



Short Communication

Emergent effects of temperature and salinity on mortality of a key herbivore

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ABSTRACT

Aquatic ecosystems are threatened by multiple stressors which might interact in non-additive ways. Two key stressors in marine systems that are likely to be mediated by ongoing climate change are temperature and salinity. Here, we experimentally examine the influence of warming and desalination on mortality rates of a key herbivorous sea urchin, *Paracentrotus lividus*, between two populations over time. Mortality rates were significantly increased by warming and desalination as individual stressors, with up to total mortality exhibited at the highest water temperature (27 °C) and lowest salinity (25). However, these stressors interacted, with desalination significantly exacerbating mortality rates at the highest temperature, but not under lower thermal regimes (21 °C and 25 °C). Mortality rates were relatively consistent between two sea urchin populations. Overall, temperature and salinity stressors can significantly interact to mediate mortality rates of key aquatic species, in ways that cannot be predicted by considering individual stressors in isolation. Future research should incorporate multiple environmental contexts to better understand and predict species responses to changing climate.

1. Introduction

Anthropogenic global change threatens aquatic ecosystems worldwide through stressors such as climate change, pollution, habitat loss and biological invasion (Sala et al., 2000; Harley et al., 2006; Seebens et al., 2021). In particular, climatic warming is resulting in myriad direct and indirect effects in highly productive coastal ecosystems, extirpating species, causing range shifts, and altering key biotic interactions (Doney et al., 2012; Wong et al., 2014). However, especially in marine systems, multiple stressors are associated with climate change (e.g., acidification, deoxygenation, desalination and warming), and these may interact in non-additive ways, with many of these interactions remaining poorly understood (O’Gorman et al., 2012; White et al., 2018). Furthermore, tolerances to multiple stressors within individual species might differ among populations, further challenging predictive efforts. That is, individual species can display high levels of plasticity in response to exposure to stressful conditions (Hufbauer et al., 2012; Wahl et al., 2016), with long-term sub-lethal exposures potentially building resilience (Vasseur et al., 2014). Accordingly, multiple stressors may manifest differently among populations, depending on the prevailing conditions of the environment.

Salinity is a primary determinant of aquatic species distributions, with organisms required to maintain homeostasis by balancing body fluid ion concentrations relative to the surrounding waters (Sutcliffe, 1978). As such, previous works have examined and harnessed salinity tolerances to better understand species’ biogeographical dynamics and potential future distribution scenarios (Paiva et al., 2018; Cuthbert et al., 2020). Temperature is also pervasive in coastal ecosystems, and can interact with salinity in mediating distributional effects on species (Einarson, 1993), as well as biotic interaction strengths (Cuthbert et al., 2019). Global surface temperatures are likely to change by between 1 °C and 3.7 °C by the end of the century (IPCC 2013), however, undulations in marine systems can be much more intense and rapid (Pansch and Hiebenthal, 2019). In particular, short-term temperature changes and extreme peaks associated with heat waves can be marked (Pansch et al., 2018), yet changes to salinity might exacerbate, or dampen, such temperature effects (Alderdice and Forrester, 1971). Accordingly, there is an urgent need for studies that investigate combined effects of these key stressors, and particularly on keystone species that disproportionately influence ecosystem structure (Paine, 1966). In turn, this can inform future species distributions as anthropogenic pressures increase, as well as possible cascading effects.

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Sea urchins are abundant and commercially-important taxa in coastal marine ecosystems (Machado et al., 2019; Yeruham et al., 2020). Given their major role in altering macroalgal assemblages, many species are considered keystone herbivores that mediate habitat availability for other taxa (Sala et al., 2012). The sea urchin *P. lividus* (Lamarck, 1816) is widespread along the northeastern Atlantic Ocean, from Scotland and Ireland to southeastern Morocco, as well as in the Mediterranean Sea (Boudouresque and Verlaque, 2007). In the Mediterranean Sea, a thermal threshold of 31 °C has been determined for this species, explaining empirical population collapse in reefs (Yeruham et al., 2015), whilst other studies have suggested a lethal temperature of around 29 °C (Pagès et al., 2017). Being sensitive to low and high salinities, upper and lower tolerances have been determined at 15 to 20 and 39 to 40, respectively (Boudouresque and Verlaque, 2007). Here, we examine emergent effects between temperature and salinity on mortality rates of *P. lividus* in the biodiverse archipelago of Madeira, Portugal. Specifically, we ask whether effects of warming are conserved across salinity regimes, or whether salinity changes offset or exacerbate warming effects. In turn, we examine how general responses are by comparing distinct sea urchin populations subject to different potential anthropogenic disturbance.

