Contrasting effects of ocean warming on different components of plant-herbivore interactions

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ABSTRACT

There is increasing uncertainty of how marine ecosystems will respond to rising temperatures. While studies have focused on the impacts of warming on individual species, knowledge of how species interactions are likely to respond is scant. The strength of even simple two-species interactions is influenced by several interacting mechanisms, each potentially changing with temperature. We used controlled experiments to assess how plant-herbivore interactions respond to temperature for three structural dominant macrophytes in the Mediterranean and their principal sea urchin herbivore. Increasing temperature differentially influenced plant-specific growth, sea urchin growth and metabolism, consumption rates and herbivore preferences, but not movement behaviour. Evaluating these empirical observations against conceptual models of plant-herbivore performance, it appears likely that while the strength of herbivory may increase for the tested macroalga, for the two dominant sea-grasses, the interaction strength may remain relatively unchanged or even weaken as temperatures rise. These results show a clear set of winners and losers in the warming Mediterranean as the complex factors driving species interactions change.

1. Introduction

Over the coming decades, the ecological impacts of global warming are expected to increase as temperatures rise (IPCC, 2013). Global average sea surface temperatures are predicted to rise by 0.75 °C by 2035 (Kirtman et al., 2013) and between 1 °C and > 3 °C by 2100 (Collins et al., 2013), relative to the reference period 1986–2005. While a large body of research has focused on the direct effects of global change on population abundances, community composition, and organismal physiology (e.g. Sala et al., 2000), global change may cause less obvious alterations to the networks of interactions among species (Tylianakis et al., 2008). Indeed, biotic interactions such as predation, herbivory, parasitism or mutualism are key in maintaining ecosystems' biodiversity, resilience and services (Bascompte et al., 2006; Dobson et al., 2011; Ives and Carpenter, 2007). The historical lack of research on the effects of warming on biotic interactions, especially in marine ecosystems (Wernberg et al., 2012, but see recent advances, e.g. Gutow

et al., 2016; Hernán et al., 2017), likely stems from difficulties in quantifying modifications in interactions compared to documenting changes in single species abundance, biodiversity or individual physiological processes (McCann, 2007; Somero, 2012; Wernberg et al., 2012). Even a simple two-species interaction is ridden with complexities, driven by a host of biological, behavioural and ecological mechanisms that can all interact in often surprising ways (Boada et al., 2017). Unravelling these mechanisms and understanding how they are likely to respond to change is far from trivial. Indeed, interactions may be particularly susceptible to warming, since they are sensitive to the relative abundances of the set of interacting species, their physiology, phenology and behaviour (Parmesan, 2006; Suttle et al., 2007; Tylianakis et al., 2007).

The interaction between a primary producer and its consumer can be used as a basic model to explore the complexity inherent in understanding the effects of changing temperatures at the community level. Plant-herbivore interactions are crucial for the evolution of both plant

and herbivore traits (e.g. Fritz and Simms, 1992), and are critical in determining the abundance of primary producers globally (Cebrián, 1999). They structure both terrestrial and marine food webs and ultimately determine whether the world is dominated by producers or consumers (Polis, 1999). Plant-herbivore interactions play a central role in driving marine ecosystem dynamics (e.g. Bakker et al., 2016), and it is far from clear how the strength of these interactions will respond to a changing climate.

For a start, trophic interactions are regulated by the autoecology of the intervening species. Temperature can alter plant and animal growth and survival rates, which influence their population abundance, playing a crucial role in determining trophic interactions (Bale et al., 2002; O'Connor, 2009; Post and Pedersen, 2008). In addition, nonlethal temperature rises tend to increase growth and production of plants (Nemani et al., 2003; Post and Pedersen, 2008; Way and Oren, 2010), given that biochemical reaction rates accelerate with temperature fuelled by an increase in kinetic energy (Janssens et al., 2015). Similarly, moderate warming will also likely result in increased growth rates of ectothermic animals (Kordas et al., 2011), decreased development time, increased herbivore population sizes and expanded geographic ranges (Bale et al., 2002; O'Connor et al., 2011). Moreover, both animal and plant respiration rates show higher thermal sensitivity compared to photosynthetic rates (Allen et al., 2005; Padilla-Gamiño and Carpenter, 2007). In addition, higher temperatures may also imply changes in animal behaviour, such as faster and longer animal movements and also increased feeding rates as metabolic needs increase (Gibert et al., 2016; Kordas et al., 2011). This raises the question whether warming will expand the spatial scale over which key species exert their influence (Welsh and Bellwood, 2012). In addition, movement patterns have been linked to the feeding capacity of some animals, with individuals that display restricted mobility having a lower impact on their resources (Hereu, 2005).

Plants respond to herbivory using a range of strategies. While some plants are well-adapted to tolerate herbivory pressure (Strauss and Agrawal, 1999), herbivory often triggers compensatory growth (Sanmartí et al., 2014; Vergés et al., 2008), or an increase in deterrent secondary metabolites (Tomas et al., 2015; Vergés et al., 2007a), thus influencing herbivore feeding choices. How each of these individual mechanisms will work together to influence the overall outcome of plant-herbivore interactions in a warming environment is an open question (Post and Pedersen, 2008). For a start, it would help to understand how the different mechanisms influencing the strength of the interaction respond to warming. Synthesizing these responses could give us a better sense of how plant-herbivore interaction strength is likely to change as temperatures increase.

As a simple heuristic, we propose a model to assess how warming is likely to change the impacts of herbivory on vegetation. At its simplest, it is possible to conceive three potential responses derived from the interplay between the individual responses of plant and herbivores to warming (see Fig. 1 and see Supplementary material): (i) if plant and herbivores respond equally to warming (in terms of individual growth, termed "performance" for the sake of simplicity), herbivore pressure will remain unchanged (Fig. 1a); (ii) if the plant's optimal performance range extends to higher temperatures than the herbivore's performance range, then herbivore pressure will decrease (Fig. 1b); (iii) and if the optimum temperature for plant performance is lower than that of the herbivore, then herbivore pressure will increase with warming (Fig. 1c). We define herbivore pressure as the fraction of primary production removed by an individual herbivore – obtained by dividing herbivore performance by plant performance.

Our study aims to explore which of the many factors that could potentially influence plant-herbivore interactions are likely to change given projected temperature scenarios in three important Mediterranean macrophytes and their sea urchin common consumer. We focus on plant growth, herbivore growth and respiration, and herbivore behaviour (movement patterns, feeding choices and rates). We

integrate these responses and compare them to the heuristic models presented above, to assess how the strength of herbivory is likely to shift as temperatures increase depending on plant species identity and characteristics. As an enclosed temperate sea, the Mediterranean is experiencing rapid temperature change (Coma et al., 2009; Garrabou et al., 2009) but we know very little of how herbivory processes are likely to be affected in these waters. We aim to fill this gap.

