© 2015. Published by The Company of Biologists Ltd | The Journal of Experimental Biology (2015) 218, 2148-2151 doi:10.1242/jeb.117705

SHORT COMMUNICATION

Energy metabolism and cellular homeostasis trade-offs provide the basis for a new type of sensitivity to ocean acidification in a marine polychaete at a high-CO_2 vent: adenylate and phosphagen energy pools versus carbonic anhydrase

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ABSTRACT

Species distributions and ecology can often be explained by their physiological sensitivity to environmental conditions. Whilst we have a relatively good understanding of how these are shaped by temperature, for other emerging drivers, such as P_{CO_2} we know relatively little. The marine polychaete *Sabella spallanzanii* increases its metabolic rate when exposed to high P_{CO_2} conditions and remains absent from the CO_2 vent of Ischia. To understand new possible pathways of sensitivity to CO_2 in marine ectotherms, we examined the metabolic plasticity of *S. spallanzanii* exposed *in situ* to elevated P_{CO_2} by measuring fundamental metabolite and carbonic anhydrase concentrations. We show that whilst this species can survive elevated P_{CO_2} conditions in the short term, and exhibits an increase in energy metabolism, this is accompanied by a significant decrease in carbonic anhydrase concentration. These homeostatic changes are unlikely to be sustainable in the longer term, indicating *S. spallanzanii* may struggle with future high P_{CO_2} conditions.

KEY WORDS: Individual approach, P_{CO_2}, Climate change, Homeostatic capacity, Annelid, Mediterranean Sea

INTRODUCTION

An understanding of a species' ecophysiological limits helps us identify the reasons underpinning species and population processes over different spatial scales. Whilst we have a relatively good understanding of how species distributions are shaped by temperature (see Bozinovic et al., 2011), for other emerging environmental drivers, such as increasing seawater partial pressure of CO_2 (P_{CO_2}), which is causing the acidification of the oceans, we know relatively little (see Calosi et al., 2013; Kroeker et al., 2011; Maas et al., 2012). Shallow water, high CO_2 vents have been used as analogues to investigate the potential ecological and evolutionary implications of ocean acidification. In particular, at the CO_2 vent of Ischia the polychaete fauna have been characterised in relation to the venting activity (e.g. Kroeker et al., 2011). Based on their distribution patterns, species found inside and outside these naturally acidified areas can be considered to be either 'tolerant' (abundant both inside and outside the low pH/high P_{CO_2} areas) or 'sensitive' (found outside the vents in similar habitat). Tolerant species include those that are able to maintain their metabolic rate levels unchanged during acute exposure to elevated P_{CO_2}, thus maintaining their energy metabolism and metabolic scope levels. In comparison, sensitive species show extreme decreases or increases in metabolic rates, corresponding to an extreme decrease of aerobic metabolism and an increase in metabolic costs, respectively, with both responses probably leading to a substantial decrease in metabolic scope (see Calosi et al., 2013 and references therein). In general, species that are poor regulators of metabolic rate under high P_{CO_2} conditions have been shown to have lesser homeostatic control, with some undergoing metabolic depression (Melzner et al., 2009). The fan worm *Sabella spallanzanii* (Gmelin, 1791) (Sabellidae) is present in the waters around Ischia (including those near the vents; M.-C.G. and P.C., personal observation), being especially abundant in areas with high nutrient levels, e.g. harbours (Bocchetti et al., 2004). It is absent from the high venting areas, despite showing the ability to increase its metabolic rates when exposed *in situ* to high P_{CO_2} conditions (e.g. Calosi et al., 2013), and thus possibly maintain its metabolic scope, unless it undergoes a physiological trade-off between energy metabolism and other important functions (e.g. enzymatic activities, osmo-ionic or pH intracellular regulation). Thus, *S. spallanzanii* allows us to investigate the biochemical mechanism underpinning a type of sensitivity to high P_{CO_2} not connected to metabolic depression, which may contribute towards explaining the distribution of this polychaete around the CO_2 vent of Ischia.

To determine the extent to which the cellular physiological condition explains the sensitivity of *S. spallanzanii* to ocean acidification, we conducted *in situ* transplant experiments (e.g. Calosi et al., 2013), transferring specimens to either control pH/P_{CO_2} or low pH/high P_{CO_2} conditions, and examined the concentration of fundamental aerobic and anaerobic metabolites and of carbonic anhydrase. Carbonic anhydrase is an essential enzyme involved in an organism's acid–base and respiratory function (see Fehsenfeld et al., 2011), which are key to defining its tolerance to high P_{CO_2}. This approach allowed us to test for the effect of high P_{CO_2} on this species' biochemical metabolic responses, enabling us to unravel possible functional trade-offs among different traits, which may help explain its sensitivity. Our use of an 'individual approach' allowed us to examine the significance of inter-individual variation in the metabolic versus enzymatic responses, which may otherwise remain masked by using an independent samples analysis (see discussion on 'the golden mean' in Bennett, 1987). Furthermore, our study is the first to provide mechanistic evidence for an alternative metabolic pathway of sensitivity to high P_{CO_2} conditions, characterised by a significant reduction in metabolic rates and energy metabolism (e.g. Ivanina et al., 2013). This mechanism seems to be

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Received 1 December 2014; Accepted 11 May 2015