2. Materials and methods

2.1. Animal collection and maintenance

We collected the sea urchin *P. lividus* from two intertidal sites along the east coast of Madeira, Portugal in February 2017, where it was found to be locally abundant (Quinta do Lorde Beach 32°44'30.3"N 16°42'31.7"W; Funchal Bay, 32°38'46.7"N 16°53'56.8"W). Conditions at both sites at the time of sampling were 18 °C and 36 salinity. These two sites were chosen due to contrasts in anthropogenic activities, with one being a less impacted habitat, close to a Marine Protected Area (Quinta do Lorde Beach) and the other subject to high levels of ship traffic and pollution (Funchal Bay). During collection, individual sea urchins were manually removed from rock pools and transported in source water to a laboratory in the Marine and Environmental Sciences Centre, Madeira. Sampling was performed at two sites to test for potential population-level differences experimentally. In the laboratory, sea urchins were acclimated in aquaria of 30 L with continuous aeration (2–2.7 ind. L⁻¹), containing 36 salinity sea water from the collection sites for four days, with water exchanged fully in the middle of this period. Conditions were 21 °C (± 1 °C) under a light:dark cycle of 12:12, with sea urchins fed with local macroalgae (i.e., *Gelidium* sp.) ad libitum every second day. Sea urchins exhibited high survivability (> 90%) during this acclimation period.

2.2. Experimental design

We employed a fully factorial experimental design to test the effects of two stressors on sea urchin mortality: temperature (i.e., warming) and salinity (i.e., desalination) (Table 1; Fig. 1). Three water temperatures (21 °C, 25 °C and 27 °C) were crossed with two salinity regimes (36 and 25). This design resulted in six discrete temperature and salinity

Table 1

Experimental treatments concerning sea urchin mortality across temperature and salinity stressors. Each stressor combination was examined for two different populations and replicated ten times.

Temperature (°C)	Salinity	Stressor
21	36	Ambient
21	25	Desalination
25	36	Warming (intermediate)
25	25	Warming (intermediate), desalination
27	36	Warming (high)
27	25	Warming (high), desalination

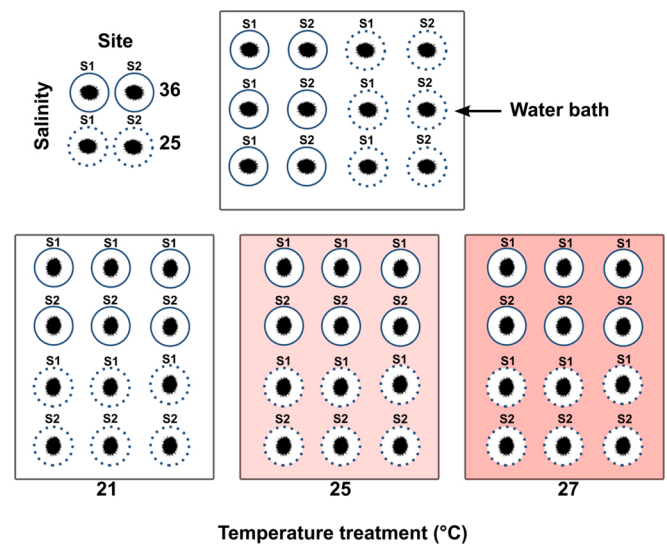


Fig. 1. Schematic representation of the experimental design. Note that the treatments within each water bath are not randomised in this figure and the sample size is reduced for simplicity. Animal silhouettes were obtained from PhyloPic (www.phylopic.org).