2. Materials and methods

2.1. Study system

Our study focuses on the subtidal photophilic environments of the Mediterranean, examining interactions between the main invertebrate herbivore in these systems and the principal canopy-forming macrophyte species in sandy and rocky bottoms. Sandy areas are typically dominated by the seagrasses *Posidonia oceanica* (L.) Delile and *Cymodocea nodosa* (Ucria) Ascherson, while rocky areas are dominated by macroalgal communities (largely *Cystoseira mediterranea* (Sauvageau)). These primary producers are all consumed by the sea urchin *Paracentrotus lividus* (Lam.), which is the most important invertebrate herbivore in the Mediterranean (Boudouresque and Verlaque, 2001).

P. oceanica is a stenohaline seagrass species with high thermal sensitivity (Gacia et al., 2007; Tomasello et al., 2009); shoot mortality is known to increase by 2% year^{-1} for each additional degree of annual maximum temperature (Marbà and Duarte, 2010), with some studies arguing it might become functionally extinct in the Mediterranean during this century as a result of warming (Jordà et al., 2012). *C. nodosa* is the second most abundant seagrass species occupying soft bottoms, and occurs mostly in coastal lagoons and sheltered bays, where it can endure a wide range of temperatures and salinities (Pagès et al., 2010; Pérez and Romero, 1992). Rocky littoral and infralittoral environments are dominated by a diverse assemblage of canopy-forming macroalgae, of which *C. mediterranea* is among the most dominant (Ballesteros, 1992). To our knowledge, little is known of its response to warming. The sea urchin, *P. lividus* is a key herbivore both in algal-dominated rocky bottoms, where it can produce barren overgrazed areas (e.g. Boada et al., 2017), and in seagrass meadows, where it can consume up to 20% of annual seagrass production (Prado et al., 2007; Tomas et al., 2005). In addition, in the presence of predators, *P. lividus* shows very restricted movements, and when released from predation pressure, browses much more extensively, which can have important consequences for the plant resources they feed on (Hereu, 2005). Despite its ecological importance, the response of this sea urchin species to warming is not clear, with adult skeletons remaining unaffected by warming (Collard et al., 2016), while larval fitness being reduced at high temperatures (García et al., 2015).

2.2. Study design

We conducted a series of modular laboratory experiments to explore the influence of temperature on different components of the interaction between macrophytes and herbivorous sea urchins. This included testing the effects of temperature on plant growth, sea urchin growth and respiration, movement behaviour, plant consumption and plant choice. The results of these controlled experiments were used to inform empirical performance curves for the three dominant macrophyte species and their principal invertebrate herbivore. We used these empirical performance curves to evaluate the direction plant-urchin interactions will likely take as temperatures increase for each of the studied plant species. We used different temperature conditions that aimed at capturing current mean and maximum summer temperatures present in the NW Mediterranean plus potential extremely warm temperatures. The analysis of the longest data series available for sea surface temperature in the Catalan coast (l'Estartit, 1975–present, data provided by J.
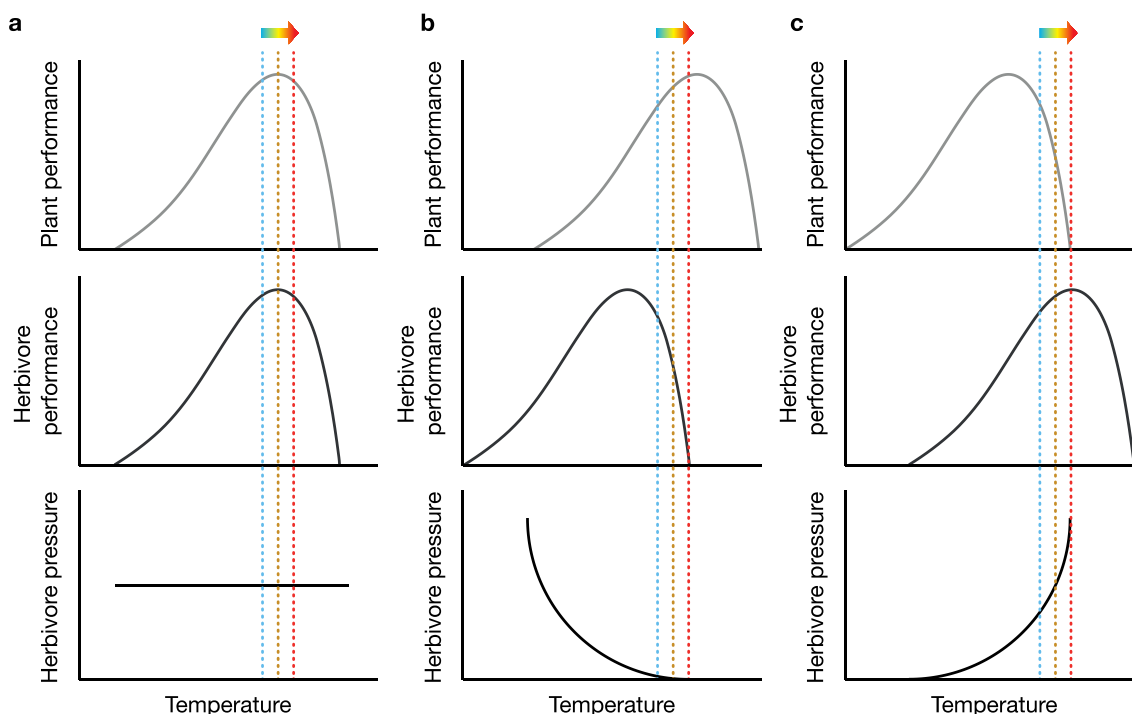
Fig. 1. Conceptual model of the potential outcomes of plant-animal interactions in a warming Mediterranean. The arrow above the dashed vertical lines show the direction of warming. (a) When both plant and herbivore thermal performance curves are of similar shape and display the same optimal temperature, warming will not produce any changes to herbivore pressure[1]. (b) If plant performs better at warmer temperatures compared to the herbivore, herbivore pressure[1] will decrease with warming. (c) In contrast, herbivore pressure[1] will increase with warming, if the herbivore performs better at warmer temperatures compared to the plant. See the Supplementary for more information on the shape of these theoretical curves.
[1]Here, we conceptually define herbivore pressure as the result of dividing herbivore performance by plant performance.

Pascual) shows that the mean summer sea surface temperature is 22 °C, with maximum temperatures in August being 23.8 °C on average and with temperatures above 28 °C being extremely rare (J. Pascual unpublished data, Garrabou et al., 2009). Using these known ranges, we determined the different temperature treatments for each of the manipulative experiments described below.

