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

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27

28 **Abstract**

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

44

45 **Keywords**

46 climate change; macroalgae; Mediterranean; seagrass; sea urchin; temperature
47

48

49 **Highlights**

50 • Multiple mechanisms influence interactions, each likely modified by temperature.

51 • Mediterranean macrophyte-herbivore interactions show complex contrasts.

52 • Herbivory on the two main Mediterranean seagrasses is expected to decrease.

53 • A key canopy-forming macroalgae however is likely to suffer increased herbivory.

54 • Warming is creating winners and losers in temperate waters as interactions change.

55

56

57 **Introduction**

58 Over the coming decades, the ecological impacts of global warming are expected to
59 increase as temperatures rise (IPCC, 2013). Global average sea surface temperatures are
60 predicted to rise by 0.75°C by 2035 (Kirtman et al., 2013) and between 1°C and more than
61 3°C by 2100 (Collins et al., 2013), relative to the reference period 1986-2005. While a
62 large body of research has focused on the direct effects of global change on population
63 abundances, community composition, and organismal physiology (e.g. Sala et al., 2000),
64 global change may cause less obvious alterations to the networks of interactions among
65 species (Tylianakis et al., 2008). Indeed, biotic interactions such as predation, herbivory,
66 parasitism or mutualism are key in maintaining ecosystems' biodiversity, resilience and
67 services (Bascompte et al., 2006; Dobson et al., 2011; Ives and Carpenter, 2007). The
68 historical lack of research on the effects of warming on biotic interactions, especially in
69 marine ecosystems (Wernberg et al. 2012, but see recent advances, e.g. Gutow et al.,
70 2016; Hernán et al., 2017), likely stems from difficulties in quantifying modifications in
71 interactions compared to documenting changes in single species abundance, biodiversity
72 or individual physiological processes (McCann, 2007; Somero, 2012; Wernberg et al.,
73 2012). Even a simple two-species interaction is ridden with complexities, driven by a host
74 of biological, behavioural and ecological mechanisms that can all interact in often
75 surprising ways (Boada et al., 2017). Unravelling these mechanisms and understanding
76 how they are likely to respond to change is far from trivial. Indeed, interactions may be
77 particularly susceptible to warming, since they are sensitive to the relative abundances of
78 the set of interacting species, their physiology, phenology and behaviour (Parmesan,
79 2006; Suttle et al., 2007; Tylianakis et al., 2007).

81 The interaction between a primary producer and its consumer can be used as a basic
82 model to explore the complexity inherent in understanding the effects of changing
83 temperatures at the community level. Plant-herbivore interactions are crucial for the
84 evolution of both plant and herbivore traits (e.g. Fritz and Simms, 1992), and are critical
85 in determining the abundance of primary producers globally (Cebrián, 1999). They
86 structure both terrestrial and marine food webs and ultimately determine whether the
87 world is dominated by producers or consumers (Polis, 1999). Plant-herbivore interactions
88 play a central role in driving marine ecosystem dynamics (e.g. Bakker et al., 2016), and
89 it is far from clear how the strength of these interactions will respond to a changing
90 climate.

91

92 For a start, trophic interactions are regulated by the autoecology of the intervening species.
93 Temperature can alter plant and animal growth and survival rates, which influence their
94 population abundance, playing a crucial role in determining trophic interactions (Bale et
95 al., 2002; O'Connor, 2009; Post and Pedersen, 2008). In addition, nonlethal temperature
96 rises tend to increase growth and production of plants (Nemani et al., 2003; Post and
97 Pedersen, 2008; Way and Oren, 2010), given that biochemical reaction rates accelerate
98 with temperature fuelled by an increase in kinetic energy (Janssens et al., 2015). Similarly,
99 moderate warming will also likely result in increased growth rates of ectothermic animals
100 (Kordas et al., 2011), decreased development time, increased herbivore population sizes
101 and expanded geographic ranges (Bale et al., 2002; O'Connor et al., 2011). Moreover,
102 both animal and plant respiration rates show higher thermal sensitivity compared to
103 photosynthetic rates (Allen et al., 2005; Padilla-Gamiño and Carpenter, 2007). In addition,
104 higher temperatures may also imply changes in animal behaviour, such as faster and
105 longer animal movements and also increased feeding rates as metabolic needs increase

106 (Gibert et al., 2016; Kordas et al., 2011). This raises the question whether warming will
107 expand the spatial scale over which key species exert their influence (Welsh and
108 Bellwood, 2012). In addition, movement patterns have been linked to the feeding
109 capacity of some animals, with individuals that display restricted mobility having a lower
110 impact on their resources (Hereu, 2005).

111

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

122

123 As a simple heuristic, we propose a model to assess how warming is likely to change the
124 impacts of herbivory on vegetation. At its simplest, it is possible to conceive three
125 potential responses derived from the interplay between the individual responses of plant
126 and herbivores to warming (see Fig. 1 and see Supplementary Material): (i) if plant and
127 herbivores respond equally to warming (in terms of individual growth, termed
128 “performance” for the sake of simplicity), herbivore pressure will remain unchanged (Fig.
129 1a); (ii) if the plant’s optimal performance range extends to higher temperatures than the
130 herbivore’s performance range, then herbivore pressure will decrease (Fig. 1b); (iii) and

131 if the optimum temperature for plant performance is lower than that of the herbivore, then
132 herbivore pressure will increase with warming (Fig. 1c). We define herbivore pressure as
133 the fraction of primary production removed by an individual herbivore – obtained by
134 dividing herbivore performance by plant performance.

135

136 Our study aims to explore which of the many factors that could potentially influence
137 plant-herbivore interactions are likely to change given projected temperature scenarios in
138 three important Mediterranean macrophytes and their sea urchin common consumer. We
139 focus on plant growth, herbivore growth and respiration, and herbivore behaviour
140 (movement patterns, feeding choices and rates). We integrate these responses and
141 compare them to the heuristic models presented above, to assess how the strength of
142 herbivory is likely to shift as temperatures increase depending on plant species identity
143 and characteristics. As an enclosed temperate sea, the Mediterranean is experiencing
144 rapid temperature change (Coma et al., 2009; Garrabou et al., 2009) but we know very
145 little of how herbivory processes are likely to be affected in these waters. We aim to fill
146 this gap.

