



Mussels show capacity for persistence under, and recovery from, marine heatwaves

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Abstract

The ability of marine organisms to persist under, and recover from, periods of stressful conditions will shape their occurrence in future oceans characterized by exacerbated marine heatwaves (MHWs). Organism persistence and recovery may, in turn, be shaped by traits of the organisms themselves including, for example, body size. In the present study, we tested the responses (survival, heart rate, Arrhenius breakpoint temperature – ABT, clearance rate, respiration rate, and condition index) of large (5 cm) and small (3 cm) *Perna viridis* mussels after exposure to a three-week marine heatwave (MHW; +4 °C) and a one-week recovery period. Exposure to elevated temperatures did not affect the survival of large or small mussels, however, at the end of the MHW both size classes exhibited increased heart rate under elevated temperatures, small mussels exhibited increased ABT, and large mussels exhibited significantly increased clearance rate. Following one week of recovery at control temperature, the altered responses had returned to be similar to those of mussels held under control conditions. The results obtained here indicate that both sizes of mussels can readily recover from exposure to short-term elevated temperatures imposed by MHWs, enabling the continued persistence of *P. viridis* mussels in future oceans.

Keywords Climate change · Warming · Temperature · Marine ecology · Asian green mussel · *Perna viridis*

Introduction

Marine organisms and the ecosystems they form are facing altered patterns of extreme environmental conditions as a result of global climate change (Parmesan and Yohe 2003). Therefore, the ability of organisms to respond to, and recover from, periods of stressful environmental conditions will likely contribute to their survival in future oceans. Although our understanding of the immediate effects of stressful conditions on the survival and functioning of organisms is improving (Abram et al. 2017), the capacity of organisms to recover following stressful conditions is uncertain (Suryan et al. 2021). Moreover, the capacity to

respond and recover from stressful periods may vary with biological characteristics, such as body size, yet such context dependencies remain rarely considered (but see Sukhotin et al. 2003). Refining our understanding of the response and recovery capacity of organisms with different biological characteristics will improve the accuracy of projected impacts of global climate change.

A significant source of stress for organisms in marine environments is change in environmental temperature, which can compromise the physiological and ecological functioning of organisms. On a global level, climate change is altering the occurrence of short-term temperature anomalies (Laufkötter et al. 2020). That is, marine heatwaves (MHWs) – anomalous warm periods of at least five days exceeding the 90th percentile of historic temperatures – are predicted to increase in severity, frequency, and duration under global climate change (Hobday et al. 2016; Oliver et al. 2018). Organisms exposed to MHWs typically have higher energetic costs to maintain growth, reproduction, and survival (e.g., Leung et al. 2019; Hemraj et al. 2020; Minuti et al. 2021). As a result, the adjustment of physiological processes associated with energy acquisition and expenditure

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can enable organisms to sustain physiological and ecological functions under MHWs (Madeira et al. 2018).

The capacity of organisms to restore physiological processes in the period following MHWs (e.g., in a recovery period) can be as influential as the adjustments performed when organisms experience the MHW itself (Hemraj et al. 2020). Following exposure to MHWs, the rate and extent to which organisms can adjust processes to pre-MHW levels may be indicative of their recovery capacity (Seifarth et al. 2021). The complete adjustment of processes during recovery ensures that functions are restored after periods of stress, such as MHWs (Giomi et al. 2016; Minuti et al. 2021; Joyce et al. 2022). In contrast, organisms displaying slower or minor changes in processes post-MHW will likely suffer from latent effects that persist beyond the MHW (Minuti et al. 2021). However, few studies to date have considered the capacity for organisms to recover from MHWs and which factors may affect this capacity (but see Hemraj et al. 2020; Minuti et al. 2021; Joyce et al. 2022).

The tolerance and recovery capacity of organisms to periods of stress can be shaped by the morphology of organisms. For example, susceptibility to MHWs can be affected by body size (Denny et al. 2011; Zardi et al. 2016). That is, larger individuals typically allocate more energy to reproductive purposes than smaller ones, which reduces the amount of energy available to compensate for elevated temperature stress (Sukhotin et al. 2003; Carey et al. 2013; Sokolova 2013). Where there are contrasting responses in organisms of different sizes, this pattern can have implications for population structure, which may have repercussions for ecosystem structure and function (Petes et al. 2008).

Changes to ecosystem structure and function will be linked to impacts on species that act as ecosystem engineers. As wide-ranging ecosystem engineers, marine bivalves increase habitat complexity and influence the biodiversity of benthic communities through the formation of biogenic reef structures (Commito et al. 2005; Borthagaray and Carranza 2007; Sousa et al. 2009). Many bivalves, such as mussels, are filter-feeders that play critical roles in the cycling of nutrients and improving water quality in coastal systems (Crooks 2002). One such mussel, *Perna viridis* (Linnaeus 1758), is abundant and widely distributed throughout the Indo-Pacific region (Siddall 1980). In addition to its ecosystem role, *P. viridis* is an economically important aquaculture species across the tropical Southeast Asia region (Rajagopal et al. 2006; FAO 2022). However, such tropical species remain understudied despite projections that tropical regions may experience the highest increase in MHW frequency in coming decades relative to other latitudes (Holbrook et al. 2019; Saranya et al. 2022). Additionally, tropical organisms may be more susceptible to temperature anomalies than their temperate counterparts (Vinagre et al. 2018; Holbrook et al. 2019; Oliver et al. 2019; Saranya et al. 2022).