treatments, run for populations from each of the two sites at the same time (Fig. 1). This lower salinity regime is experienced by *P. lividus* in its native range (Chafik et al., 2001). Animals with an endoskeleton size class from 2.5 cm to 4.0 cm were selected for the experiment, to size-match individuals as far as possible. At the start of the experiment, individual sea urchins were placed in plastic arenas of 300 mL capacity (i.e., cups of ~8 cm diameter; $n = 10$ individuals per experimental group; 120 total experimental units). Water baths of 52 L volume were used to manipulate temperature conditions, evenly across the other treatment groups (site and salinity), whilst salinity was adjusted by diluting sea water with aged tap water (for the 25 group). The site and salinity treatments were randomised within each water bath (i.e., temperature treatment). All experimental arenas received continual air supply. The water temperatures were controlled by temperature loggers (T-logger, HOBO Pendant® Temperature Data Logger), with salinity and temperature verified daily using a WTW conductometer (cond 330i; WTW). Water was fully exchanged every second day in each treatment, but topped up daily to account for evaporative losses. The duration of the experiment was 16 days, with mortality assessed daily. An individual was considered dead when no movement of the spines could be observed, and the water inside the cups was often opaque. During the experiment, animals were fed ad libitum with macroalgae (i.e., *Gelidium* sp.) after each water exchange.

2.3. Data analyses

Sea urchin mortality rates over time were analysed using sigmoidal curves fit via the following equation:

$$y = 100 / [1 + e^{-Z(t-Q)}] \quad (1)$$

where Z is the slope of the mortality, t is time and Q is the onset of mortality (Briski et al., 2008, 2011). Best-fitted curves were constructed using S-Plus 6.1 (S-Plus® 6.1, 2002; Insightful Corp., Seattle, WA, USA).

Mortality rates, at the end of the experiment, were analysed using binomial generalised linear models with logit links, given data were recorded on a binary scale (i.e., dead or alive). Owing to complete separation (i.e., total survival or mortality across certain treatment groups), bias reductions were employed to allow for robust parameter estimations (Kosmidis, 2020). Temperature (3 levels), salinity (2 levels) and site (2 levels) were included as explanatory terms for mortality, as

well as their interactions. Non-significant terms were removed from the model stepwise, such that the final model included only significant single and interacting terms (i.e., $p < 0.05$). Likelihood ratio tests were used to compute main coefficients, with Tukey comparisons used *post-hoc* via estimated marginal means (Lenth, 2020). Statistical analyses were computed in R v4.0.2 (R Core Team, 2020).

3. Results

Mortality rates of sea urchins differed substantially over the course of the experiment (Fig. 2). Survival was at least 90% under ambient (i.e., control) conditions (Fig. 2, blue curve), and therefore we are confident that experimental mortality was driven by temperature and salinity regime shifts, particularly given our regular water exchanges (i.e., every two days). Under the most stressful condition (27 °C and 25; Table 1; Fig. 2, red curve), mortality rates increased rapidly to 70% and 100% between sites. Mortality rates were also generally elevated at the highest temperature without additional salinity stress (27 °C and 36), but exhibited a slower increase and a reduced magnitude (Fig. 2, black curve). For lower temperatures, sea urchin mortality rates were always at or below 10% over the course of the experiment (Fig. 2). One slight exception to this was the low salinity treatment at the intermediate temperature for one sea urchin population (25 °C and 25; Fig. 2b, green curve).

Mortality rates at the end of the experiment (Fig. 3) did not differ significantly between sites overall ($\chi^2 = 0.401$, $df = 1$, $p = 0.527$), or with sites in interaction with temperature and salinity (all $p > 0.05$). Mortality was, however, significantly affected by temperature ($\chi^2 = 47.854$, $df = 2$, $p < 0.001$) and salinity ($\chi^2 = 6.32$, $df = 1$, $p = 0.012$) singularly, as well as through the ‘temperature \times salinity’ interaction between those terms ($\chi^2 = 6.596$, $df = 2$, $p = 0.037$) (Fig. 3). As such, the effects of salinity reductions were influenced by temperature, whereby desalination had no significant effect at 21 °C ($p = 0.340$) or 25 °C ($p = 0.506$), yet was significant at 27 °C ($p = 0.016$). Desalination effects were emergent with warming, whereby end-point mortality rates were over twice as high under low (85%) as compared to high (40%) salinities at the highest temperature across sites (Figs. 2, 3). Total mortality was exhibited at Quinta do Lorde Beach at the highest temperature and lower salinity (Fig. 3).