All the urchins, *C. mediterranea*, and *P. oceanica* samples used in the manipulative experiments were collected near Blanes (41°40′ N, 2°48′ E). *C. nodosa* samples were collected in a bay in the Ebre delta (40°35′ N, 0°37′ E). To minimise inter-seasonal influences all the sampling was done in spring or early summer between 2014 and 2016 depending on the experiment (the average SST at that time is 13–16 °C). Water temperature treatments in all of the aquaria were achieved by increasing or decreasing water temperatures by 1 °C every 6 h until treatment temperatures were reached, to prevent plants or animals from suffering a thermic shock.

2.3. Plant growth

The effect of increasing temperature on plant growth was assessed by determining either leaf elongation or biomass change in each of the three plant species under different temperature conditions. We collected 30 *P. oceanica* shoots in the field and placed them in 6 aerated flow-through 200 L aquaria within an hour (5 shoots per aquarium). We randomly assigned each aquarium to two growing temperature treatments (18 °C or 25 °C). Aquaria were placed in full sunlight and the shoots were weighted down to ensure they remained submerged. All shoots were marked near the ligula with a needle to assess leaf elongation over 15 days (modified Zieman method, see e.g. Pérez and Romero, 1994). A similar procedure was used for *C. nodosa* seagrass shoots. 45 shoots were harvested from the field and placed in 9 aquaria (5 shoots per aquarium). We randomly assigned each aquarium to 3 temperature treatments (20, 30, 35 °C). Again, all shoots were marked

near the ligula with a needle to assess leaf elongation over 15 days as described above. Note that we used higher temperature treatments for *C. nodosa*, given this species lives in shallower, often enclosed bays. Finally, for *C. mediterranea*, we collected 10 thalli and randomly allocated each of them to one of two aerated flow-through temperature treatment aquaria (18 °C or 25 °C) (5 thalli per treatment). 200 L aquaria were placed in full sunlight and the thalli were weighted down to ensure they remained submerged. Growth of *C. mediterranea*, was estimated as the change in biomass (as fresh weight, g) of each alga from the start to the end of the experiment (5 weeks). Even if all thalli from the same treatment were placed in the same aquarium, aquaria were big enough (200 L) to allow sufficiently spatial heterogeneity (i.e. differences in temperature of 0.2 °C) to avoid pseudoreplication (Hurlbert, 1984).

Plant growth data was analysed in R with linear models containing the response variable 'plant growth' and the predictor variable 'temperature' coded as a fixed factor with 2 levels for *P. oceanica* and *C. mediterranea*, and with 3 levels for *C. nodosa*. We tested if the random grouping variable 'aquarium' should be added to the linear models, but Akaike Information Criterion (AIC) and Log Likelihood Ratio recommended dropping random effects (Zuur et al., 2009) from all the models except for the analysis of *C. nodosa* growth. Assumptions of normality and homoscedasticity were checked graphically and fulfilled in all cases (in the case of *C. nodosa* growth, data was square root transformed).

2.4. Herbivore growth and respiration

The effect of temperature on sea urchin growth was assessed by comparing the growth of urchins at different water temperatures. Sea urchins of different sizes were collected in the field, randomly allocated to different aquaria for each temperature treatment (16, 19, 22, 25, 28 and 31 °C treatments, 6 aquaria per treatment) and fed ad libitum a mix

of algae every three days, for the entire duration of the experiment. Each aquarium had two small (< 3 cm), two medium (3–5 cm) and two large (> 5 cm) individuals. We photographed all individuals from each aquarium and temperature treatment at the start of the experiment (216 individuals) and after two months (< 200). Some individuals did not survive for the entire duration of the experiment and were excluded from the analyses. Images were taken with the aboral side of each individual facing upwards and with a ruler as measure reference. We used imageJ to estimate urchin test diameter to the nearest millimetre. Growth was calculated as the increase in test diameter of each individual sea urchin from the start to the end of the experiment.

The effect of temperature on sea urchin respiration was assessed by comparing oxygen concentration before and after a 90-minute incubation of three replicate individuals per temperature treatment (16, 19, 22, 25 and 28 °C) and for three different sea urchin sizes (small [< 3 cm], medium [3–5 cm], large [> 5 cm]), placed in hermetic 1 L glass containers. Sea urchins were collected from the field and fed ad libitum a mix of algae for the entire duration of the experiment. An incubation time of 90 min was determined in pilot studies to assess the kinetics of decline in dissolved oxygen levels in the container. Oxygen concentration (mg/L) was measured at the start and the end of the experimental period with an optical dissolved oxygen meter (YSI, ProOBOD) placed inside the container. Sensor calibration and salinity corrections were done following manual instructions. Oxygen saturations below 80% were not observed in the trials. Shaking avoided temperature and oxygen gradients developing within the container during measurements. Oxygen consumption was calculated following the equation:

$$\text{Oxygen consumption (mg ind}^{-1}\text{ h}^{-1}) = [(O_0 - O_t) * V/T]$$

where O_0 and O_t are the initial and final oxygen concentrations (mg O_2 L^{-1}) measured, T is the incubation time (h) and V is the volume (L) of the container.

The response variables 'sea urchin growth' and 'sea urchin respiration' were analysed in R with linear models. Given that in this case we had 5–6 levels of the predictor variable temperature, we treated it as a continuous variable instead of a factor. This allowed us to test not only the linear effect of temperature on growth and respiration rates, but also the quadratic term. Sea urchin size was used as a covariate. Assumptions of normality and homoscedasticity were checked graphically and fulfilled in both cases.

2.5. Herbivore movement behaviour

A separate laboratory experiment was performed to assess the effect of temperature on *P. lividus* movement patterns. Sea urchins of a similar size (between 2 and 3 cm) were collected and placed in large aquaria with seawater either at 18 °C or at 25 °C for acclimation, and fed a mix of *P. oceanica* leaves and macroalgae. To test their movement patterns at different temperatures, we placed urchins in 1-metre circular tanks (void of food) either at 18 °C ($n = 21$) or 25 °C ($n = 14$). Each sea urchin was tested only once and urchins were transferred from the acclimating aquaria to tanks of the same temperature. The arenas were lit with fluorescent light sources and urchin movements were recorded using stop-motion filming (one image taken every 30 s) from above. Urchins were placed at the centre of the arena at the beginning of each trial and their movement was tracked until they reached 10 cm from the edge of the tank. The tank was emptied, and carefully cleaned at the end of each day of tests to ensure that cues from the previous trial did not influence subsequent trials (e.g. Yerramilli and Johnsen, 2010).

The movement response of sea urchins to warming was determined by analysing a total of 3292 images that resulted from the experiment. The x and y coordinates of each urchin were obtained using an image processing toolbox in Matlab (Mathworks Ltd.) and then analysed with the adehabitatLT package in R (Calenge, 2011). This package computes the increments in the x and y axis for each step of the trajectory (time

interval = 30 s). The x and y coordinates of each individual trajectory were used to assess the movement behaviour of sea urchins in each condition. We used a general numerical approach based on the analysis of the qth order long-range correlations in sea urchin displacements (for more information see Supplementary information and Seuront and Stanley, 2014).