Here, the responses of *P. viridis* of two size classes were assessed at the end of a simulated MHW and recovery period in a laboratory experiment. The considered responses – including survival, heart rate, Arrhenius breakpoint temperature (ABT), clearance rate, respiration rate, and condition index – were used to understand if MHWs drove shifts in organism persistence and physiology at the end of a MHW and a recovery period. We were testing the hypothesis that if we exposed large and small mussels to the MHW, then at the end of this event the mussels would have altered survival and physiological processes (increased heart rate, higher ABT, increased clearance rate, increased respiration rate), with the susceptibility being size-dependent. We also anticipated that following a recovery period after the MHW, the physiological rates of both large and small mussels would return to be similar to those of organisms that had not experienced the event, and survival would be unaffected while condition index would be reduced in those organisms that had experienced the MHW. Detrimental changes to the survival or physiological state of these organisms could have extensive repercussions on associated ecosystems as MHWs may hinder the ability of these organisms to provide habitat complexity, cycle nutrients, and improve water quality. As a result, elucidating the effects of MHWs is key to understanding the capacity of organisms and their ecological functions to endure and recover from MHWs.

Methods

Mussel collection and maintenance

Large (mean \pm SE; 5.06 ± 0.49 cm, min–max; 4.56–6.03 cm and weighing $0.154 \pm <0.001$ g in dry weight mean \pm SE) and small (3.02 ± 0.39 cm; 2.56–3.53 cm and weighing $0.053 \pm <0.001$ g in dry weight) Asian green mussels, *Perna viridis*, were collected during low tide from Tolo Harbour, Hong Kong SAR, China ($22^{\circ}24'23.4''N$ $114^{\circ}13'08.7''E$) in January 2022. These mussels represent two size classes abundant at the same tidal range during the season of collection in the region (for further detail regarding seasonal dynamics of *P. viridis* in Hong Kong see Lee 1985), with organisms of this size recognized to be sexually mature (Walter 1982). Following collection, mussels were acclimated to laboratory conditions in tanks (W 39 cm \times D 28 cm \times H 28 cm; ~ 22 L volume) filled with sand-filtered, aerated seawater maintained at 21.4 ± 0.3 °C and salinity of $31 \pm <1$ ppt for five days to acclimate organisms to ambient laboratory conditions at this time of year. Water temperature in all tanks was maintained using either 150-W or 50-W bar heaters. Animals were cleaned of all epibionts during laboratory acclimation. Throughout the acclimation and experimental period, mussels were fed once daily with

a phytoplankton diet (Reed MaricultureLPB™ Shellfish diet®). Rations were calculated as 2% of mussel dry flesh weight (g) in dry weight of algae feed (g.L⁻¹) to obtain the appropriate volume as per the manufacturer instructions, who provide further information regarding the dietary content (<https://reedmariculture.com/products/lpb-shellfish-diet>). Temperature and salinity were monitored daily using a digital thermometer (HI98128, Hanna Instruments Inc., USA) and a refractometer (ATC, Aichose Brix Refractometer), respectively (Table 1). All tanks received a daily 50% water change.

Experimental design

To understand how *P. viridis* of different sizes respond to, and recover from, MHWs we used a factorial experimental design with two factors: temperature (control vs. elevated), and period (heatwave vs. recovery), with six replicate tanks per experimental group. Each tank contained 10 mussels of either the large or small size classes. After five days in the laboratory, the temperature of the experimental tanks were gradually increased by 1 °C per day until they reached mean summer temperature (target 26.8 °C, calculated from surface water data collected nearest our sampling site of “Tolo Harbour and Channel TM2” from 1986 to 2021 between April to October: <https://cd.epic.epd.gov.hk/EPICRIVER/marine/download/>; measured 26.3 ± 0.3 °C) for one week. Summer (April to October as per the EPD: https://www.afcd.gov.hk/english/conservation/con_tech/files/eiao_7.pdf) conditions were used as the control because MHWs are predicted to increase in frequency the most during summer, with such warming events at this time of year having the greatest potential to exceed the upper thermal limits of organisms, including mussels (Thorvald et al. 2022). The rate of initial warming was selected as it avoids intense physiological stress on organisms, and has been shown to enable them to survive this process (see, for example, Leung et al. 2021). Indeed, mussels maintained 100% survival during

the increase of temperature and subsequent holding period. Following this, the elevated temperature treatment was achieved by increasing temperature in these tanks from 26.5 to 30.0 °C at a rate of ~ 1 °C per hour (a rate aligned with that used in Joyce et al. 2022). The elevated temperature treatment of 30 °C represents a water temperature hotter than the mussels would have recently experienced, as temperatures here ranged from 21.3 to 31.6 °C over the last year, with an average of 26.3 °C and the hottest temperature experienced six months prior to the sampling (<https://cd.epic.epd.gov.hk/EPICRIVER/marine/download/>). Elevated temperatures were maintained for 21 days, and the biological responses of *P. viridis* were measured on the final two days (hereafter referred to as ‘at the end of the MHW’) to determine the outcomes of exposure as has been done in previous studies considering the effects of MHWs (Minuti et al. 2021; Joyce et al. 2022; He et al. 2023). After the heatwave period, temperatures of the heatwave tanks were returned to control temperature at a rate of ~ 1 °C per hour. After a one-week recovery period, biological responses of mussels were measured again on the final two days (hereafter referred to as ‘the end of the recovery period’).