147

148 **Materials and Methods**

149 *Study system*

150 Our study focuses on the subtidal photophilic environments of the Mediterranean,
151 examining interactions between the main invertebrate herbivore in these systems and the
152 principal canopy-forming macrophyte species in sandy and rocky bottoms. Sandy areas
153 are typically dominated by the seagrasses *Posidonia oceanica* (L.) Delile and *Cymodocea*
154 *nodosa* (Ucria) Ascherson, while rocky areas are dominated by macroalgal communities
155 (largely *Cystoseira mediterranea* (Sauvageau)). These primary producers are all

156 consumed by the sea urchin *Paracentrotus lividus* (Lam.), which is the most important
157 invertebrate herbivore in the Mediterranean (Boudouresque and Verlaque, 2001).

158

159 *P. oceanica* is a stenohaline seagrass species with high thermal sensitivity (Gacia et al.,
160 2007; Tomasello et al., 2009); shoot mortality is known to increase by 2% year⁻¹ for each
161 additional degree of annual maximum temperature (Marbà and Duarte, 2010), with some
162 studies arguing it might become functionally extinct in the Mediterranean during this
163 century as a result of warming (Jorda et al., 2012). *C. nodosa* is the second most abundant
164 seagrass species occupying soft bottoms, and occurs mostly in coastal lagoons and
165 sheltered bays, where it can endure a wide range of temperatures and salinities (Pagès et
166 al., 2010; Pérez and Romero, 1992). Rocky littoral and infralittoral environments are
167 dominated by a diverse assemblage of canopy-forming macroalgae, of which *C.*
168 *mediterranea* is among the most dominant (Ballesteros, 1992). To our knowledge, little
169 is known of its response to warming. The sea urchin, *P. lividus* is a key herbivore both in
170 algal-dominated rocky bottoms, where it can produce barren overgrazed areas (e.g. Boada
171 et al., 2017), and in seagrass meadows, where it can consume up to 20% of annual
172 seagrass production (Prado et al., 2007; Tomas et al., 2005). In addition, in the presence
173 of predators, *P. lividus* shows very restricted movements, and when released from
174 predation pressure, browses much more extensively, which can have important
175 consequences for the plant resources they feed on (Hereu, 2005). Despite its ecological
176 importance, the response of this sea urchin species to warming is not clear, with adult
177 skeletons remaining unaffected by warming (Collard et al., 2016), while larval fitness
178 being reduced at high temperatures (García et al., 2015).

179

180 *Study design*

181 We conducted a series of modular laboratory experiments to explore the influence of
182 temperature on different components of the interaction between macrophytes and
183 herbivorous sea urchins. This included testing the effects of temperature on plant growth,
184 sea urchin growth and respiration, movement behaviour, plant consumption and plant
185 choice. The results of these controlled experiments were used to inform empirical
186 performance curves for the three dominant macrophyte species and their principal
187 invertebrate herbivore. We used these empirical performance curves to evaluate the
188 direction plant-urchin interactions will likely take as temperatures increase for each of
189 the studied plant species. We used different temperature conditions that aimed at
190 capturing current mean and maximum summer temperatures present in the NW
191 Mediterranean plus potential extremely warm temperatures. The analysis of the longest
192 data series available for sea surface temperature in the Catalan coast (l'Estartit, 1975–
193 present, data provided by J. Pascual) shows that the mean summer sea surface temperature
194 is 22°C, with maximum temperatures in August being 23.8°C on average and with
195 temperatures above 28°C being extremely rare (J. Pascual unpublished data, Garrabou et
196 al., 2009). Using these known ranges, we determined the different temperature treatments
197 for each of the manipulative experiments described below.

198

199 All the urchins, *C. mediterranea*, and *P. oceanica* samples used in the manipulative
200 experiments were collected near Blanes (41°40' N, 2°48' E). *C. nodosa* samples were
201 collected in a bay in the Ebre delta (40°35 'N, 0°37' E). To minimise inter-seasonal
202 influences all the sampling was done in spring or early summer between 2014 and 2016
203 depending on the experiment (the average SST at that time is 13-16°C). Water
204 temperature treatments in all of the aquaria were achieved by increasing or decreasing

205 water temperatures by 1°C every 6 hours until treatment temperatures were reached, to
206 prevent plants or animals from suffering a thermic shock.

207

208 *Plant growth*

209 The effect of increasing temperature on plant growth was assessed by determining either
210 leaf elongation or biomass change in each of the three plant species under different
211 temperature conditions. We collected 30 *P. oceanica* shoots in the field and placed them
212 in 6 aerated flow-through 200 L aquaria within an hour (5 shoots per aquarium). We
213 randomly assigned each aquarium to two growing temperature treatments (18°C or 25°C).
214 Aquaria were placed in full sunlight and the shoots were weighted down to ensure they
215 remained submerged. All shoots were marked near the ligula with a needle to assess leaf
216 elongation over 15 days (modified Zieman method, see e.g. Pérez and Romero, 1994). A
217 similar procedure was used for *C. nodosa* seagrass shoots. 45 shoots were harvested from
218 the field and placed in 9 aquaria (5 shoots per aquarium). We randomly assigned each
219 aquarium to 3 temperature treatments (20, 30, 35°C). Again, all shoots were marked near
220 the ligula with a needle to assess leaf elongation over 15 days as described above. Note
221 that we used higher temperature treatments for *C. nodosa*, given this species lives in
222 shallower, often enclosed bays. Finally, for *C. mediterranea*, we collected 10 thalli and
223 randomly allocated each of them to one of two aerated flow-through temperature
224 treatment aquaria (18°C or 25°C) (5 thalli per treatment). 200 L aquaria were placed in
225 full sunlight and the thalli were weighted down to ensure they remained submerged.
226 Growth of *C. mediterranea*, was estimated as the change in biomass (as fresh weight, g)
227 of each alga from the start to the end of the experiment (5 weeks). Even if all thalli from
228 the same treatment were placed in the same aquarium, aquaria were big enough (200L)

229 to allow sufficiently spatial heterogeneity (i.e. differences in temperature of 0.2°C) to
230 avoid pseudoreplication (Hurlbert, 1984).

