



**Universitat**  
de les Illes Balears

## **MASTER'S THESIS**

# **TEMPERATURE-DEPENDENCE OF THE PURPLE SEA URCHIN PARACENTROTUS LIVIDUS: A BEHAVIOURAL APPROACH**

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**Master's Degree in Marine Ecology**

**(Specialisation/Pathway *Global Change*)**

**Centre for Postgraduate Studies**

**Academic Year 2021-22**

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## Abstract

Climate change is increasingly impacting species and communities around the globe. Ocean warming is particularly threatening for marine ecosystems and many species of marine invertebrates are especially sensitive to raising temperatures. We studied the behavioural response of the purple sea urchin (*Paracentrotus lividus*), a common herbivore of the Mediterranean Sea, to a thermal regime by performing an experiment under controlled laboratory conditions. We evaluated changes in weight and the behaviour of sea urchins after 11 days of exposure to four targeted temperatures under a sublethal range (20, 23, 26, and 29 °C). Sea urchins modified their behavioural responses when exposed to increasing temperatures, while no significant results for changes in weight were found. Increasing temperatures induced higher mobility and activity, while longer times were required for the righting response. These results suggest a strong temperature-dependence of the behaviour of *P. lividus* and reveal the need for further studies on consequences of climate change on marine invertebrates.

## Introduction

Climate change has become one of the major threats for the environment due to the release of increasing CO<sub>2</sub> emissions to the atmosphere (Brothers and McClintok, 2015; García et al., 2015). Climate change particularly threatens marine ecosystems, with increasing sea surface temperature (SST) as one of its major dangers (Brothers and McClintok, 2015; García et al., 2015; Yeruham et al., 2015; Anton et al., 2020; Ding et al., 2020; Santos et al., 2020). Over the last decade, oceans experienced the warmest temperatures ever reached and the projection is that marine heatwaves will keep occurring with longer duration and increasing intensity (Frölicher, Fischer & Gruber, 2018). Marine heatwaves can exert devastating impacts on marine ecosystems due to elevated temperatures surpassing the lethal limits of species (Yeruham et al., 2015; 2020). For instance, the marine heatwave of 2015-2016 caused more than 40% of coral mortality in the Southern

Red Sea (Anton et al., 2020). Similarly, the 2003 European heatwave caused widespread mortality of the endemic Mediterranean seagrass *Posidonia oceanica* (Marbà and Duarte, 2010).

The Mediterranean Sea is particularly vulnerable to ocean warming due to its geographical position and its dependency on currents and water influx from the Atlantic Ocean (Giorgi and Lionello, 2008; Fox-Kemper et al., 2021). It is located in a transition zone between the arid climate of North Africa and the temperate and rainy climate from central Europe (Giorgi and Lionello, 2008). Furthermore, it is affected by interactions between mid-latitude and tropical processes. The Mediterranean region has shown large climate shifts in the past (Luterbacher et al., 2006) and it is because of these features that it is considered a hot-spot in terms of future predictions of global warming and climate change (Luterbacher et al., 2006; Giorgi and Lionello, 2008; Yeruham et al., 2015; Fox-Kemper et al., 2021). The mean SST in summer between 2002-2010 in the Western Mediterranean has increased  $1,05 \pm 0,37^{\circ}\text{C}$  compared to the temperatures relative to years 1980-2000 (Marbà and Duarte, 2010; Jordà, Marbà and Duarte, 2012). Predictions developed at the moment show an increase not only in the mean SST of the Mediterranean, but also in the maximum temperatures reached in the hottest season (Lionello, 2012; Lionello et al., 2014; Savva et al., 2018). It is predicted an average increase of  $2^{\circ}\text{C}$  by 2050 and around  $3,4^{\circ}\text{C}$  by 2100 in the Western Mediterranean under the 2.6 and 8.5 RCP scenarios, which are being used to drive climate model simulations according to the evolution of the atmospheric composition (Meinshausen et al., 2011; IPCC 2007; 2013; García et al., 2015). This will drive into an average SST in summer of  $29-30,5^{\circ}\text{C}$  by the end of the century (Jordà, Marbà and Duarte, 2012; Savva et al., 2018), which surpasses (or it is close to) the lethal thermal threshold of several Mediterranean species (Savva et al., 2018). Predictions show that the increase of SST is an important stressing factor on marine invertebrates, manifested at a molecular and ecological level (Brothers and McClintok, 2015).

In temperate seas, echinoderms species play a key role as important herbivores, controlling the structure and functioning of benthic communities (Crook, 2003; Gianguzza et al., 2010; Bonaviri et al., 2011; Yeruham et al., 2015; Pagès et al., 2018; Boudouresque

and Velarque, 2020). The purple sea urchin *Paracentrotus lividus* (Lamarck, 1816) (Echinodermata: Echinoidea) is a key-stone species marine invertebrate widely distributed in the Mediterranean Sea. Its thermal range spans from 10-15°C in winter and 18-25°C in summer (Boudouresque and Velarque, 2020). *P. lividus* dominates intertidal rocky bottoms and shallow water seagrasses beds (e.g., meadows dominated by *Posidonia oceanica* or *Cymodocea nodosa*), with a maximum depth of 20 meters and an upper limit marked by desiccation (Crook, 2003; Yeruham et al., 2015; Boudouresque and Velarque, 2020).