Response variables

Survival was monitored daily. Mussel mortality was recorded when individuals displayed continuous gaping despite physical stimulus, after which mussels removed from the experimental tanks.

To measure physiological responses of heart rate, clearance rate, and respiration rate, the same four individuals were used at the end of the heatwave and recovery periods when possible unless the mussel died during the recovery period and needed to be replaced. To measure Arrhenius breakpoint temperature, four random mussels (different to those used for the other responses) were chosen at the end of each period due to the mortality of mussels occurring during temperature ramping preventing repeatable measurements. Similarly, condition index was measured for two randomly chosen mussels in each tank only at the end of the recovery period due to the required sacrifice of mussels. A regression analysis between length and dry flesh weight was calculated at the end of the experiment using the surviving mussels to generate a regression coefficient. The calculated coefficient was then used to standardize the relevant response variables (i.e., clearance and respiration rates) of mussels in the experiment for gram of dry flesh weight using the length of each mussel (Hawkins et al. 1999; Sylvester et al. 2005; Arrieche et al. 2020).

The heart rate of four mussels was measured per replicate tank at the end of each period (i.e., heatwave and recovery) using noninvasive infrared sensors (Newshift, Portugal) linked to a Picoscope amplifier (Pico Technology,

Table 1 Abiotic conditions of temperature and salinity (average ± SEM) in tanks for each size class and temperature combination considered during heatwave and recovery periods

Size	Temperature	Period	Temperature	Salinity
Large	Control	Heatwave	26.1 ± 0.1	34 ± < 1
		Recovery	26.2 ± 0.1	35 ± < 1
	Elevated	Heatwave	30.2 ± 0.1	34 ± < 1
		Recovery	26.8 ± 0.1	35 ± < 1
Small	Control	Heatwave	26.3 ± 0.2	34 ± < 1
		Recovery	26.3 ± < 0.1	35 ± < 1
	Elevated	Heatwave	30.3 ± 0.1	34 ± < 1
		Recovery	26.8 ± 0.1	35 ± < 1

UK) (as in Cheng et al. 2018). The sensors were attached to mussel shells above the heart (i.e., near the mid-dorsal posterior hinge; see Burnett et al. 2013) to detect the electromagnetic waves produced by the heartbeat of mussels. Large and small mussels were individually placed into either 500 mL or 250 mL beakers, respectively, with aerated seawater, and the beakers were then placed into programmable water baths (Julabo PURA 22, Germany) preheated to the temperature the mussels had been experiencing (either 26.5 or 30.0 ± 0.5 °C). Mussels were allowed to rest for 20 min after which heartbeat traces were recorded. Resting heartbeats (beats min^{-1}) were recorded and counted for 3 min and averaged.

The Arrhenius breakpoint temperature (ABT) was measured at the end of each period (i.e., heatwave and recovery) by increasing temperatures in the water baths used to measure heart rate (above) from control temperatures until all individuals did not display visible heartbeat traces and were unresponsive to physical stimulus. So that all animals were beginning from the same temperature, mussels from the elevated treatment at the end of the heatwave period were cooled to 26 °C over an hour. Temperatures were raised by 0.2 °C per minute, and heart rates measured every 5 min (i.e., after each 1 °C increment) for one minute. In addition to the mussels whose heart rates were measured, one additional mussel per treatment was used to measure body temperature by inserting thermocouples (Omega K-type, Teflon insulated, tip diameter 0.25 mm) connected to a digital thermometer (Lutron TM-903A, Taiwan) into the mantle cavity of the mussel. Arrhenius plots were drafted, with natural-log heart rates (in beats min^{-1}) against the reciprocal of body temperature of the mussel in Kelvin (1000/K) and fitted by segmented linear regressions using the “segmented” package in R (Muggeo 2017). The intercept of these regression lines, which indicates the point at which there is a break in the increase in heart rate with increasing temperature, was defined as the Arrhenius breakpoint temperature (ABT; Stillman and Somero 1996).

The clearance rate of four mussels was measured per replicate tank at the end of each period (i.e., heatwave and recovery). Large mussels were placed into 1L beakers with 500 mL of seawater while small mussels were placed into 600 mL beakers with 250 mL of seawater. For both, the seawater was preheated (26.5 or 30.0 ± 0.5 °C, depending on treatment), 1.2 μm filtered, and continuously aerated using air stones supplied with air from a compressor (HIBLOW HP-200). Temperatures were maintained by placing beakers inside a water bath set to the appropriate temperature. Each mussel was allowed to rest for 20 min before adding a fixed concentration of algal solution ($\sim 80,000$ cells mL^{-1}), following which 5 mL of seawater was immediately sampled. A second sample was taken after 30 min. The number of algal cells in the water samples was quantified using

a haemocytometer (Neubauer, Marienfeld, Germany). A beaker containing no mussels was also used for each tank to account for any changes in background cell concentration. For each sample, algal cells were counted twice and the values averaged. Clearance rates were then calculated using the following equation:

$$CR = \ln\left(\frac{C_1}{C_2}\right) \times V/(w \times t)$$

(per Coughlan 1969) where C_1 and C_2 are the cell concentrations at the beginning and end of each interval, V is volume of water (i.e. 0.5 or 0.25 L), w is the dry flesh weight (in grams) of each individual, and t is the interval time in hours (i.e. 0.5).