231

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

240

241 *Herbivore growth and respiration*

242 The effect of temperature on sea urchin growth was assessed by comparing the growth of
243 urchins at different water temperatures. Sea urchins of different sizes were collected in
244 the field, randomly allocated to different aquaria for each temperature treatment (16, 19,
245 22, 25, 28 and 31 °C treatments, 6 aquaria per treatment) and fed ad libitum a mix of
246 algae every three days, for the entire duration of the experiment. Each aquarium had two
247 small (<3 cm), two medium (3-5 cm) and two large (>5 cm) individuals. We
248 photographed all individuals from each aquarium and temperature treatment at the start
249 of the experiment (216 individuals) and after two months (<200). Some individuals did
250 not survive for the entire duration of the experiment and were excluded from the analyses.
251 Images were taken with the aboral side of each individual facing upwards and with a ruler
252 as measure reference. We used imageJ to estimate urchin test diameter to the nearest

253 millimetre. Growth was calculated as the increase in test diameter of each individual sea
254 urchin from the start to the end of the experiment.

255

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

269
$$\text{Oxygen consumption (mg ind}^{-1} \text{ h}^{-1}) = [(O_0 - O_t) * V / T]$$

270 Where O_0 and O_t are the initial and final oxygen concentrations ($\text{mg O}_2 \text{ l}^{-1}$) measured, T
271 is the incubation time (h) and V is the volume (l) of the container.

272

273 The response variables 'sea urchin growth' and 'sea urchin respiration' were analysed in
274 R with linear models. Given that in this case we had 5-6 levels of the predictor variable
275 temperature, we treated it as a continuous variable instead of a factor. This allowed us to
276 test not only the linear effect of temperature on growth and respiration rates, but also the

277 quadratic term. Sea urchin size was used as a covariate. Assumptions of normality and
278 homoscedasticity were checked graphically and fulfilled in both cases.

279

280 *Herbivore movement behaviour*

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

294

295 The movement response of sea urchins to warming was determined by analysing a total
296 of 3292 images that resulted from the experiment. The x and y coordinates of each urchin
297 were obtained using an image processing toolbox in Matlab (Mathworks Ltd) and then
298 analysed with the adehabitatLT package in R (Calenge, 2011). This package computes
299 the increments in the x and y axis for each step of the trajectory (time interval = 30
300 seconds). The x and y coordinates of each individual trajectory were used to assess the
301 movement behaviour of sea urchins in each condition. We used a general numerical

302 approach based on the analysis of the q^{th} order long-range correlations in sea urchin
303 displacements (for more information see Supplementary Information and Seuront and
304 Stanley, 2014).

305

306 Finally, for each replicate sea urchin we calculated the mean sea urchin speed and the
307 straightness index. The straightness index (I_s), a measure of path tortuosity, is a
308 dimensionless number that ranges from 1 (maximum straightness) to 0 (maximum
309 tortuosity). It is the ratio of the Euclidian distance between the initial and final point of
310 the trajectory, and the sum of Euclidian distances between pairs of points separated by a
311 given time. Since different windows of time result in different I_s (Benhamou 2004), we
312 calculated this index for a range of window widths. Comparisons between experiments
313 were consistent regardless of window width and, we only present the I_s for a window of
314 1 step (30 seconds).

315

316 The significance of the differences between the empirical values of the function $\zeta(q)$ was
317 analysed with a linear model, considering as a response variable the ‘slope of the
318 exponents of the q^{th} order moments ($\zeta(q)$)’ and the fixed factor ‘temperature’ (2 levels:
319 18°C and 25°C) as the predictor. Each individual sea urchin was considered a replicate.
320 The response variables mean sea urchin speed and tortuosity were analysed with a linear
321 model to assess the effects of the predictor temperature (fixed factor, 2 levels). Normality
322 and homoscedasticity were assessed graphically and fulfilled in all cases.

323

324 *Herbivore consumption*

325 The effect of temperature on consumption was assessed by comparing the amount of
326 seagrass *P. oceanica*, *C. nodosa* and algae *C. mediterranea* eaten by the urchin *P. lividus*

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

341

342 The effects of the fixed factor ‘temperature’ (3 levels: 15, 20, 25°C) on the response
343 variable ‘sea urchin consumption’ of the seagrass *P. oceanica* was analysed with a
344 generalised linear mixed effects model with a Poisson distribution, due to the high number
345 of zeros of the response variable. ‘Sea urchin consumption’ was the result of subtracting
346 the initial plant biomass by the final biomass in each compartment and corrected by
347 subtracting any autogenic change (estimated from the biomass change in control
348 compartments). We used the function `glmer` from the package `lme4` (Bates et al., 2017).
349 The random effect ‘aquarium’ could not be dropped from the model according to the
350 Akaike Information Criterion (AIC) and the Log Likelihood Ratio (Zuur et al., 2009). We
351 used a similar generalised linear model to assess the effect of the fixed factor ‘temperature’

352 (3 levels: 15, 20, 25°C) on the consumption of *C. nodosa*. However, in this case we used
353 a negative binomial distribution due to the response variable being overdispersed (Zuur
354 et al., 2009). Again, we could not drop the random effect 'aquarium' according to AIC
355 and the Log Likelihood Ratio. Finally, to analyse the effects of temperature on the
356 consumption of *C. mediterranea*, we used a simple linear model. Assumptions of
357 normality and homoscedasticity were checked graphically and fulfilled in all cases.

358

359 *Herbivore choice experiments*

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

377 change, given that there was no difference in length or weight of plant material in any of
378 the controls at the end of each experiment.

