Predator response diversity to warming enables ecosystem resilience in the Galápagos

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Abstract

An important impact of global warming in nature is the decline of ecological functions such as primary production, habitat provision, and carbon sequestration. These functions can be disrupted when the species that perform them are impaired by anthropogenic warming or other stressors. Where there is a diversity of responses to warming among the species filling these roles, the function is more likely to be maintained despite the loss of the least tolerant species. However, the response diversity to warming of key functions is generally unknown, particularly for the roles played by predatory and marine species. Here we show that the thermal sensitivity of predation to acute warming varies substantially among four marine invertebrate carnivores: three whelks and a sea star that inhabit rocky reefs around the Galápagos islands. Two of the four predators were clearly adapted to cooler temperatures and their functional performance declined dramatically with experimental warming. In contrast, predation by two whelks, and one in particular, improved with warming, including beyond temperatures expected in 2100 under the most pessimistic emissions scenario. These results suggest that a high level of temperature response diversity of predation could help maintain this critical function in a variable and changing environment.

Introduction

The core functions of natural ecosystems — that ultimately provide the services humans depend on — are performed by groups of species with similar characteristics, e.g., pollinators and decomposers [1,2]. Warming and numerous other aspects of climate change impair these species and their ability to perform ecological functions [3–8]. Due to the universality of metabolic scaling between temperature and the metabolism of ectothermic organisms, the rates of many ecosystem functions also scale with temperature [9,10]. This temperature-function relationship is typically unimodal, initially increasing with temperature up to a threshold (known as the thermal optimum), then declining rapidly [10]. The tipping

point at which functioning declines is determined by the thermal sensitivity of the species most tolerant of warming.

The diversity of warming responses among the species that make up a functional group (i.e., "ecological response diversity") is believed to influence the resilience of ecosystem functions to disturbance and environmental change [11–14]. If most or all species within a functional group have similar tolerances of and responses to warming, most of the group and the function itself will be lost if temperature increases (Fig 1). In contrast, a diversity of responses and thermal niches, and in particular the presence of one or more species tolerant of warming, can help maintain functioning even if species richness declines [11,13] (Fig 1).

Response diversity can be, but is not necessarily related to species richness [11,13]. For example, Tilman and Downing [15] demonstrated that temperate grassland plots with greater species richness were more likely by chance to include drought-tolerant species. Therefore, when a drought occurred, the most diverse experimental plots were the most resistant to reductions in rainfall and were able to maintain ecological functions like primary production and habitat provision. In contrast, even on the world's most biodiverse coral reefs there is very little variation in thermal tolerance among species within functional groups such as the fast-growing and habitat-providing acroporid corals [16]. Anthropogenic heatwaves only one or two degrees C above typical conditions can kill off hundreds of species within this and other functional groups of reef corals [17]. In this case species richness is a poor predictor of ecosystem resistance to warming, because although functional redundancy is very high (i.e., many species can fill the same functional role), response diversity is low.

Moreover, the ability of an organism or species to survive an acute or chronic disturbance is not necessarily indicative of its ongoing functional performance; the per capita performance of a species can be low or even zero even though it is still technically present in a community. Therefore, ecological response diversity cannot be inferred indirectly by measuring species richness or even the presence of

functionally important species and instead must be measured directly. As a result, very little is known about the functional response diversity of complex ecological functions in nature [13,16,18,19].

There is some prior work in marine systems on response diversity and climate resilience. For example, Nash et al. [20] found that when response diversity of herbivorous fishes that inhabit coral reefs is high, top-down control of seaweeds is maintained even when heat waves reduce the abundance of smaller parrotfishes, apparently benefitting larger-bodied herbivores. Moreover, coral communities at those locations recover more rapidly. Likewise, a modeling study [21] found that response diversity to warming and other disturbances among tropical corals can support ecological resilience. Coral communities comprised of species with high resistance as well as species able to recovery rapidly, were more resilient to disturbance. In the model, the two types of corals facilitated recovery by the other through "competitor-enabled rescue".

