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Upper thermal limits and risk of mortality of coastal Antarctic ectotherms

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Antarctic marine animals face one of the most extreme thermal environments, characterized by a stable and narrow range of low seawater temperatures. At the same time, the Antarctic marine ecosystems are threatened by accelerated global warming. Determining the upper thermal limits (CT_{max}) is crucial to project the persistence and distribution areas of the Antarctic marine species. Using thermal death time curves (TDT), we estimated CT_{max} at different temporal scales from 1 minute to daily and seasonal, the predict vulnerability to the current thermal variation and two potential heatwave scenarios. Our results revealed that CT_{max} at 1 min are far from the temperature present in the marine intertidal area where our study species, showing Echinoderm species higher CT_{max} than the Chordata and Arthropods species. Simulations indicated that seasonal thermal variation from the intertidal zone contributed to basal mortality, which increased after considering moderate scenarios of heatwaves (+2°C) in the Shetland Archipelago intertidal zone. Our finding highlighted the relevance of including exposure time explicitly on the CT_{max} estimates, which deliver closer and more realistic parameters according to the species that may be experiencing in the field.

KEYWORDS

upper thermal limits, heatwave, Antarctic peninsula, marine ectotherms, temperature mortality

Introduction

Global warming (GW) poses one of the greatest threats to biodiversity (Pecl et al., 2017), leading by anthropogenic activities that are likely to increase the frequency of mean temperatures and extreme heatwaves in regions such as the Antarctic continent (Robinson et al., 2020; González-Herrero et al., 2022; Turner et al., 2022). Polar areas such as Antarctica Peninsula have experienced the increasing effect of GW due to anthropogenic activities worldwide affecting surface seawater temperature variation in the last 50 years to about ~ 2°C

(Meredith and King, 2005; Cook et al., 2016; Morley et al., 2020). These extreme zones are also characterized by marine species adapted to relatively stable and isolated conditions, which are harmed due to the increased temperature associated with GW (Peck, 2018). The increased seawater temperature and their impact on Antarctic animals, represent an ideal scenery to understand the impact of increased GW on habitats and species adapted to low temperatures.

Because the shape of thermal performance is determined by multiple sensitive biological rates (Lefevre et al., 2021), this biological phenomenon is ultimately linked with the thermal limits for life and death in ectotherms experience. Also, thermal windows that a species can successfully tolerate providing a good insight into the thermal niche of taxa (Rezende et al., 2014), helping determine species distribution modeling and predict response to GW (Sunday et al., 2012; Liao et al., 2021; Ørsted et al., 2022). Determining the consequences of GW on Antarctic marine communities is crucial to building a detailed description of the organismal performance in challenger thermal conditions, which aids in predicting the thermal tolerance responses from species under thermal stress (Sinclair et al., 2016). Based on the intimate nature of intensity and time of exposition that thermal stress had, Thermal Death Time curves (TDTs) have been explicitly formalized to evaluate the impact of time on the critical response to thermal stress (Rezende et al., 2014; Jørgensen et al., 2021). Recently, a detailed description of upper thermal limits from 39 ectotherm marine species belonging to the Antarctic ecosystem has revealed differences in thermal sensitivity among taxa (Molina et al., 2022). This approach using TDTs explicitly considers exposure time to thermal stress on an ecological scale. This remarkable methodological tool allows for specifying relevant temporal windows of thermal stress. Then, the risk of extirpation due to the temperature increment in bounded time, such as extreme heatwave events, may be determined (Hobday et al., 2016; Hobday et al., 2018). For animals that inhabit outer regions, thermal sensitivity is an urgent need due to assessing the magnitude of time effects to obtain a precise estimate of CT_{max} (Peralta-Maraver and Rezende, 2021), which is valuable information to predict temperature mortality in field conditions (Rezende et al., 2020).

Southern ocean species inhabitant constantly cold environments characterized by thermal stenothermality (Peck, 2005), and slight differences in thermal environment can be enough to cause differences between species (Bilyk and DeVries, 2011; Sandersfeld et al., 2017), populations (Morley et al., 2009), and spatial distribution (Morley et al., 2010). Several phenomena, such as interspecific differences, trophic levels position, and body size variation, significantly affect thermal limits (Peck et al., 2009). The mismatch with the upper thermal limits and the temperature that Antarctic animals experience in the field (Peck et al., 2009; Beers and Jayasundara, 2015) may be attributable to sub-estimated the effect of exposure time in the experimental trial (Molina et al., 2022). According to the evidence above, this work aims to evaluate the upper thermal limits of seven marine ectotherm Antarctic species (Chordata 3 spp., Arthropoda 2 spp., and Echinodermata 2 spp.), standardizing by the exposition time (T_{ko} 1 min) making the measures comparable among experimental trial and species (Rezende et al., 2014). Thus, based on *in situ* records of seawater intertidal temperature variation (Kuklinski and Balazy, 2014), and an analytic approach to evaluate

