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Functional and energetic consequences of climate change on a predatory whelk

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ABSTRACT

The increasing rise in sea surface temperature caused by human activities currently represents the major threat to biodiversity and natural food webs. In this study we used the Lessepsian mussel *Brachidontes pharaonis,* one of the most recent invaders of the Mediterranean Sea, as a model to investigate the effect of a novel prey and a chronic increase in temperatures on functional parameters of local consumers, compared to the native mytilid species *Mytilaster minimus*. In particular we focused on the whelk *Stramonita haemastoma*, a widespread Mediterranean intertidal predator that actively preys on bivalves, barnacles and limpets, by studying the direct effects of such multiple stressors on feeding and growth rate, projected into a future climate change scenario (RCP8.5) relative to 2046–2065 with higher hypothesized temperatures of 2 °C. Gastropods showed a significantly higher feeding rate (ADFR) on *M. minimus* at high (6.45 ± 0.43) *vs* low temperatures (5.15 ± 0.33) compared to *B. pharaonis* (2.84 ± 0.37 *vs* 2.48 ± 0.27). Ingestion rate (ADIR), however, recorded higher values for *B. pharaonis* at high (1.71 ± 0.22) and low (1.49 ± 0.16) temperatures, compared to *M. minimus* (0.17 ± 0.01 *vs* 0.14 ± 0.01). Prey significantly influenced growth rate, condition index and the length-weight relationship (LWR) of whelks, while only ADFR seemed to be influenced by higher temperatures. In conclusion the extra amount of energy from the novel prey, together with temperature side effects, successfully influenced growth rates and reproductive events, positively affecting the global fitness of whelks.

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1. Introduction

Biotic interactions of local species are naturally shaped by environmental variability (Vasseur et al., 2007; Post, 2013). Seawater temperature, through the fundamental influence on metabolic machinery (Brown et al., 2004), plays a prominent role in driving functional and life history (LH) traits of most ectotherms, affecting their local persistence over time (*sensu* Sibly et al., 2012). Increasing temperature, as a consequence of future climate change (CC; IPCC, 2014), will probably determine cascading effects within natural communities, modifying current biodiversity (Gooding et al., 2009; Yamane and Gilman, 2009). Intertidal shores are harsh habitats with regard to temperature; the body temperatures of ectotherms can vary greatly according to daily tidal cycles and seasonal weather conditions (Helmuth, 1998, Helmuth and Denny, 1999). Intertidal organisms are, for this reason, considered to live “on the edge” and thus CC is expected to modify the structure and species composition of those communities. CC may favour the spread of much more thermo-tolerant alien marine species, such as jellyfishes, bivalves and fishes by increasing the likelihood of reinforcing facilitation mechanisms (Southward et al., 1995; Stachowicz et al., 2002; Galil et al., 2015) or through the availability of empty niches in the invaded range (Hierro et al., 2005). Invasive species originated from the Red Sea (also called Lessepsian) and introduced to the Mediterranean Sea through the Suez Canal, are considerably more thermo-tolerant and better able to cope with highly changing thermal conditions than most Mediterranean species (Zerebecki and Sorte, 2011). Thus, when these species interact with local ecological equivalents, they will be advantaged by their major innate ability to survive under harsher conditions (Sarà et al., 2008). Invaders may then be able to replace native species in the local food webs (Simberloff et al., 2013) and

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consequently, local native consumers may count on a larger selection of prey. Nonetheless, local consumers, for their part, will also have to cope with increasing temperatures due to CC. However, although the effect of temperature is essentially pervasive (Gillooly et al., 2001), there is still little research to investigate the crossed effect between an alien prey and the increasing temperature on feeding behaviour (e.g. prey preference and consumption rate) of a local consumer apart from a single study dealing with the planktonic food webs (Seifert et al., 2014). According to theory (e.g. Arrhenius law; Kooijman, 2010; Sarà et al., 2014), increasing temperature should be particularly effective in enhancing the consumption rates in ectotherms (Sibly et al., 2012; Seifert et al., 2014). As a consequence, it is possible that an altered scheme of consumption dynamics of an abundant local predator has important local implications for the destabilization of the entire community equilibria (Vasseur and McCann, 2005; Seifert et al., 2014). Consumers are widely believed as able to adapt their feeding behaviour, and in particular the quality and quantity of food consumed in order to adjust their energy intake as a response to a varying environment (Tylianakis et al., 2008; Kordas et al., 2011; Kaspari et al., 2012). Ecologists use the term “plasticity” to describe this ability of organisms to modify their feeding behaviour, with compensatory feeding patterns, e.g. increased predation or ingestion rate to compensate for low quality resources or stressful conditions (Duarte et al., 2015). The same kind of plasticity can also be observed when consumers maximize consumption of high quality resources (Jacobsen and Sandjensen, 1994; Falkenberg et al., 2013) at the same time satisfying their energetic requirements and enhancing the individual fitness as suggested by classical ecological theory (Optimal Foraging Theory; Pyke, 1984). Here, we designed an experimental set-up to test if a widespread intertidal carnivorous gastropod, *Stramonita haemastoma*, when fed with an invasive bivalve, *Brachidontes pharaonis* (Sarà et al., 2000, 2003) under constant increased temperature of a few degrees (IPCC, 2014; RCP8.5 scenario relative to 2046–2065), will show any difference in the individual fitness with respect to when it fed with the native ecological equivalent prey, the bivalve *Mytilaster minimus*. Thus, we investigated whether (i) functional traits, such as those involved in feeding processes (i.e. predation and ingestion) were modified, and (ii) if any repercussions on life history (LH) traits, such as growth and fecundity, were evident. *Brachidontes* and *Mytilaster* (and *Stramonita*) represent a perfect model for this study: the former is one of the first time invaders (Pallary, 1912; Sarà et al., 2000, 2003), forms dense clusters on lower mid-littoral and subtidal rocks where *Stramonita* lives and spreads to the Western Basin (Sarà et al., 2013; Porporato et al. accepted, 2017). If present, it out-competes *M. minimus* (Safriel et al., 1980) that usually, in the absence of the alien species, proliferates and represents one of the most frequent items in the *Stramonita* diet (Safriel et al., 1980). Results from the present experiment comprise an important tool to evaluate the species colonization process and predict future spread, but will also be useful when assessing the potential expansion of Lessepsian species under higher temperatures and salinity conditions in the Mediterranean Sea, as a result of current global warming, where Lessepsian species would have a distinct advantage over native species (Sarà et al., 2008).