379

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

387

388 *Plant performance, herbivore performance and herbivore pressure conceptual curves*

389 In order to model both plants' and urchins' thermal performance curves, we used
390 modified Gaussian functions obtained from Angilletta (2006). We parameterised each
391 function with values chosen to best reflect the empirical optima observed in our
392 experiments (using data from Fig. 2 for the plants, and from Fig. 3 and 4 for the
393 herbivores). These parameter values do not bear biological meaning, but were used to
394 observe the shape of the resulting curves (see supplementary information), using the web
395 app Geogebra (www.geogebra.org). For the herbivorous sea urchins, we modelled two
396 types of performance curves depending on whether sea urchin feeding preferences were
397 influenced by the incubation temperature of their feeding source (see supplementary
398 information): a continuous modified Gaussian function was used when sea urchins did
399 not modify their preference when offered plants incubated at warm temperatures; while a
400 stepwise function was used to impose a truncation of the thermal performance curves of
401 sea urchins, to mimic the effect of offering them plants incubated at warm temperatures

402 (i.e. less preferred). The stepwise function behaves as a modified Gaussian for $x < 2$, but
403 otherwise it quickly drops to 0 (and then negative values, with no biological meaning in
404 this case). Finally, to obtain the herbivore pressure curve, we divided the thermal
405 performance function of sea urchins by the thermal performance function of each plant
406 (see supplementary).

407

408 **Results**

409 *Plant Growth*

410 Temperature significantly affected the growth rates of the three plants studied. *P.*
411 *oceanica* and *C. mediterranea* displayed significantly lower growth rates at warmer
412 temperatures (25 vs 18°C; Fig. 2a,c, Table 1). In contrast, *C. nodosa* displayed higher
413 growth rates at temperatures as high as 30°C, compared to cooler and warmer treatments
414 (20 and 35°C) (Fig. 2b, Table 1).

415

416 *Herbivore growth and respiration*

417 Temperature significantly affected both the growth and respiration of the herbivorous sea
418 urchin *P. lividus* (Fig. 3, Table 1). The best model fitting our data included the quadratic
419 term of temperature, highlighting a temperature that maximises both processes at ca. 22°C.
420 Sea urchin size also significantly affected both growth and respiration rates (see
421 supplementary Fig. S1a,b).

422

423 *Herbivore behaviour*

424 Sea urchin movement patterns in the lab did not change significantly between temperature
425 treatments. Their trajectories were similar in terms of tortuosity (Fig. 4a), and long range
426 correlations (Fig. 4c). There was a faint trend of slower velocities at warmer temperatures

427 (Fig. 4b), but this was not significant at $\alpha = 0.05$. As is typical for this species (Pagès,
428 2013) their trajectories were in the realm of superdiffusive movements, nearer to ballistic
429 than Brownian motion (Fig. 4c).

430

431 *Herbivore consumption and feeding choice experiments*

432 Sea urchin feeding rates on both seagrass species were maintained from 15 to 20°C, but
433 then plunged at the warmest treatment (25°C) (Fig. 5a,c, Table 1). Moreover, for both
434 seagrass species, sea urchins preferred seagrass leaves that had been incubated at cooler
435 temperatures (Fig. 5b,d, Table 1). In contrast, sea urchin feeding rates on the alga *C.*
436 *mediterranea* were sustained even at higher temperatures, although with a negative trend
437 towards the warmest treatments (Fig. 5e, Table 1). Sea urchins did not display any
438 preferences between algae incubated at cool or warm treatments (Fig. 5f).

439

440 **Discussion**

441 Increasing temperatures are likely to trigger a complex suite of responses in the dynamics
442 of plant-herbivore interactions, with potentially far-reaching consequences for
443 Mediterranean macrophyte communities. While it is clear that some plant species, like
444 *Posidonia oceanica* and *Cystoseira mediterranea* will be pushed beyond their optima and
445 show decreased growth, *Cymodocea nodosa* may actually benefit due to its high thermal
446 optimum. Together with the other responses to temperature evidenced here, which
447 include sea urchin growth, respiration, feeding rates and plant susceptibility to
448 consumption, it appears that while the strength of the plant-sea urchin interaction may
449 weaken for seagrass species – quite considerably in the case of *C. nodosa* – herbivory
450 pressure may actually increase on the macroalga (see these results using the framework
451 of our heuristic models in Fig. 6).

452

453 As plant-herbivore interactions are the outcome of several processes acting together,
454 changes in any one of these processes could influence the interaction. The picture further
455 gains in complexity because as found elsewhere (Sentis et al., 2015; Van De Velde et al.,
456 2016), not all processes are equally influenced by temperature. While growth and feeding
457 showed clear directional responses, plant susceptibility to being consumed exhibited
458 contrasting responses, and urchin movement did not change. In addition, these responses
459 were highly species specific, dependent on the inherent tolerance limits of each species
460 (Kordas et al., 2011). Thus, while both *P. oceanica* and *C. mediterranea* showed higher
461 growth at lower temperatures (as is typical for most temperate species, Lee et al., 2007),
462 *C. nodosa* grew best at 30°C. The responses of their common sea urchin consumer to
463 increasing temperatures varied. Surprisingly, while growth and respiration were highest
464 at intermediate temperatures (ca. 22°C, see Fig. 3), *P. lividus* did not modify its movement
465 behaviour with increasing temperatures. Consumption rates did not correspond well with
466 urchin growth either; at 25°C, urchins had practically stopped eating. Mismatches
467 between consumption and metabolism/growth are common in many species including
468 urchins, likely representing physiological limits to plasticity (Lemoine and Burkepile,
469 2012). In addition, while the palatability of the two seagrass species apparently declined
470 (possibly as a result of increased production of secondary compounds (Vergés et al.,
471 2007b), but see Hernán et al., 2017), this was not true for the macrophyte *C.*
472 *mediterranea*. These differences can lead to differential susceptibilities of species to
473 herbivory pressure across the seascape as temperature increases (Peñuelas and Staudt,
474 2010; Poore et al., 2013).