Finally, for each replicate sea urchin we calculated the mean sea urchin speed and the straightness index. The straightness index (Is), a measure of path tortuosity, is a dimensionless number that ranges from 1 (maximum straightness) to 0 (maximum tortuosity). It is the ratio of the Euclidian distance between the initial and final point of the trajectory, and the sum of Euclidian distances between pairs of points separated by a given time. Since different windows of time result in different Is (Benhamou 2004), we calculated this index for a range of window widths. Comparisons between experiments were consistent regardless of window width and, we only present the Is for a window of 1 step (30 s).

The significance of the differences between the empirical values of the function ζ(q) was analysed with a linear model, considering as a response variable the 'slope of the exponents of the qth order moments (ζ(q))' and the fixed factor 'temperature' (2 levels: 18 °C and 25 °C) as the predictor. Each individual sea urchin was considered a replicate. The response variables mean sea urchin speed and tortuosity were analysed with a linear model to assess the effects of the predictor temperature (fixed factor, 2 levels). Normality and homoscedasticity were assessed graphically and fulfilled in all cases.

2.6. Herbivore consumption

The effect of temperature on consumption was assessed by comparing the amount of seagrass *P. oceanica*, *C. nodosa* and algae *C. mediterranea* eaten by the urchin *P. lividus* at different water temperatures in separate experiments. In each experiment, 200 L aquaria were divided into 6 compartments, 5 of which contained a sea urchin with plant biomass and the 6th compartment was maintained as control, with only plant material to account for plant losses not due to consumption by sea urchins. Two aquaria were allocated to one of 3 treatments in experiments using *C. nodosa* and *P.oceanica*, 15, 20 or 25 °C and 4 treatments for *C. mediterranea*, 15, 22, 25 or 28 °C. Urchins were starved for 3 days before a known amount of plant material was placed in each compartment. After 2–8 days (depending on the plant species) all remaining plant material in each compartment was removed and weighed to estimate the biomass eaten. This was repeated twice for *P. oceanica* and *C. mediterranea*, and three times for *C. nodosa*. While the possibility of changes in plant palatability in the course of the feeding experiment cannot be ruled out, we think it very unlikely given the short duration of our feeding trials compared to the rate of change in plant metabolites and toughness (i.e. in the order of weeks to months, Hernán et al., 2017).

The effects of the fixed factor 'temperature' (3 levels: 15, 20, 25 °C) on the response variable 'sea urchin consumption' of the seagrass *P. oceanica* was analysed with a generalized linear mixed effects model with a Poisson distribution, due to the high number of zeros of the response variable. 'Sea urchin consumption' was the result of subtracting the initial plant biomass by the final biomass in each compartment and corrected by subtracting any autogenic change (estimated from the biomass change in control compartments). We used the function glmer from the package lme4 (Bates et al., 2017). The random effect 'aquarium' could not be dropped from the model according to the Akaike Information Criterion (AIC) and the Log Likelihood Ratio (Zuur et al., 2009). We used a similar generalized linear model to assess the effect of the fixed factor 'temperature' (3 levels: 15, 20, 25 °C) on the consumption of *C. nodosa*. However, in this case we used a negative binomial distribution due to the response variable being overdispersed (Zuur et al., 2009). Again, we could not drop the random effect 'aquarium' according to AIC and the Log Likelihood Ratio. Finally, to

analyse the effects of temperature on the consumption of *C. mediterranea*, we used a simple linear model. Assumptions of normality and homoscedasticity were checked graphically and fulfilled in all cases.

2.7. Herbivore choice experiments

An herbivore choice experiment was undertaken to determine if changes in water temperature affected plant defence mechanisms. Shoots of the seagrasses *P. oceanica* and *C. nodosa* were collected and stored in either 22 °C or 30 °C treatment aquaria for 3 weeks to allow changes to plant metabolites. Seagrass traits generally respond within these time frames to changes in environmental conditions (Hernán et al., 2017, Hernán et al., 2016; Jordi F Pagès et al., 2010; Ruiz et al., 2001). The alga *C. mediterranea* was collected and stored in aquaria at 18 °C and 25 °C, since thalli could not survive the 30 °C treatment. Experiments were conducted by placing 20 cm of seagrass or 1 g of algae from each temperature treatment at either end of 5 L aquaria containing an urchin and ambient flow through water. This was done for 36 aquaria containing *P. oceanica* treatments, 23 containing *C. nodosa* incubated at 22 and 30 °C treatments and 25 aquaria containing *C. mediterranea* incubated at 15 and 25 °C treatments. Seagrass and algae were measured or weighed to determine the amount consumed by urchin after half of all the plant material in each aquarium had been eaten or 10 days had elapsed. Each aquarium was treated as a replicate but aquaria where no plants were eaten after 10 days were removed from the analysis. For each plant species 5 aquaria containing plant material but no urchins were used as controls for autogenic change. However, we did not need to correct for any autogenic change, given that there was no difference in length or weight of plant material in any of the controls at the end of each experiment.

To assess if there was a preference for plants incubated at each temperature treatment, we calculated the difference between consumption at lower and higher temperature treatments. We then checked the normality of these differences and applied a *t*-test or a Wilcoxon rank test depending on whether normality was fulfilled or not respectively. Both statistical analyses test whether the vector of differences in consumption are significantly different from zero (alpha = 0.05). A significant difference indicates a preferred choice.

2.8. Plant performance, herbivore performance and herbivore pressure conceptual curves

In order to model both plants' and urchins' thermal performance curves, we used modified Gaussian functions obtained from Angilletta (2006). We parameterised each function with values chosen to best reflect the empirical optima observed in our experiments (using data from Fig. 2 for the plants, and from Figs. 3 and 4 for the herbivores). These parameter values do not bear biological meaning, but were used to observe the shape of the resulting curves (see Supplementary information), using the web app Geogebra (www.geogebra.org). For the herbivorous sea urchins, we modelled two types of performance curves depending on whether sea urchin feeding preferences were influenced by the incubation temperature of their feeding source (see Supplementary information): a continuous modified Gaussian function was used when sea urchins did not modify their preference when offered plants incubated at warm temperatures; while a stepwise function was used to impose a truncation of the thermal performance curves of sea urchins, to mimic the effect of offering them plants incubated at warm temperatures (i.e. less preferred). The stepwise function behaves as a modified Gaussian for $x < 2$, but otherwise it quickly drops to 0 (and then negative values, with no biological meaning in this case). Finally, to obtain the herbivore pressure curve, we divided the thermal performance function of sea urchins by the thermal performance function of each plant (see Supplementary).

3. Results

3.1. Plant growth

Temperature significantly affected the growth rates of the three plants studied. *P. oceanica* and *C. mediterranea* displayed significantly lower growth rates at warmer temperatures (25 vs 18 °C; Fig. 2a,c, Table 1). In contrast, *C. nodosa* displayed higher growth rates at temperatures as high as 30 °C, compared to cooler and warmer treatments (20 and 35 °C) (Fig. 2b, Table 1).