Temperature is an abiotic variable that affects sea urchins (Brothers and McClintok, 2015; Yeruham et al., 2015; Zhang et al., 2017; Pagès et al., 2018; Ding et al., 2019; Santos et al., 2020). In the absence of food constraints, temperature can control physiological responses involved in metabolic processes, including respiration and feeding rates and somatic and gonadal growth (Yeruham et al., 2015; 2020; Santos et al., 2020;). Even though they are a eurythermal species that can tolerate a wide range of extreme temperatures (4-30°C) (Yeruham et al., 2015; 2020; Boudouresque and Velarque, 2020), sea urchins have an optimal temperature at which different traits of performance peak (Boudouresque and Velarque, 2020; Santos et al., 2020). Increasing temperatures (within the nonlethal range) commonly rise the metabolic activity of organisms, leading to the increase of the activity of their organisms as well as their velocity (Gibert et al., 2016; Pagès et al., 2018). It has been demonstrated that changes in the environmental temperature can affect the behaviour of ectotherm organisms and alter their body size (Gibert et al., 2016; Zhang et al., 2017; Ding et al., 2020). Movement patterns, such as velocity, as well as feeding rates may also present changes at higher temperatures (Kordas, Harley and o'Connor, 2011; Gibert et al., 2016; Pagès et al., 2018), though it is difficult to assess (Lejeusne et al., 2009).

Sea urchins present neuromuscular-mediated behaviours such as righting responses and foraging behaviours, that can be used as proxies of their health status and their capacity to protect themselves from environmental stresses (Brothers and McClintock, 2015; Ding et al., 2020). There are studies assessing the response of behavioural traits of sea urchins regarding temperature (Zhang et al., 2017; Pagès et al., 2018; Ding et al., 2020). The

righting response - the capacity to coordinate tube feet and spine movements to invert themselves onto their oral side (Bayed et al., 2005; Ding et al., 2020) - is a common behaviour used as an indicator of their physiological status in relation to environmental changes as well as a health measure in relation to the stress level of the organisms (Lawrence and Cowell, 1996; Bayed et al., 2005). It is measured in the laboratory by inverting the organisms onto their aboral side and quantifying the time (seconds) they require to turn back into their oral side using the tube feet and spines (Kleitman, 1941; Lawrence and Cowell, 1996; Bayed et al., 2005; Ding et al., 2020). Righting response can be used to assess the general physiological status of sea urchins because urchins must have a minimum degree of coordination between the tube feet and spines (Kleitman, 1941; Lawrence and Cowell, 1996; Bayed et al., 2005). This degree of coordination may vary along the temperature gradient.

Foraging behaviour refers to the behavioural responses displayed by sea urchins in relation to availability or presence of food and it has been used to assess the effect of environmental variables such as temperature on movement patterns of echinoids (Pagès et al., 2018; Ding et al., 2020). We are assessing two foraging behaviours in this study: foraging time – time required for the sea urchin to reach food – and foraging velocity – distance travelled by the sea urchin to reach food. Other studies have previously measured these behavioural responses in sea urchins (Pagès et al., 2018; Ding et al., 2020) and they are considered appropriate behavioural responses to get a general knowledge of the fitness and health status of sea urchins, as well as to find the optimal temperature of their activity (Pagès et al., 2018; Ding et al., 2020).

Despite the ecological importance of urchins, as well as their economic value, not many quantitative studies have investigated their behavioural ecology with regard to temperature (Crook, 2003). This study aims to quantify the effects of sublethal temperatures in the behaviour of the purple sea urchin *Paracentrotus lividus*. A laboratory experiment was performed in the Institute of Advanced Mediterranean Studies (IMEDEA, Mallorca, Spain), where several sea urchins were exposed to temperatures ranging from 20 to 29°C for 11 days. Growth and three behavioural responses were measured and

analysed to measure their relationship with temperature. Thus, we worked under the hypothesis that temperature had an effect in the behaviour of sea urchins.

## Material and methods

### *Collection and maintenance of sea urchins*

A total of 20 sea urchins (*Paracentrotus lividus*) were collected in Port de Valldemossa, Mallorca (39° 43' 04''N, 2° 35' 13'' E) (Figure 1) on May 16<sup>th</sup> 2022 between 0,5 and 3 m depth over a rocky substrate. This urchin collection was authorized by the local authorities (Government of Balearic Islands; GOIB). Salinity (37,4 PSU) and temperature (20,4°C) were measured *in situ* to acclimatize the urchins to similar conditions in the laboratory as those in the field. Urchins were fed with *Padina pavonica*, a brown algae widely distributed in the Mediterranean Sea, which is a known food preference of *P. lividus* (García et al., 2015; Boudouresque and Velarque, 2020).