We quantified the functional response diversity of marine carnivores to ocean warming. We measured the effects of warming on the metabolism and predation rates of four invertebrate carnivores from rocky subtidal reefs of the Galápagos including three whelks and one sea star (Fig 2). Our results indicate a high degree of functional response diversity among marine carnivores in this system and suggest this characteristic could enable functional resilience to anthropogenic warming.

Materials and Methods

Predation experiment

To measure the species-specific effect of temperature on feeding, we quantified the predation rates of four invertebrate carnivores: *Vasula melones*, *Tribulus planospira*, *Hexaplex princeps*, and *Heliaster cumingi* (hereafter referred to by their respective genus). These species share a similar diet of barnacles and other prey such as smaller herbivorous snails. All experiments were performed inside laboratory aquaria at the Galapagos Science Center (GSC) on San Cristóbal Island, Galápagos. *Vasula*, *Tribulus* and *Heliaster* were collected from Bahía Tijeretas on the southwestern coast of San Cristóbal (0° 53'

17.0" S, 89° 36' 25.0" W) at depths of 1-4 m. *Hexaplex* was collected from La Barcaza (0°40' 16.9" S, 89° 15' 54.5" W, Fig S1), a small island off the northwestern coast of San Cristóbal at 8 m depth.

In the predation experiment, *Tribulus*, *Hexaplex*, and *Heliaster* were fed barnacles (*Megabalanus peninsularis*), while *Vasula* were fed small herbivorous snails (*Columbella haemastoma* and *Engina pyrostoma*). Although the largest *Vasula* typically consume barnacles, those used in the experiment were smaller and thus were fed smaller prey. Barnacles were collected at an 8 m depth from La Barcaza and intertidally at Kicker Rock (0° 46' 41.7" S, 89° 31' 06.9" W). The herbivorous snails used as prey were collected from Tijeretas.

We measured predator feeding rates inside 16 L glass aquaria during May, June, and July of 2021 and 2023. Each aquarium was filled with seawater that was pumped from the nearby ocean, held inside two 2000 L tanks, and filtered using a high-quality filtration system (RainHarvest Systems Triple 20 Inch Big Blue Filter Assembly, Blue, L-R, 20 µm pleated sediment filter, a 5 µm pleated sediment filter, and a 1 µm activated carbon block filter; SKU 17695) to reduce microbial metabolic activity. We replaced ⅓ of the water in each aquarium three times a week and monitored salinity levels twice daily. Throughout the predation experiments, individuals were exposed to 12 hours of both light and darkness. Water inside the aquaria was oxygenated using air stones (Marina 1-inch Cylinder Air Stone, model A962) and experimental temperatures were maintained with a thermostat control system (Inkbird ITC-308 Digital Temperature Controller 2-Stage Outlet Thermostat Heating and Cooling). Once the temperature inside a given aquarium deviated by ± 0.3°C from the desired experimental temperature, the system activated a centralized chiller (AquaEuroUSA Max Chill-1/13 HP Chiller) or an individual submersible heater (Tetra HT30 Submersible Aquarium Heater & Electronic Thermostat, one per aquarium), respectively, to bring the temperature back to the experimental temperature.

The selection of experimental temperatures varied (Table 1) among predators based on field observations and pilot studies, which indicated that some species could not tolerate higher temperatures.

Due to space and other resource limitations in the laboratory, all temperature incubations and experiments across the four predator species were conducted asynchronously.

For the predation experiments with *Tribulus*, *Hexaplex*, and *Heliaster*, barnacle prey were epoxied (Z SPAR Splash Zone 2-Part Epoxy Compound) to small stones and placed in the aquaria. For the *Vasula* treatment, five herbivorous snails were added to each aquarium. Predation was monitored daily by checking for the presence of consumed prey, and any consumed prey were replaced within 24 hours. To assess the effect of temperature on prey mortality, one control aquarium was included for each temperature incubation, where prey were exposed to the same conditions as the experimental trials but without predators. No significant effect of temperature on prey mortality was observed; no prey died in the control aquarium at any temperature.

