



# Response of native and invasive grazers to global warming: marine heatwaves vs. gradual trends

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**ABSTRACT:** Ecological responses to global warming are likely driven by a combination of gradual warming trends and extreme climate events, which are increasing in frequency and intensity. Specifically, heatwaves may amplify the impact of ongoing warming, and thus affect species' physiological responses, behaviour and eventually survival. Here, we tested the hypothesis that a tropical invasive grazer snail, *Cerithium scabridum*, will be more resilient to the effects of future gradual warming and marine heatwaves (MHWs) than its native congener *C. lividulum*, co-occurring in rocky intertidal pools along the Levantine coast. Survival and faecal production (as a proxy for feeding rate) of the 2 species were measured under 4 experimental temperature conditions: ambient summer mean (31°C), predicted warming scenario (ambient +3°C), and short-term MHWs (+5°C) added to either ambient or warming treatments, followed by a recovery period. No effect of warming alone was detected on either species, whereas MHW reduced faecal production only in the native *C. lividulum*. During the recovery period, *C. lividulum* survival dropped, but the few surviving individuals recovered from the heat stress as indicated by the increase in faecal production. Neither snail species survived under the combination of warming and MHW. These results suggest that both species, living in a thermally fluctuating and often extreme environment, can tolerate a +3°C gradual warming, but only the invasive snail can withstand a +5°C heatwave. However, neither species can endure a severe heatwave on top of predicted gradual warming, potentially leading to population collapse among both species in the region.

**KEY WORDS:** Marine heatwaves · Climate change · Global warming · Invasive species · *Cerithium* spp. · Feeding · Recovery capacity

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## 1. INTRODUCTION

Anthropogenic climate change is rapidly and globally impacting oceans by increasing their temperature (Poloczanska et al. 2013, IPCC 2019), affecting

marine organisms both directly (i.e. physiologically) and indirectly (i.e. through shifts in species interactions) (Poloczanska et al. 2013). Ecological responses to global warming are likely to be driven by a combination of gradual warming trends and extreme climate

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events (Jentsch et al. 2007, Ghedini et al. 2015), which are increasing in frequency and intensity (Smale et al. 2019, Oliver et al. 2021, Smith et al. 2023). There is broad recognition that extreme disturbances, rather than gradual trends, are likely to produce more dramatic changes in marine ecosystems due to their abrupt and catastrophic effects (Jentsch et al. 2007, Leung et al. 2017). This is because mean trend effects can affect ecosystems over relatively long periods (years to decades) (Thompson et al. 2013), potentially allowing for organism acclimation, adaptation and, ultimately, evolution (Jentsch et al. 2007, Veilleux et al. 2015). However, gradual warming can cause significant changes in the distribution of species, leading to shifts in the composition and functioning of ecosystems. As a consequence, community reconfiguration may occur particularly where warm-adapted species have rapidly colonized communities previously dominated by cold-adapted species (Vergés et al. 2014, Wernberg et al. 2016). These changes may impact important ecosystem processes, but it is still uncertain whether these transformed communities maintain the same functions as the ones they have replaced and how warming will affect ecosystem functioning in the near future (Gilson et al. 2021).

Conversely, extreme climatic events are associated with significant immediate biological and ecological consequences. Among extreme climatic events, marine heatwaves (MHWs) are defined as discrete periods, lasting at least 5 d, in which seawater temperature is anomalously higher than the 90th percentile based on a given historical baseline period (30 yr) (Hobday et al. 2016). Despite their short-term nature, MHWs have been shown to potentially drive significant changes in marine ecosystems (Hobday et al. 2016, Smith et al. 2023) and lead to a rapid collapse of marine communities (e.g. kelp forests in Western Australia; Wernberg et al. 2013), or to dramatic mass mortality events (e.g. benthic invertebrate communities in the Mediterranean Sea; Garrabou et al. 2009, 2022) or, ultimately, to local or regional extinction (Gutschick & BassiriRad 2003). When extreme events are added to the ongoing gradual warming, they may amplify its impacts at the species, population and community levels (Smale & Wernberg 2013, Boucek & Rehage 2014), possibly resulting in complex and catastrophic responses (Harris et al. 2018).

Long-term and abrupt temperature shifts can also affect species indirectly by influencing species interactions (Lemoine & Burkepille 2012, Bommarito et al. 2023, Díaz-Morales et al. 2023). Grazing is among the ecological interactions rapidly responding to thermal stress due to the direct effects of temperature

on metabolic functions (Brown et al. 2004). According to the metabolic theory of ecology (Brown et al. 2004), moderate warming will increase organism metabolic activity until a threshold is exceeded, beyond which energy intake and organism performance will be impaired (Angilletta et al. 2010, Mertens et al. 2015). Therefore, increasing temperature can alter producer–consumer interactions by directly enhancing consumer metabolism and, consequently, grazing rates (O'Connor 2009). Further temperature increases, however, may reduce or even reverse such effects on consumption, especially if consumption does not scale equally with metabolism (Lemoine & Burkepille 2012).

In marine ecosystems, Mertens et al. (2015) showed that after an initial increase, the feeding rate in gastropods declines under further gradual warming, indicating a possible metabolic depression as a response to increasing thermal stress. Nevertheless, the impact of gradual warming alone on feeding rate is not always significant, as shown by Ghedini et al. (2015), who detected a significant positive effect of heatwaves on gastropod consumption rate. This positive effect might result from increased grazer metabolism, highlighting the potential of extreme events to change the strength of interactions over short periods. However, the ecological effects of gradual changes and extreme events can considerably differ depending on the investigated species and are difficult to anticipate, as indicated by the different response of grazers to thermal stress (Table 1). In addition, the combined effects of extreme climatic events with gradual warming trends remain poorly investigated, as they are considered separately in most climate change experimental studies (Harris et al. 2018; Table 1).