3.2. Herbivore growth and respiration

Temperature significantly affected both the growth and respiration of the herbivorous sea urchin *P. lividus* (Fig. 3, Table 1). The best model fitting our data included the quadratic term of temperature, highlighting a temperature that maximises both processes at ca. 22 °C. Sea urchin size also significantly affected both growth and respiration rates (see Supplementary Fig. S1 a,b).

3.3. Herbivore behaviour

Sea urchin movement patterns in the lab did not change significantly between temperature treatments. Their trajectories were similar in terms of tortuosity (Fig. 4a), and long range correlations
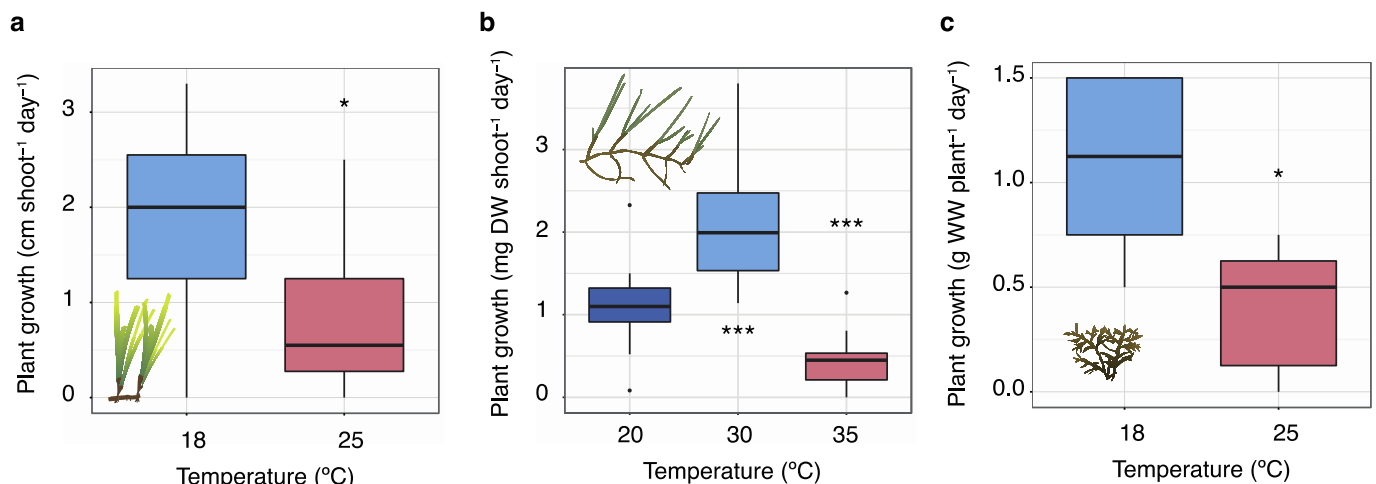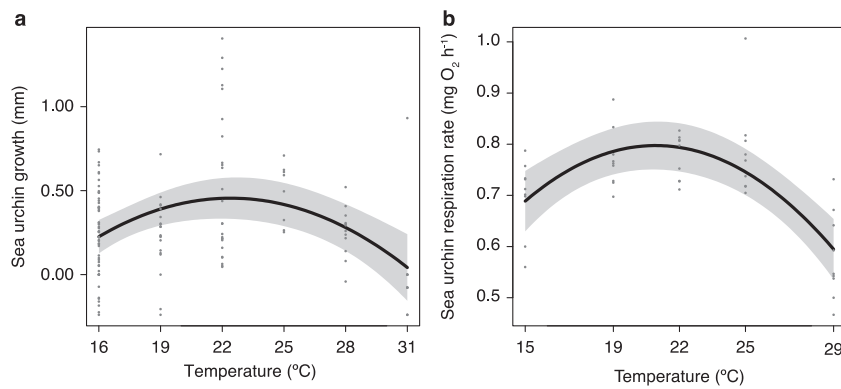

Fig. 2. Plant growth at different incubating temperatures. (a) *Posidonia oceanica* seagrass, (b) *Cymodocea nodosa* seagrass, (c) *Cystoseira mediterranea* macroalgae. Asterisks denote significant differences. Significance codes $p < 0.001$ '***', $p < 0.05$ '*'.

Fig. 3. Sea urchin thermal performance curves (a) for growth and (b) respiration rates. Solid lines correspond to the predictions of a linear model applied to the data sets using the quadratic term of temperature as a predictor, hence the parabolic shape of the curve. Shaded areas define the 95% confidence intervals around fitted values. Sea urchin size significantly affected both growth and respiration curves as well (see Fig. S1 from the Supplementary).
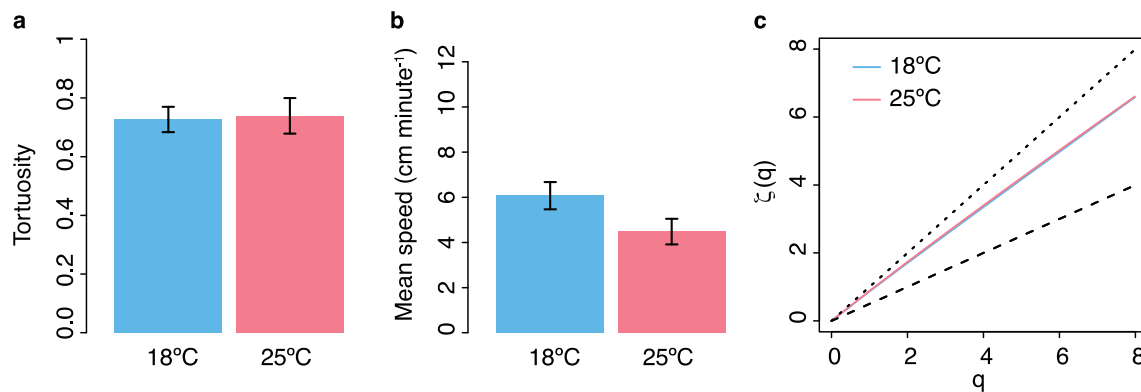
Fig. 4. Sea urchin movement behaviour at cool and warm water temperatures. (a) Temperature did not affect the tortuosity of sea urchin trajectories, (b) nor their mean speed. (c) The analysis of sea urchin trajectories at different scales (see methods) did not find any differences between the trajectories of urchins wandering in cool (blue solid line) or warm (red solid line) conditions. The dotted line denotes a ballistic trajectory, while the dashed line represents Brownian motion. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 4c). There was a faint trend of slower velocities at warmer temperatures (Fig. 4b), but this was not significant at $\alpha = 0.05$. As is typical for this species (Pagès, 2013) their trajectories were in the realm of superdiffusive movements, nearer to ballistic than Brownian motion (Fig. 4c).