Respiration measurements

We also measured the species-specific effect of temperature on metabolism measured as respiration in ecophysiology chambers at eleven temperatures (16, 20, 24, 26, 28, 30, 32, 34, 36, 40, 42 °C). Individuals were collected from their aforementioned locations the day before experiments were conducted and held overnight in seawater at a constant temperature of 16 °C, close to the ambient temperature of the seawater *in situ*. We performed the respirometry experiments on a single species per day, and all measurements were recorded during July 2022. Nine individuals (i.e., n = 9 per species) were randomly selected and assigned to one of ten acrylic 680-mL respirometry chambers containing filtered seawater. A final tenth chamber was left empty as the control to measure any background metabolic activity (i.e., by microbes in the seawater). This background rate was later used as a baseline and subtracted from the rates of all other chambers at that experimental temperature. To maintain water circulation and oxygen saturation inside each chamber, a magnetic stir bar rotated at ~200 rpm once stationed above a motorized table system, which was designed and built by the Australian Institute of Marine Science, Townsville, Australia. This table was then placed inside a 142-L cooler (Quick and Cool 150 Qt Cooler Item #: 00044363) which was filled with seawater at an identical temperature to insulate chambers and maintain uniform temperatures. Oxygen consumption was measured inside each chamber

every 1 s for ~15 min with a PreSens Oxygen Meter System (OXY-10 SMA (G2) Regensburg, Germany). Temperature was maintained to within ± 0.3 °C of the experimental temperature for a given incubation by a thermostat that controlled a water heater and chiller. Any measurement abnormalities (e.g., the organism or a bubble touching the oxygen probe causing a false oxygen spike) were noted and later eliminated from the data prior to analysis.

After each temperature incubation, individuals were kept in their respective chambers (with the lid unscrewed to allow for oxygen circulation) and held inside a 120 L container filled with filtered seawater at the previous incubation's temperature (to help standardize potential acclimation effects) for 10–20 min while the water in the cooler that contained the table system was warmed to the next temperature. Air stones were used to aerate and help circulate the water. Once the seawater had warmed to the next experimental temperature, the ten chambers were replenished and situated in their respective table positions for the following incubation. After the final temperature incubation, study organisms were euthanized by placing them in a labeled ziplock bag overnight in a 5 °C freezer. The following day, they were desiccated at 60 °C for 24 hrs in a drying oven (Memmert UFE 400 Sterilizer Laboratory Oven) and incinerated at 500 °C for 4 hr in a muffle furnace (Optic Ivymen System Laboratory Furnace 8.2/1100). Post-burn weights (g) were subtracted from pre-burn weights to normalize respiration rates by Ash-Free Dry Weight (AFDW).

Thermal performance curves and analysis

We used repeated local linear regressions with the *LoLinR* package in R to quantify respiration rates recorded from PreSens oxygen measurements. After obtaining these regressions, we performed corrections for chamber water volume displacement (i.e., by each individual) and rates from control chambers, and normalized each rate by its respective individual's AFDW. These rates were then log-transformed preceding their fit to a modified Sharpe–Schoolfield equation for high-temperature inactivation using a nonlinear least squares regression. Fits were determined using the '*nls.multstart*' R package [22,23] to generate random starting values for thermal parameters, wherein Akaike information criterion (AIC) assisted in model selection for the best-fitting parameter set [22,23]. After obtaining model

fits, we used 95% confidence intervals (CIs) to estimate T_{opt} for each species [as in 24]. Once T_{opt} values were obtained, we visually assessed their distribution using histograms and quantile-quantile plots. The interquartile range (IQR) method, substituting the median and IQR for mean and standard deviation (SD)[25,26], was used to identify and remove outliers from each species. We then constructed four TPCs as the average metabolic response by each species across the temperature gradient.