Biological responses to warming are indeed linked to organism thermotolerance, which can vary among species with different geographical or phylogenetic origins (Bozinovic et al. 2011, Seebacher et al. 2015) despite inhabiting the same habitat (Leung et al. 2019). Under ocean warming, in temperate aquatic ecosystems, fast-growing invasive species may be promoted (Stachowicz et al. 2002) and, in some cases, poised to outperform native species (Sorte et al. 2013, McKnight et al. 2021). In particular, tropical invasive species, pre-adapted to warmer conditions in their original range of distribution, are expected to be more capable of withstanding high temperatures than their temperate native counterparts. Within the Mediterranean Sea, the Levantine Basin can be considered a 'distinct ecoregion' (Spalding et al. 2007) and a global hotspot of warming and biological invasions (Rilov et al. 2022), mainly due to the prox-

Table 1. Results of experimental studies on the effects of gradual warming trends and marine heatwaves (MHWs) on the performance of marine grazers using different response variables (consumption, energy budget, body condition, respiration, survival, growth, faecal production). Increase, Decrease, and Neutral relate to whether the rates of the tested response variable increased, decreased, or did not change relative to the control, respectively

Species	Response variable	Gradual warming			MHWs				Reference
		Increase	Decrease	Neutral	Increase	Decrease	Neutral	Recovery	
<i>Turbo undulatus</i>	Consumption			×	×			Not tested	Ghedini et al. (2015)
<i>Turbo undulatus</i>	Consumption		×				Not tested		Mertens et al. (2015)
<i>Thalotia conica</i>	Energy budget		Not tested			×		Not tested	Leung et al. (2017)
	Body condition					×			
	Survival					×			
<i>Heliocidaris erythrogramma</i>	Survival		×				Not tested		Hariato et al. (2018)
	Respiration		×						
<i>Austrocochlea concamerata</i>	Consumption		Not tested			×		Yes	Leung et al. (2019)
	Respiration					×		Yes	
<i>Austrocochlea constricta</i>	Consumption		Not tested			×		No	
	Respiration					×		No	
<i>Nerita atramentosa</i>	Consumption		Not tested				×		
	Respiration					×		Yes	
<i>Turbo militaris</i>	Survival			×			Not tested		Mamo et al. (2019)
	Growth			×					
<i>Trochus sacellum</i>	Survival		Not tested			×		Not tested	Hemraj et al. (2020)
	Respiration						×		
<i>Astraliium haematragum</i>	Survival		Not tested			×			
	Respiration						×		
<i>Heliocidaris erythrogramma</i>	Consumption		Not tested			×		×	Minuti et al. (2021)
	Respiration							×	
	Faecal production							×	Partial
	Survival					×			No
<i>Chlorostoma argyrostoma</i>	Survival		×				Not tested		Falkenberg et al. (2021)
	Consumption			×					
	Respiration			×					
<i>Lunella argyrostoma</i>	Survival		×				Not tested		
	Consumption			×					
	Respiration			×					
<i>Phorcus turbinatus</i>	Survival		×				Not tested		Rilov et al. (2022)
	Respiration		×						
<i>Phorcus articulatus</i>	Survival		×				Not tested		
	Respiration		×						
<i>Patella caerulea</i>	Survival		×				Not tested		
	Respiration		×						
<i>Cellana rota</i>	Survival			Up to 35°C			Not tested		
	Respiration	×							

imity to the Suez Canal which has enabled the passage of hundreds of taxa since its opening (Zenetos et al. 2022). This region represents the southeastern (trailing) edge of the distribution of most Mediterranean and Atlanto-Mediterranean species (Rilov 2016) and is characterized by naturally extreme conditions (highest temperature and salinity, and lowest primary productivity in the Mediterranean) (Coll et al. 2010). As a result, many native species occupying this fast-warming basin may be exposed to temperatures close to their upper thermal limits, and this might induce

their possible retraction and, in worst-case scenarios, a total collapse under extreme warming conditions as was demonstrated for native sea urchins and molluscs in the region (Rilov 2016, Yeruham et al. 2020, Albano et al. 2021). By contrast, invasive thermophilic species from warmer regions might benefit from global warming and become dominant in fast-warming regions such as the Levant (Walther et al. 2009, Belmaker et al. 2013).

The combination of gradual warming and increasing extreme events (i.e. MHWs) in the Levantine basin

might thus have detrimental effects on the local species and their interactions. Specifically, in the near future, rocky intertidal (and tidepool) species are predicted to be more threatened by warming than subtidal species, mainly due to their exposure to temperatures nearing their upper lethal limits and reduced ability to acclimate to warming under fluctuating conditions (Somero 2010). On the other hand, given the highly variable temperature conditions experienced by intertidal species, they may adapt to some extent and resist environmental change, such as warming or heatwaves (Stillman 2002, Rilov et al. 2022, Khosravi et al. 2023).

Here, we evaluated how the separate and combined effects of gradual (future warming scenario) and abrupt (MHWs) changes in temperature affect faecal production (as a proxy for feeding rate) and survival of 2 abundant Mediterranean tidepool snail grazers, the native *Cerithium lividulum* Risso, 1826 and the invasive Indo-Pacific *Cerithium scabridum* R. A. Philippi, 1848. *C. lividulum* has a wide distribution in the Mediterranean Sea (Fig. 1), with few records in the Eastern Atlantic Ocean (Gofas et al. 2001). *C. scabridum* is an Indo-Pacific species that entered the Mediterranean Sea via the Suez Canal soon after it was opened and is considered one of the earliest, most successful Lessepsian migrants (Karachle et al. 2016). In its native range, *C. scabridum* has been found in the Red Sea, Persian Gulf and Indian Ocean, while in the Mediterranean, it has spread to Israel, Egypt, Lebanon, Syria, Turkey, Sicily (Italy) (Barash & Danin

1982), north Cyprus (Cecalupo & Quadri 1996), southern Tunisia (Enzenross & Enzenross 2001), the north-eastern Aegean (Albayrak 2001) and Malta (Mifsud & Sammut 2006) (Fig. 1). These 2 species co-occur in the rocky intertidal pools along the Levantine coast, where they regularly experience highly variable temperatures (Amsalem & Rilov 2021) and rarely desiccating conditions (G. Rilov pers. obs.). On the Israeli coast, while *C. lividulum* can only be found inside tidepools, the invasive *C. scabridum* can be found in tidepools as well as on shallow subtidal reefs (Rilov et al. 2018).