3.4. Herbivore consumption and feeding choice experiments

Sea urchin feeding rates on both seagrass species were maintained from 15 to 20 °C, but then plunged at the warmest treatment (25 °C) (Fig. 5a,c, Table 1). Moreover, for both seagrass species, sea urchins

Table 1
Summary of the different analyses performed. Model: type of model used in R (either linear [lm()/lme()], generalized linear with Poisson distribution [glmer()], generalized linear with negative binomial distribution [glmer.nb()] or non-parametric Kruskal-Wallis [kruskal.test()]). Random: type of random effects introduced into the model. Resp. Transf.: type of transformation applied to the response variable. Df: degrees of freedom. Statistic: depending on the model used the statistic used was Fisher's F, Chi-squared, or the Kruskal-wallis.
Significance codes $p < 0.001$ '***', $p < 0.01$ '**', $p < 0.05$ '*', $p > 0.05$ ' '.

Response variable	Model	Random	Resp. transf.	Effect	Sum squares	Df	Statistic	p-Value
P. oceanica growth	Linear	–	–	Temperature	6.53	1	7.55	0.010 *
				Residuals	24.23	28		
C. nodosa growth	Linear	1 | Aquarium	sqrt(x)	Temperature	–	2	21.12	$2.6\ 10^{-5}$ ***
C. mediterranea growth	Linear	–	–	Temperature	1.14	1	7.48	0.026 *
				Residuals	1.22	8		
Sea urchin growth	Linear	–	–	Temperature	1.70	1	18.89	$2.9\ 10^{-5}$ ***
				I(temperature^2)	1.74	1	19.33	$2.4\ 10^{-5}$ ***
				Size class	1.21	2	6.74	0.002 **
				Residuals	10.99	122		
Sea urchin respiration	Linear	–	–	Temperature	0.15	1	36.48	$4.6\ 10^{-7}$ ***
				I(temperature^2)	0.17	1	41.69	$1.2\ 10^{-7}$ ***
				Size class	2.62	2	319.38	$< 2\ 10^{-16}$ **
				Residuals	0.16	39		
P. oceanica consumption	glm Poisson	1 | Aquarium	round(x*100)	Temperature	–	2	32.28	$9.8\ 10^{-8}$ ***
				Size class	–	1	11.48	0.0007 ***
C. nodosa consumption	glm negative binomial	1 | Aquarium	round(x ∗ 10)	Temperature	–	2	9.95	0.007 **
C. mediterranea consumption	Linear	–	–	Temperature	6.99	3	21.19	$2.0\ 10^{-6}$ ***
				Residuals	2.20	20		
Difference in consumption *P.oceanica*	*t*-Test	–	–	–	–	21	2.10	0.047 *
Difference in consumption *C. nodosa*	Wilcoxon	–	–	–	–	20	155.5	0.050 *
Difference in consumption *C. mediterranea*	*t*-Test	–	–	–	–	23	0.517	0.610
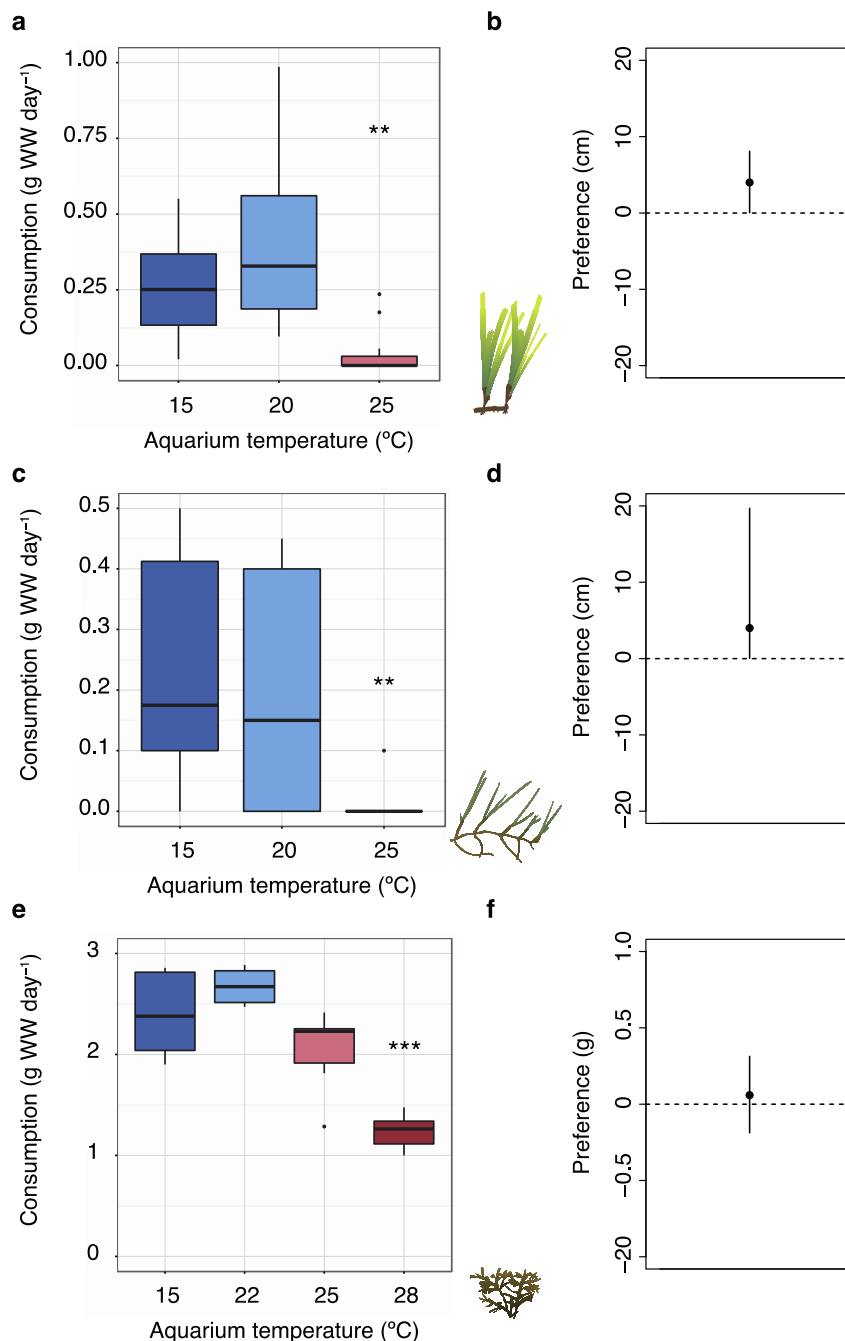
Fig. 5. Sea urchin consumption rate at increasing temperatures and sea urchin choice of plants incubated at cool and warm temperatures. (a, b) correspond to the seagrass *Posidonia oceanica*, (c, d) to the seagrass *Cymodocea nodosa*, and (e, f) to the macroalgae *Cystoseira mediterranea*. Significance codes $p < 0.001$ '***', $p < 0.01$ '**', $p < 0.05$ '*'. For the preference plots (b, d, f), effects are significant ($p \leq 0.05$) where confidence intervals do not intercept 0.

preferred seagrass leaves that had been incubated at cooler temperatures (Fig. 5b,d, Table 1). In contrast, sea urchin feeding rates on the alga *C. mediterranea* were sustained even at higher temperatures, although with a negative trend towards the warmest treatments (Fig. 5e, Table 1). Sea urchins did not display any preferences between algae incubated at cool or warm treatments (Fig. 5f).