Results and Discussion

We found a high degree of response diversity to acute warming. Our results suggest that despite the potential of functional decline of species intolerant of high temperatures (i.e., with continued ocean warming), other species could fill their role and maintain the ecological function (in this case predation). Two of our four experimental species (the sea star *Heliaster* and the whelk *Hexaplex*) are clearly cold-adapted and highly sensitive to warming. For both, predation was greatest at ~21-22°C (Fig 3C). For example, predation by *Hexaplex* was low at 16°C (Fig 3C), peaked at 21°C, then declined with temperatures typical of warmer periods and seasons in the Galápagos (i.e., 26°C and 28°C, Fig 4). *Heliaster* predation (which on a per capita basis was the highest of the four experimental species) was greatest at 22°C and declined to nearly zero at 25°C (Fig 3C). At the highest experimental temperature for *Heliaster* (25°C) several experimental individuals showed signs of stress and died after lesions were observed on their dorsal surface. We have also observed *Heliaster* with these lesions in the field when ocean temperature exceeds ~24ºC, for example during the 2023-24 El Niño event. The lesions appear similar to the typical signs of sea star wasting disease [27,28]; a common temperature-related disease of sea stars in the U.S. Pacific Northwest.

Two of the whelk species (particularly *Vasula*) were far more tolerant to higher temperatures. Predation by *Tribulus* was low at 19°C, peaked around 28°C and declined at 31°C. *Vasula* did not feed at all at 19°C (Fig 3C) and in contrast to the other three species, its predation continued to increase to the

highest experimental temperature for the predation experiment (32°C), indicating an especially high thermal tolerance.

We also estimated the thermal optima (T_{opt}) of respiration in respirometry chambers as an indicator of the metabolic responses of each predator to warming. T_{opt} for respiration ranged from 22ºC for *Heliaster* to nearly 40ºC for *Vasula* (Fig 3B). More important than the specific values, the respiration T_{opt} rankings correspond closely to the relative scaling of predation rate with temperature: *Tribulus* and *Vasula* had far higher respiration T_{opt} values than *Hexaplex*, and especially *Heliaster* (Fig 3B). Respiration rates also mirrored the same patterns across species (Fig 3A) in relation to T_{opt} and predation rates. This suggests that the observed variation in the temperature-dependence of functional performance is related to (possibly mechanistically) species-specific metabolic sensitivity to temperature. It is often implicitly assumed, if rarely demonstrated, that measured physiological sensitivity to warming is indicative of the relative temperature-dependence (e.g., among species) of other organismal rates (e.g., growth, movement, consumption, etc.). Our results suggest that, at least for these functions and species, the relative thermal sensitivity of metabolism is predictive of the relative sensitivity of the ecological functions species fulfill in communities (that are typically much more difficult to measure).

The temperature of the surface and shallow waters of the sea surrounding the Galápagos islands is incredibly dynamic [29]. This is due to the complex interplay of oceanographic phenomena acting at different spatial and temporal scales including the ENSO cycle and seasonal variation in the strength of ocean currents such as the Humbolt current that delivers cold water from the Southern Ocean [29–31]. As a result, ocean surface temperature can be as cool as 12 or 13ºC in the La Niña phase of the ENSO cycle and as warm as 32ºC during El Niño (Fig 4). In addition, the strength of upwelling (the delivery of cool, nutrient rich water from depth) can vary at a scale of tens of meters or minutes, causing variation in seawater temperature of several degrees (ºC) between nearby locations or during a given day [29].

The implication of this variability for the performance of ectothermic organisms is that most species will only function near their T_{opt} for a relatively small proportion of the thermal conditions they experience. Our results suggest that predation by the two cold-adapted species (*Hexaplex* and *Heliaster*) would be negligible when habitat temperature was above ~25ºC (Fig 3C), such as during the warm months of La Niña years (e.g., in March of 2021 and 2022, Fig 4) and for most of the year under El Niño conditions (e.g., from April 2023 to March 2024, Fig 4). In fact, during the most recent El Niño, benthic seawater temperatures exceeded the observed predation T_{opt} of Hexaplex and Heliaster 98% and 83% of the time, respectively (Table S1). Conversely, predation by the two experimental species most tolerant of higher temperatures (*Tribulus* and *Vasula*) should be minimal when environmental temperatures are below ~20-22ºC (Fig 3C) — much of the year under La Niña conditions (Fig 4, Table S1). This implies that the diverse responses to temperature facilitates continued predation over a broader range of thermal conditions, ensuring functional continuity even when the performance of individual species is low.