To compare the response of the 2 snails to future gradual warming and MHWs, we performed feeding assays where faecal production was used as a proxy for feeding rate. *C. lividulum* and *C. scabridum* were exposed to experimentally manipulated temperature conditions, including a predicted future temperature scenario (Representative Concentration Pathway [RCP] 8.5, 'business-as-usual' scenario according to IPCC 2019) and 2 short-term MHWs (one on top of ambient temperature and another one on top of the RCP 8.5 scenario), followed by recovery under ambient and future gradual warming scenario conditions, respectively. The reason for including the recovery of both snail species was to assess post-stress effects. We hypothesized (1) that given the subtropical origin of *C. scabridum*, this invasive snail would have a higher thermal tolerance compared to the native species, as well as a better capacity to recover after the heatwave; (2) a stronger negative effect of extreme events (i.e. MHWs) on the perform-

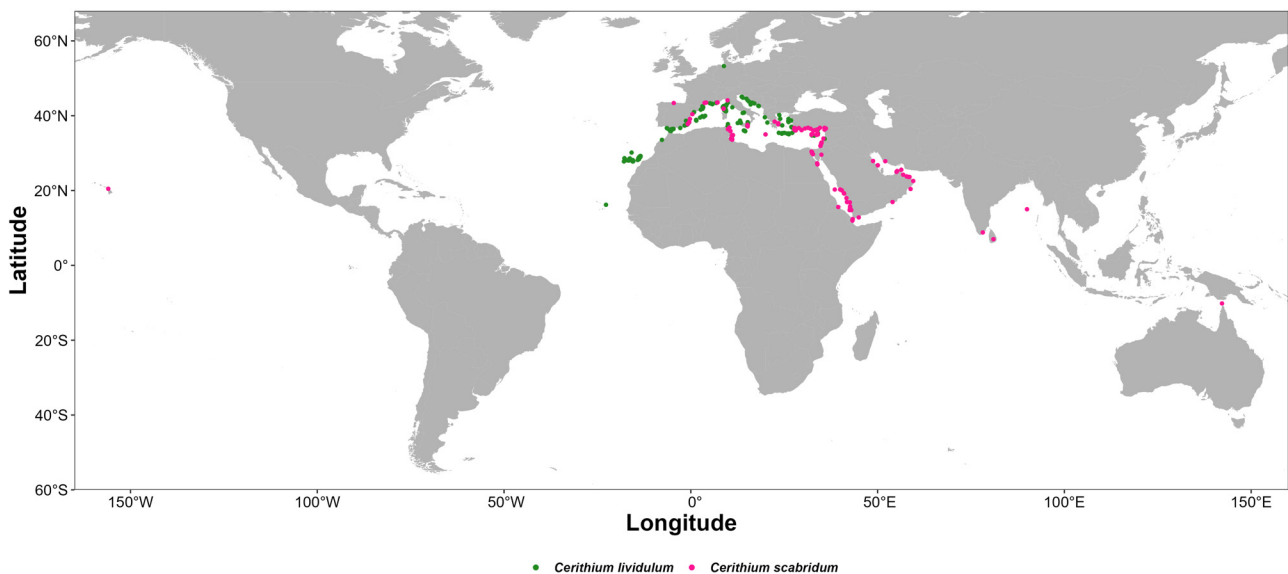


Fig. 1. Worldwide known distribution of *Cerithium lividulum* Risso, 1826 (green dots) and *Cerithium scabridum* R. A. Philippi, 1848 (purple dots). Data on *C. lividulum* and *C. scabridum* from GBIF Secretariat (2023). GBIF Backbone Taxonomy. Checklist data set <https://doi.org/10.15468/39omei>

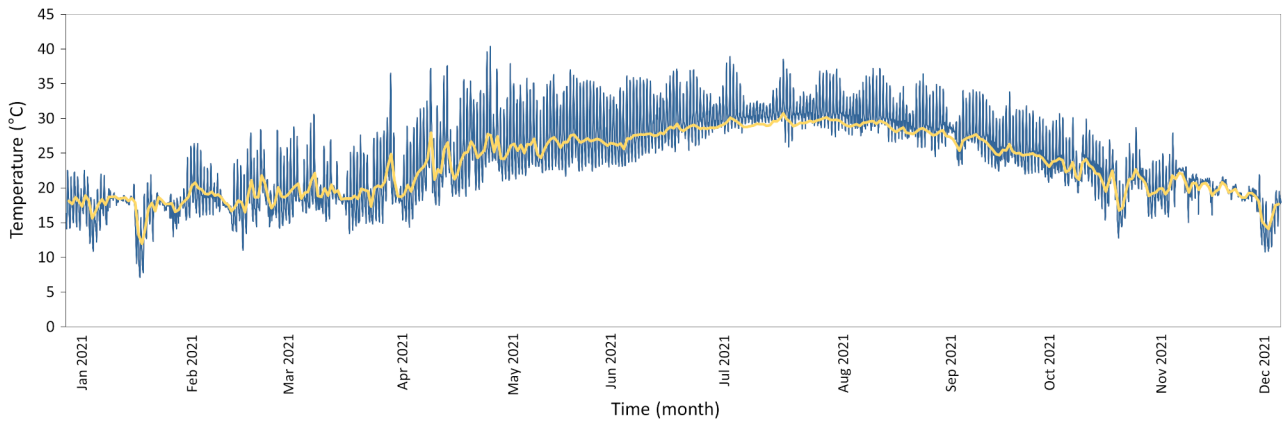


Fig. 2. Hourly (blue line) and daily mean (yellow line) changes in temperatures ( $^{\circ}\text{C}$ ) in a large tidepool where both snail species (*Cerithium lividulum* and *Cerithium scabridum*) were abundant on the intertidal reef in Shikmona, Haifa, Israel, between January and December 2021

ance (faecal production and survival) of the 2 snail species compared to the effects of projected gradual warming; and (3) that an MHW, when superimposed on the future gradual warming scenario, would lead to increased mortality in both snail species.

## 2. MATERIALS AND METHODS

### 2.1. Tidepool thermal conditions

The Israeli coast is characterized by a semi-diurnal tide cycle and a maximal tide amplitude of 40 cm. Coastal water salinity is around 39 PSU (Guy-Haim et al. 2016). A yearly record of tidepool water temperature for this region is shown in Fig. 2. Temperature measurements were recorded every hour (from January to December 2021) with an EnvLogger (model T2.4, ElectricBlue), deployed at 0.3 m depth inside a typically closed tidepool (during low tide and calm seas) at the back of a vermetid reef where the snails are common. The maximum temperature measured was  $40.4^{\circ}\text{C}$  in May and the minimum was  $7.1^{\circ}\text{C}$  in January. The maximum daily temperature range during the sampled year was  $17.6^{\circ}\text{C}$  (greatest variability occurs in the spring), the minimum was  $0.4^{\circ}\text{C}$  (lowest variability occurs in summer or early winter), and the average daily range was  $7.8^{\circ}\text{C}$  (compared to around  $1^{\circ}\text{C}$  as measured in the summer in open water on the reef wall at 0.5 m depth, see Rilov et al. 2022).