To measure respiration rate, individual mussels were placed in sealed 500 mL plastic tubs equipped with an oxispot (a planar sensor spot with an oxygen sensitive coating; SP-PSt3-NAU-D5-YOP, PreSens) and filled with aerated seawater at the treatment temperature. Similar to previous studies, mussels were allowed to rest undisturbed for 20 min, after which oxygen concentration was measured after 0, 15, and 30 min, using a fiber optic oxygen sensor (Fibox4 trace, PreSens) (Wang et al. 2011; Ibarrola et al. 2022). The oxygen saturation in the containers did not fall below 75% over 30 min, with the rate of decline similar for small and large mussels. Plastic tubs without mussels were used to account for background respiration rate, which was deducted from the respiration rates of mussels. Respiration rate for each mussel was then corrected using the dry weight of mussels according to the following equation:

$$\text{Respiration rate} = \frac{(O_2^{\text{start}} - O_2^{\text{end}})}{w \times t}$$

where O_2 refers to the concentration of oxygen (in mg O_2), w refers to dry flesh weight (in grams) and t refers to the duration of the measurement time (in hours).

To quantify condition index at the end of the experiment, mussel flesh was excised from the shell and both parts were dried in an oven at 60 °C for 48 h, after which they were weighed to the nearest 0.0001 g. Condition index (CI) was then calculated as:

$$CI = \frac{fW}{sW} \times 100$$

where fW is the dry flesh weight and sW is the dry shell weight of each individual (in grams).

Statistical analysis

To test the effect of heatwave exposure on the survival of mussels of different sizes, a survival analysis was conducted using the “survival” package in R (v. 3.4–0), which was

followed by a cox proportional hazards model, to determine the effect of temperature (control vs elevated) on each size class. Cox proportional hazards models allow determination of how independent factors influence the rate of an event (i.e. mortality) occurring over time. Statistical significance of the temperature effect on survival probability for each mussel size was assessed using Chi-square tests using the "car" package (Fox et al. 2019). To test the effect of temperature and period on mussel responses we used permutational analysis of variance (PERMANOVA) run with Primer 7 + PERMANOVA. To avoid potentially confounding effects associated with body size on the responses considered, the analyses on mussel size classes were run separately. To analyze the effects of temperature and period on heart rate, clearance rate and respiration rate, we used the fixed factors of temperature (two levels – control vs elevated), and period (two levels – heatwave vs recovery), with tank as the level or replication and a random factor (nested within temperature). Due to the mortality of mussels at the end of the thermal ramp used to obtain ABT measurements and quantifying condition index, for these responses the effects of temperature but not period were analyzed using a PERMANOVA with a single fixed factor of temperature. When significant results were obtained, PERMANOVAs were followed by pair-wise post-hoc tests.

Results

Survival probability

The survival probability of mussels from both size classes (large and small) was not significantly different between mussels exposed to elevated temperatures and mussels exposed to control temperatures (Chi square test, large:

$X^2=0.16$, $p=0.682$, Fig. 1a and Table S1; small $X^2=3.14$, $p=0.107$, Fig. 1b and Table S1).

Heart rate

The heart rate of large and small mussels was significantly affected by an interactive effect between temperature (i.e. elevated, control) and experimental period (i.e. at the end of the heatwave and recovery) (large: $F_{(1,10)}=35.094$, $p<0.05$, Fig. 2a and Table S2; small: $F_{(1,10)}=11.391$, $p<0.05$, Fig. 2b and Table S2). For both sizes, heart rate was higher for those mussels experiencing elevated temperatures at the end of the heatwave period compared to those at control temperature at this time, with those of large mussels increasing by 39% compared to the control, while those of small mussels increased by 16% (Fig. 2). However, at the end of the recovery period when temperature had returned to the control level, heart rate of those mussels that had experienced the elevated temperature were similar to those that had not experienced the elevated temperature (Fig. 2).

Arrhenius breakpoint temperature (ABT)

The ABT of large mussels tended to be higher for those experiencing elevated temperatures compared to those experiencing control temperatures at the end of the heatwave period (Fig. 3a), however the difference was not significant ($F_{(1,6)}=3.898$, $p>0.05$, Fig. 3a and Table S3). The ABT of large mussels were similar between temperature treatments at the end of the recovery period ($F_{(1,6)}=4.075$, $p>0.05$, Fig. 3a and Table S3). For small mussels, the ABT was significantly higher for those experiencing elevated temperatures compared to those maintained at control temperature after the MHW period ($F_{(1,6)}=12.309$, $p<0.05$, Fig. 3b and Table S3), but was not significantly different between temperature treatments after the recovery period ($F_{(1,6)}=2.453$,