Given the large degree of temporal temperature variance, the anthropogenic warming trend is more difficult to discern in the Galápagos compared to less variable regions [32]. A recent study detected ocean surface water warming of 1.2ºC (on average) for the region between 2002 and 2018 [30]. However, some regions of the Galápagos have warmed at nearly twice this rate — specifically the waters around the far northern islands of Darwin and Wolf. Moreover, climate models project substantial near-future warming, especially under the high emissions SSP5-8.5 scenario of CMIP6. Under these conditions, median ensemble sea surface temperatures could increase by another 2-3ºC by 2100 [33,34].

Our results indicate that warming of only a few degrees could exceed the tolerance of two of the four common invertebrate predators in our study. Both species could plausibly survive at low densities, possibly as sink populations, but would contribute little to top-down control of prey populations. However, warming could actually increase the performance of the two warm-adapted species,

particularly *Vasula*, thereby compensating for the functional loss of *Hexaplex* and *Heliaster*. This suggests that the observed response diversity of predators and predation in this system could improve the resilience of the community to anthropogenic warming.

An important caveat is that this inference assumes little or no future adaption to natural seasonal variation in temperature or ocean warming due to greenhouse gas emissions. Marine invertebrates are clearly able to increase their thermal tolerance via adaptation, acclimatization, and other adaptive mechanisms [35–37], although most do not appear to be doing so fast enough to keep up with environmental change. Adaptation could enable species more sensitive to high temperatures to maintain functioning as the system warms, to some degree alleviating the benefits of response diversity. A related caveat is that our experiment exposed predators to different temperatures for 21 days. In the context of ocean warming, this acute temperature treatment mimics the anthropogenetic heat waves, but not necessarily the longer-term (decadal) warming trend.

The fingerprint of greenhouse gas emissions and global warming is complex in some regions of the Galápagos. For example, Fernandina and Isabela Islands, the western-most portion of the Galápagos Islands, has cooled rapidly due to the strengthening (possibly anthropogenic) of the Equatorial Under Current [30,38]. Thus, recent and possible near-future changes in the marine thermal environment of the Galápagos range from rapid cooling to extreme warming. Given these opposing temperature trends, a high degree of thermal response diversity — including the presence of cold-adapted species that will thrive in the western Galápagos with continued cooling — appears crucial to maintain functioning, and not just in warming areas. A diversity of organismal responses to temperature (essentially a broad range of largely non-overlapping thermal niches within a given functional group) can lead to the maintenance of predation across a complex and variable thermal seascape.

In summary, our results demonstrate the value of functional response diversity, and the importance of conserving species expected to fill crucial roles in a warmer world. A diversity of responses to marine

heat waves in which species more tolerant of higher temperatures can functionally compensate for declines in cold-adapted species can increase ecosystem resilience to environmental change [13]. A growing body of work is beginning to suggest that community characteristics like functional response diversity are better predictors of ecological resilience than more traditional measures of biodiversity like species richness [11,13]. Untangling the relationship between ecosystem resilience to global warming and trait diversity should be a priority for field ecology.

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Table and Figures

Table 1. Details for experiments that measured the effects of temperatures on predation.

Predator species	**Temperatures (°C)**	**Sample size (n)**	**Duration (d)**
Vasula melones	19, 23, 26, 29, 32	8	7
Tribulus planospira	19, 22, 25, 28, 31	8	7
Hexaplex princeps	16, 21, 26, 28	8 for 16 and 26°C and 6 for 21 and 28°C	21 for 16 and 26°C and 15 for 21 and 28°C
Heliaster cumingi	16, 23, 26	5	7