risk of mortality to Antarctic marine species (Molina et al., 2022), we quantify vulnerability to the current condition of thermal variation and two scenarios (+2°C 10 days and 30 days) of moderate heatwaves (Hobday et al., 2016) that those ectotherm species may experience in field conditions.

Methods

Animal collection

Fieldwork was carried out in January 2020 in the lower intertidal zone off the South Shetland Island, Fildes Bay, King George Island (62°11'S, 58°59'W). A total of 20 Antarctic juvenile fishes were collected from three species *Harpagifer antarcticus* (12), *Trematomus newnesi* (6) and *Lepidonotothem nudifrons* (2), and 14 arthropods individuals from two species *Bovallia gigantea* (4), and *Glyptonotus antarcticus* (10), and 19 echinoderms from two species *Odontaster validus* (9) and *Sterechinus neumayeri* (10). All animals were caught using a 12-inch aquarium fish net and hands turning over rocks off the intertidal zone. After, animals were immediately deposited in coolers with constant aeration and carried alive to the laboratories infrastructures of Instituto Antártico Chileno (INACH) in Escudero Antarctic Scientific Station. This laboratory facility includes several 50 L tanks with circulating and filtered, aerated seawater. The animals were transferred to aquariums with seawater at a controlled temperature ($1 \pm 0.3^\circ\text{C}$), salinity of 33 (± 0.5) psu, under natural photoperiod, and no feeding. These conditions were maintained for at least 48 hours to allow them to be acclimated to captivity conditions before undergoing the thermal trials. All animals were kept in separated 50 L aquariums during captivity before the thermal trials.

TDT curves to CT_{max}

All animals individually were subjected to a temperature ramp, to fishes and arthropods with an increment of $0.07^\circ\text{C min}^{-1}$ and echinoderms, a ramp of $0.08^\circ\text{C min}^{-1}$. The experimental trial stopped when animals presented signals of thermic stress such as loss of equilibrium, defined as the inability of fish and arthropods to maintain dorso-ventral orientation for at least 1 min (Beitinger et al., 2000), and to echinoderms loss of adhesion to the surface of the metabolic chamber or showed lack of evident movement of tube feet or spines (Peck et al., 2009). These procedures were repeated until all individuals were measured during the experiment time. At the end of trial routines, all individuals were euthanized using an overdose of BZ20, following bioethics protocols of Universidad Andres Bello, and body mass and length were recorded using a caliper and analytical balance.

To obtain a proper estimate that reflects both upper thermal critical temperature and exposition time, we combine the CT_{max} observation (i.e., the temperature that would result in knockdown or death) from the ramping experiment with the respective recorded time (t). Using these two parameters (CT_{max} and t), we build the thermal death time (TDT) curves (eq. 1) (Rezende et al., 2014) to estimates Standardized T_{ko} ranges.