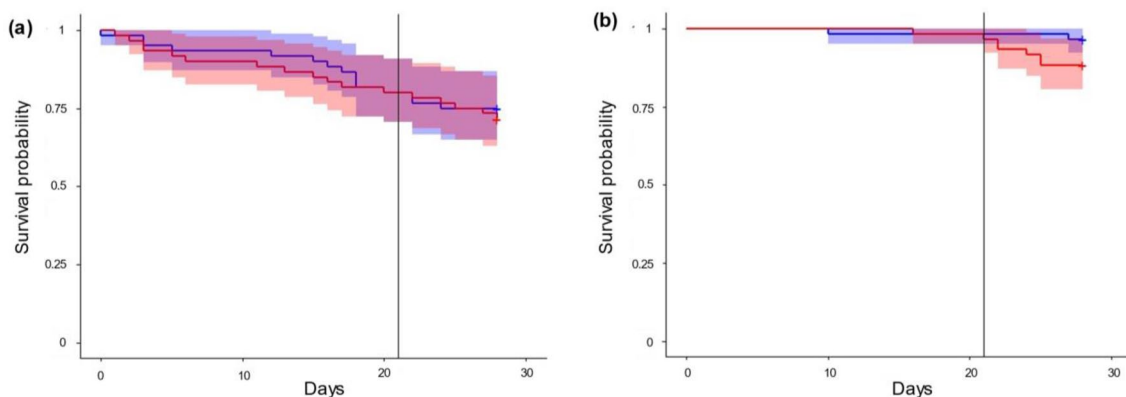


Fig. 1 Survival probability ($\pm 95\%$ CI) of **a** large and **b** small mussels exposed to either control (blue) or elevated (red) temperatures during the three-week heatwave period and after one week recovery period (start of recovery delimited by black vertical line)

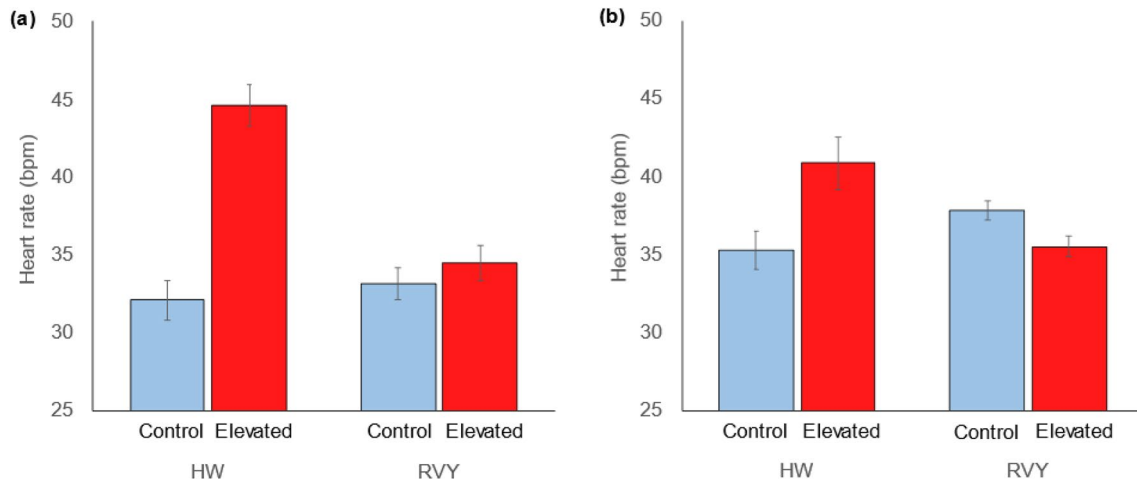


Fig. 2 Mean heart rate (beats per minute) \pm SEM of **a** large and **b** small mussels exposed to either control (blue) or elevated (red) temperatures at the end of a simulated heatwave (HW) and recovery (RVY) period

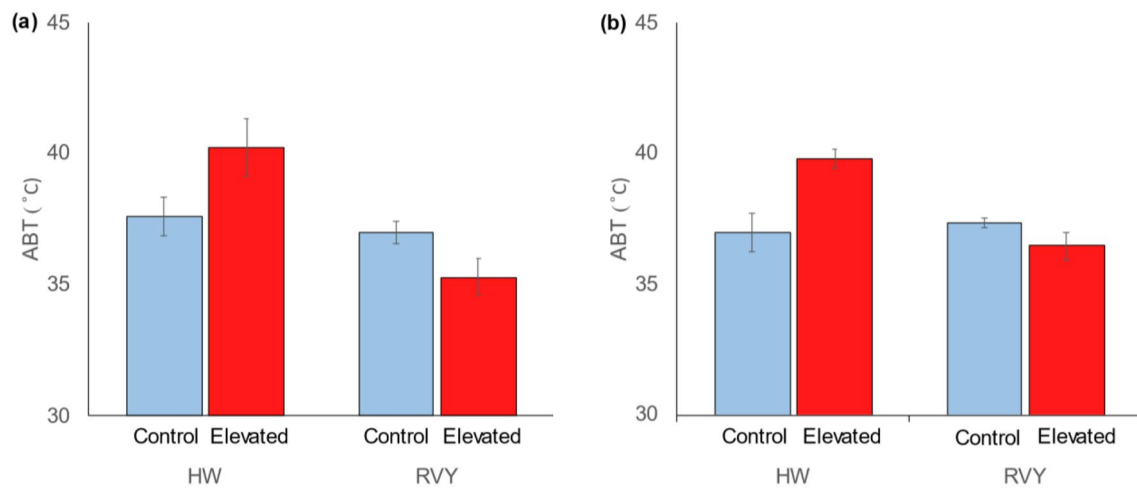


Fig. 3 Mean Arrhenius breakpoint temperature (ABT) \pm SEM of **a** large and **b** small mussels exposed to either control (blue) or elevated (red) temperatures at the end of a simulated heatwave (HW) and recovery (RVY) period