475

476 Global warming is changing the odds for Mediterranean macrophytes by creating clear
477 ‘winners’ and ‘losers’ among the species that dominate these waters at present. What is
478 interesting, though, is that these patterns arise not as a result of a single mechanism or
479 process that changes with temperature, but because of the interplay between several
480 mechanisms that together shape the plant-herbivore interaction. Thus, the expected
481 decrease in herbivory pressure with temperature for *C. nodosa* (see Fig. 6b), results not
482 merely from a faster growth, and thus increased productivity, but also because it reduces
483 its palatability to urchins (Figs. 5d) and because sea urchins consume much less at higher
484 temperatures (Fig. 5c, independent of seagrass palatability). Consequently, *C. nodosa* is
485 likely to be released from herbivory pressure as temperatures increase (Fig. 6b).
486 Similarly, while the growth of *P. oceanica* decreases at higher temperatures (Fig. 2a),
487 given that in parallel urchin growth decreases (Fig. 3a), as does consumption (Fig. 5a)
488 and palatability is reduced (Fig. 5b), the impact of herbivory may still decrease or remain
489 unchanged for this species (Fig. 6a). In sharp contrast, the canopy-forming macroalga, *C.*
490 *mediterranea* is probably most at risk from increasing temperatures, once again as a result
491 of a suite of changes in mechanisms affecting plant-herbivore interactions. Thus, while it
492 reduces its growth in elevated temperature conditions (Fig. 2c), urchin consumption
493 remains high until 25 °C (Fig. 5e), while palatability does not decrease at the highest
494 temperatures (Fig. 5f). If anything, the strength of this algae-herbivore interaction is set
495 to increase with ocean warming (Fig. 6c). This is particularly worrying, given that of all
496 the systems we studied, benthic macroalgal systems are most prone to state shifts, often
497 precipitated by urchin overgrazing (Boada et al., 2017; Pinnegar et al., 2000).

498

499 In interpreting these results, it is essential to remember that there are several additional
500 mechanisms that we have not considered. Our laboratory experiments and the

501 performance curves test the current tolerance limits of the species in question to changing
502 conditions. Of course, as temperatures change, it is quite possible for species to acclimate
503 within the limits of their phenotypic plasticity, or genetically adapt to increasing
504 temperatures by selection of the fittest genotypes (Lee et al., 2007). While most plants
505 show considerable capacity to adjust their photosynthetic traits to enhance their
506 performance, this ability varies considerably between species (Lee et al., 2007).
507 Consumers, in contrast, tend to be more sensitive to warming (Voigt et al., 2003). The
508 consumer *P. lividus*, however, is a thermal generalist that experiences a wide range of
509 environmental temperatures, ranging from 10 to 30°C (Boudouresque and Verlaque,
510 2001), and is potentially exposed to extremes of temperatures in shallow coastal bays.
511 How plants and animals acclimate or adapt to increasing temperatures will significantly
512 change performance optima and result in further changes in the plant-animal interaction.
513 As species are pushed to the edge of their tolerance limits, we should expect a host of
514 individual and population-level consequences that will also be critical to ecosystem
515 functioning (Bennett et al., 2015; Tylianakis et al., 2008). However, in a field experiment
516 using a thermal plume, Garthwin et al. (2014) showed that a meadow of the seagrass
517 *Zostera muelleri* that had been exposed to sustained higher temperatures for 30 years had
518 similar levels of growth and herbivory than un-impacted meadows nearby. Similarly,
519 Morelissen and Harley (2007) found that even though individual species may be
520 influenced by temperature, plant–herbivore interactions may not necessarily be. Other
521 studies, in contrast, have found that warming tends to increase interaction strength
522 between producers and consumers (O’Connor et al., 2009; Poore et al., 2013). Our
523 heuristic models help to explain why warming may or may not modify plant-herbivore
524 interaction strength by influencing some of the components of these interactions (see
525 rationale at the end of introduction). Moreover, our results show that the same amount of

526 warming might have opposing effects on Mediterranean macrophyte-herbivore
527 interactions contingent on species specific thermal performance. We must apply caution
528 when interpreting our heuristic models (Fig. 6), given the low number of temperature
529 levels used in the plant growth experiments (see Fig. 2). As a sensitivity exercise, we
530 examined the effect of shifting the plants' thermal performance curves around their
531 optima, leaving the urchins' performance curves unchanged (see results in the
532 supplementary, Figs. 8-10). The sensitivity analysis confirmed the results observed in
533 Fig. 6, given that the changes to the resulting herbivore performance curves changed
534 minimally. In the future, however, we might have to introduce more actors into the
535 picture, as the sparid *Sarpa salpa* (L.) and the thermophilous black sea urchin *Arabacia*
536 *lixula* (L.) will also likely be affected by warming (Gianguzza et al., 2011; Privitera et al.,
537 2011). Moreover, warming is already causing a host of tropical species, such as the
538 herbivorous rabbitfish (*Siganus luridus* and *S. rivulatus*), to migrate to temperate areas
539 (Vergés et al., 2014), altering local interactions and potentially precipitating algal barrens
540 (Sala et al., 2011).

541

542 As far as we are aware, this is the first study to explicitly examine how warming mediates
543 key plant-animal interactions (that structure Mediterranean macrophyte communities in
544 this case) at this diversity of scales (from the behavioural, metabolic, to individual level).
545 Moreover, the inclusion of these responses in simple heuristic models demonstrates that
546 the complex effects of warming on plant-animal interactions are the result not merely of
547 their effect on each individual species' survival, but also of temperature changing a suite
548 of plant and animal responses (including palatability and potentially behaviour [not in
549 this case]) that are difficult to predict *a priori*. This can lead to unexpected results.
550 Ecological interactions have developed over evolutionary time scales and are the

551 consequence of a dynamic interplay between each species attempting to adjust to
552 environmental changes as well as ensuring its own evolutionary success. Rapid
553 environmental changes are accelerating this dynamic process, stretching the ability of
554 species to cope with the rate of these changes. How these interactions play out in real-
555 world scenarios, where several species interact both directly and indirectly in a dizzyingly
556 complex network of interactions, is difficult to conceive, especially given that warming
557 experiments generally assume that individual organisms that have been experimentally
558 warmed in short-term experiments, will respond in a similar way as individuals whose
559 ancestors have been exposed to the same level of warming over decades. In any case, our
560 results show that not all of these consequences are going to be negative, since some
561 species may be able to compensate for the effects of temperature, leaving the interaction
562 itself unchanged. Some structural species, like *C. nodosa* in the case of this study, may
563 even emerge as clear winners in these scenarios. Much will depend on the plasticity and
564 adaptive capacity of the individual actors within the interaction to this change. It may be
565 useful to think of interactions themselves as having an inherent plasticity, adapting in a
566 coupled way to changing conditions. There will be limits to this joint plasticity, breaking
567 down either as its individual actors cross tolerance thresholds, or when the interaction
568 itself becomes too strong or too weak (see Fig. 6). Clearly, as human-induced rapid
569 environmental change continues apace, it is pushing us to investigate more carefully what
570 governs species interactions, in order to understand how they will respond to change.
571 Knowing what to expect of these ecosystems in the near future, may help us manage them
572 more effectively. We believe we can be moderately optimistic for Mediterranean seagrass
573 communities given their expected unchanged or reduced herbivore pressure as warming
574 continues. However, our study should serve as an early warning for Mediterranean
575 macroalgal communities, which are already subject to strong top-down control due to the

576 loss of top-predators (Pinnegar et al., 2000), but which are likely to be subjected to even
577 higher herbivore pressure.

