Journal of Experimental Marine Biology and Ecology 501 (2018) 109–117

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Prior heat accumulation reduces survival during subsequent experimental heat waves

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ARTICLE INFO

Keywords:
Heat waves
Heat accumulation
Tigriopus californicus
Thermal history
Survival
Energetics

ABSTRACT

Heat waves, i.e., periods of extremely hot weather, are expected to increase in frequency and duration under climate change. Repeated exposure to thermal stress events such as heat waves can affect population dynamics and even population persistence. Understanding whether recent thermal history bolsters or hinders demographic responses such as survival or growth during heat waves is crucial for predicting population persistence in the face of climate change. We tested for differential mortality following an experimental heat wave in populations of the splash pool copepod, *Tigriopus californicus*, inhabiting pools that differ in their recent thermal history. We observed differences in survivorship that were correlated with differences in thermal history. Among multiple metrics of thermal history, daily degree-hours (a measure of heat accumulation) best explained heat wave survival such that a higher number of degree-hours resulted in reduced heat wave survival. This finding is consistent with the hypothesis that repeated exposure to sublethal temperatures reduces thermal tolerance. Increasing heat wave intensity and duration, or warmer conditions that increase heat accumulation followed by heat waves may negatively impact population persistence by exacerbating the demographic effects of heat waves. The results of this study emphasize the need to integrate mechanistic physiology within the realm of population ecology to bolster the ability to predict population-level responses to climate change.

1. Introduction

Extreme weather events may strongly affect populations due to the large magnitude of change over short periods of time (Parmesan et al., 2000; Jentsch et al., 2007; Helmuth et al., 2014). Periods of extremely hot weather ("heat waves") are predicted to increase in frequency and duration as climate change accelerates (Frich et al., 2002; Meehl and Tebaldi, 2004). Understanding how heat waves affect population persistence is critical for projecting ecological and evolutionary responses to changing weather patterns associated with climate change. This entails linking the physiology of heat stress responses to demographic processes that influence population growth and adaptation.

Predicting the effect of heat waves on individual survival and performance may require more than understanding physiological stress responses to acute or short-term temperature conditions associated with the heat wave event, such as heat wave intensity (i.e., maximum daily temperature) and duration (length of the heat wave). Heat wave survival may reflect thermal experiences prior to the heat wave event itself (Huber et al., 2010). For example, exposure to sublethal but physiologically stressful temperatures may increase thermal tolerance through the physiological processes of heat "hardening" or acclimatization (Lindquist and Craig, 1988; Bowler, 2005; Loeschcke and Sørensen, 2005). In this case, exposure to sublethal temperature stress before a heat wave is expected to increase survival during and following the heat wave. In contrast, thermally stressful exposures may lower thermal tolerance due to energetic constraints associated with declines in aerobic scope, the amount of energy available beyond the maintenance of basal metabolic costs, under physiologically stressful conditions (Coma et al., 2009; Pörtner, 2010; Sokolova et al., 2012). In this context, heat waves following a series of sublethal thermal stress events would be expected to cause higher mortality than heat waves following benign conditions.

An individual's time-course of body temperatures (thermal history) shapes its tolerance to future heat stress events (Ward and Stanford, 1982; Huey and Kingsolver, 1989; Angilletta et al., 2002; Terblanche et al., 2006; Schulte et al., 2011; Dowd et al., 2015; Kingsolver and Woods, 2016; Sinclair et al., 2016). Physiological responses to thermal history may explain why thermal tolerance increases following one set of thermal exposures and declines following another. For example, brief exposures to stressful temperatures that initiate the subcellular heat shock response can protect cells against subsequent exposures to high temperatures by elevating concentrations of heat shock proteins

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https://doi.org/10.1016/j.jembe.2018.01.012
Received 1 June 2017; Received in revised form 17 December 2017; Accepted 27 January 2018
Available online 12 February 2018
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(Lindquist and Craig, 1988; Feder and Hofmann, 1999). Longer-term temperature acclimatization can involve changes at many levels of biological organization, such as biochemical changes (e.g., metabolic reorganization) and structural changes (e.g., changes in cell membrane fluidity) (Somero, 2002). In contrast, exposure to high temperatures that reduce aerobic scope may diminish energy reserves via impacts on energy allocation and production, especially when high temperatures are experienced over an extended exposure duration (Pörtner, 2010; Sokolova et al., 2012). Impacts on energy reserves may reduce the efficacy of physiological stress responses (Hand and Hardewig, 1996) and reduce thermal tolerance.

In this study, we examined the influence of recent thermal history on mortality during experimental heat waves in populations of the splash pool copepod, *Tigriopus californicus*. *T. californicus* is fully aquatic and exhibits restricted thermoregulatory behaviours and low thermal inertia (i.e., the rate at which an individual reaches equilibrium body temperature after a change in environmental temperature), making it reasonable to equate *T. californicus* body temperature to the surrounding water temperature (Huey et al., 1999; Fitzgerald and Nelson, 2011). To characterize splash pool thermal history, we used hourly water temperature measurements to estimate average daily maximum temperatures, average daily mean temperatures, average daily minimum temperatures, average daily degree-hours (a time-based integral of daily heat accumulation), the standard deviation in daily temperature, the frequency of days with temperature exceeding 26 °C and days exceeding 32 °C, and the absolute maximum weekly temperature.