$p > 0.05$, Fig. 3b and Table S3). The ABT of large mussels was 37.51 ± 0.57 °C (average \pm SE) whereas small mussels had an ABT of 37.64 ± 0.39 °C (Fig. 3), with rates dependent upon treatments as noted above.

Clearance rate

The clearance rates of large but not small mussels were significantly affected by the interaction effect between temperature (i.e. elevated, control) and experimental period (i.e. at the end of the heatwave and recovery) (large: $F_{(1,10)} = 15.085$, $p < 0.01$, Fig. 4a and Table S4; small: $F_{(1,10)} = 1.016$, $p > 0.05$, Fig. 4b and Table S4). Specifically, the clearance rate of large mussels was higher for those experiencing elevated temperatures at the end of the

MHW period compared to those at control temperature, which then decreased to similar levels observed for those that has not experienced elevated temperatures (Fig. 4a). Clearance rates of small mussels, however, were not statistically different between temperature treatments within both the MHW and recovery periods (Fig. 4b). Despite no statistically significant differences, small mussels exposed to elevated temperatures did exhibit a trend towards higher clearance rates compared to those exposed to control temperatures after the heatwave period, with similar clearance rates then observed following the recovery period (Fig. 4b). Overall, the large mussels typically had lower clearance rates (ranging from ~ 1 to 3.5 L gDWT $^{-1}$ h $^{-1}$; Fig. 4a), than did the small mussels (ranging from ~ 5 to

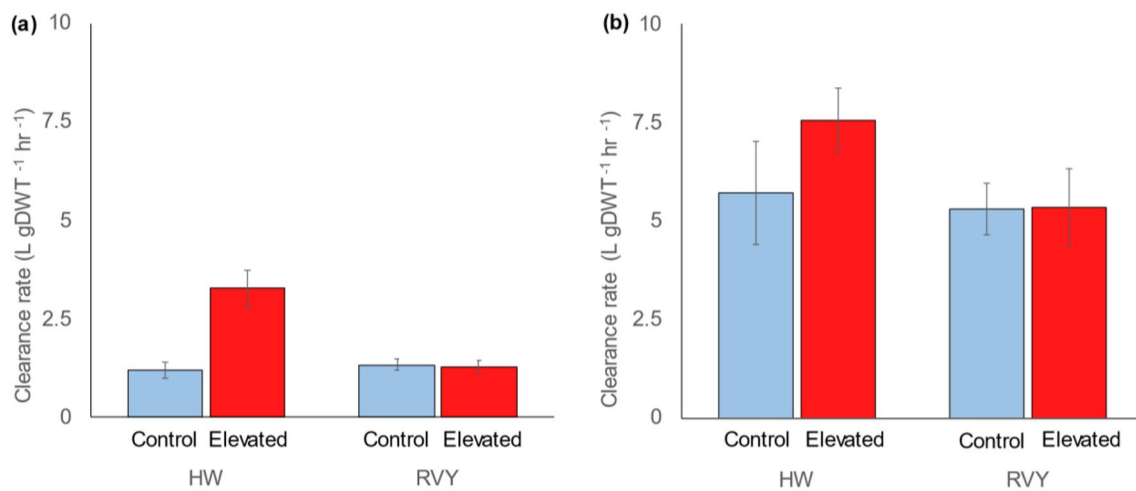


Fig. 4 Mean clearance rate \pm SEM of **a** large and **b** small mussels exposed to either control (blue) or elevated (red) temperatures at the end of a simulated heatwave (HW) and recovery (RVY) periods

7.5 L gDWT⁻¹ h⁻¹; Fig. 4b) with rates dependent upon treatment as noted above.

Respiration rate

The respiration rate of large mussels was significantly different between periods ($F_{(1,10)} = 26.498$, $p < 0.01$, Fig. 5a and Table S5). Larger mussels exposed to elevated temperatures exhibited a trend towards increased respiration rates compared to those at control temperatures at the end of the MHW period, which likely drives the significant overall effect between the time periods (Fig. 5a). For small mussels there was no effect of period ($F_{(1,10)} = 0.356$, $p > 0.05$, Fig. 5b and Table S5) on respiration rates.

Condition index

No significant differences were observed in the condition index of mussels exposed to elevated temperatures compared to mussels exposed to control temperatures in either large ($F_{(1,10)} = 0.441$, $p > 0.05$; Table S6) or small ($F_{(1,10)} = 0.282$, $p > 0.05$, Table S6) mussels.