578

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595

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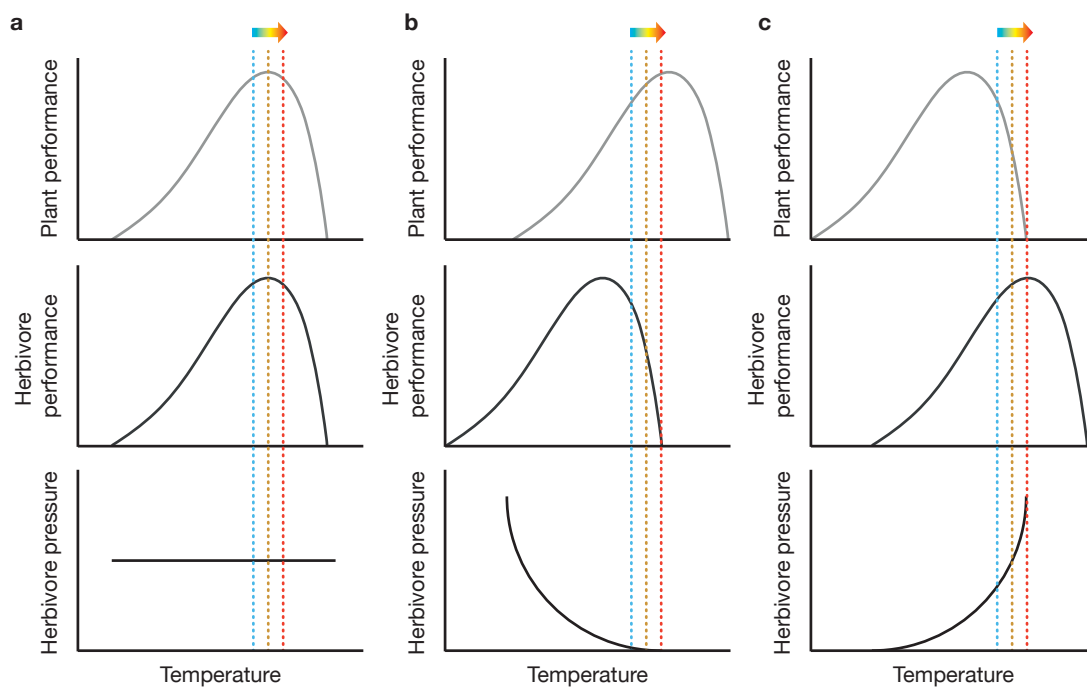
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834 **Figure legends**

835 **Fig. 1.** Conceptual model of the potential outcomes of plant-animal interactions in a warming
836 Mediterranean. The arrow above the dashed vertical lines show the direction of warming.
837 When both plant and herbivore thermal performance curves are of similar shape and display the
838 same optimal temperature, warming will not produce any changes to herbivore pressure¹. (b) If
839 plant performs better at warmer temperatures compared to the herbivore, herbivore pressure¹ will
840 decrease with warming. (c) In contrast, herbivore pressure¹ will increase with warming, if the
841 herbivore performs better at warmer temperatures compared to the plant. See the supplementary
842 for more information on the shape of these theoretical curves.

843 ¹Here, we conceptually define herbivore pressure as the result of dividing herbivore performance by plant performance.
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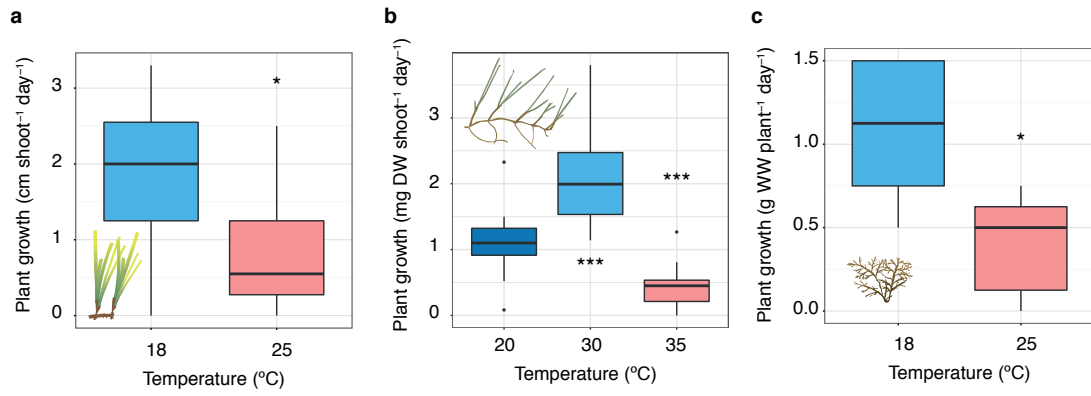


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847 **Fig. 2.** Plant growth at different incubating temperatures. (a) *Posidonia oceanica* seagrass, (b)
848 *Cymodocea nodosa* seagrass, (c) *Cystoseira mediterranea* macroalgae. Asterisks denote
849 significant differences. Significance codes $p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