### 2.2. Organism collection and identification

Specimens of *Cerithium lividulum* and *C. scabridum* were collected in October 2021, when coastal water

temperature was  $30^{\circ}\text{C}$ , i.e. just below maximum summer temperatures that are around  $31\text{--}32^{\circ}\text{C}$  in very shallow waters on this coast (Rilov et al. 2022), from different closed tidepools on the rocky intertidal reef, located in Tel Shikmona, Haifa, Israel ( $32^{\circ} 49' 32.3'' \text{N}$ ,  $34^{\circ} 57' 18.2'' \text{E}$ ). Depths of the tidepools ranged between 0.2 and 0.3 m, and the pools were located at 10–30 m distance from each other. Snails were collected from the pools during the low tide, which, at the time of sampling, occurred at 13:00 h.

After collection, snails were immediately transported to the facilities of the Israel Oceanographic and Limnological Research (IOLR) Institute and acclimated to peak summer (August) average ambient temperature ( $31^{\circ}\text{C}$ ) for 5 wk in an outdoor mesocosm system with a continuous seawater flow, to ensure they were not suffering from any stress caused by temperature changes. All individuals were fed ad libitum with fresh *Ulva* sp. collected from algal culture tanks within the same facility. The species identity was confirmed by morphology-based identification and DNA barcoding using the cytochrome c oxidase subunit I mitochondrial gene following the protocol described by Rabi et al. (2020).

### 2.3. Experimental set-up: future scenarios and heatwaves

Four temperature regime treatments were applied to test the effects of thermal stress on faecal matter production and survival of *C. lividulum* and *C. scabridum* and their ability to recover from thermal stress as follows: (1) mean summer ambient ( $31^{\circ}\text{C}$ ), (2) RCP 8.5 business-as-usual scenario ( $34^{\circ}\text{C}$ ) according to the IPCC (2019) projections, (3) a short (8 d) MHW super-



imposed on the ambient treatment (36°C) and (4) a short MHW superimposed on the RCP 8.5 scenario (RCP 8.5 + MHW; 39°C).

The magnitude of temperature change used for the heatwave was chosen following a study describing trends and spatial distribution of MHW events in the Eastern Mediterranean Basin from 1982 to 2020 (Ibrahim et al. 2021). Those authors defined an MHW as 'prolonged discrete anomalously warm water event that can be described by its duration, intensity, rate of evolution, and spatial coverage' (Ibrahim et al. 2021, p. 2) and they used the sea surface temperature (SST) data obtained from the National Oceanic and Atmospheric Administration Optimum Interpolation ([NOAA] OI SST V2.1). They showed that in the region, the MHW frequency trend increased by 1.2 events per decade between 1982 and 2020, while the cumulative intensity trend increased by 5.4°C-days per decade. Ibrahim et al. (2021) also showed that the most intense MHW event in the Eastern Mediterranean Basin was located south of Rhodes (maximum intensity = 6.35°C). This heatwave event was associated with 2 other extreme events located in the Levantine Basin, which co-occurred in May 2020 with very high intensities (maximum intensity = 5.66 and 4.74°C, respectively). Therefore, in our study, we chose to simulate an MHW of 5°C magnitude lasting 8 d, superimposed on either ambient summer conditions or on a scenario of a 3°C warmer summer.

After the 5 wk acclimation period in large tanks of an outdoor mesocosm system, snails were transferred for an additional 3 d acclimation period at summer ambient temperature (31°C) in the experimental outdoor system which consisted of 20 l thermobaths in which submerged holding jars were placed (see detailed descriptions by Guy-Haim et al. 2016 and Amsalem & Rilov 2021). Six independent experimental units, consisting of 300 ml glass jars, completely filled with seawater and each containing 3 snails, were set per species and temperature (6 jars per snail species,  $n = 12$  jars per thermobath;  $n = 8$  thermobaths). Two thermobaths were randomly assigned to each temperature treatment, resulting in 36 individual snails per treatment and species (4 temperature treatments  $\times$  2 species, total  $n = 288$ , Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m748p069\\_supp.pdf](http://www.int-res.com/articles/suppl/m748p069_supp.pdf)). Jars were filled with aerated temperature-equilibrated seawater (exchanged every 48 h) and covered with a net to prevent snails from escaping. All snails were previously measured and weighed using digital callipers (FUJI Digital Caliper 0–150 mm) and an analytic scale (analytical balance BPS-1000-C2V2), respectively, and fed ad libitum with *Ulva* sp.

After an acclimation to ambient summer temperature and holding conditions, snails were acclimated to the different treatments (i.e. scenarios). The thermobaths assigned to the ambient and MHW treatments (2 thermobaths per treatment) were kept at ambient temperature (31°C) for 12 d (Fig. 3). In the RCP 8.5 and RCP 8.5 + MHW treatments, a gradual acclimation to predicted future warming (34°C) was performed increasing by 1°C d<sup>-1</sup> (Fig. 3), which corresponds to a lower rate than the ambient diurnal temperature fluctuations in tidepools. Once the target baseline temperatures were reached, the snails were allowed to acclimate to these conditions for 8 d (Fig. 3). Afterwards, an MHW was superimposed on the MHW and RCP 8.5 + MHW treatments. The MHW was simulated by increments of 2.5°C d<sup>-1</sup> until the target temperatures of 36 and 39°C were reached in the MHW and RCP 8.5 + MHW treatments, respectively (Fig. 3).

During acclimation, in the RCP 8.5 + MHW treatment, massive mortality of both *C. lividulum* and *C. scabridum* was recorded on Day 1 and Day 5, respectively, after the target temperature was reached (see Fig. 3). Consequently, the RCP 8.5 + MHW experimental units were excluded from the following procedures. The heatwave simulated for the MHW treatment lasted 8 d and then gradually decreased by 2.5°C per day until reaching the ambient temperature (31°C). Once the temperature was reached, the snails of all remaining treatments were kept under a recovery phase for 8 d (see Fig. 3). Complete water exchange occurred every 48 h by transferring the snails to jars filled with temperature pre-equilibrated water. Water parameters (temperature and oxygen) were monitored before and after the water change with a multimeter (WTW 3420). Mortality was recorded weekly, and dead individuals were removed from the experimental units.