4. Discussion

Anthropogenic environmental changes are the greatest threats to global biodiversity (Dirzo et al., 2014; Urban, 2015). However, predicting how the effects of multiple stressors combine is challenging, yet is key to informing management strategies for threatened and

economically-important species. Owing to their ecological and commercial importance, sea urchins have been extensively researched in marine systems (Hereu et al., 2012), for example being common bio-indicators (Carballera et al., 2011). Factors such as predator abundance, pollution and overexploitation have been linked to declines (Boudouresque and Verlaque, 2007; Yeruham et al., 2020).

In the present study, mortality rates of a widespread herbivorous sea urchin were found to be driven by temperature and salinity interactively. Both warming and desalination significantly heightened mortality rates in isolation, however, the inclusion of salinity stresses disproportionately exacerbated effects of warming. These effects were relatively consistent between two distinct island populations of sea urchins that are potentially subject to different environmental conditions owing to differences in human activity. Given increasing extreme events and high environmental heterogeneity in coastal marine ecosystems (Pansch et al., 2018), our results suggest that populations of *P. lividus* may be compromised should temperatures increase beyond 27 °C under certain salinity regimes. Nevertheless, we found slight differences in responses between the two populations, with a steeper mortality onset over time exhibited in populations from Quinta do Lorde Beach at the highest temperature compared to Funchal Bay. The latter is subjected to a greater degree of disturbance through pollution and ship traffic, while Quinta do Lorde Beach is less disturbed and proximal to a Marine Protected Area. Although non-significant overall, the slower mortality onset in the more impacted site therefore may represent a greater stress resilience in areas subjected to anthropogenic disturbance (Hufbauer et al., 2012).

Whilst mortality rates are useful indicators of extreme species' physiological end points, alterations to key behaviours might also occur at sub-lethal temperatures that compromise ecosystem functions. Indeed, previous works have identified ocean warming to reduce the performance of *P. lividus* in terms of respiration and consumption (Yeruham et al., 2020). In particular, compromised sea urchin populations could cause trophic cascades, favouring increases in macroalgae that would otherwise be grazed extensively (Boudouresque and Verlaque, 2007). Recently, population crashes of *P. lividus* have been documented following temperatures consistently exceeding 30 °C, coupled with competitive pressures from invasions (Yeruham et al., 2020). Similarly, in the eastern Atlantic (Madeira to Canary Islands), mass sea urchin mortality events have been reported, whereby high sea water temperatures have enabled widespread pathogenic bacterial infections (Clemente et al., 2014). Our results suggest that salinity regime shifts act as an additional, overlooked stressor that further weakens tolerances to warming, and potentially to other stressors.

P. lividus populations are naturally found under a very broad range of thermal regimes, from 4 °C in the northeast Atlantic to 30 °C in the Mediterranean Sea (Boudouresque and Verlaque, 2007). Similarly, in the Atlantic Ocean, *P. lividus* has been found to exist under salinities that fluctuate from 24 to 34 (Chafik et al., 2001), however, populations also occur where salinity falls below 20 (Bayed et al., 2005). Another study found mass mortality of *P. lividus* following an extreme rainfall event that lowered salinities to 7 (Fernandez et al., 2003). Although the present study examined two populations from the same island, we did not find any significant differences in responses to stressors. Nevertheless, this does not preclude the possibility of other, more disparate populations having greater susceptibility to stressor effects, and particularly northern populations with potentially lower critical thermal maxima than those assessed here. Conversely, populations that exist in areas subject to greater salinity and temperature fluctuations may be more robust to variations through time. In that context, Atlantic populations of *P. lividus* have been shown to be more tolerant to lower salinities (Bressan et al., 1995; Pétinay et al., 2009), and therefore Mediterranean populations could die-off at different salinities than assessed here. The mode of exposure to regime shifts might also influence susceptibilities, with chronic exposures potentially yielding different effects than acute changes. That is because species exposed to changes (e.g., marine heat