*Figure 1. Sampling area of Paracentrotus lividus (Port de Valldemossa, Mallorca, Spain).*



Specimens were transported to IMEDEA within one hour of collection. Specimens were weighed and put into different aquariums inside a temperature chamber (Figure 2). The 20 sea urchins were randomly distributed in five 15 L aquariums (length x width x height: 25 cm x 25 cm x 30 cm) from Blau Aquaristic's equipment (Blau aquaristic: Cubic panoramic; [www.blau-aquaristic.com](http://www.blau-aquaristic.com)). Each aquarium with four urchins was disposed inside large tanks (length x width x height: 80 cm x 35 cm x 34,5 cm) with fresh water, where the temperature was controlled (objective  $T^a(^{\circ}\text{C}) \pm 0,5$ ) using IKS-Aquastar system ([www.iks-aqua.de](http://www.iks-aqua.de)) to control de temperature. Daily water changes (3 L) were made during the experiment, as well as daily measures and adjustments of salinity ( $37,5 \pm 0,3$  PSU). To maintain the water in the aquariums clean, a water filter was set inside each aquarium and a bubbler was included to maintain normoxia conditions during the experiment. The photoperiod was programmed to settle 13 hours of light and 11 hours of night.



*Figure 2. Disposition of tanks and aquariums during the experiment, inside the temperature chamber, in IMEDEA.*

Two grams of *P. pavonica* were administrated *ad libitum* to each aquarium every 2 o 3 days during the experiment to feed the urchins but they were starved for 24h before taking behavioural measurements to standardize the hunger level across urchins.

### *Experimental design*

The urchins were acclimated for seven days, and an increase of 1°C/day was made in each aquarium until reaching the targeted-temperatures of 20°C, 23°C, 26°C, and 29°C. Measurements were taken individually on each urchin the first day they reached the targeted temperature and 11 days after being exposed to that temperature.

On each sea urchin we measured growth and three behavioural responses: weight change (gr/day), standardized weight change (%), righting response (s), foraging time (s) and foraging velocity (mm/min) (Table 1). Behavioural responses were measured in 6 L individual aquariums, filled with 50% fresh sea water and 50% water from their treatment aquarium.

**Table 1. Description of the response variables of the experiment.**

Variable type	Response variable	Description	Unit
physiological	weight	Change in weight after 11 days of exposure	grams (gr)
physiological	standardized weight	Percentage of weight loss or gained weight	%
behavioural	righting response	Time a sea urchin takes to invert themselves onto its oral side after being turned upside down	seconds (s)
behavioural	foraging time	Time a sea urchin took to reach the food incentive	seconds (s)
behavioural	foraging velocity	Distance a sea urchin reached in a minute	mm/min

An additional aquarium with four urchins was maintained at 20 °C during the experiment and used as a control treatment. Same measurements as taken for the experiment were taken the first day and the last day of the experiment.

### *Righting response*

All behavioural responses were measured in the 6 L aquariums by setting a GOPRO Hero 5 camera on top of the aquariums. Righting response was quantified by setting each sea urchin onto his aboral side and measuring the time (s) they took to invert themselves onto their oral using a timer and not for more than 15 min.

### *Foraging time*

Foraging time was considered the time (s) each sea urchin took to reach the food (*Padina pavonica*) After the righting response was measured, a food incentive was disposed inside the aquarium at a known distance from the urchin. The movement of the individuals was recorded for 30 min. When the sea urchins did not reach the food, a value of 1800 s was noted. Data was extracted from the analysis of the videos.

### *Foraging velocity*

The foraging velocity was considered a behavioural response related to the exposure to a food incentive. It was calculated with the data extracted from the videos taken during the experiment following this formula:

$$\text{Velocity (mm/min)} = \frac{\text{distance covered (mm)}}{\text{time of movement in 30' (minutes)}}$$

### *Weight of sea urchins*

Weight was measured in grams using a balance from the laboratory. Weight measurements were also taken the day urchins were collected so urchins could be distributed across treatments with comparable weights.

Changes in weight were calculated following the formula:

$$\Delta W = \frac{(W2 - W1)}{\text{days of exposure}}$$

where W1 is the weight from the first measure and W2 the weight at the end of the exposure.

Weight change was also standardized by weight to get a percentage of weight change per urchin using this formula:

$$\Delta W(\%) = \frac{(W2 - W1)}{W1} \times 100$$

### *Statistical analysis*

All statistical analysis and graphics were carried out either using R studio or Excel. In table 2 the response variables used are described.

Temperature was considered a continuous variable to perform linear models in R studio and allow us to test the linear effect of temperature on the response variables. In order to perform linear regressions in R, the function *lm()* was used following this structure:

```
linealgressionX <- lm (responsevariable ~ temperature, data = mydatabase)
```

Linear regressions were plotted using *ggplot*.