#### 2.4. Feeding bioassay and faecal production

Feeding bioassays were used to assess the functioning (performance) response of *C. scabridum* and *C. lividulum* exposed to the different treatments and their potential for recovery from thermal stress. Here, faecal matter production was chosen as a proxy for feeding since it is not affected by sloppy feeding behaviour of grazers and renders a distinction between unconsumed and consumed food (Wahl et al. 2020). In addition, defecation rate was found to be linearly positively correlated to ingestion rates (Ayukai & Nishizawa 1986, Besiktepe & Dam 2002, Güllow

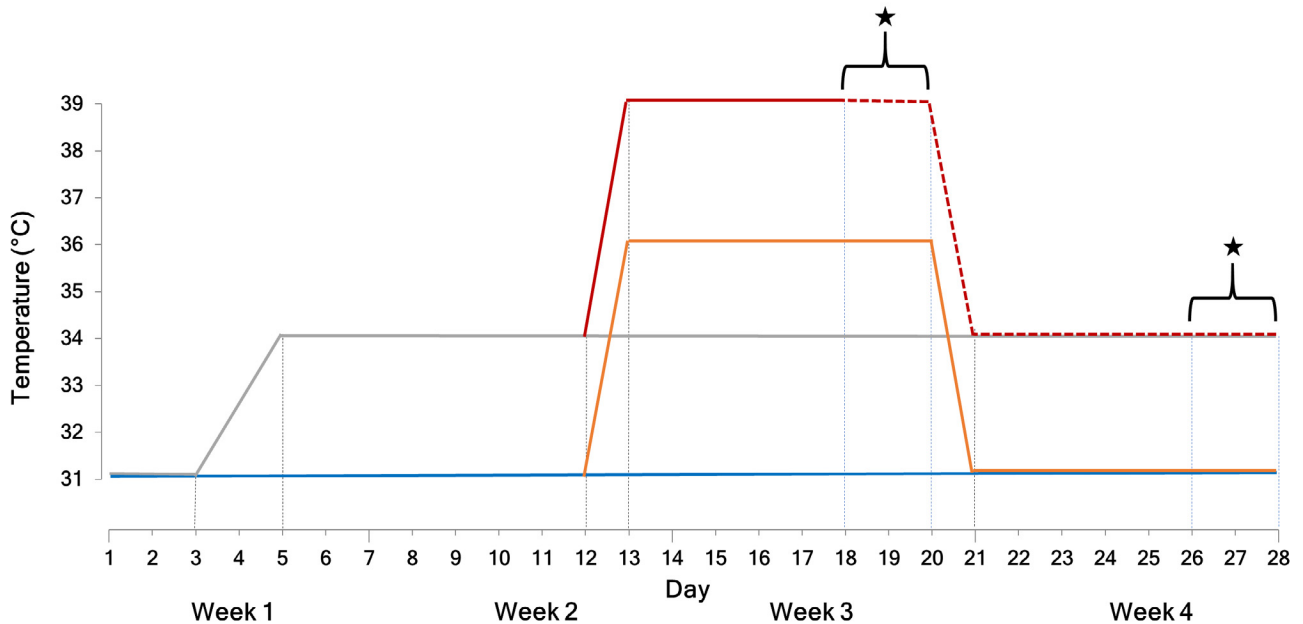


Fig. 3. Magnitude and duration of the experimental temperature treatments: Ambient (31°C, in blue), RCP 8.5 (34°C, in grey), marine heatwave (MHW; 36°C, in orange), RCP 8.5 + MHW (39°C, in red). Stars indicate the time at which feeding assays were run to quantify faecal matter production during the 4 wk experimental period. The dashed red line starting on Day 18 indicates that the RCP 8.5 + MHW treatment was removed from the experiment due to the massive snail mortality recorded

2015) and, given the relatively short duration of the feeding assays (48 h) described here, coprophagy and degradation of faecal matter can be neglected (Besiktepe & Dam 2002).

Feeding assays were run twice during the experiment. The first was conducted on Day 18, after the 6 d exposure to MHW and coinciding with the end of the 2 wk exposure to the RCP 8.5 scenario (see Fig. 3). The second feeding assay was run on Day 26, after 6 d of recovery from the MHW, and coincided with the end of the 3 wk exposure to the RCP 8.5 scenario (see Fig. 3). Before each feeding assay, snails were starved for 6 d so that their guts would have been empty during the assay and then fed with fresh *Ulva* sp. pieces of similar size, under their respective treatment conditions. The starvation time (6 d) adopted here was chosen as a reasonable time period to standardize hunger levels based on the observations derived from a previous pilot study, where after 10 d of food deprivation under ambient temperature conditions (31°C), both snail species ( $n = 80$ ) continued to produce faecal matter and no mortality was recorded.

After 48 h, snails were removed from the jars together with the remaining pieces of algae. Faeces were collected, transferred to 50 ml plexiglass beakers, and inspected under a stereomicroscope (Nikon SMZ1500) to separate faecal matter from any undigested matter (e.g. algal residues). Water contain-

ing the faeces was then filtered with a vacuum pump (MRC VP-17) using pre-weighed and pre-combusted glass microfibre filters (GF/F, Whatman™,  $\varnothing$  25 mm). The filters were then rinsed with deionized water to remove the remaining salt. The filters were finally oven-dried at 80°C for 12 h and reweighed.

## 2.5. Statistical analyses

Statistical analyses were performed in R (version 4.1.2) (R Core Team 2021). Differences in survival between treatment groups at each weekly time point for the 2 snail species were assessed using the non-parametric Kruskal-Wallis test followed by Dunn's multiple comparison test. The variance in faecal matter production was modelled using linear mixed models (LMMs) with a Gaussian distribution with the function 'lmer' from the R package 'lme4' (Bates et al. 2015) and restricted maximum likelihood (REML) as the estimation method (Corbeil & Searle 1976). Mixed-effects models were chosen since they allow the inclusion of both fixed and random effects as predictor variables. The full model included temperature treatment and species as fixed factors and their interaction, whereas thermobath (i.e. tank units) was set as a random factor. For temperature treatment and species effect size calculations, ambient treatment (31°C) and *C.*

*lividulum* were set as the reference level, respectively. Model assumptions were evaluated using the diagnostics tool from the 'DHARMA' package (Hartig 2018), which provides quantile-quantile plots with the Kolmogorov-Smirnov test to detect deviations from normality, outliers and dispersion tests. The model met the assumptions of normality and homogeneity of variance. Therefore, no transformation was applied to the response variable. Effect sizes (standardized mean difference following Pustejovsky et al. 2014) were visualized using the 'plot\_model' function from the 'sjPlot' package (Lüdtke 2021). Post hoc pairwise comparisons based on estimated marginal means (Searle et al. 1980) were run to assess the significance of differences between pairs of group means using the function 'emmeans' within the 'emmeans' package (Lenth 2022). This statistical approach was applied separately to each feeding assay.