2. Materials and methods

Specimens of *S. haemastoma* were collected alive at low tide during the month of June 2014 from the intertidal shores near San Vito Lo Capo and the natural reserve of Monte Cofano (Castelluzzo, TP) (LAT: 38° 6′23.42″N; LONG: 12°42′17.84″E), where the mussels *B. pharaonis* and *M. minimus* were both present, although with different densities. As in surveys conducted along 100-m transects, whelks were relatively abundant in this site with a density of ~0.56 ind./m^2 (Giacoletti et al., 2016), while *M. minimus* reached densities of ~19,753.3 ± 9445 ind./m^2 (G. Sarà, unpublished data), and *B. pharaonis* showed an occasional distribution. Whelks were brought back to the Experimental Aquaculture Facility at IAMC-CNR in Messina, and acclimated at room temperature (20–22 °C) and seawater salinity (37–38), and starved for one week to reduce stress generated by manipulation and transport (Garton and Stickle, 1980), before being transferred to experimental tanks (1350 L). The first tank (Tank A) was equipped with a 1500 W electric heater in order to maintain a higher temperature of 2 °C than the second tank (Tank B), which received water at ambient temperature. Water from each tank (A, B) was distributed into 16 1 L plastic compartments, divided in two groups of 8, each containing a single whelk. Natural variation of temperatures due to the open water flow were continuously monitored through the use of temperature data loggers (model: iButton G1, prec. ± 1 °C, res. ± 0.5 °C, http://www.alphamach.com). Each group of whelks was fed for the first 7 days with *B. pharaonis* or *M. minimus*, respectively, in order to allow whelks to experience handling with their prey (Rovero et al., 1999). After this last period of adaptation, animals were starved for another week prior to the start of the experiment: this step allowed for hunger levels to be standardized (Garton and Stickle, 1980). No drill mortality was detected during the experiment.

2.1. Prey-size selection

Size-classes for each prey species (*M. minimus* and *B. pharaonis*) used during the experiment were determined through a preliminary prey-choice test, following the experimental design proposed by Underwood and Clarke (2005). In practice, we tested 36 specimens of *S. haemastoma* of the same size, and acclimated as above. In the first experiment two size-classes of *M. minimus* (5–10 mm and >10 mm) were offered simultaneously, without replacement, to each single whelk in their respective 1-L plastic compartment. The experiment was replicated twice. In the second experiment, four size-classes of *B. pharaonis* (10–15, 15–20, 20–25 and 25–30 mm) were offered simultaneously to each single whelk, with the same experimental setting. These prey class-sizes were chosen as they corresponded to the most common sizes observed in the field where the whelks were observed feeding (unpubl. obs.). Each experiment was replicated twice. Attacks were considered to start when the prey was put in the arena, and ended as soon as specimens of *S. haemastoma* had made their choice. To meet the independence criterion (*sensu* Underwood, 1997), each whelk was used only once, and later they were killed by gentle freezing.

2.2. Growth rates and fecundity

The experiment involved 48 medium size (30–40 mm) individuals of *S. haemastoma*, and lasted for 135 days, from July 2nd to November 19th, 2014, in order to evaluate the influence of prey and temperature on the growth rate of our model predator. As before detailed, water from each experimental fiberglass tanks was distributed in two groups of 8 whelks, and each group was fed with a different diet. The first diet (D1) consisted of a fixed daily density (n = 12) of the indigenous mussel *M. minimus*, while the second diet (D2) involved the same density of the Lessepsian mussel *B. pharaonis*. Each day consumed items were replaced, in order to maintain a constant density of the prey, allowing the whelks to feed *ad libitum*. Specimens of *S. haemastoma* were weighed and measured every two weeks, by taking five different variables (Fig. 1): total weight (TW), shell length (SL), shell width (SW), aperture height (AH), and aperture width (AW) (Chiu et al., 2002),

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