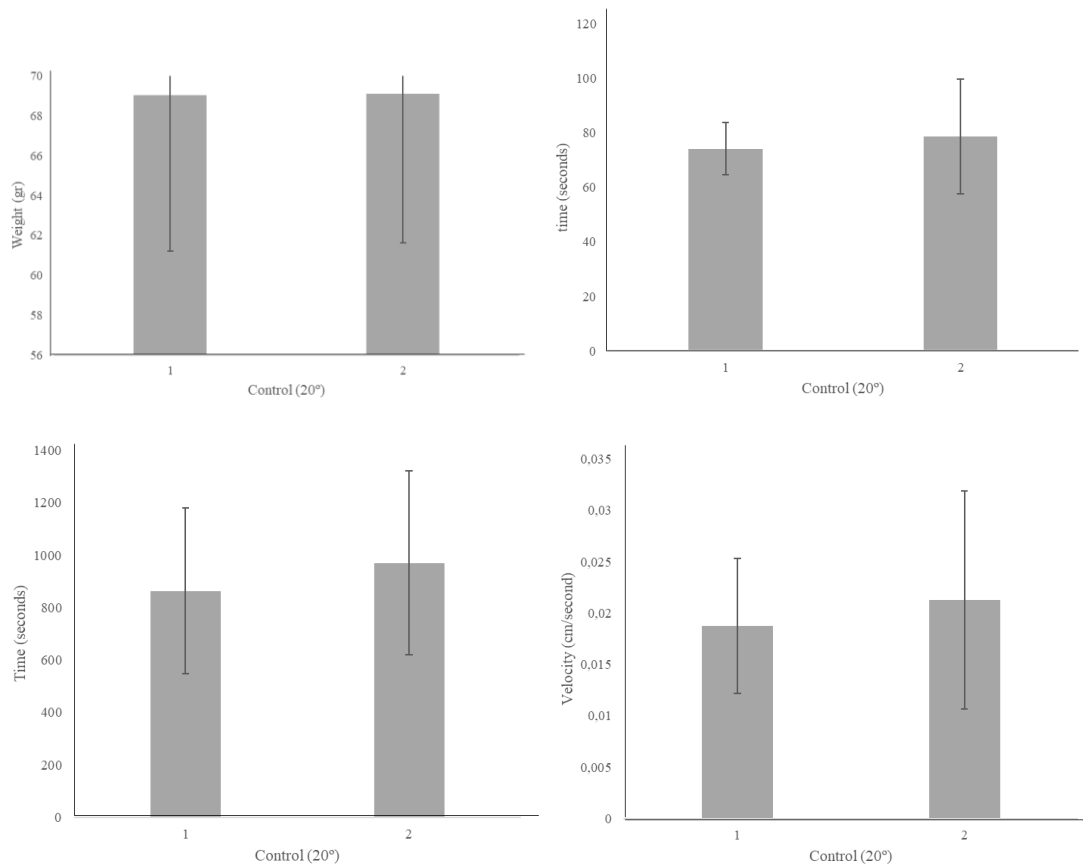
**Table 2. Description of the response variables measured in our study.**

Response variable	n	Minimum	Maximum	Mean ± SE
Weight	4	-0,485	0,155	-0,039 ± 0,068
Stardarized weight	4	-5,731	1,597	-0,548 ± 0,798
Righting response	4	39	565	138,933 ± 69,894
Foraging time	4	101	1800	1011,063 ± 321,062
Foraging velocity	4	0	41,584	11,213 ± 6,396

## Results

### *Control treatment*

For the control treatment, it was verified that there were no changes in the response variables during the duration of the experiment. No significant differences were found between the two sampling times for changes in weight or the behavioural variables using the analysis of the variance (ANOVA) (Table 3;  $p$  value  $< 0,05$ ).



**Figure 3.** Bar plots for all variables used in the experiments at 20°C (control temperature), measured two times along the experiment: (1) first day they reached 20°C and (2) after 32 days of exposure to 20°C.

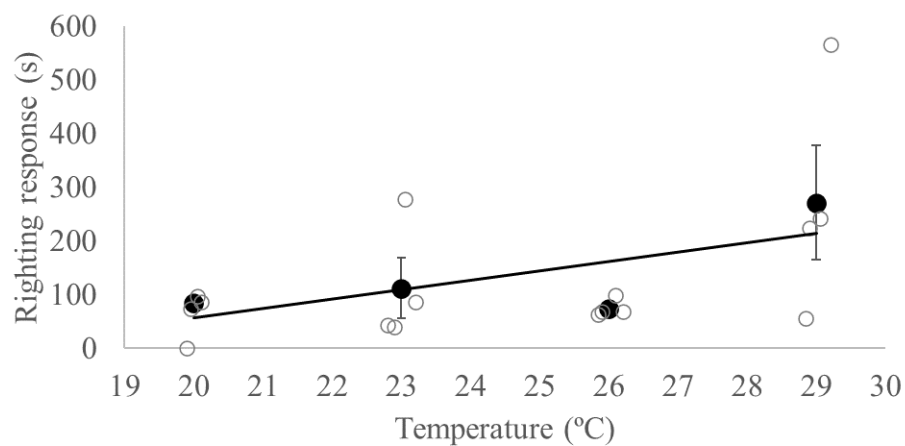
**Table 3. Results of the analysis of the variance (ANOVA) run for the four variables treated.**

response variable	Analysis of the Variance		
	Df	F value	p value
weight	1	0	0,995
righting response	1	0,038	0,852
foraging time	1	0,051	0,829
foraging velocity	1	0,066	0,806

Notes of spines lost and whether they had eaten or not were taken to keep track of signs on health issues or stress. No mortality or stress signs were seen during the experiment.

