger et al., 2019b), which was respectively adapted to fit the requirements of the project. The code itself consisted of two stages, the first being the complete processing and cleaning of the data in order to create raw TPCs for visualization and interpretation using the '*lme4*' package. We are currently working on the next stage which involves running Bayesian models to determine the TPC parameters mentioned before (Topt, E and Eh) to statistically compare them between the study species, seasons, and habitats. This will be achieved by using the log-transformed Sharpe-Schoolfield modified equation and One-way ANOVAs for each parameter (Silbiger et al., 2019a; Silva Romero et al., 2021). All temperature, time series data, and oxygen consumption rates, were organized into CSV files, which subsequently went through a process of cleaning before importing into R Studio. This process involved trimming time series data as to remove noisy segments at the beginning and at the end of each experiment to ensure correct calculations. Also, oxygen consumption rates were calculated using a regression method.

To facilitate comparability throughout the analyses, the respiration rates were normalized to organic biomass (AFDW), which is a common practice in other similar studies (de Boer, 2000; Zhu & Lee, 1997). Additionally, rates were converted into (μ mol/cm^{2*}hr) and control respiration rates (Blanks) were subtracted from experimental rates in order to account for microorganism respiration as mentioned in the previous section. The final output of the this first stage results in a complete dataset with the required components to produce raw TPC graphs for each species.

RESULTS

All curves from the intertidal zone displayed a unimodal shape with visibly steep negative slopes (deactivation energy). However, in the subtidal zone only *B. grande* displayed a typical unimodal shape. TPCs from *T. coccinea* and *M. peninsularis* did not have a sharp negative slope, and in some cases there was no visible negative slope at all (particularly for subtidal *T. coccinea,* which displayed incomplete curves). This indicates that metabolic rates did not decline even at the highest temperatures measured (41°C) (**[Figure](#page-20-0)** *2*). The respiration rates varied from from species to species, but in general the average rates laid between 1 and 4.5 Log μ mol O2 g−1 hr−1.

Specifically, in *B. grande*, TPCs from each season ranged from 2 (lowest average value registered) to 4 (highest average value registered) Log µmol O2 g−1 hr−1. Similarly, *T. coccinea*'s TPCs, also had a rate starting point of aproximately 2-2.5 Log µmol O2 g−1 hr−1, however intertidal individuals reached a max average value of aproximately 4.5 Log µmol O2 g−1 hr−1 during the warm season and less than 3 Log µmol O2 g−1 hr−1 during the cool season, while subtidals only registered a max average value of 3.5 Log µmol O2 g−1 for both seasons. *M. peninsularis* TPCs displayed the lowest average rates of the three species with both intertidals and subtidals starting from 1 and 1.5 Log μ mol O2 g−1, respectively. Intertidal individuals only registered a max avergae rate of **<** 2.5 Log µmol O2 g−1 hr−1 and subtidals had a higher max average rate of 3 Log µmol O2 g−1 hr−1 (**[Figure](#page-20-0)** *2*).

Seasonal comparison

Respiration rates for all species and habitats were not universally higher during the warm season. Out of the six assessed TPCs, only the intertidal *T. coccinea*'s TPC showed higher respoiration rates (**[Figure](#page-20-0)** *2*). This was concluded for it being the only graph were the confidence intervals did not overlap. The rest of the TPCs did not reveal sufficient noticeable differences between the cool and warm seasons (all confidence interval margins overlapped). Interestingly, *T. coccinea*'s subtidal TPCs exhibited the most similar seasonal respiration rates, with its curves being near identical on both the cool and warm season (**[Figure](#page-20-0)** *2*).

Habitat comparison

There was no visible general trend for significant variations between intertidal and subtidal respiration rates, with once again only *T. coccinea* showing differences between habitats, with intertidal rates being higher in the warm season. *Bunodosoma grande*'s TPCs showed strikingly similar respiration rates on both subtidal and intertidal graphs, and in the case of *M. peninsularis*, the respiration rates for the intertidal TPCs was found to be actually slightly lower than the subtidal TPCs on both seasons.

Figure 2. Thermal Performance Curves for respiration rates (Log µmol O2 g−1 hr−1) for *Bunodosoma grande*, *Megabalanus peninsularis*, and *Tubastraea coccinea*. Red lines represent the respiration rates measured during the warm season and blue ones during the cool season. Gray margins represent the 95% confidence intervals.

DISCUSSION

Our study's prediction that the respiration rates of the three species would be higher during the warm season (compared to the cool season) did not prove to be a universal phenomenon. In fact, it was only observed in *T. coccinea* on the intertidal zone. These unexpected results may stem from a lack of plasticity potential in the study species. This can be attributed to many factors such as significant differences in intrapopulation acclimatation capacity, resulting in a sampling effort that might not reflect the species actual overall plasticity potential (Crickenberger et al., 2015). Also, on the molecular level, several studies have found that genetic diversity facilitaded by effective gene flow is crucial in conferring subpopulations with acclimation capabilities, thus highlighting the necessecity to explore the genetic side of thermal performance (Donelson et al., 2019; Foo & Byrne, 2016).

Additionally, the temperature difference between the cool and warm seasons (7°C) may not have been substantial enough to trigger acclimatization, or the duration of each season (less than six months) might have been too short for a significant acclimatization process. It should be taken into account that our study species were not exposed to common seasonal temperature changes: the cool season sampling was carried out during a prolonged La Niña event, which had started in 2020 (Shi et al., 2023). Therefore, the warm season months did not reach their normal peaks in temperature in previous years, and high temperature acclimatization may have been weakened as a result.