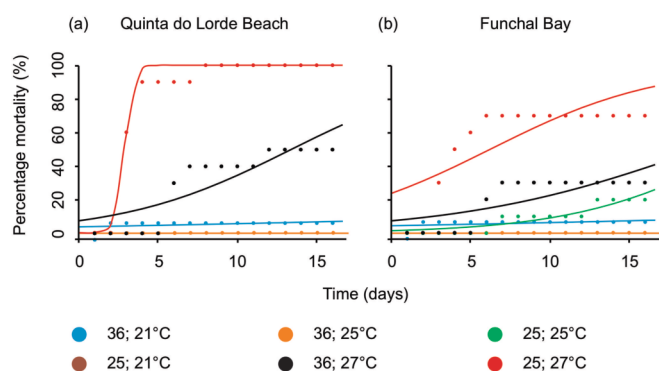


Fig. 2. Sea urchin *Paracentrotus lividus* mortality rates through time across different temperature and salinity treatments, and between two sites (a) and (b) in Madeira, Portugal. Note that overlapping treatments with zero mortality are shown in a single colour [i.e., 25, 21 °C; 36, 25 °C; 25, 25 °C for part (a), and 25, 21 °C; 36, 25 °C for part (b)].

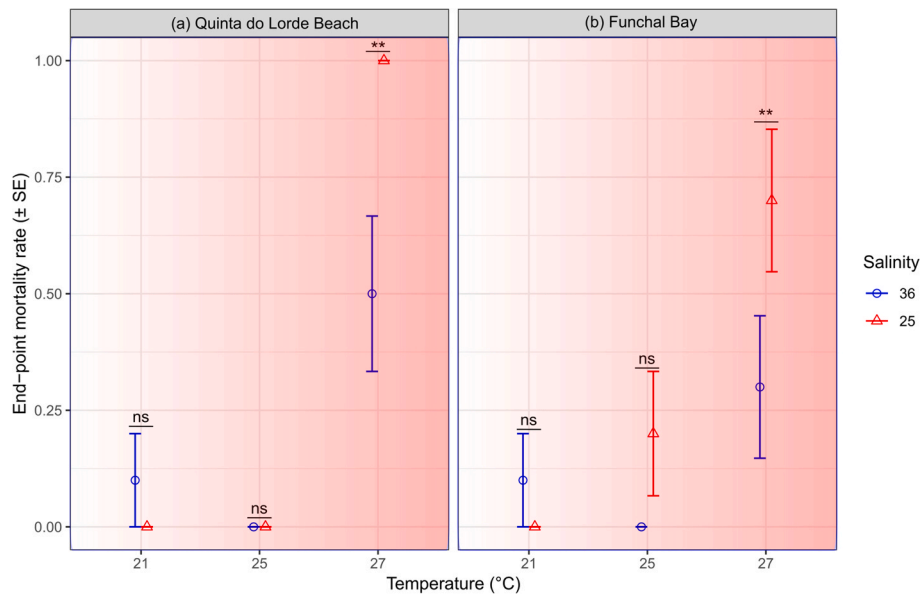


Fig. 3. Mean mortality rates of sea urchin *Paracentrotus lividus* collected from two sites (a, b) in Madeira, Portugal across warming and desalination stressors. Values are reported on the last day of the experiment (i.e., day 16). Abbreviations: ns = non-significant ($p > 0.05$); ** = $p < 0.01$; pairwise according to salinity within each temperature and site grouping.

waves; Hobday et al., 2016) over a longer period may have a greater capacity to adapt, while rapid short-term fluctuations may be more detrimental (Vasseur et al., 2014). As such, future works should consider increasing climatic variabilities, as well as resilience built over time, when inferring responses to stressors.

Future salinity conditions in the Atlantic are projected to shift considerably (Skirris et al., 2020). Although *P. lividus* has been reported to exist at salinities lower than examined here (Chafik et al., 2001), suboptimal salinities, coupled with future warming and extreme weather events (i.e., heat waves and heightened surface runoff), could compromise keystone sea urchin populations with both ecological and economic ramifications. Future works are required to further elucidate these effects in the context of additional biotic and abiotic stressors.

Data availability statement

All data generated or analysed during this study are included in this published article [and its supplementary information files].

Declaration of Competing Interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2021.102126>.

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