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Feeding behaviour of an intertidal snail: Does past environmental stress affect predator choices and prey vulnerability?

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ABSTRACT

Predation is one of the most important factors in determining structure and dynamics of communities on intertidal rocky shores. Such regulatory role may be of special relevance in novel communities resulting from biological invasions. Non-indigenous species frequently escape natural predators that limit their distribution and abundance in the native range. However, biological interactions also can limit the establishment and spread of non-native populations. There is a growing concern that climate change might affect predator–prey interactions exacerbating the ecological impacts of non-indigenous species. However, mechanisms underlying such interactions are poorly understood in marine ecosystems. Here, we explored if past environmental stress, i.e., increasing temperature and decreasing pH, could affect the vulnerability of two mussel prey, the native *Mytilus galloprovincialis* and the non-indigenous *Xenostrobus securis*, to predation by the native dogwhelk *Nucella lapillus*. In addition, we evaluated the consequences on the feeding behaviour of *N. lapillus*. First, we exposed monospecific assemblages of each mussel species to combined experimental conditions of increasing temperature and decreasing pH in mesocosms for 3 weeks. Then assemblages were placed on a rocky shore and were enclosed in cages with dogwhelks where they remained for 3 weeks. Despite the lack of preference, consumption was much greater on the native than on the invasive mussels, which barely were consumed by dogwhelks. However, this trend was diverted when temperature increased. Thus, under a coastal warming scenario shifts in dogwhelks feeding behaviour may help to contain invader's populations, especially in estuarine areas where these predators are abundant.

1. Introduction

On intertidal rocky shores, patterns of distribution of species are determined by complex interactions between biological and physical forces (Connell, 1961). Among these forces, predation is one of the most important factors in determining structure and dynamics of communities (Menge, 1983; Wieters and Navarrete, 1998). The most evident effect of predation encompasses changes on prey density and distribution limits, while indirectly it can change diversity within the community (Sih et al., 1985; Wieters and Navarrete, 1998). Nevertheless, the effect of predators on prey populations often varies in intensity across space and time due to different factors, e.g., variation in predator densities at population level, indirect interactions, differential foraging efficiency, or feeding preferences (Hines et al., 2009; López et al., 2010; Menge, 1983; Shinen et al., 2009).

The regulating role of predators is of special relevance in novel communities resulting from the establishment of non-indigenous species (NIS) (López et al., 2010; Rilov, 2009; Rodriguez, 2006; Shinen et al., 2009) since a number of complex novel interactions can be established due to the arrangement of new set of species. For instance, native predators can facilitate invasion of a NIS via consumption of native competitors if they fail to recognize a novel species as a potential prey (Keane and Crawley, 2002). Alternatively, strong preferences for NIS may release native species from potential new competitors or enemies (Rodriguez, 2006), or open the possibility of novel responses, such as associational susceptibility or defence within a community (Shinen et al., 2009). Feeding preferences can determine to a great extent, both the per individual and the total effect of predators on prey assemblages invaded by NIS. Thus how predators choose their diets and hunting efficiency are crucial to our understanding of predator–prey interactions, particularly with regard to stabilizing properties (Sih, 1987). Knowing whether or not predator behaviour is caused by preference might also help ecologists to understand how predator–prey interactions may be modulated by environmental changes (Jackson and Underwood, 2007).

Predator food preference is a combination of characteristics of both the predator and the prey traits (e.g., prey size, prey vulnerability, prey quality or profitability, handling time, availability or the past experience of the predator and prey) (Hughes and Dunkin, 1984a; López et al, 2010; Munari and Mistri, 2011). The vulnerability or ability of a prey species to avoid predation may be also conditioned by physical

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environmental conditions (Munari and Mistri, 2011; Sanford et al., 2014). In stressful environments, prey may be more vulnerable to predation if their response to attack is hindered or if their ability to find a refuge is reduced as a consequence of environmental stress (Tallqvist, 2001). For instance, oysters are more susceptible to predation by snails when exposed to increasing pCO_2 (Sanford et al., 2014).

Of the many environmental variables, temperature and pH are some of the most critical stressors in coastal systems, especially in estuarine environments (Halpern et al., 2008). If the current trajectory of global emissions continues, an increase of SST of more than 3 °C and a reduction in ocean pH by 0.3–0.4 units are expected by the end of this century (IPCC, 2013). The impacts of such changes are very variable and include from shifts in physiological and behavioural responses of species to changes in species interactions and distributions or even alterations of food webs (Munari and Mistri, 2011; Ries et al., 2009; Schiel et al., 2004). For instance, acidification could cause structural and compositional changes in shells of molluscs making them more vulnerable to predators (Tunnicliffe et al., 2009). Acidified seawater may also disrupt the capability of certain gastropods to express induced defences, increasing their vulnerability to predation (Bibby et al., 2007). If invasive species tend to be more tolerant to climatic change, then the per capita effects of predators on their native counterparts might increase as a consequence of stress experienced by native prey species (Sanford et al., 2014).