Likewise, La Niña events are characterized by a substantial increase in nutrient concentration in the water by upwelling (Dueñas et al., 2021), leading to a greater availability of nutrients during the cool months, which might have buffered the aclimatization potential between seasons. For instance, *M. peninsularis*, showed slightly higher respiration rates during the cold season and it has been reported that past La Niña events greatly benefited this species, allowing significant recruitment levels (Edgar et al., 2010; Witman et al., 2010). Little is known on the nutrient dependency of *T. coccinea* and *B.grande,* nevertheless, studies on the influence of biotic factors on TPCs have showed that generally the effect of nutrient availability is usually overlooked, when it can be just as important (if not more) on TPC results (Litchman & Thomas, 2023). Regardless, our results hold important implications in a context of climate change, since they suggest sessile filter feeders might be more vulnerable than previously thought to ocean warming. It is possible that conducting similar studies over more extended periods of heat, such as during El Niño events, might yield more definitive results (Harianto et al., 2021).

On the other hand, the unique results of *T. coccinea's* thermal performance might be related to its pantropical distribution. *T coccinea,* originally from the Indo-pacific, can be nowadays found in all oceans at tropical latitudes and is considered a cryptogenic species in the Galápagos (Carlton, 2019). Research on the thermal tolerance of this species has been carried out in several sites along the Atlantic, where it is categorized as an invasive species. One study found that *T.coccinea* populations from the Gulf of Mexico had a higher tolerance to temperature and pH stress than the native populations from the Indo-pacific, suggesting a potential to displace endemic populations (Strychar et al., 2021). Another study, which took place in Brazil, found no evidence of *T. coccinea* having greater thermal plasticity compared to native cnidarians. It mainly attributed the species successful invasion to its r-selectted life history traits (Almeida Saá et al., 2020). These findings suggest that although *T. coccinea* populations might not consistently display greater thermal acclimatization on all its distributions, it does however have exceptionally robust traits that have facilitated its invasion to many locations in the tropics. Galápagos harbours its own species of endemic Tubastraea such as *T. tagusensis* and *T. floreana*. These congeners are currently considered endangered and its populations were severely impacted during the strong 1982/83 El Niño event (Feingold & Glynn, 2014). In contrast, there were no records of *T. coccinea*'s populations being impacted by this ENSO event, and it is considered the most common ahermatypic coral species of the entire archipelago (Glynn et al., 2009). As the effects of climate change continue, the composition of ahermatypic corals in Galápagos could potentially shift towards a *T. coccinea* dominated landscape.

Our second prediction suggesting higher respiration rates of intertidal organisms during both warm and cool seasons did not generally hold true. In fact, for *M. peninsularis*, the overall respiration rates were higher in subtidal individuals. Similar results were observed in a study comparing Upper-mesophotic and shallow coral reefs, which did not find variation in thermal sensitivity between depths (Gould et al., 2021) and in a study comparing the thermal performances of several tropical and temperate rocky shore organisms, which found higher warming tolerance for subtidal species than for intertidal species (Vinagre et al., 2016). One potential explanation for this trend is that many intertidal species already live at their thermal limits, making them more sensitive when exposed to higher temperatures, leading to a sharp declines in the negative slope of their TPCs after surpassing their thermal optima (Leung et al., 2021; Vinagre et al., 2016). Indeed, when comparing the respiration curves between habitats, there is a noticeable tendency for steeper declines in the intertidal zone compared to the subtidal zone, which further supports this explanation. This phenomenon is particularly common in organisms that cannot use behaviour to buffer exposure to extreme temperatures such as sessile species (Buckley & Huey, 2016).

In regards to other thermal performance studies carried out in the Galápagos Islands, we have found a similar respiration rate ranges from other ectotherms such as pencil urchins (*Eucidaris galapagensis*). In a 2021 study (Silva Romero et al., 2021), sampling was perfomed in warm and cold locations throughout the archipelago. Here the urchins' average rates were recorded from 2-4 Log µmol O2 g−1 hr−1 in all locations, which aligns with our study species ranges (1-4.5 Log µmol O2 g−1 hr−1).

Drawing broad conclusions that apply to an entire group of organisms can be challenging. Therefore, we recommend conducting more assessments for each specific species. This approach is particularly crucial for sessile filter-feeding animals, such as the three we studied (that, in fact, are some of the most common sessile animals of the whole archipelago). These organisms contribute significantly to nutrient cycling and water quality maintenance by removing plankton and organic particles from it (Petersen, 2004). They also play a pivotal role in controlling plankton populations and act as a link between microscopic and macroscopic organisms in their ecosystems (Gili & Coma, 1998). Thus, in the context of ocean warming, these species might face additional stress that could pottentially affect their population fitness, such as limited reproductive success, increased mortality, and scarcity of food (Edgar et al., 2010), consequently causing impacts on the higher levels of the trophic chain. Hence, a detailed understanding of their thermal tolerance and adaptability is vital for predicting and managing the effects of climate change on marine ecosystems.

CONCLUSIONS

The present study reveals that the respiration rates of our study species do not uniformly increase during the warm season of the Galapagos Islands. These results challenge the assumption of a generalized a phenotypic plasticity mechanism, were metabolic rates increase in response to higher temperatures across different species. Contrary to expectations, our findings also highlight that the respiration rates of intertidal organisms are not uniformly higher than those of subtidal organisms, in fact it might suggest the opposite in some cases. These results suggest that species with the highest thermal limits usually posses the lowest warming tolerance, as has been suggested in similar studies. Our study emphasizes the inherent complexity of thermal responses among marine sessiles and the importance of more detailed species-specific research when evaluating the impacts of climate change. These insights are crucial for better understanding the resilience of marine trophic chain interactions and the adaptability of marine ecosystems when faced with environmental changes.

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