### 3. RESULTS

#### 3.1. Survival

Mortality did not occur during the first 2 experimental weeks for either *Cerithium lividulum* or *C. scabridum* (Fig. 4), but 100% mortality was recorded for both species during the third week under the RCP 8.5 + MHW treatment (Fig. 4). In this treatment, all native snails died on the first day of the MHW, while all invasive snails died after 5 d under the MHW. During the third week, *C. lividulum* survival was reduced to 89% under the MHW-only scenario (Fig. 4A), whereas *C. scabridum* survival decreased only slightly to 94.4, 97.2 and 91.6% under the ambient, RCP 8.5, and MHW treatments, respectively (Fig. 4B). In the fourth week (post-MHW period), *C. lividulum* survival decreased further to 77.7 and 13.9% under RCP 8.5 and MHW treatments, respectively (Fig. 4A), whereas *C. scabridum* survival remained relatively high at 88.8, 91.7 and 83.3% under ambient, RCP 8.5 and MHW treatments, respectively (Fig. 4B). Differences in *C. scabridum* and *C. lividulum* survival between treatment groups were statistically significant during the third and fourth week (Kruskal-Wallis test,  $p < 0.0001$ ). Specifically, *C. scabridum* survival was significantly lower under the RCP 8.5 + MHW treatment compared to the other 3 temperature treatments (Ambient, RCP 8.5 and MHW, Dunn's test,  $p < 0.0001$ ), during the third and fourth week. Also, survival of *C. lividulum* was significantly lower under the RCP 8.5 + MHW treatment compared to the other 3 temperature treatments (Ambient, RCP 8.5 and MHW, Dunn's test,  $p < 0.0001$ ), during the

third and fourth experimental week. In addition, pairwise comparisons showed significant differences in *C. lividulum* survival during the fourth week, between the following treatment groups: Ambient vs. MHW (Dunn's test,  $p < 0.0001$ ), Ambient vs. RCP 8.5 + MHW (Dunn's test,  $p < 0.0001$ ), MHW vs. RCP 8.5 (Dunn's test,  $p = 0.002$ ), RCP 8.5 vs. RCP 8.5 + MHW (Dunn's test,  $p < 0.001$ ).

#### 3.2. Faecal production

During the first feeding assay (third week of the experiment), faecal matter production in the invasive snail *C. scabridum* was generally higher compared to that of *C. lividulum* in all treatments (Fig. 5A). Specifically, LMM showed that faecal production of *C. scabridum* was significantly higher than that of *C. lividulum* under the MHW treatment (estimate = 3.03, CI = 1.42–4.64,  $p < 0.001$ ; Table S1, Fig. S2). Consistent results were obtained from post hoc pairwise comparisons which showed significant differences in fae-

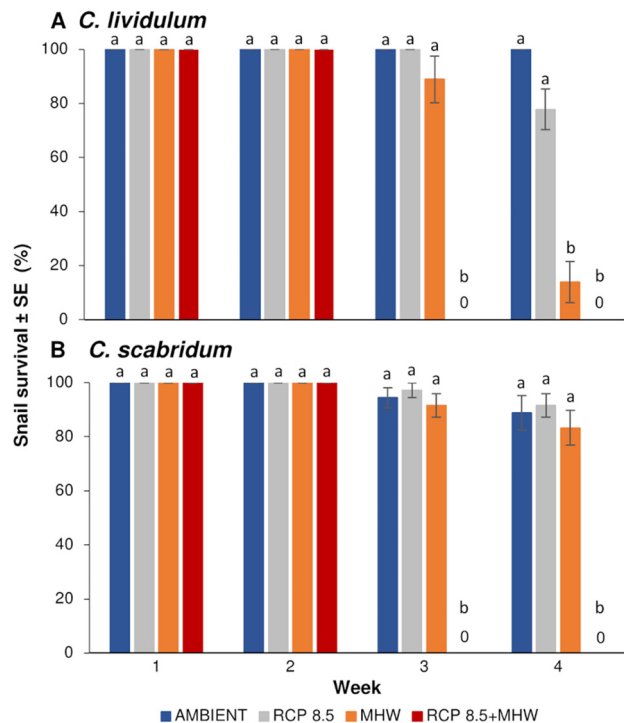


Fig. 4. Survival (%)  $\pm$  SE of (A) *Cerithium lividulum* and (B) *C. scabridum* ( $n = 36$  per species and treatment) over a 4 wk experimental period. Blue, grey, orange, and red bars represent survival of snails exposed to Ambient, RCP 8.5, marine heatwave (MHW) and RCP 8.5 + MHW treatments, respectively. Bars labelled with the same letters refer to values that do not differ significantly ( $p > 0.05$ ), according to Dunn's post hoc test



cal production between *C. lividulum* and *C. scabridum* under the MHW treatment (estimate =  $-3.9437$ ,  $t_{60} = -7.020$ ,  $p < 0.0001$ ; Table S2).

During the recovery period (fourth week), faecal production of the invasive snail *C. scabridum* was significantly higher than that of *C. lividulum* overall (LMM, estimate =  $2.18$ , CI =  $0.51-3.84$ ,  $p = 0.011$ ; Fig. 5B; Table S3, Fig. S3); the analysis includes only the surviving *C. lividulum* ( $n = 69$ ). However, the LMM did not show any significant impact of temperature treatment on faecal production (Table S3, Fig. S3). Post hoc comparisons detected significant differences in faecal production between the 2 species only within the ambient treatment (Table S4), with *C. scabridum* producing more faeces than *C. lividulum* (estimate =  $-2.176$ ,  $t_{54} = -2.623$ ,  $p = 0.011$ ; Table S4).

#### 4. DISCUSSION

Gradual warming trends and extreme climatic events have been repeatedly reported to lead to substantial ecological changes at species, population and community levels of biological organization (Jentsch et al. 2007, Harris et al. 2018, Garrabou et al. 2022).

However, given their catastrophic and destructive nature, extreme events are predicted to drive more significant changes in marine ecosystems rather than gradual climatic trends (Jentsch et al. 2007). Our results suggest that (1) both the native and invasive species may not survive a strong MHW superimposed on the future much warmer ocean ( $+8^{\circ}\text{C}$ ); (2) both native and invasive snails may be relatively resilient to future gradual temperature increases ( $+3^{\circ}\text{C}$ ); (3) a relatively short (8 d) MHW ( $+5^{\circ}\text{C}$  above ambient) can cause considerable reduction in performance and eventual mortality in the native but not in the invasive snail; (4) during the recovery period, under ambient temperatures, the invasive *Cerithium scabridum* has higher feeding rates than the native *C. lividulum*; and (5) the performance of native snails that do survive a short MHW can be recovered when temperature returns to current summer ambient conditions.