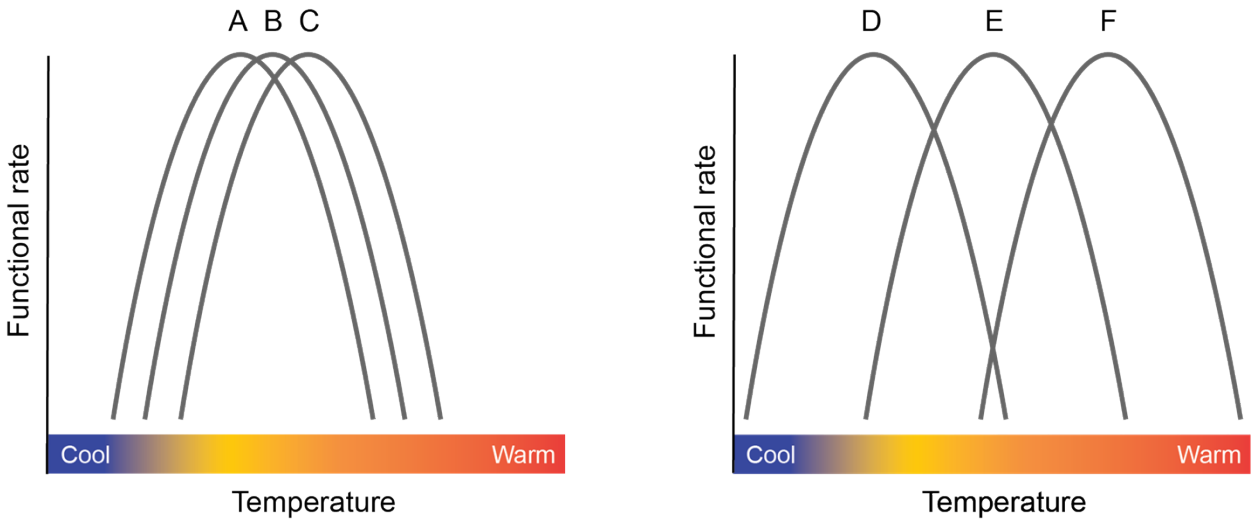

Figure 1. A theoretical model illustrating the concept of ecological response diversity and how it can vary among locations and communities. Each curve represents the functional response of a species (A-F) within a single functional group, e.g., herbivores or detritivores. Left: the functional responses of the three species are very similar and response diversity is low. Right: functional response diversity is greater and this community is likely to be more resistant to warming (in this case) or another type of disturbance or environmental change. Note the functional response of these species is often measured as metabolism or fitness. This can be informative, but it is often better to directly measure the species' actual functional performance based on its specific ecological role, e.g., herbivory.