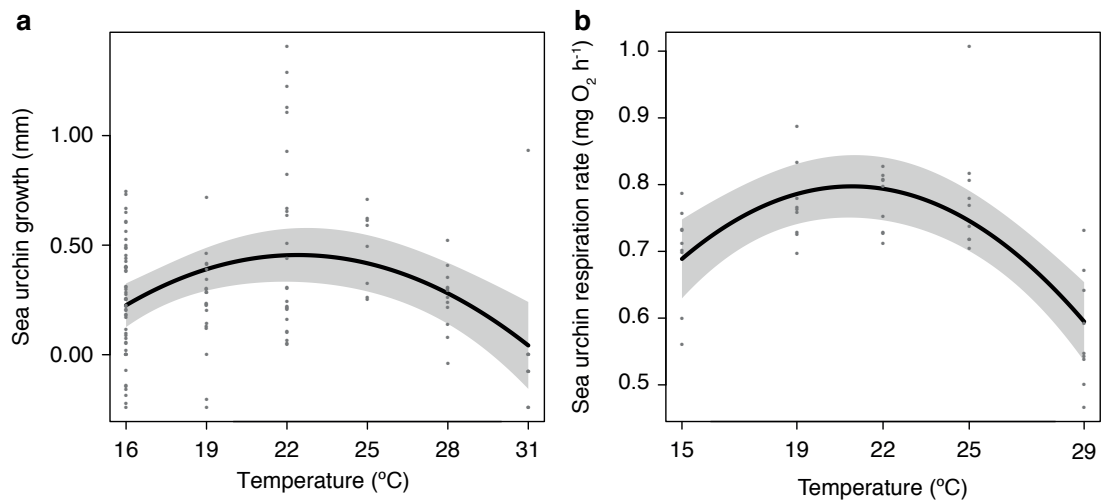
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853 **Fig. 3.** Sea urchin thermal performance curves (a) for growth and (b) respiration rates. Solid lines
854 correspond to the predictions of a linear model applied to the data sets using the quadratic term
855 of temperature as a predictor, hence the parabolic shape of the curve. Shaded areas define the
856 95% confidence intervals around fitted values. Sea urchin size significantly affected both growth
857 and respiration curves as well (see Fig. S1 from the supplementary).

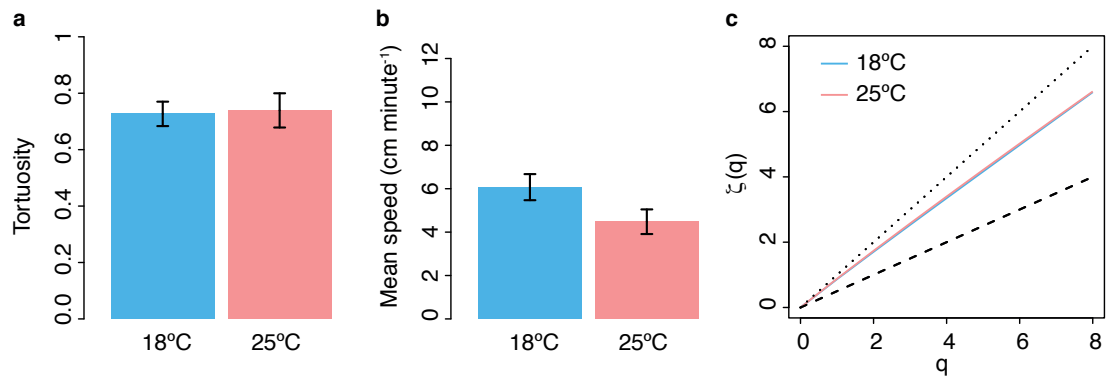


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861 **Fig. 4.** Sea urchin movement behaviour at cool and warm water temperatures. (a) Temperature
862 did not affect the tortuosity of sea urchin trajectories, (b) nor their mean speed. (c) The analysis
863 of sea urchin trajectories at different scales (see methods) did not find any differences between
864 the trajectories of urchins wandering in cool (blue solid line) or warm (red solid line) conditions.
865 The dotted line denotes a ballistic trajectory, while the dashed line represents Brownian motion.