It is increasingly recognized that gradual warming and extreme climatic events do not act separately but in combination, with the potential to push systems across tipping points (Harris et al. 2018). Thus, these 2 stressors may act synergistically, substantially reducing the fitness and, ultimately, survival of sensitive species. Here, we provided novel experimental

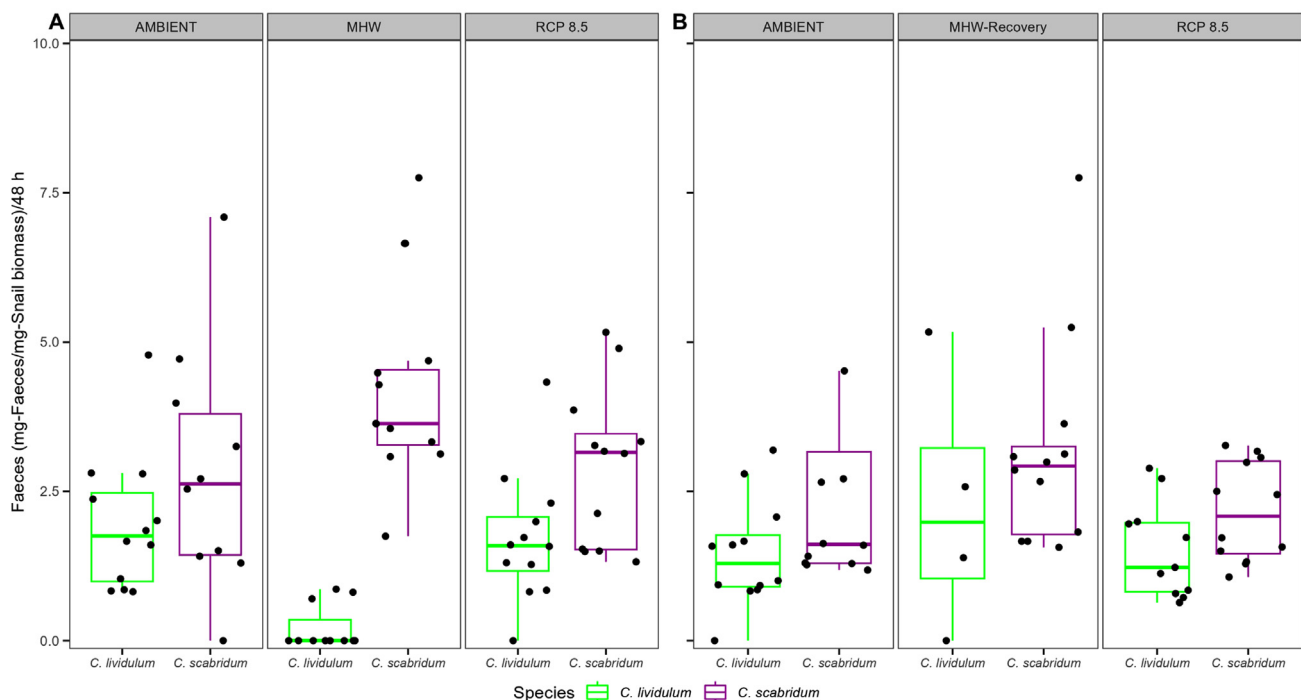


Fig. 5. Faecal matter production (DW in mg) of *Cerithium lividulum* (green) and *C. scabridum* (purple) in 48 h standardized per snail biomass (WW), exposed to 3 temperature treatments (Ambient, marine heatwave [MHW] and RCP 8.5), (A) after 8 d exposure to MHW and 2 wk exposure to the RCP 8.5 scenario temperatures (Day 20,  $n = 104$  of *C. lividulum* and  $n = 100$  of *C. scabridum*) and (B) after 8 d of recovery from MHW and after 3 wk exposure to the RCP 8.5 scenario (Day 28,  $n = 68$  of *C. lividulum* and  $n = 94$  of *C. scabridum*). Black dots represent arithmetic means of individual replicates per experimental unit, horizontal lines are the medians within the interquartile range (boxes), and whiskers indicate minimum and maximum values

evidence that the combined effect of gradual warming and MHW not only impaired the performance and survival of the sensitive native species *C. lividulum* but also produced lethal effects on the highly thermophilic species *C. scabridum*. Our results suggest that the extreme temperatures (39°C) experienced by *C. lividulum* and *C. scabridum*, when the heatwave was added on top of the RCP 8.5 scenario, exceeded the lethal threshold of both species, inducing mortality of all individuals. This means that in the Levantine intertidal rocky shore, summer temperatures, which can reach 39°C and beyond during daytime in tidepools less connected to the sea, might pose a mortality risk even to thermophilic invaders, such as *C. scabridum*. Hence, although tropical invaders are expected to be the absolute winners in such a region under near-future warming conditions (Rilov et al. 2022), the interaction of gradual climate trends and heatwaves has the potential to induce population collapse even among invasive tropical species within tidepools. However, because the invasive *C. scabridum* also has shallow subtidal populations (unlike the native species that only occurs in tidepools) and such extreme temperatures are not expected in the more open sea in the foreseeable future, we can anticipate that these populations will persist while the native species might disappear. In addition, the persistence of subtidal population of *C. scabridum* in the region can potentially allow for a re-seeding of the affected tide pool populations following extreme warming events.

The fact that continuous prolonged exposure to gradual warming (+3°C, RCP 8.5 scenario) did not have any effect on snail survival is perhaps unsurprising, as in the tidepools and during daytime warming, they are currently exposed to short periods of very high temperatures (see Rilov et al. 2022), which are followed by a cooling relief at night. During the summer, in the southeastern Mediterranean, the lower-mid-intertidal zone experiences relatively stable temperatures that closely mirror those of the nearby coastal waters, with little exposure to air. This is mainly due to minimal tidal fluctuations and a constant sea breeze, that produce nearly continuous wavy conditions, characteristic of the summer season (see Rilov et al. 2022). However, in spring and autumn, when the sea is calm or when winds blow from land, prolonged desiccation events can be frequent (see Zamir et al. 2018). These events disconnect many tidepools from the open sea for long periods, creating highly stressful conditions including temperatures that can often reach 34°C and above (see Amsalem & Rilov 2021). These conditions may have primed the 2 snails to

withstand the thermal conditions they were exposed to in the +3°C treatment.