$$T_{ko} = CT_{max} - z \text{Log}_{10} t, \quad (1)$$

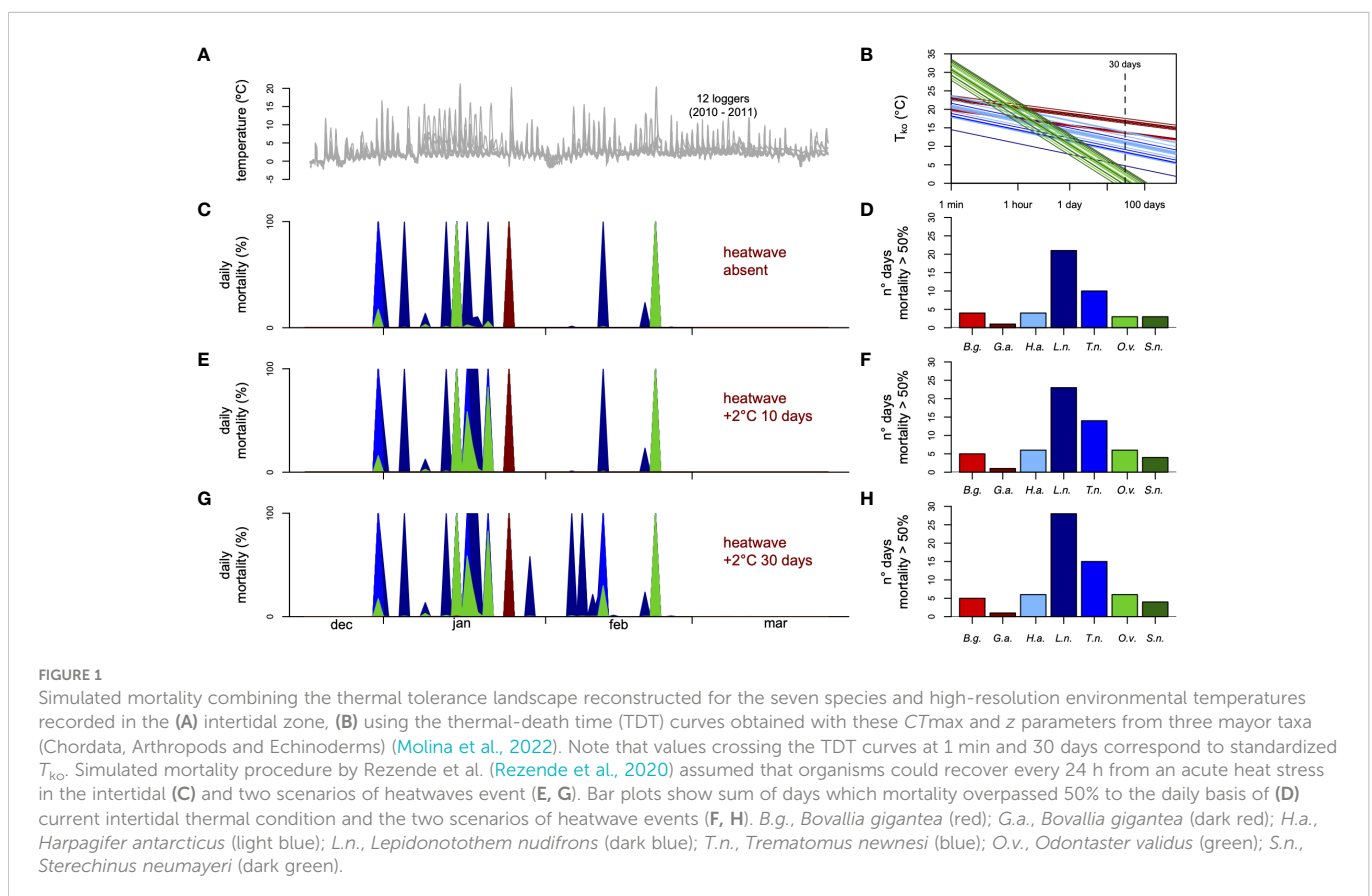
To thermal sensitivity parameter (z), which describes how thermal tolerance decays with the duration of the heat challenge (i.e., the net reduction in T_{ko} resulting from a tenfold increase in exposure time), we used the z estimates from Antarctic ectotherm marine species nearly related with the species studied here (Molina et al., 2022). Then, we mapped this slope back onto the experimental estimated of T_{ko} and standardized t to estimate the expected tolerance temperature at $t = 1$ minute, 10 days, and 30 days (eq. 1) on a species-specific basis. Then we built a single TDT per individual per the seven species considered in this study, obtained a total of 53 curves (Figure 1B).

Predicting thermal mortality

Combining standardized T_{ko} from the experimental essay with thermal sensitivity reported in literature and field temperatures in Antarctica, we were able to determine if these organisms could be experiencing thermal mortality under the current condition as well as two moderate marine heatwaves episodes scenarios (Hobday et al., 2016).

Thermal scenarios were built using temperature data obtained temperatures with a 1-min resolution from these datasets *via* interpolation and calculated the ‘instantaneous mortality’ associated with these temperatures as described in (Rezende et al., 2020). Intertidal temperature records were obtained from 12 dataloggers covering the whole tidal range of Admiralty Bay, King George Island, with a resolution of 5 min between December 2010 and March 2011 (Kuklinski and Balazy, 2014). Because the main goal of this analysis is to determine if current recorded temperatures can lead to thermal