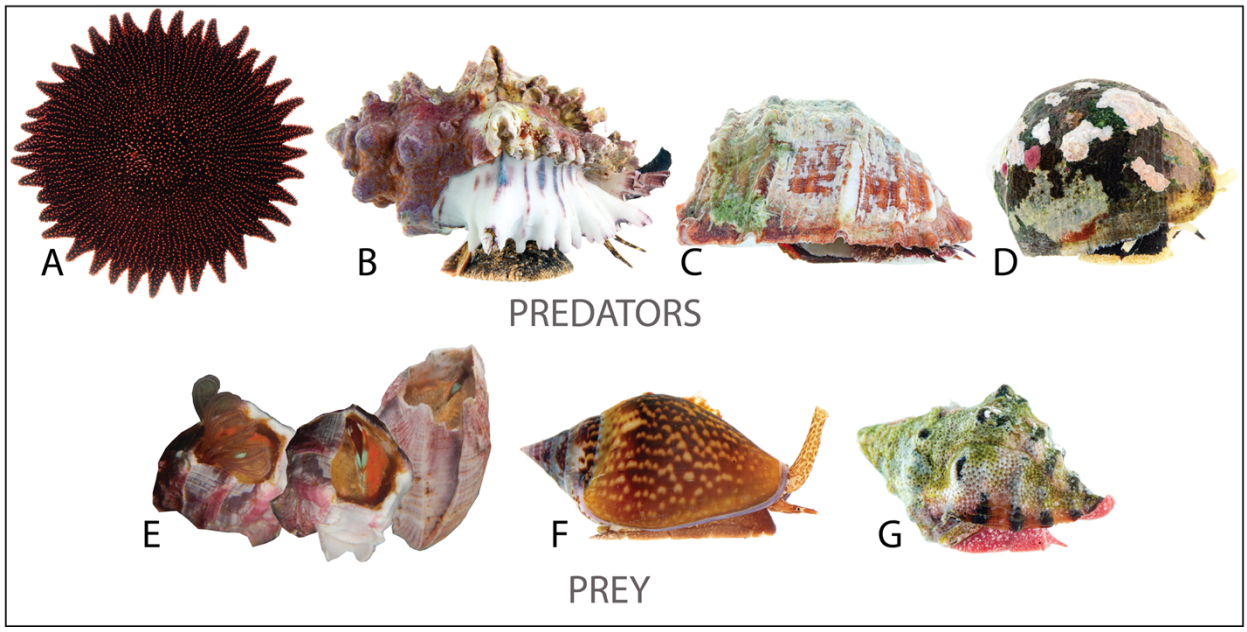

Figure 2. The study species used in the predation experiments that quantified the effect of temperature on predation rate by four marine carnivores that inhabit rocky, subtidal reefs of the Galápagos. (A) *Heliaster cumingi,* (B) *Hexaplex princeps*, (C) *Tribulus planospira*, and (D*) Vasula melones*. The three prey species used were (E) *Megabalanus peninsularis*, (F) *Columbella haemastoma* (note this image is of the visually very similar congener *C. fuscata*), and (G) *Engina pirostoma*. In the experiments, predator species A-C were fed *Megabalanus* and *Vasula* was fed the two small herbivorous snails (F and G). Species sizes, including their relative sizes, are not to scale. Photos A-D, F and G were taken by Jose Vieira. E was taken by Favio Rivera.