Mussels are organisms of commercial interest and provide key ecological services on rocky shores (e.g., ecosystem engineering, nutrient cycling, reduction of anthropogenic eutrophication) (Sousa et al., 2009). In several rias (sensu Vilas et al., 2005) along the Galician coast (NW of Spain) the intense commercial culture of *Mytilus galloprovincialis* (Lamarck, 1819) produces around 270.000 tonnes of mussels per year. In the Ria de Vigo, part of this production comes from the estuarine area where *M. galloprovincialis* co-occurs with the introduced black-pygmy mussel *Xenostrobus securis* (Lamarck, 1819) on rocky shores. These mussel populations suffer predation pressure by multiple species, being the dogwhelk *Nucella lapillus* (Linnaeus, 1758) and the crab *Carcinus maenas* (Linnaeus, 1758), two of the most abundant benthic predators (Gestoso et al., 2013). If native predators prefer the native over the invasive mussel, then invasion of *X. securis* might be indirectly facilitated by predators. Previous experimental work showed that *C. maenas* consumed more native than invasive mussels, probably due to differences in handling time and profitability between the two species (Veiga et al., 2011). As other muricids, dogwhelks drill holes in shells of their prey, usually either above the most nutritious or most easily accessible point of the shell (Morton, 2008 and references therein). Nevertheless, differences in shell shape of prey may determine prey preference by dogwhelks (López et al., 2010). Although previous observations have documented *M. galloprovincialis* and *X. securis* consumption by the dogwhelk *N. lapillus* in the inner part of the Galician Rias Baixas (Gestoso et al., 2014) no studies have experimentally evaluated the intensity of predation on the 2 prey species. Both prey species present different shell morphology and composition in terms of mineralogical compounds. Whereas *X. securis* has a subcylindrical shell with ventral arcuate margin and almost terminal umbones, *M. galloprovincialis* has an oval, subtriangular shell, with prominent umbones, pointed and slightly curved ventrally (Veiga et al., 2011). In addition, shells of *X. securis* are specially enriched in aragonite, whereas shells of *M. galloprovincialis* present a greater percentage of calcite (Gestoso et al. in prep.). Such differences may potentially influence predator feeding behaviour and susceptibility of prey (Carter et al., 1998; Elner and Hughes, 1978). Nevertheless, shell properties can be modified under environmental stress. Ocean acidification, particularly in combination with warming, increases the energetic costs of calcification and calcified structures may become thinner or weaker (Byrne and Przeslawski, 2013; Rodolfo-Metalpa et al., 2011). For example under these conditions, calcification of aragonite-enriched shells could be strongly affected since aragonite is more soluble than calcite (Gazeau et al. 2013). Reduced shell thickness or strength could decrease the effort or amount of time necessary for boring predators to penetrate mollusc shells and thus enhance susceptibility to predation. However, species display complex and divergent patterns of energy allocation to defences (i.e., shell properties) that may influence predator–prey interactions. Until now, interactions between predators and the two mussel prey exposed to warming and acidification have not yet been experimentally tested.

The aim of this study was to explore interactions between the predator *N. lapillus* and the two mussel prey, *M. galloprovincialis* and *X. securis*. Firstly, we evaluated if past environmental stress (i.e., decreasing pH and increasing temperature) affected predator choices and prey vulnerability. Secondly, we analysed feeding behaviour of *N. lapillus*. We used synthetic assemblages of different species composition that resembled mussel assemblages found on rocky shores of the inner part of Ria de Vigo. First, we exposed monospecific assemblages of each species to combined experimental conditions of increasing temperature and decreasing pH in mesocosms for 3 weeks. Then assemblages were placed on a rocky shore and were enclosed in cages with dogwhelks where they remained for 3 weeks.

2. Material and methods

2.1. Mesocosm system

Experimental setup was established using four 350-L PVC tanks, filled up with 1 μm filtered-seawater, renewed once a week. Each tank was equipped with its own mechanical and biological filter system. The whole setup was placed at the Laboratory of Coastal Biodiversity, at CIIMAR in Porto (Portugal) and received natural light under a 12/12 h light/dark photoperiod.

Climate change scenario was achieved by manipulating two climate-change factors, temperature and pH. The experimental set-up included two temperature levels (low: average ambient temperature of 16 °C and high: increased temperature of 21 °C, simulating a rise in temperature within the range predicted of 2 to 6.4 °C by 2099 (Sokolov et al., 2009) and two pH levels (ambient pH: 8 and reduced pH: 7.65) (Fig. 1A, B). Temperature in each tank was controlled with titanium aquarium chillers–heaters with UV sterilizer (TECO TC-15) and carbonate chemistry of seawater in the reduced pH treatments was manipulated by diffusing 100% CO_2 from a gas tank to the experimental tanks. The gas flux was controlled through a pH stat system (Aqua Medic AT Control) by opening or closing a solenoid valve when the pH readings in the experimental tanks deviate from the predetermined set points by 0.1 pH units. Submersible pumps (3000 L h^{-1}) located at the bottom of tanks ensured the diffusion of CO_2 and also facilitated water motion.

2.2. Environmental parameters in mesocosms

Temperature and pH were continuously monitored using probes and data-logger function of the controller. The pH electrodes were standardised against Tris seawater buffers (ionic strength of 0.7 M). Salinity was measured at least three times a week using a refractometer and water from each tank was sampled twice a week to analyse total dissolved inorganic carbon (TDIC). Each water sample was introduced into serum vials capped without head space after filtered through a 0.2 μm pore size glass microfiber filter. Samples were analysed with a Licor LI-7000 CO_2 analyzer within 3 days after collection, and TDIC was then partitioned into CO_2, bicarbonate, alkalinity, and carbonate from salinity, temperature and pH using the program csys.m (Zeebe and Wolf-Gladrow, 2001). As calcium salinity ratio in seawater is nearly conservative (Doney et al., 2009), calcium concentration was estimated from the salinity according to ion concentrations in seawater (Pilson, 2013). Saturation states of calcite (Ω_{ca}) and aragonite (Ω_{ara}) were calculated using the thermodynamic solubility product of calcite and