4. Discussion

Increasing temperatures are likely to trigger a complex suite of responses in the dynamics of plant-herbivore interactions, with potentially far-reaching consequences for Mediterranean macrophyte communities. While it is clear that some plant species, like *Posidonia oceanica* and *Cystoseira mediterranea* will be pushed beyond their optima and show decreased growth, *Cymodocea nodosa* may actually benefit due to its high thermal optimum. Together with the other responses to

temperature evidenced here, which include sea urchin growth, respiration, feeding rates and plant susceptibility to consumption, it appears that while the strength of the plant-sea urchin interaction may weaken for seagrass species – quite considerably in the case of *C. nodosa* – herbivory pressure may actually increase on the macroalga (see these results using the framework of our heuristic models in Fig. 6).

As plant-herbivore interactions are the outcome of several processes acting together, changes in any one of these processes could influence the interaction. The picture further gains in complexity because as found elsewhere (Sentis et al., 2015; Van De Velde et al., 2016), not all processes are equally influenced by temperature. While growth and feeding showed clear directional responses, plant susceptibility to being consumed exhibited contrasting responses, and urchin movement did not change. In addition, these responses were highly species specific, dependent on the inherent tolerance limits of each species (Kordas et al., 2011). Thus, while both *P. oceanica* and *C. mediterranea* showed
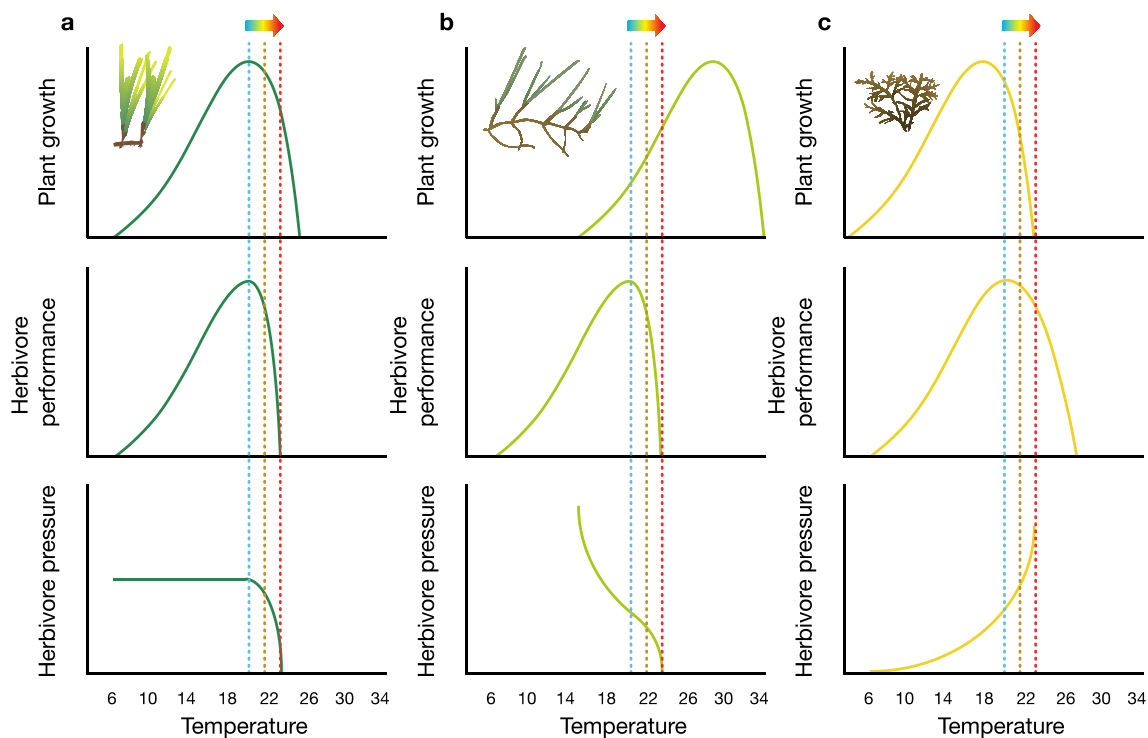
Fig. 6. Conceptual model of the outcomes of plant-animal interactions in a warming Mediterranean. The arrow above the dashed vertical lines show the direction of warming. (a) We expect herbivore pressure on *Posidonia oceanica* seagrass to keep unchanged with warming, given that both the sea urchin and the seagrass display similar optimal temperatures of performance; however, sea urchins' feeding rates plunge when offered *P. oceanica* seagrass leaves from plants incubated at warm temperatures, hence the decrease in herbivore pressure when warming increases (from the blue to the red dotted lines). (b) We expect the herbivore pressure between urchins and the seagrass *Cymodocea nodosa* to decrease with warming given the warmer optimal temperature of performance of the seagrass compared to the herbivore. The herbivore pressure curve is expected to be especially steep at higher temperatures, given the lower feeding rates of urchins when offered plants incubated at warm temperatures. (c) We expect the herbivore pressure between the macroalga *Cystoseira mediterranea* and the sea urchin to increase with warming, given the low performance of the macroalga at warm temperatures, while sea urchins still display high feeding rates (see also Fig. 5). See Materials and methods and Supplementary materials for more information on the shape of these curves. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

higher growth at lower temperatures (as is typical for most temperate species, Lee et al., 2007), *C. nodosa* grew best at 30 °C. The responses of their common sea urchin consumer to increasing temperatures varied. Surprisingly, while growth and respiration were highest at intermediate temperatures (ca. 22 °C, see Fig. 3), *P. lividus* did not modify its movement behaviour with increasing temperatures. Consumption rates did not correspond well with urchin growth either; at 25 °C, urchins had practically stopped eating. Mismatches between consumption and metabolism/growth are common in many species including urchins, likely representing physiological limits to plasticity (Lemoine and Burkepile, 2012). In addition, while the palatability of the two seagrass species apparently declined (possibly as a result of increased production of secondary compounds (Vergés et al., 2007b), but see Hernán et al., 2017), this was not true for the macrophyte *C. mediterranea*. These differences can lead to differential susceptibilities of species to herbivory pressure across the seascape as temperature increases (Peñuelas and Staudt, 2010; Poore et al., 2013).