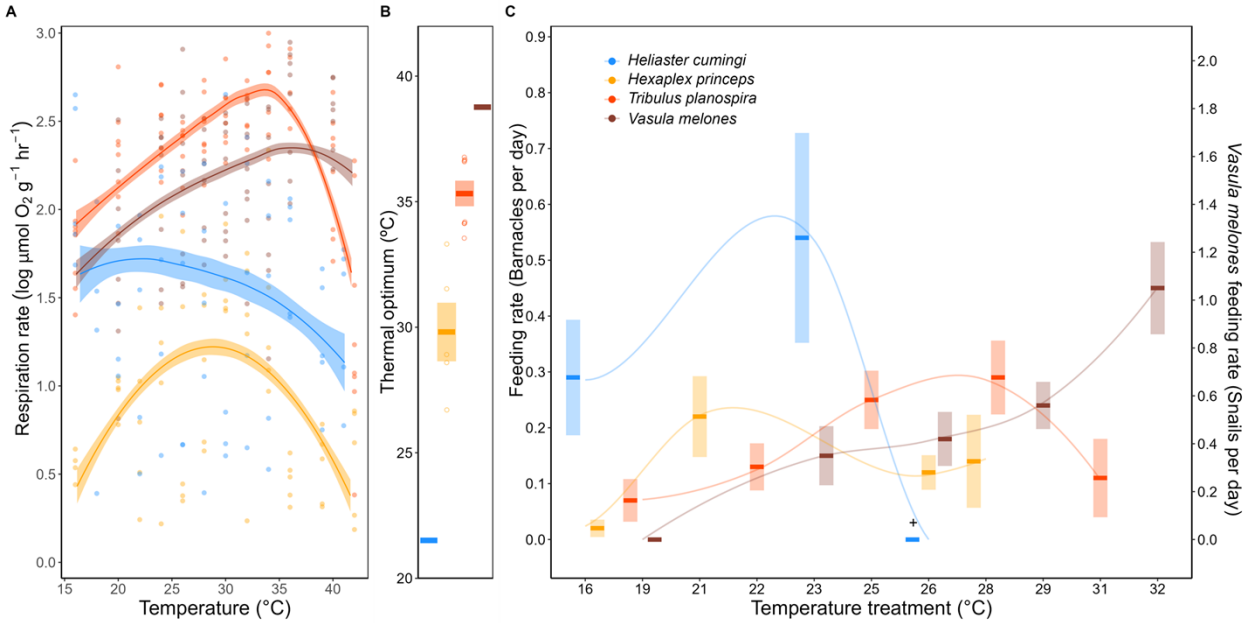

Figure 3. Effects of temperature on the respiration and predation of four common invertebrate carnivores found on shallow subtidal rocky reefs of the Galápagos. **A)** Thermal Performance Curves (TPCs) for each species based on measurement of mass-normalized respiration across a range of temperatures. **B)** The thermal optima (T_{opt}) of respiration for the four predators, calculated from the TPCs. **C)** Functional responses of predation to temperature. *Vasula* was fed two snail prey (*Engina pirostoma* and *Columbella haemastoma*) and the other three predators were fed the barnacle *Megabalanus peninsularis.* Predation trials were performed in laboratory mesocosms at the Galapagos Science Center and each temperature trial lasted two weeks (samples sizes ranged from 5 to 8, Table 1). Trials for each species were performed independently. In **B** and **C** Solid horizontal lines are mean values and associated vertical shaded bars are ±1SE, while in **A** shaded bars 95% confidence intervals. We fit curves for each species in **C** using the geom_smooth function in ggplot2 to help visualize the predation TPCs. See Supplementary Information for additional details about the predation experiments and respiration measurements.

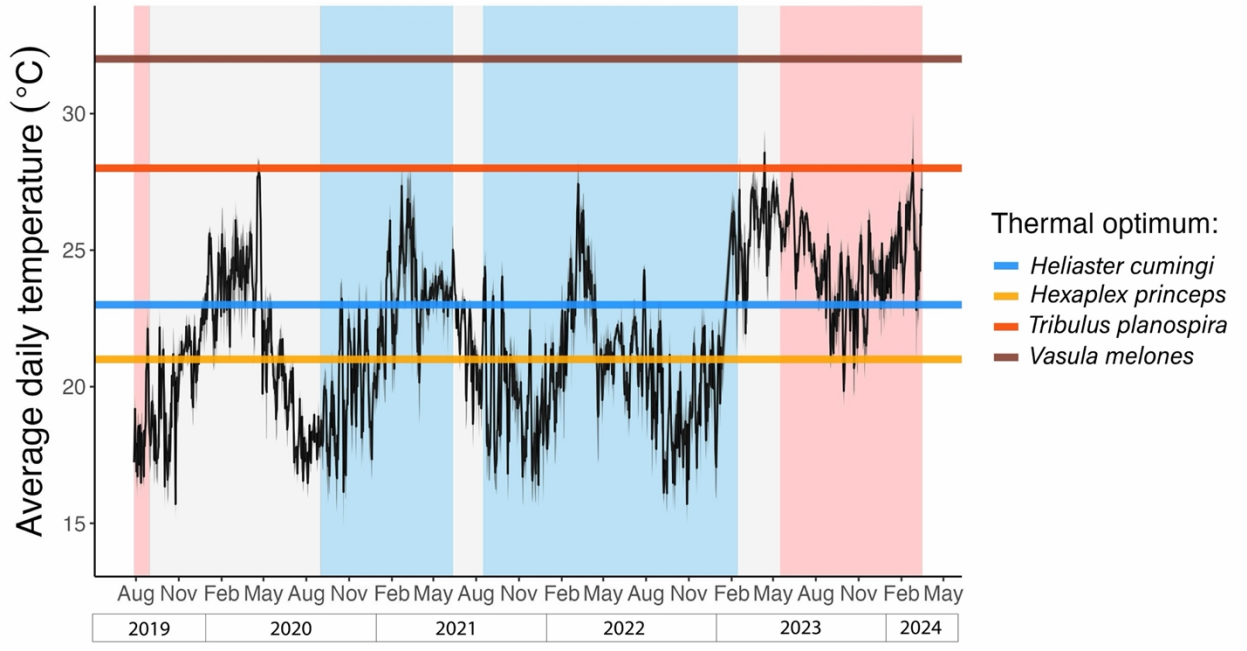

Figure 4. Recent benthic temperature at Cerro Mundo reef, San Cristóbal island, Galápagos at 10m depth. Shaded areas of the graphic indicate the status of the ENSO cycle during the study period (El Niño red, La Niña blue, and neutral conditions in light grey) based on NOAA's Oceanic Niño Index (ONI) https://www.climate.gov/news-features/understanding-climate/climate-variability-oceanic-nino-index). The four horizontal lines overlaying the temperature data are the estimated mean thermal optima for predation (as show in Fig 3C) by the four experimental carnivores.

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