Discussion

The impact of marine heatwaves (MHWs) on the survival of organisms is associated with their physiological ability to respond to thermal stress (Frölicher and Laufkötter 2018). In the current study, mussel survival for both large and small

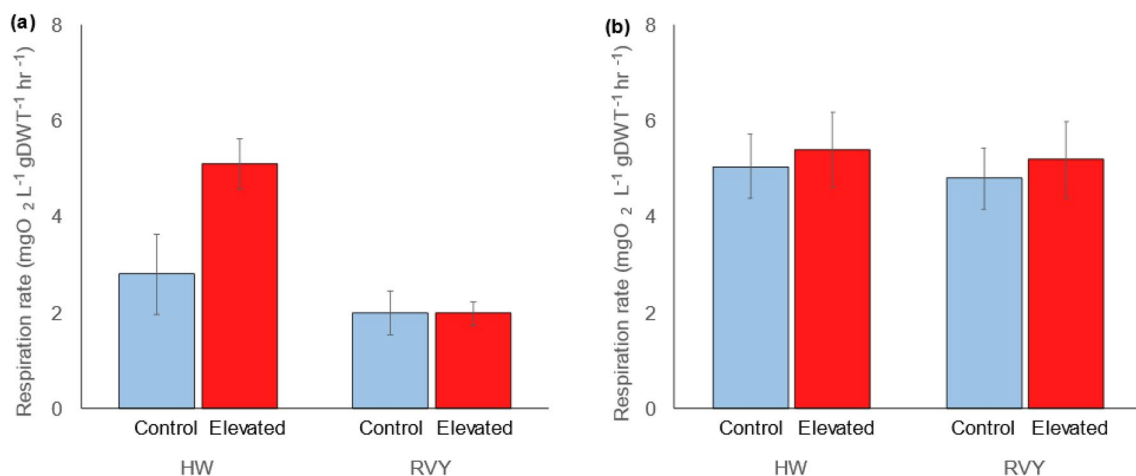


Fig. 5 Mean respiration rate \pm SEM of **a** large and **b** small mussels exposed to either control (blue) or elevated (red) temperatures at the end of a simulated heatwave (HW) and recovery (RVY) period

individuals was not negatively affected by experiencing a simulated MHW, which was in contrast to our anticipated response. While survival was not modified, mussels exposed to elevated temperatures showed some anticipated physiological responses, specifically increases in heart rate (significantly for both large and small mussels), ABT (significantly in small mussels, and a trend towards this in large mussels), and clearance rate (significantly in large mussels, and a trend toward this in small mussels) at the end of the MHW. Surprisingly, some of the responses showed no difference in mussels of either size (respiration rate). Notably, following the marine heatwave recovery period, all modified traits (heart rate, ABT, and clearance rate) of organisms exposed to elevated temperatures returned to levels similar to those that had not experienced the event as anticipated, and unexpectedly the condition index of mussels at the end of the experiment was the same regardless of their MHW exposure. Together, this high survival rate, maintained condition index, and rapid adjustment of physiological processes across size classes indicates that these mussels and their community structure may persist under MHW events that last days to weeks.

Experiencing thermal stress, as occurs during MHWs, has the potential to negatively affect the survival of organisms. However, here we found that the survival of *P. viridis* was unaffected by exposure to heatwave conditions, which aligns with previous studies of *P. viridis* (Goh and Lai 2014; Cheng et al. 2018; Wang et al. 2018). Further examples demonstrating the tolerance of marine organisms to short-term warming events include other bivalves (Hicks and McMahon 2002), gastropods (Joyce et al. 2022), and crustaceans (Tepolt and Somero 2014). There is variability in observed responses, however. Previous studies have also shown that mussel species in temperate regions experience high rates of mortality when exposed to heatwaves of similar magnitude to those considered here (Seuront et al. 2019). Differences in findings among studies on temperate bivalves and the present study on a tropical population may be attributed to the consistently high environmental temperatures experienced by *P. viridis*, contrasting to more fluctuating thermal conditions found in temperate systems (Deutsch et al. 2008; Tewksbury et al. 2008). The maintenance of survival observed here may reflect the adjustment of sublethal physiological processes required for organism function.

The physiological responses measured in this study were observed to readily adjust in response to temperature conditions. Specifically, heart rate (in both large and small mussels), ABT (in small mussels), and clearance rate (in large mussels), increased significantly in response to elevated temperatures and decreased when temperatures returned to recovery conditions. The optimization of physiological processes under different temperatures has been proposed to contribute towards the predicted capacity of the mussel *P.*

viridis to thrive in warmer future oceans, as well as invade and establish in new habitats (Cheng et al. 2018). The capacity of *P. viridis* to adjust physiological processes rapidly and effectively in response to increased ambient temperature is characteristic of ectothermic organisms (Angilletta et al. 2002). Since mussels have limited strategies for behavioral thermoregulation, adjustment of heart rate, ABT, and clearance rate, may be the primary mechanism by which they can avoid unnecessary energetic intake or output.