### *Righting response*

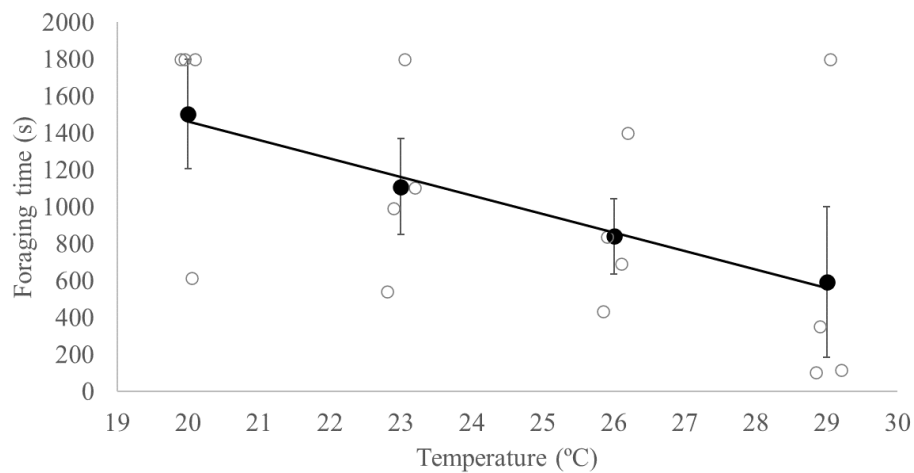
The righting response resulted to have a marginally significant dependence on temperature (Figure 4; p value = 0,102; Adjusted R<sup>2</sup> = 0,130), showing a positive relationship.



**Figure 4. Linear regression between temperature (°C) and righting response (s) of the sea urchin *P. lividus* after 11 days of exposure to four different temperature treatments. Black solid dots indicate the mean ( $\pm$ SE) while grey circles represent raw measurements.**

### *Foraging time*

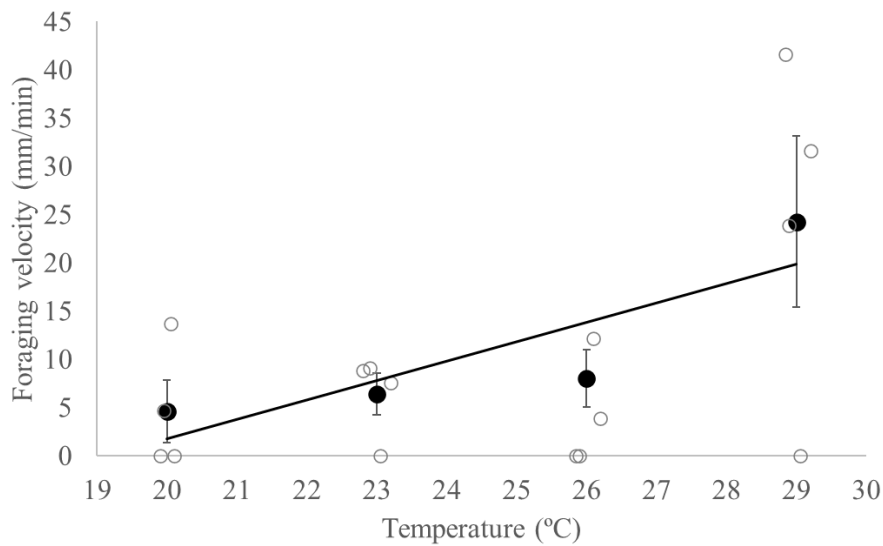
The relation between foraging times and increasing temperatures was positive and significant (Table 4, Figure 5; Adjusted  $R^2 = 0,241$ ; p value = 0,031).



**Figure 5.** Linear regression between temperature (°C) and foraging time (s) of the sea urchin *P. lividus* after 11 days of exposure to four different temperature treatments. Black solid dots indicate the mean ( $\pm$  SE) while grey circles represent raw measurements.

### *Foraging velocity*

Results for foraging velocity were similar to those of foraging time. We found that a positive and significant relationship between velocity of sea urchins and temperature (Table 3; Figure 7; p value = 0,02; Figure 6).



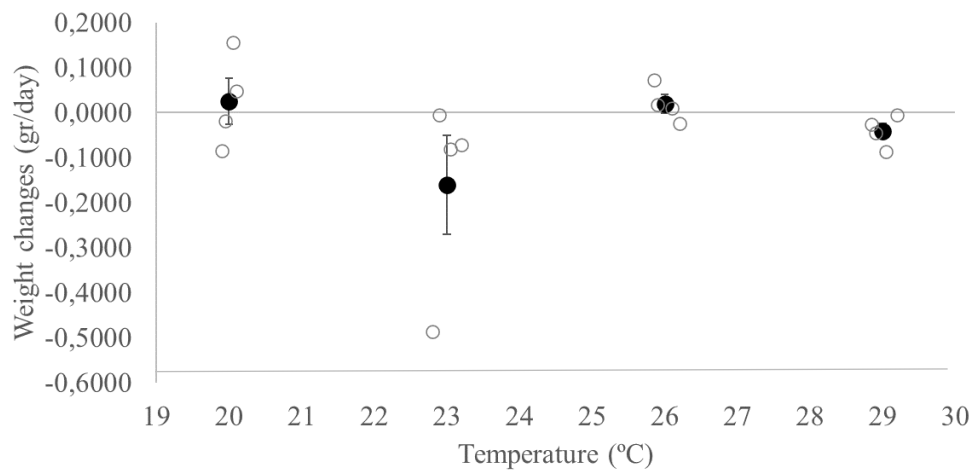
**Figure 6. Linear regression between temperature (°C) and foraging velocity (mm/min) of the sea urchin *P. lividus* after 11 days of exposure to four different temperature treatments. Black solid dots indicate the mean ( $\pm$ SE) while grey circles represent raw measurements.**