mortality in Antarctica, we selected these locations as they are representative of warmer waters within the Western Antarctic Peninsula (Barnes and Peck, 2008) and used records from the austral summer between December and March in subsequent analyses. With the interpolated temperature data with a 1-min resolution at hand, we estimated the predicted thermal mortality for an ‘average’ individual organism belonging to each of seven species of chordate, arthropod, and echinoderm. As explained in detail elsewhere (Rezende et al., 2020), this procedure involved (1) using the mean CT_{max} and z to obtain a generic TDT for each species, (2) simulating the tolerance landscape from these TDTs assuming that knockdown times at each measurement temperature are normally distributed with $CV = 0.25$ ($CV = \text{standard deviation [SD]}/\text{mean}$) [see Supplementary Information in (Rezende et al., 2020)], and then (3) running the dynamic.landscape function combines the tolerance landscapes with the ambient temperature records to estimate the predicted mortality under these field conditions. We performed simulations for all species under three contrasting scenarios. First, under the highly variable thermal conditions, with the temperature data from the 12 data loggers deployed in the intertidal zone and assuming that animals recover when the temperatures drop at night (this is accomplished by calculating daily survival iteratively and resetting the survival curve at 00:00). Second, under two scenarios of a moderate marine heatwave as is described in (Hobday et al., 2016), with an average increment of seawater of $+2^\circ\text{C}$ for a period of 10 days and 30 days. As vulnerability indices, we calculated each species’ average mortality across days along loggers for the intertidal records ($n = 12$ loggers per species). All analyses were performed in R environment (R Development Core Team, 2019)



Results

Thermal tolerance and TDTs estimates

Body sizes (fresh weight) of animals collected ranged between 0.88 - 37.1 g. Echinoderms (*Odontaster validus* and *Sterechinus neumayeri*) were the bigger animals measured with a body size mean of $18.34 \pm 8.84\text{SD}$ and ranged between 5.49 - 37.1 g., followed by Chordata (*Harpagifer antarcticus*, *Trematomus newnesi* and *Lepidonotothem nudifrons*) animals with a body size mean of $8.84 \pm 5.22\text{SD}$ and ranged between 2.38 - 25.25 g., and Arthropoda (*Bovallia gigantea*, and *Glyptonotus antarcticus*) with a body size mean of $3.58 \pm 1.54\text{SD}$ and ranged between 0.88 - 6.049 g. Having a rough estimate of upper thermal limits with the dynamic essay and the thermal sensitivity obtained from Molina et al. (Molina et al., 2022), we then proceeded to calculate expected T_{ko} following 1 min exposure to compare among the major taxa which species belong at the same temporal scale. The mixed model ANOVA with phylum as a random effect revealed significant differences among Echinoderms, Chordata, and Arthropod species ($F_{2,4} = 57.95$, $p = 0.011$). Pairwise comparison indicated differences between Echinoderms and Chordata ($t = -10.291$, $p = 0.0011$) and Arthropods species ($t = -5.766$, $p = 0.0011$), and absence of differences between Arthropods and Chordata ($t = 2.787$, $p = 0.1024$). The Echinoderm species showed higher T_{ko} 1 min with *S. neumayeri* $31.18 \pm 2.10\text{SD}$ and *O. validus* $30.65 \pm 1.29\text{SD}$, followed by Arthropods species *G. antarcticus* with 22.42 ± 1.21 and *B. gigantea* $19.81 \pm 0.14\text{SD}$, and Chordata species *H. antarcticus* $21.04 \pm 1.86\text{SD}$, *L. nudifrons* $17.57 \pm 4.33\text{SD}$ and *T. newnesi* $19.08 \pm 1.59\text{SD}$.

Predicted mortality in the field

We estimated predicted daily mortalities over 100 days during the Austral summer for the intertidal zones. Our simulations suggest that current temperatures can elicit some thermal mortality depending on the TDT profiles of different species. In our field thermal stress scenario (Figure 1A), mortality surpassed 50% on five occasions for arthropods *B. gigantea* (4) and *G. antarcticus* (1), 35 occasions for chordates *L. nudifrons* (4), *H. antarcticus* (21), *T. newnesi* (10), and 6 for echinoderms *O. validus* (3) and *S. neumayeri* (3) and all these instances involved primarily loggers at higher tide locations (Figures 1C, D). Accordingly, the mean daily mortality estimated per logger differed significantly across species based on regular analysis of variance ($F_{6,77} = 6.45$, $p = 6.34 \times 10^{-6}$), suggesting that one arthropod (*B. gigantea*) and chordates are more susceptible to high-temperature fluctuations than other species. Note that, even though pairwise differences between species were not always statistically significant (Figure 1), the inclusion of loggers with less extreme temperatures decreases the statistical power of this analysis as mortality in these circumstances is nearly zero for all groups. For simulations assuming heatwaves with sea water warming of $+2^\circ\text{C}$ by a duration of at 10 days and 30 day the increment in days when mortality surpassed 50% was over of 29% and 42% respectively (Figures 1E, G), in both cases mainly driven by increment in

