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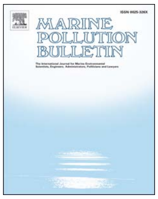

# Contrasting effects of ocean warming on different components of plant-herbivore interactions

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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 seagrasses, 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

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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.