### *Weight of sea urchins*

After 11 days of exposure to the four different temperatures, no significant results were found for changes in weight (Table 4; p value = 0,956; adjusted  $R^2 = -0,07$ ) in relation to the temperature treatments. The regression model for the growth in *P. lividus*, measured in weight changes after 11 days of exposure to each treatment, is presented in figure 7.

There was no significant relationship between weight changes (standardized by weight of the urchin) and temperature (Table 4; p value = 0,986; adjusted  $R^2 = -0,07$ ).





**Figure 7. Weight change in the sea urchin *P. lividus* after 11 days of exposure to the four targeted-temperatures. Black solid dots indicate the mean ( $\pm$ SE) while grey circles represent raw measurements.**

*Table 4. Linear regression results for all response variables.*

variables	lineal regression			
	Df	F statistic	p value	Adj R <sup>2</sup>
<b>Weight changes (gr/day)</b>	1	0,003	0,956	-0,070
<b>Righting response (s)</b>	1	3,098	0,102	0,130
<b>Foraging time (s)</b>	1	5,767	0,031	0,241
<b>Foraging velocity (mm/min)</b>	1	7,19	0,02	0,323
<b>Weight (%)</b>	1	0,0003	0,986	-0,071

## Discussion

Increasing temperatures can trigger complex dynamics in marine communities, including changes of behaviour in marine invertebrates. In our experiment, we document a strong temperature-dependence of the behaviour of the urchin *Paracentrotus lividus*.

Temperature affected the foraging behaviour of *P. lividus*, both in terms of foraging time and foraging velocity. Foraging time decreased and foraging velocity increased along a temperature gradient spanning from 20 to 29 °C, meaning the urchins got to the food faster at higher temperatures. Previous experiments assessing the effect of temperature in the foraging behaviour of different species of sea urchins show mixed results (Pagès et al., 2018; Ding et al., 2020). For instance, Pagès et al., (2018) reported that the consumption rates – another measurement of the foraging behaviour of sea urchins - of *P. lividus* are strongly related to temperature. On the other hand, results from Ding et al., (2020) showed no significant difference in the foraging behaviour of the sea urchin *Mesocentrotus nudus* after being exposed to three temperatures (10 °C, 15 °C, 20 °C). Even though for both of those experiments and ours the targeted temperatures were below the lethal threshold, our experiment included a high temperature treatment close to thermal threshold of *P. lividus* in the eastern Mediterranean of 30,5 °C (Yeruham et al., 2015), which might explain the strong temperature-dependence of urchin behaviour found in our results. Nevertheless, the grazing activity of these herbivores can shape the structure and functioning of marine benthic communities (Lawrence, 1975; Duggins, 1981; Benedetti-Cecchi and Cinelli, 1995; Schiel, Steinbeck and Foster, 2004; Hereu, 2005), and changes in their foraging behaviour related to ocean warming might trigger unexpected changes in the Mediterranean coastal communities.

Our results showed that the urchins took longer to turn around as temperature increased. The righting response time more than tripled from 20°C to 29°C (righting response increased from 85 to 271 s at 20 °C and 29 °C respectively), but no optimum for righting response was found. The experiment performed by Brothers and McClintok (2015) showed higher righting response times for the sea urchin *L. variegatus* when exposed to

28 °C as compared to 32 °C, showing a similar response that found in our experiment, where higher righting response times were found as temperatures approached to the upper limit of 30,5 °C described by Yeruham et al., (2015). The ability of righting themselves up has been related to their defence against predators. Lower righting response times related to increasing temperatures might have great consequences due to the interaction of the sea urchins with their ecosystem – a reduced ability of righting themselves up might make *P. lividus* a vulnerable prey that could trigger a decrease of urchin density in benthic ecosystems, potentially affecting community structure and ecosystem functioning by causing trophic cascades.

We did not find changes in the growth rate of *P. lividus* after being exposed to targeted temperatures for 11 days along a temperature gradient. It is known that metabolic rates of sea urchins tend to increase at warmer temperatures as long as it does not surpass the species thermal limit (Lemoine and Burkepile, 2012; Gibert et al., 2016; Pagés et al., 2018; Boudouresque and Velarque, 2020; Santos et al., 2020), which we did not exceed in our experiment. However, 11 days might not have been enough time to observe changes in the weight of the sea urchins. Pagés et al., (2018) exposed *P. lividus* for two months to the targeted-temperatures between 16 and 31 °C and reported a quadratic response with an increase in body weight from 16 °C up to an optimum of 22 °C followed by a steadily weight decrease from 23 to 31 °C.