mortality to *B. gigantea* (1 day both scenarios), *L. nudifrons* (2 days both scenarios), *H. antarcticus* (2 days and 7 days respectively), *T. newnesi* (4 days and 5 days respectively), *O. validus* (3 days both scenarios) and *S. neumayeri* (2 days both scenarios) (Figures 1G, H). Similarly, mean predicted daily mortality differed significantly between species ($F_{6,77} = 6.475$, $p = 1.47 \times 10^{-5}$), once again supporting differences in susceptibility to warm waters between groups (Figure 1).

Discussion

Precise estimates of upper thermal limits are essential to determine the impact of GW on Antarctic species, either because they have evolved in habitat characterized by narrow and extreme thermal environments or because their habitats are changing rapidly (Morley et al., 2020). Here, we combined an experimental essay on Antarctic organisms with thermal sensitivity to build an accurate and comparable estimate of upper thermal limits through the taxa. Our results evidence a clear difference in thermal tolerance among Arthropods Chordata and Echinoderms, as well as the relevance of distinguishing the time effect (i.e., T_{ko} 1 min, T_{ko} 1 day and 30 days) on the vulnerability to warming conditions (Richard et al., 2012; Molina et al., 2022). In addition, under the tolerance landscape framework (Rezende et al., 2020), we showed that temperature variation from the intertidal area did affect the predicted mortality to the studied species, though in different intensities depending on the taxa. Also, conservative scenarios of extreme marine warming events (heatwaves) during an Austral summer at the Antarctic archipelago did impact predicted mortality (Figure 1A), showing the vulnerability of the Antarctic marine species to GW on an ecological scale.

According to previous evidence about thermal tolerance to Antarctic species (Peck et al., 2009), we found that estimators of thermal limits such as CT_{max} are above the temperature these animals experience in natural conditions. Our approach explicitly followed a correction by time exposure and used estimates of thermal sensitivity to Antarctic species (Molina et al., 2022). It is one step forward because TDT curves allow building an estimate of time scale with ecological significance, either daily, monthly, or seasonally temporal window (Figure 1B). That is important because the role of exposure time in determining temperature tolerance is a perspective little studied in the literature (Lefevre et al., 2021), but essential if we want to evaluate the impact of GW on Antarctic species (Morley et al., 2020). For instance, our study is the first to show evidence of upper thermal limits to Malacostraca Arthropods such as the amphipodan *Bovallia gigantea* and the isopoda *Glyptonotus antarcticus*. Despite the interspecific difference among Antarctic arthropods, our findings cover the wide range of thermal limits reported in the literature, from 32.5°C to 6.7°C (Lahdes et al., 1993; Peck, 2004; Peck et al., 2009; Peck et al., 2010; Toullec et al., 2020). Also, our results on Chordata animals such as *Harpagifer antarcticus*, *Lepidonotothem nudifrons*, and *Trematomus newnesi* are according to the wide range of upper thermal limits Antarctic nototenids from 21.58°C to 5°C (Somero and

DeVries, 1967; Peck et al., 2009; Beers and Sidell, 2011; Bilyk and DeVries, 2011; Joyce et al., 2018). Likewise, the Echinoderms *Odontaster validus* and *Sterechinus neumayeri* showed upper thermal limits, as reported previously, in a range of 24.7°C to 10.9°C (Peck et al., 2009; Peck et al., 2010; Morley et al., 2012). Undoubtedly, species comparison allows us to visualize the diversity of the thermal tolerance capacity that Antarctic species must possess, which underpins different physiological architectures. However, discrepancies in methodological approaches and traits evaluated may obscure another phenomenon in the variation in thermal tolerance limits (Williams et al., 2016), making it difficult to build proper interspecific comparisons. Comparison among species that inhabit the same environments may differ in physiological strategies to cope with environmental thermal stress, constrained to a specific ecological scale (Peck, 2011; Byers, 2020). Therefore, physiological and genetic mechanisms are needed to understand the variation in thermal tolerance and distinguish phenotypic thermal strategy from adapting to extreme and cold Antarctic habitats, including physiological, molecular mechanisms (González-Aravena et al., 2021; Saravia et al., 2021), and behavioral responses influenced changes in distribution ranges (Morley et al., 2010).