Nonetheless, the lack of change in faecal production under gradual warming was less expected. In accordance with the metabolic theory of ecology, climate warming is expected to increase marine ectotherm metabolic activity (Dillon et al. 2010, Yvon-Durocher et al. 2010, Seebacher et al. 2015), translating into energy gain by enhanced feeding (Sanford 2002, Brown et al. 2004). Other studies have also found that moderate warming (+2.5°C above ambient) does not affect gastropod feeding rates, but instead significantly reduces survival (Falkenberg et al. 2021). Here, the lack of significant effects of gradual warming treatment on both survival and faecal production of the 2 *Cerithium* species suggests that the acclimation time (24 d) to the target temperatures, although relatively short, was sufficient to allow the snails to acclimate to near future conditions, enhancing their resilience and reducing their sensitivity to elevated temperatures (Stillman 2003, Seebacher et al. 2015).

While gradual warming by 3°C did not affect the performance of the 2 snail species, a drastic reduction in faecal production was detected in the native grazer (*C. lividulum*) during the first feeding assay under the abrupt +5°C MHW treatment. This suggests that abrupt changes (and/or the greater temperature change) in seawater temperature induced by the MHW might have prompted a stronger physiological response in *C. lividulum* than gradual warming, impairing its ability to acclimate to elevated temperature over a short time period likely by decreasing its feeding. In a previous study, Ghedini et al. (2015) showed that gradual warming changes (+3°C above ambient temperature) did not affect gastropod consumption, which, by contrast, peaked during the heatwave they induced, possibly due to increased consumer metabolism. In our study, the reduction in *C. lividulum* faecal production during the MHW probably reflected a decrease in its feeding activity, contrasting the findings of Ghedini et al. (2015). Indeed, since feeding is a hump-shaped function of temperature, it is expected to increase until a threshold is exceeded and to decrease beyond that point (Englund et al. 2011). Different species-specific thermal optima may find the tested species at different points on that curve. This may explain why the studied grazers show contrasting responses by increasing (Ghedini et al. 2015), decreasing (Leung et al. 2019) or showing no change (Leung et al. 2019, Minuti et al. 2021) in their feeding when exposed to warming.

Here, we showed that the more sensitive native species (*C. lividulum*) considerably reduced its per-

formance during the MHW, while the thermophilic invader (*C. scabridum*) was able to maintain its metabolism under the same conditions. Superior physiological performance (i.e. survival and metabolic rates) of a tropical invasive fish (*Siganus rivulatus*) over a native one (*Sarpa salpa*) was previously shown under increasing seawater temperature (Marras et al. 2015), as well as for invasive intertidal topshells and limpets on the Israeli Mediterranean coast (Rilov et al. 2022). Similarly, a recent meta-analysis (McKnight et al. 2021) provided evidence that non-native species, originating from warmer regions, outperform natives in coastal marine ecosystems subjected to elevated temperature. Such findings strengthen the hypothesis that future ocean warming might benefit thermophilic invasive species, enhancing their spread and success. This might explain why here the invasive *C. scabridum* did not exhibit any reduction in its metabolic performance even when temperature reached 36°C under the MWH treatment.

Interestingly, the survival of *C. lividulum* was not considerably affected during the heatwave itself, which caused a reduction in survival of only 11% of individuals during the third week of the experiment (see Fig. 4A). However, most of the mortality (~86%) in *C. lividulum* occurred in the following week, during the post-heatwave period, when the temperature was brought back to ambient conditions, as a consequence of the negative carryover effects of the heatwave. A similar response was reported for the sea urchin *Heliocidaris erythrogramma*, which showed a decrease in food consumption and faecal production under heatwave conditions, followed by increased mortality during the recovery period (Minuti et al. 2021). In response to intense heat stress, consumers are expected to enhance their energy intake by increasing vital biological rates (e.g. food consumption, growth, and reproduction) to keep up with rising metabolic demand and to survive (Brown et al. 2004, Leung et al. 2020). However, growing evidence has shown that at high temperatures, consumer metabolism increases faster than consumption, indicating the inability of certain individuals to cope with thermal stress, which leads them to decrease their feeding in response to elevated energy demand (Lemoine & Burkepile 2012, Minuti et al. 2021). Thus, a temperature-induced mismatch of metabolism and consumption can result in a decrease in consumer fitness and, ultimately, its survival (Lemoine & Burkepile 2012). Accordingly, it is likely that less resilient individuals of *C. lividulum*, even though surviving while exposed to extreme heat stress, succumbed during the re-

covery period, likely as a result of their reduced feeding and the consequent lack of energy supply.

It is worth noting that the relatively long period of food starvation (6 d) applied here, before each feeding assay, might have added some initial stress for the snails, potentially affecting, to some degree, their ability to withstand the heat stress (Delorme et al. 2020). This was a necessary procedure to put all tested individuals at similar starting points as has been done in many similar studies (e.g. Núñez-Pons et al. 2012). However, the fact that no mortality was recorded in the snails exposed to ambient temperature treatment and under the same starvation regime, coupled with similar observations obtained from a previous pilot study (see Section 2), strengthens the idea that warming induced by the MHW was very likely the main stressor affecting the observed snail response.

Even more interesting were the *C. lividulum* individuals that survived the recovery period (~14% of the total individuals) and also recovered their feeding performance as indicated by the increase in faecal production during the post-heatwave period (see Fig. 5B). It has been shown that intertidal gastropods can modify their physiology and activate molecular defence, not only to accommodate the impacts of a sudden increase in temperature induced by heatwaves, but also to recover once the heat stress subsides (Leung et al. 2019). The within-species variability, evident in our study, suggests that the surviving individuals may have had either higher adaptive ability (more resistant genotypes) or higher phenotypic plasticity deriving from the use of residual reserves and food availability. More generally, the return to ambient temperature conditions after a heatwave clearly does not allow for the recovery of the entire population. Substantial physiological stress might have compromised the fitness of most individuals and, ultimately, their survival, suggesting that further increase in warming and MHW intensity might reduce the viability of the native species in the region.

Overall, this study emphasizes the importance of considering the joint effects of gradual warming and extreme climatic events when forecasting ecological response in climate change research. Deeper insights into the response of marine species to extreme events, such as heatwaves, in conjunction with gradual warming trends, is needed for predicting and mitigating climate change effects on marine ecosystems. However, as long as experimental research remains based on studies focused on either of the 2 aspects separately, the ecological effects produced by the interaction of gradual changes and extreme events

remain difficult to anticipate, especially in a fast-warming and highly vulnerable region such as the Levantine basin.

The next step in such experimental studies is to incorporate realistic variability of the environmental parameters into the experimental design, such as the inclusion of fine-scale natural fluctuations as well as exposing the tested organisms to repeated heatwaves of different strengths or durations (see Smith et al. 2023). Such experiments will further improve our predictions of future climate change effects on coastal species and communities.

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