No urchins died during our experiment, indicating that the thermal limit of this population of urchins from the western Mediterranean was not reached at 29° C. Unfortunately, in our experiment we were unable to identify the optimum temperature of any of the performance traits assessed since the relations with temperature were linear (increasing or decreasing) instead of quadratic. However, we were able to demonstrate that the behaviour of *P. lividus* is strongly affected by temperature.

Therefore, we believe further investigation needs to be taken to find the optimum temperature of *P. lividus* in the Western Mediterranean. The simulation of more complex scenarios (e.g., adding other trophic levels such as predators and resources) might be key to understand the dynamics involved in the behaviour of sea urchins in shallow coastal ecosystems under climate change scenarios.

Despite their ecological importance, the behaviour of sea urchins has rarely been quantified in relationship to temperature. Given the importance of echinoids as key-stone species in shallow coastal ecosystems, it is necessary to have a better understanding of the complex dynamics that could develop in a rapidly warming ocean.

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## References

- Anton, A., Randle, J. L., Garcia, F. C., Rossbach, S., Ellis, J. I., Weinzierl, M., & Duarte, C. M. (2020). Differential thermal tolerance between algae and corals may trigger the proliferation of algae in coral reefs. *Global Change Biology*, *26*(8), 4316-4327.
- Barnes, D. K., Crook, A., O'Mahoney, M., Steele, S., & Maguire, D. (2001). Sea temperature variability and *Paracentrotus lividus* (Echinoidea) population fluctuations. *Journal of the Marine Biological Association of the United Kingdom*, *81*(2), 359-360.
- Bayed, A., Quiniou, F., Benrha, A., & Guillou, M. (2005). The *Paracentrotus lividus* populations from the northern Moroccan Atlantic coast: growth, reproduction and health condition. *Journal of the Marine Biological Association of the United Kingdom*, *85*(4), 999-1007.
- Benedetti-Cecchi, L., & Cinelli, F. (1995). Habitat heterogeneity, sea urchin grazing and the distribution of algae in littoral rock pools on the west coast of Italy (western Mediterranean). *Marine Ecology Progress Series*, *126*, 203-212.
- Bonaviri, C., Vega Fernández, T., Fanelli, G., Badalamenti, F., & Gianguzza, P. (2011). Leading role of the sea urchin *Arbacia lixula* in maintaining the barren state in southwestern Mediterranean. *Marine Biology*, *158*(11), 2505-2513.
- Boudouresque, C. F., & Verlaque, M. (2020). *Paracentrotus lividus*. In *Developments in aquaculture and fisheries science* (Vol. 43, pp. 447-485). Elsevier.
- Brothers, C. J., & McClintock, J. B. (2015). The effects of climate-induced elevated seawater temperature on the covering behavior, righting response, and Aristotle's lantern

reflex of the sea urchin *Lytechinus variegatus*. *Journal of Experimental Marine Biology and Ecology*, 467, 33-38.

Brothers, C. J., & McClintock, J. B. (2015). The effects of climate-induced elevated seawater temperature on the covering behavior, righting response, and Aristotle's lantern reflex of the sea urchin *Lytechinus variegatus*. *Journal of Experimental Marine Biology and Ecology*, 467, 33-38.

Cohen-Rengifo, M., Agüera, A., Detrain, C., Bouma, T. J., Dubois, P., & Flammang, P. (2018). Biomechanics and behaviour in the sea urchin *Paracentrotus lividus* (Lamarck, 1816) when facing gradually increasing water flows. *Journal of Experimental Marine Biology and Ecology*, 506, 61-71.

Crook, A. C. (2003). Individual variation in the covering behaviour of the shallow water sea urchin *Paracentrotus lividus*. *Marine Ecology*, 24(4), 275-287.

Ding, J., Zheng, D., Sun, J., Hu, F., Yu, Y., Zhao, C., & Chang, Y. (2020). Effects of water temperature on survival, behaviors and growth of the sea urchin *Mesocentrotus nudus*: new insights into the stock enhancement. *Aquaculture*, 519, 734873.

Domenici, P., González-Calderón, D., & Ferrari, R. S. (2003). Locomotor performance in the sea urchin *Paracentrotus lividus*. *Journal of the Marine Biological Association of the United Kingdom*, 83(2), 285-292.

Duggins, D. O. (1981). Sea urchins and kelp: The effects of short term changes in urchin diet 1. *Limnology and Oceanography*, 26(2), 391-394.

Fox-Kemper, B., H.T. Hewitt, C. Xiao, G. Aðalgeirsdóttir, S.S. Drijfhout, T.L. Edwards, N.R. Golledge, M. Hemer, R.E. Kopp, G. Krinner, A. Mix, D. Notz, S. Nowicki, I.S. Nurhati, L. Ruiz, J.-B. Sallée, A.B.A. Slangen, and Y. Yu, 2021: Ocean, Cryosphere and

Sea Level Change. In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1211–1362, doi:10.1017/9781009157896.011.

Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, *560*(7718), 360-364.

García, E., Clemente, S., & Hernández, J. C. (2015). Ocean warming ameliorates the negative effects of ocean acidification on *Paracentrotus lividus* larval development and settlement. *Marine Environmental Research*, *110*, 61-68.

Gianguzza, P., Bonaviri, C., Milisenda, G., Barcellona, A., Agnetta, D., Fernández, T. V., & Badalamenti, F. (2010). Macroalgal assemblage type affects predation pressure on sea urchins by altering adhesion strength. *Marine Environmental Research*, *70*(1), 82-86.

Gibert, J. P., Chelini, M. C., Rosenthal, M. F., & DeLong, J. P. (2016). Crossing regimes of temperature dependence in animal movement. *Global Change Biology*, *22*(5), 1722-1736.

Giorgi, F., & Lionello, P. (2008). Climate change projections for the Mediterranean region. *Global and planetary change*, *63*(2-3), 90-104.

Hereu, B. (2005). Movement patterns of the sea urchin *Paracentrotus lividus* in a marine reserve and an unprotected area in the NW Mediterranean. *Marine Ecology*, *26*(1), 54-62.



Hoegh-Guldberg, O., R. Cai, E.S. Poloczanska, P.G. Brewer, S. Sundby, K. Hilmi, V.J. Fabry, and S. Jung, 2014: The Ocean. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Barros, V.R., C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L.White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1655-1731

Jordà, G., Marbà, N., & Duarte, C. M. (2012). Mediterranean seagrass vulnerable to regional climate warming. *Nature climate change*, 2(11), 821-824.

Kleitman, N. (1941). The effect of temperature on the righting of echinoderms. *The Biological Bulletin*, 80(3), 292-298.

Kordas, R. L., Harley, C. D., & O'Connor, M. I. (2011). Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology*, 400(1-2), 218-226.

Lawrence, J. M., & Cowell, B. C. (1996). The righting response as an indication of stress in *Stichaster striatus* (Echinodermata, Asteroidea). *Marine & Freshwater Behaviour & Phy*, 27(4), 239-248.

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F., & Pérez, T. (2010). Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in ecology & evolution*, 25(4), 250-260.

Lemoine, N. P., & Burkepile, D. E. (2012). Temperature-induced mismatches between consumption and metabolism reduce consumer fitness. *Ecology*, 93(11), 2483-2489.

Lionello, P. (Ed.). (2012). *The climate of the Mediterranean region: From the past to the future*. Elsevier.

Lionello, P., Abrantes, F., Gacic, M., Planton, S., Trigo, R., & Ulbrich, U. (2014). The climate of the Mediterranean region: research progress and climate change impacts. *Regional Environmental Change*, 14(5), 1679-1684.

Luterbacher, J., Xoplaki, E., Casty, C., Wanner, H., Pauling, A., Küttel, M., ... & Ladurie, E. L. R. (2006). Mediterranean climate variability over the last centuries: a review. *Developments in Earth and environmental Sciences*, 4, 27-148.

Marbà, N., & Duarte, C. M. (2010). Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. *Global change biology*, 16(8), 2366-2375.

Marbà, N., & Duarte, C. M. (2010). Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. *Global change biology*, 16(8), 2366-2375.

Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L., Lamarque, J. F., ... & Van Vuuren, D. P. P. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic change*, 109(1), 213-241.

Pachauri, R. K., & Reisinger, A. (2007). IPCC fourth assessment report. *IPCC, Geneva*, 2007.

Pages, J. F., Smith, T. M., Tomas, F., Sanmarti, N., Boada, J., De Bari, H., ... & Alcoverro, T. (2018). Contrasting effects of ocean warming on different components of plant-herbivore interactions. *Marine pollution bulletin*, 134, 55-65.

- Santos, P. M., Albano, P., Raposo, A., Ferreira, S. M., Costa, J. L., & Pombo, A. (2020). The effect of temperature on somatic and gonadal development of the sea urchin *Paracentrotus lividus* (Lamarck, 1816). *Aquaculture*, 528, 735487.
- Savva, I., Bennett, S., Roca, G., Jordà, G., & Marbà, N. (2018). Thermal tolerance of Mediterranean marine macrophytes: Vulnerability to global warming. *Ecology and evolution*, 8(23), 12032-12043.
- Schiel, D. R., Steinbeck, J. R., & Foster, M. S. (2004). Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology*, 85(7), 1833-1839.
- Yeruham, E., Rilov, G., Shpigel, M., & Abelson, A. (2015). Collapse of the echinoid *Paracentrotus lividus* populations in the Eastern Mediterranean—result of climate change?. *Scientific reports*, 5(1), 1-6.
- Yeruham, E., Shpigel, M., Abelson, A., & Rilov, G. (2020). Ocean warming and tropical invaders erode the performance of a key herbivore. *Ecology*, 101(2), e02925.
- Zhang, L., Zhang, L., Shi, D., Wei, J., Chang, Y., & Zhao, C. (2017). Effects of long-term elevated temperature on covering, sheltering and righting behaviors of the sea urchin *Strongylocentrotus intermedius*. *PeerJ*, 5, e3122.