Predicting ectotherm species' response to GW is key to understanding the global anthropic effect on biodiversity (Pecl et al., 2017). Identified as an anthropic global driver affecting the polar marine ecosystem, such as in the Antarctic peninsula, where increments until 2°C on the current pattern of temperatures are expected shortly (Hellmer et al., 2017; Moffat and Meredith, 2018). Here, the higher variation in temperature records to the intertidal zone may be linked with a daily higher sensibility to the tidal pattern experienced in this coastal area (Figure 1), which has been described as an extended pattern along the marine coast (Byers, 2020; Liao et al., 2021). As an atmospheric event to date, heatwaves have been related to the Antarctic continent (Robinson et al., 2020; González-Herrero et al., 2022; Turner et al., 2022), and the recurrence of extreme marine heatwaves worldwide (Hobday et al., 2018) makes it possible to expect those events around Antarctica. Due to that, GW heatwaves in marine ecosystems affect the biological communities (Paganini et al., 2014; Hobday et al., 2016; Roberts et al., 2019; Magel et al., 2020), and exposure time is urgently needed to quantify the effect of thermal stress on organismal performance (Williams et al., 2016; Lefevre et al., 2021). We used TDT curves that use the exposure time linked with thermal limits (Rezende et al., 2014), which combine real-time scales to thermal stress, allowing us to predict the effect of thermal variation in the ecological scale (Rezende et al., 2020). We modeled mortality in a window of 24 hours along with the 100 days considered from the Austral summer, then the relevant time scale of T_{ko} built from TDTs curve was from 1 to 1440 minutes to estimate mortality. The cumulated effect on a daily scale was enough to produce mortality, and this rise when moderate heatwaves (Hobday et al., 2018) were considered into the daily variation (Figure 1). Based on the higher thermal sensitivity (z) of the echinoderm *O.validatus* (T_{ko} 1 min = 30.65; T_{ko} 1 day = 10.41) and *S. neumayeri* (T_{ko} 1 min = 31.18; T_{ko} 1

day = 10.93), this mayor taxa seems to be better adapted to future warming events, which may be linked with the sessile condition and less capabilities to escape to local thermal stress (Sunday et al., 2011; Molina et al., 2022). Although lower thermal sensitivity may impact long-term response from the three Chordata *L. nudrifrons* (T_{ko} 1 min = 17.57; T_{ko} 1 day = 10.91), *H.antarticus* (T_{ko} 1 min = 21.04; T_{ko} 1 day = 14.39), *T. newnesi* (T_{ko} 1 min = 19.81; T_{ko} 1 day = 13.15) and the two Arthropods *B. gigantea* (T_{ko} 1 min = 19.81; T_{ko} 1 day = 15.61) and *G. antarticus* (T_{ko} 1 min = 22.41; T_{ko} 1 day = 18.20), the lower temperature which those species responded to the experimental thermal challenge, determine higher vulnerability to increment of temperature in a daily scale and its cumulative effect on the entire Austral summer intertidal area as well as the effects of the moderate heatwave.

In overview, precise predictions of the Antarctic fauna responses to global warming are a priority to conservation and decision-makers because of the pristine condition of the continent and the evolutionary and ecological process that has built its unique biological diversity. Our finding reveals that Antarctic marine species may be under thermal stress under less temperature but on a more extended time scale, such as heatwaves events, indeed, temperatures that may be organisms experienced at the current time in the wild. In line, differences among species are influenced by the thermal sensitivity parameter (Rezende et al., 2014), which summary the phenotypic response to the thermal difference in a specific time (minutes). We interpreted these interspecific differences as a consequence of the morphological, physiological, and behavioral adaptations that distinguish the species studied to face thermal stress in the Antarctic marine ecosystem as consequences of global warming due to human activities worldwide.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://datadryad.org/stash/share/CdFlhwoocjOslIlgf5dzjb9OjJa2V7EzLtiqxyuPokw>.

Ethics statement

The animal study was reviewed and approved by Comité de Bioética, Universidad Andrés Bello.

Author contributions

MC: Conceptualization, Investigation, Writing – original draft, Writing – review & editing, Visualization, Data curation. MRG-H: Investigation, Writing – review & editing. MA: Writing- Reviewing and Editing. ER: Writing- Reviewing and Editing, Funding acquisition. FB:

Writing- Reviewing and Editing. CG-M: Writing- Reviewing and Editing, Funding acquisition. JP: Supervision, Writing- Reviewing and Editing, Resources, Funding acquisition. All authors contributed to the article and approved the submitted version.

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