Cardiac activity was adjusted in response to changes in temperature in the present experiment. Specifically, heart rate of mussels in both size classes increased during the marine heatwave for those organisms that experienced the events, and decreased following the recovery period to be similar to those that had not experienced the heatwave. Increased heart rate is indicative of changes in the circulatory system, as elevated cardiac activity enables a greater supply of blood, which provides organisms with more oxygen, metabolites, and nutrients to cope with the costs of elevated temperature (Pörtner et al. 2005). Although an enhanced supply of metabolites may support critical organism functions in the short term, it also contributes to longer term changes through acclimation (Camacho et al. 2006). Smaller mussels also showed adjustments to ABT in response to MHWs. ABT refers to the upper thermal limit of physiological processes considered, with an increased ABT indicating smaller mussels were able to maintain cardiac activity at higher temperatures when exposed to elevated temperatures, reflecting the acclimatory capacity of mussels (Cheng et al. 2018). As a result, the observed changes in heart rate and ABT indicate that cardiac function is capable of adjusting to, and recovering from, MHW conditions. The ability to adjust cardiac activity may allow mussels to maintain the functioning of organs involved the circulatory system, which is closely associated with individual performance and higher ecological functions such as feeding, growth, and reproduction (Spooner and Vaughn 2008).

In response to elevated temperatures, organisms typically experience an increase in physiological activity, including feeding and respiration rate, that help maintain processes such as growth and reproduction (Sokolova 2013). As a result, energy reserves are closely associated with the capacity of individuals to persist under thermal stress (Sokolova 2013; Leung et al. 2017; Madeira et al. 2018). Similarly to cardiac processes, mussels displayed rapid adjustments in whole-individual physiological processes in response to MHW exposure. The significant increase of clearance rates in large mussels, and the trend observed toward this in small mussels, may confer *P. viridis* the ability to maintain sufficient energy intake under higher temperatures (Sokolova 2013). The trend towards increased respiration rate in larger mussels at the end of the heatwave compared to control individuals is also indicative of the physiological stress incurred

in this period, as mussels require higher oxygen reserves to deal with the disruption of systemic oxygen balance under elevated temperatures (Pörtner 2001; Kassahn et al. 2009). Higher respiration rates improve oxygen delivery capacity, which reduce oxidative stress that may occur as a result of impaired mitochondrial function under higher temperatures (Dimitriadis et al. 2012). Small mussels did not alter their respiration rates, which may be indicative that they maintained sufficient oxygen balance and sustained mitochondrial functions under elevated temperatures (Kassahn et al. 2009). The ability of mussels to limit physiological costs by adjusting clearance and respiration rates provides the ability to persist under MHW conditions without weakening or losing associated ecological functions and cascading to community- or ecosystem-wide impacts (Smale et al. 2017; Brodeur et al. 2019). Notably, the ability to sustain or increase clearance rates by mussels under elevated temperatures may also benefit other organisms in coastal systems as MHWs often drive phytoplankton blooms and increase eutrophication (Gao et al. 2017; Cottingham et al. 2023).

In this study, we found that both tested size classes of mussels responded similarly to a MHW in terms of their survival and physiology. However, previous studies have demonstrated that smaller sized bivalves may have higher stress tolerance compared to larger individuals (e.g., Sukhotin et al. 2003; Peck et al. 2013). Nonetheless, the absence of differences between the size classes considered in the current study may suggest that the cohorts of *P. viridis* populations they represent may be maintained under MHW conditions. In order to consider population stability in its entirety, it would also be important to incorporate studies of potentially susceptible early life history stages such as spat and juveniles into future work. Promisingly, mussels have been shown to possess extensive thermal tolerance beginning at the larval stage (Limbeck 2003; Verween et al. 2005).

In coastal systems mussels will not, however, exist in isolation from other abiotic stressors and organisms, but rather occur in complex ecosystems. This will shape both the response and the implications of the impact of MHWs. That is, where there is lower resource availability, this will likely directly limit the physiological adjustments observed in this study, and may thus affect the capacity of mussels to tolerate various environmental stressors including MHWs (Fitzgerald-Dehoog et al. 2012; Cheng et al. 2018). Moreover, interactions with other species may affect the thermal tolerance of mussels. For instance, parasitic endoliths are recognized to increase the thermal tolerance of mussels, which may affect their stress response in future oceans (Zardi et al. 2016). Where mussels are tolerant and persist under MHWs, this will benefit broader marine ecosystems due to the disproportionately influential role of bio-engineers. Specifically, the continuity of ecosystem services including shelter, water circulation and filtering, and habitat

provisioning provided by bivalves including *P. viridis* may limit the detrimental impacts of worsened MHWs and facilitate the survival of associated organisms (Nicastro et al. 2012; Wyatt et al. 2020). Therefore, the favorable physiological adjustments made by bio-engineers such as *P. viridis* at the end of and following MHWs which enable their survival may potentially scale to population and ecosystem level processes, stabilizing biological communities exposed to MHWs.

The findings of the present study offer valuable insights into the capacity of *P. viridis* to avoid latent negative impacts of MHWs through the capacity to recover from stressful conditions. Specifically, *P. viridis* displayed high tolerance and capacity to recover from exposure to elevated temperatures through adjustments of physiological processes that enabled individuals to withstand energetically costly conditions. Further research into the impacts of different stressors across life stages and the implications of complex stressor combinations and interactions with other species may improve our understanding of how *P. viridis* and other bio-engineers may persist in a rapidly changing world.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

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