We predicted that higher experimental mortality would occur during and after heat waves with increasing heat wave intensity, and we predicted that mortality rates would vary regionally, correlated with regional differences in thermal history. We expected that if beneficial effects of acclimatization or heat hardening were important, we would observe lower mortality in experimental heat waves associated with populations from splash pools having recently experienced higher daily temperatures. In contrast, if negative effects of energetic limitations on thermal tolerance were more important, we would observe higher mortality in populations from splash pools that experience higher daily degree-hours.

2. Materials and methods

2.1. Study system, site descriptions and field collection

T. californicus is distributed from Baja California to Southeast Alaska. Populations occupy splash pools in the supralittoral zone of the high intertidal – a zone characterized by large fluctuations in the abiotic environment. The replenishment of splash pools with seawater may only occur during the highest tides each tidal cycle or with storm events, one or two days per month (Egloff, 1966; Dybdahl, 1994).

Splash pool water temperature was measured during the early summer in four regions along the southern coast of Vancouver Island, British Columbia (Fig. 1). This area spans a regional thermal cline. Cooler temperatures are found towards the oceanic end of the Straight of Juan de Fuca and temperatures progressively warm as one moves into the eastern parts of the Salish Sea (Harley, 2011). We glued Ibutton temperature loggers (Embedded Data Systems, LLC) using epoxy into 38 splash pools nested within four regions along the thermal cline (N = 11, 7, 10 and 10 for Botany Bay, Fishboat Bay, Saxe Point Park and Neck Point Park, respectively). These were deployed within three days of each other in mid-May 2016 and recorded hourly temperatures for the following 13 weeks.

We used temperature data from the final seven days of field conditions to characterize splash pool thermal history for several reasons. First, it is unlikely that *T. californicus* individuals collected at the end of summer experienced the thermal conditions recorded earlier in the summer. *T. californicus* populations likely underwent extinction and recolonization metapopulation dynamics consistent with the evaporation and re-filling of splash pools (Johnson, 2001; Altermatt et al., 2012). Moreover, individual life-span in *T. californicus* is approximately 50–90 days (Powlik et al., 1997), and individuals alive in May were unlikely to still be alive in August. Furthermore, temperature in coastal localities tends to be temporally autocorrelated, which leads to periods of above average temperatures and periods of below average temperatures as opposed to a scenario of no temporal autocorrelation, where the variance in temperature is equally distributed around the mean temperature over the full duration of the time series (Vasseur and Yodzis, 2004). Thus, even in splash pools that did not evaporate, populations from those splash pools are less likely to be affected by temperature conditions from earlier in the summer relative to the more recent conditions they have experienced. Finally, heat shock proteins can have deleterious effects at high concentrations that reduce future thermal tolerance (Krebs and Feder, 1997). These costs arise by interfering with cellular processes, especially during development when cell growth and division is proceeding at high rates, or by incurring a high energetic cost that depletes a cell's energy and nutrient stores (Feder and Hofmann, 1999). Elevated heat shock protein concentrations have been found to persist in the cell for periods lasting up to 50 h post-heat stress in the marine gastropod *Tegula sp*. (Tomanek and Somero, 2000), and for periods up to 96 h post-heavy metal exposure in *T. japonicas* (Kim et al., 2014). In *T. californicus*, both the naupliar and copepodid developmental stages last for 7–10 days each (Powlik et al., 1997), and individual thermal tolerance may be negatively affected by high concentrations of heat shock proteins persisting in the cell after their upregulation in response to heat stress. Consequently, these features of *T. californicus* life history and the time course of heat shock protein effects strongly suggest that seven days is an appropriate period over which to assess the demographic consequences of acute physiological responses to thermal history. We also tested for an effect of thermal history on heat wave survival by characterizing thermal history over additional time-frames (3, 14, and 28 days; Supplementary Appendix B).

T. californicus populations were collected from every splash pool that contained populations with sufficiently high densities for collection. This excluded 19 splash pools that had completely evaporated or contained too few individuals to collect. Thus, *T. californicus* populations were collected from 19 out of the 38 splash pools (N = 6, 2, 5, and 6 for Botany Bay, Fishboat Bay, Saxe Point Park and Neck Point Park, respectively). Individuals were transported back to the University of British Columbia in 120 mL sample cups. Copepods were fed ground *Spirulina* algae (Max Pro brand fish food), and held at room temperature (20–21 °C) for 3–4 days before being subjected to experimental heat waves.

2.2. Experimental heat waves

To test for an effect of thermal history on survival during an experimental heat wave, we subjected individuals to one of two heat wave treatments corresponding to a daily maximum temperature of 26 °C or 32 °C. The experimental heat waves reflect temperature profiles observed in the field (Fig. 2). Daily fluctuations of experimental heat waves included a six-hour gradual increase from the minimum temperature (20 °C), 1 h at the maximum temperature (26 °C or 32 °C), and a six-hour decline back to the minimum temperature (Supplementary Fig. 1). The maximum experimental heat wave temperatures were selected to span a range of high temperatures encountered in the field. Field summer temperature data show that 26 °C is in the 50th percentile of daily maximum temperature and 32 °C is in the 5th percentile of daily maximum temperature (Supplementary Table 1). The thermal environments in the lab were created with a Panasonic M1R-154 programmable incubator.

From each source population, 60–104 individuals (mean: 84.5

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