Global warming is changing the odds for Mediterranean macrophytes by creating clear 'winners' and 'losers' among the species that dominate these waters at present. What is interesting, though, is that these patterns arise not as a result of a single mechanism or process that changes with temperature, but because of the interplay between several mechanisms that together shape the plant-herbivore interaction. Thus, the expected decrease in herbivory pressure with temperature for *C. nodosa* (see Fig. 6b), results not merely from a faster growth, and thus increased productivity, but also because it reduces its palatability to urchins (Figs. 5d) and because sea urchins consume much less at higher temperatures (Fig. 5c, independent of seagrass palatability). Consequently, *C. nodosa* is likely to be released from herbivory pressure as temperatures increase (Fig. 6b). Similarly, while the growth of *P.*

oceanica decreases at higher temperatures (Fig. 2a), given that in parallel urchin growth decreases (Fig. 3a), as does consumption (Fig. 5a) and palatability is reduced (Fig. 5b), the impact of herbivory may still decrease or remain unchanged for this species (Fig. 6a). In sharp contrast, the canopy-forming macroalga, *C. mediterranea* is probably most at risk from increasing temperatures, once again as a result of a suite of changes in mechanisms affecting plant-herbivore interactions. Thus, while it reduces its growth in elevated temperature conditions (Fig. 2c), urchin consumption remains high until 25 °C (Fig. 5e), while palatability does not decrease at the highest temperatures (Fig. 5f). If anything, the strength of this algae-herbivore interaction is set to increase with ocean warming (Fig. 6c). This is particularly worrying, given that of all the systems we studied, benthic macroalgal systems are most prone to state shifts, often precipitated by urchin overgrazing (Boada et al., 2017; Pinnegar et al., 2000).

In interpreting these results, it is essential to remember that there are several additional mechanisms that we have not considered. Our laboratory experiments and the performance curves test the current tolerance limits of the species in question to changing conditions. Of course, as temperatures change, it is quite possible for species to acclimate within the limits of their phenotypic plasticity, or genetically adapt to increasing temperatures by selection of the fittest genotypes (Lee et al., 2007). While most plants show considerable capacity to adjust their photosynthetic traits to enhance their performance, this ability varies considerably between species (Lee et al., 2007). Consumers, in contrast, tend to be more sensitive to warming (Voigt et al., 2003). The consumer *P. lividus*, however, is a thermal generalist that experiences a wide range of environmental temperatures, ranging from 10 to 30 °C (Boudouresque and Verlaque, 2001), and is potentially exposed to extremes of temperatures in shallow coastal bays. How

plants and animals acclimate or adapt to increasing temperatures will significantly change performance optima and result in further changes in the plant-animal interaction. As species are pushed to the edge of their tolerance limits, we should expect a host of individual and population-level consequences that will also be critical to ecosystem functioning (Bennett et al., 2015; Tylianakis et al., 2008). However, in a field experiment using a thermal plume, Garthwin et al. (2014) showed that a meadow of the seagrass *Zostera muelleri* that had been exposed to sustained higher temperatures for 30 years had similar levels of growth and herbivory than un-impacted meadows nearby. Similarly, Morelissen and Harley (2007) found that even though individual species may be influenced by temperature, plant–herbivore interactions may not necessarily be. Other studies, in contrast, have found that warming tends to increase interaction strength between producers and consumers (O'Connor et al., 2009; Poore et al., 2013). Our heuristic models help to explain why warming may or may not modify plant-herbivore interaction strength by influencing some of the components of these interactions (see rationale at the end of introduction). Moreover, our results show that the same amount of warming might have opposing effects on Mediterranean macrophyte-herbivore interactions contingent on species specific thermal performance. We must apply caution when interpreting our heuristic models (Fig. 6), given the low number of temperature levels used in the plant growth experiments (see Fig. 2). As a sensitivity exercise, we examined the effect of shifting the plants' thermal performance curves around their optima, leaving the urchins' performance curves unchanged (see results in the Supplementary, Figs. 8–10). The sensitivity analysis confirmed the results observed in Fig. 6, given that the changes to the resulting herbivore performance curves changed minimally. In the future, however, we might have to introduce more actors into the picture, as the sparid *Sarpa salpa* (L.) and the thermophilous black sea urchin *Arabacia lixula* (L.) will also likely be affected by warming (Gianguzza et al., 2011; Privitera et al., 2011). Moreover, warming is already causing a host of tropical species, such as the herbivorous rabbitfish (*Siganus luridus* and *S. rivulatus*), to migrate to temperate areas (Vergés et al., 2014), altering local interactions and potentially precipitating algal barrens (Sala et al., 2011).

As far as we are aware, this is the first study to explicitly examine how warming mediates key plant-animal interactions (that structure Mediterranean macrophyte communities in this case) at this diversity of scales (from the behavioural, metabolic, to individual level). Moreover, the inclusion of these responses in simple heuristic models demonstrates that the complex effects of warming on plant-animal interactions are the result not merely of their effect on each individual species' survival, but also of temperature changing a suite of plant and animal responses (including palatability and potentially behaviour [not in this case]) that are difficult to predict a priori. This can lead to unexpected results. Ecological interactions have developed over evolutionary time scales and are the consequence of a dynamic interplay between each species attempting to adjust to environmental changes as well as ensuring its own evolutionary success. Rapid environmental changes are accelerating this dynamic process, stretching the ability of species to cope with the rate of these changes. How these interactions play out in real-world scenarios, where several species interact both directly and indirectly in a dizzyingly complex network of interactions, is difficult to conceive, especially given that warming experiments generally assume that individual organisms that have been experimentally warmed in short-term experiments, will respond in a similar way as individuals whose ancestors have been exposed to the same level of warming over decades. In any case, our results show that not all of these consequences are going to be negative, since some species may be able to compensate for the effects of temperature, leaving the interaction itself unchanged. Some structural species, like *C. nodosa* in the case of this study, may even emerge as clear winners in these scenarios. Much will depend on the plasticity and adaptive capacity of the individual actors within the interaction to this change. It may be useful to think of interactions themselves as having an inherent plasticity, adapting in a coupled way

to changing conditions. There will be limits to this joint plasticity, breaking down either as its individual actors cross tolerance thresholds, or when the interaction itself becomes too strong or too weak (see Fig. 6). Clearly, as human-induced rapid environmental change continues apace, it is pushing us to investigate more carefully what governs species interactions, in order to understand how they will respond to change. Knowing what to expect of these ecosystems in the near future, may help us manage them more effectively. We believe we can be moderately optimistic for Mediterranean seagrass communities given their expected unchanged or reduced herbivore pressure as warming continues. However, our study should serve as an early warning for Mediterranean macroalgal communities, which are already subject to strong top-down control due to the loss of top-predators (Pinnegar et al., 2000), but which are likely to be subjected to even higher herbivore pressure.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2017.10.036.

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