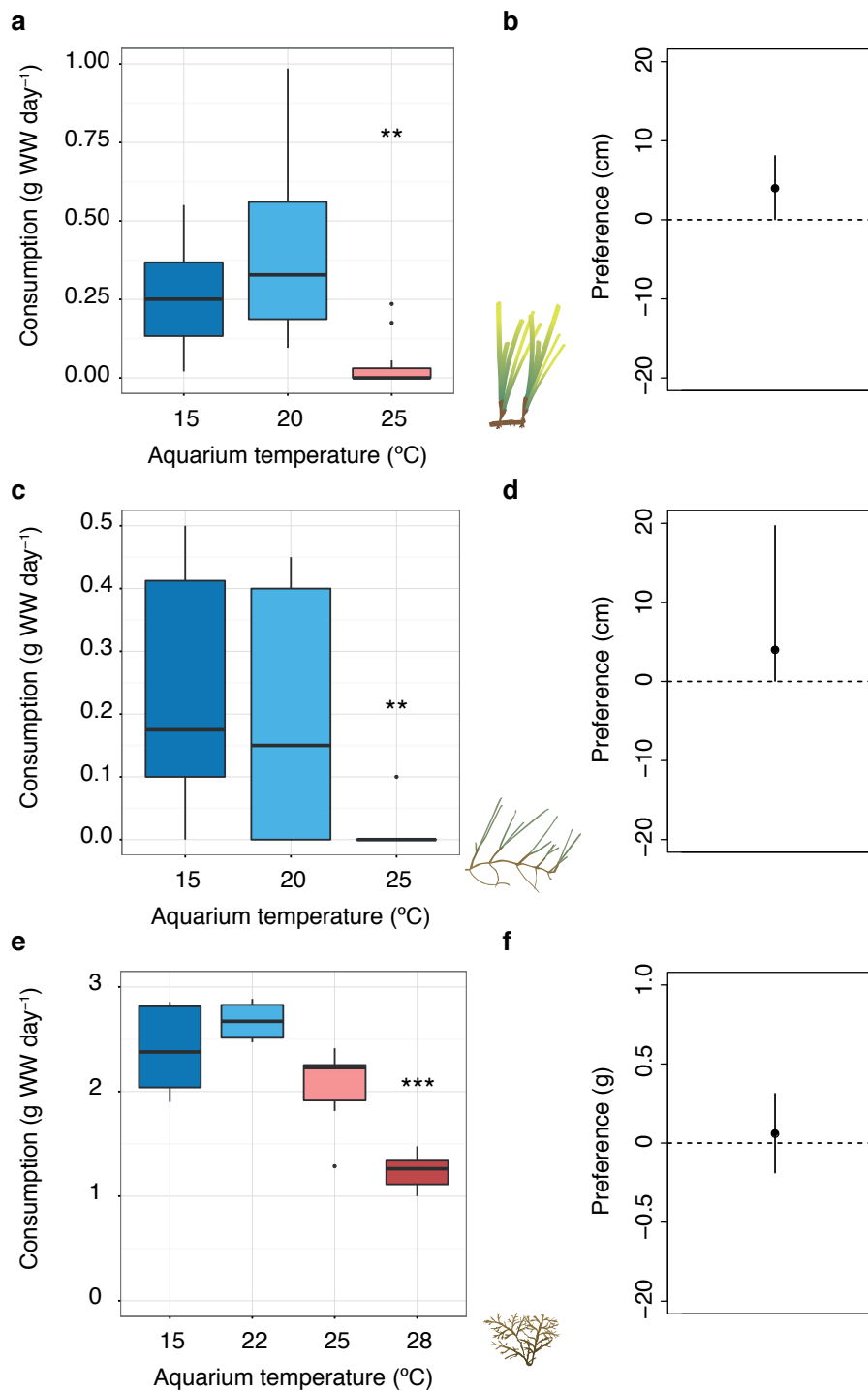


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869 **Fig. 5.** Sea urchin consumption rate at increasing temperatures and sea urchin choice of plants
 870 incubated at cool and warm temperatures. (a, b) correspond to the seagrass *Posidonia oceanica*,
 871 (c, d) to the seagrass *Cymodocea nodosa*, and (e, f) to the macroalgae *Cystoseira mediterranea*.
 872 Significance codes $p < 0.001$ ‘***’, $p < 0.01$ ‘**’, $p < 0.05$ ‘*’. For the preference plots (b,d,f),
 873 effects are significant ($P \leq 0.05$) where confidence intervals do not intercept 0.

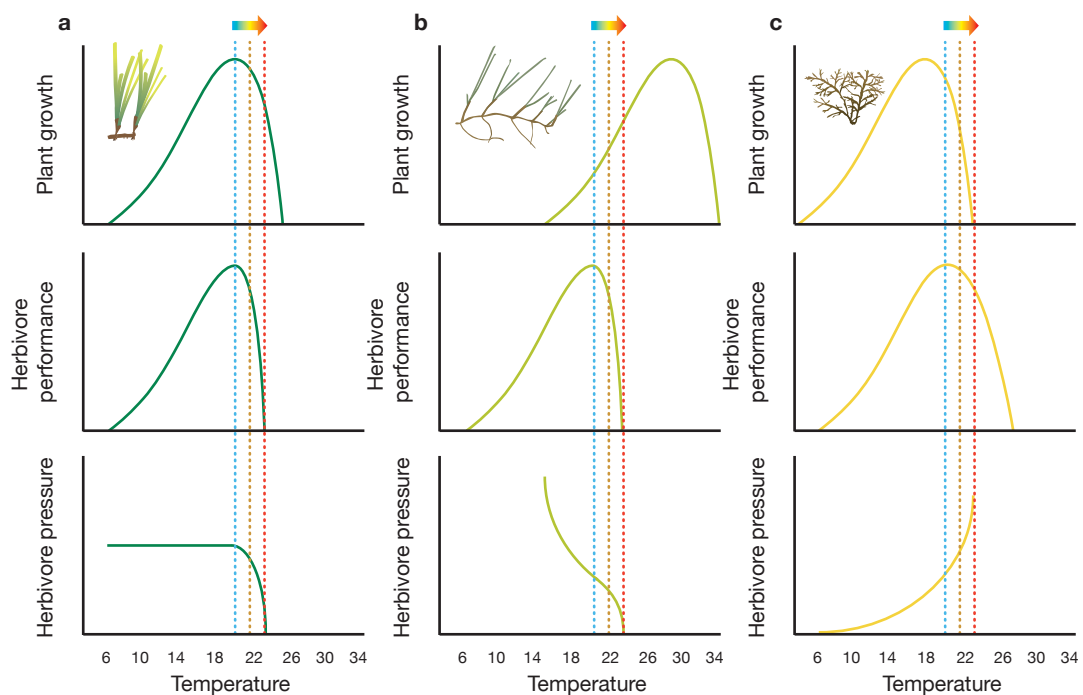


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876 **Fig. 6.** Conceptual model of the outcomes of plant-animal interactions in a warming
877 Mediterranean. The arrow above the dashed vertical lines show the direction of warming.
878 We expect herbivore pressure on *Posidonia oceanica* seagrass to keep unchanged with warming,
879 given that both the sea urchin and the seagrass display similar optimal temperatures of
880 performance; however, sea urchins' feeding rates plunge when offered *P. oceanica* seagrass
881 leaves from plants incubated at warm temperatures, hence the decrease in herbivore pressure
882 when warming increases (from the blue to the red dotted lines). (b) We expect the herbivore
883 pressure between urchins and the seagrass *Cymodocea nodosa* to decrease with warming given
884 the warmer optimal temperature of performance of the seagrass compared to the herbivore. The
885 herbivore pressure curve is expected to be especially steep at higher temperatures, given the lower
886 feeding rates of urchins when offered plants incubated at warm temperatures. (c) We expect the
887 herbivore pressure between the macroalga *Cystoseira mediterranea* and the sea urchin to increase
888 with warming, given the low performance of the macroalga at warm temperatures, while sea
889 urchins still display high feeding rates (see also Fig. 5). See methods and supplementary materials
890 for more information on the shape of these curves.

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922	<i>C. nodosa</i>	glm negative	1 Aquarium	round(x*10)	Temperature	-	2	9.95	0.007 **
923	consumption	binomial							
924									
925	<i>C. mediterranea</i>	Linear	-	-	Temperature	6.99	3	21.19	2.0 10 ⁻⁶ ***
926	consumption				Residuals	2.20	20		
927									
928	Difference in	t-test	-	-	-	-	21	2.10	0.047 *
929	consumption								
930	<i>P.oceanica</i>								
931									
932	Difference in	Wilcoxon	-	-	-	-	20	155.5	0.050 *
933	consumption								
934	<i>C. nodosa</i>								
935									
936	Difference in	t-test	-	-	-	-	23	0.517	0.610
937	consumption								
938	<i>C. mediterranea</i>								
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