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Physiological responses of a population of *Sargassum vulgare* (Phaeophyceae) to high pCO_2/low pH: implications for its long-term distribution

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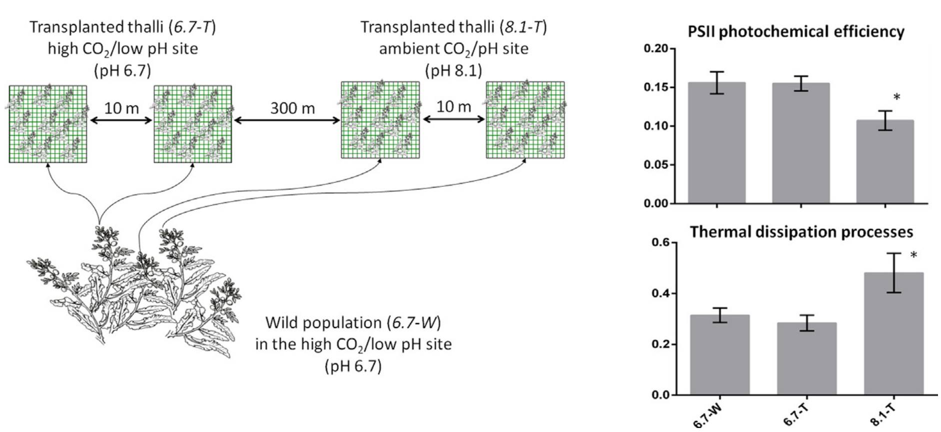
HIGHLIGHTS

- Long-term responses of species to ocean acidification are difficult to predict.
- CO_2 seeps may help to reveal adaptive strategies to cope with high CO_2/low pH.
- Photosynthetic performance and stress response were assessed on decadal exposure.
- Stress response and a decreased photochemistry was observed from pH 6.7 to 8.1.
- High pCO_2 allowed a rapid adaptation in a fast changing ocean pH.

GRAPHICAL ABSTRACT



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ABSTRACT

Ocean Acidification (OA) is likely to affect macroalgal diversity in the future with species-specific responses shaping macroalgal communities. In this framework, it is important to focus research on the photosynthetic response of habitat-forming species which have an important structural and functional role in coastal ecosystems. Most of the studies on the impacts of OA involve short-term laboratory or micro/mesocosm experiments. It is more challenging to assess the adaptive responses of macroalgal community to decreasing ocean pH over long-term periods, as they represent the basis of trophic dynamics in marine environments. This work aims to study the physiological traits of a population of *Sargassum vulgare* that lives naturally in the high pCO_2 vents system in Ischia (Italy), in order to predict the species behaviour in a possible OA future scenario. With this purpose, the photosynthetic performance of *S. vulgare* was studied in a wild, natural population living at low pH (6.7) as well as in a population transplanted from native (6.7) to ambient pH (8.1) for three weeks. The main results show that the photochemical activity and Rubisco expression decreased by 30% after transplanting, whereas the non-photochemical dissipation mechanisms and the photosynthetic pigment content increased by 50% and 40% respectively, in order to compensate for the decrease in photochemical efficiency at low pH. Our data indicated a stress condition for the *S. vulgare* population induced by pH variation, and therefore a reduced acclimation capability at different pH conditions. The decline of the PS_{II} maximum quantum yield (F_v/F_m) and the increase of PARP enzyme activity in transplanted thalli further supported this hypothesis. The absence of the species at ambient pH

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conditions close to the vent system, as well as the differences in physiological traits, suggest a local adaptation of *S. vulgare* at pH 6.7, through optimization of photosynthetic performance.

1. Introduction

Ocean acidification (OA) is an emerging threat for marine ecosystems. Atmospheric CO_2 uptake by the oceans is causing an unprecedented fast change in pH and carbon chemistry over the past 300 million years (Honisch et al., 2012; Turley et al., 2006). It has been estimated that between the years 1751 and 1994, surface ocean pH decreased from approximately 8.25 to 8.04, representing an increase of 30% in H^+ ion concentration in the world's oceans (Hall-Spencer et al., 2008). Future projections show that it will increase by 120% by 2100 (IPCC, 2007), equivalent to a reduction in pH of 0.4 units (Fabry et al., 2008; Meehl et al., 2007). At present, many studies have focused on the response of macroalgae to OA as they represent the most abundant primary producers along rocky shores (Mineur et al., 2015) and play a bottom-up control on coastal communities, supplying organic carbon to the food webs, contributing to nutrients recycling and providing habitat for larvae and other organisms (Cheminée et al., 2013; Duggins et al., 1989; Gattuso et al., 1998; Ritson-Williams et al., 2009; Xiao et al., 2015). An updated synthesis of the impacts of OA on marine biodiversity (Aze et al., 2014) as well as several studies find that a loss of 75% of the macroalgal biodiversity can be expected with OA (Baggini et al., 2014; Bellissimo et al., 2014; Porzio et al., 2011). Among macroalgae, Fucales (brown algae) are one of the most endangered groups due to their high sensitivity to pollution (Bianchi et al., 2014; Thibaut et al., 2015). It has been demonstrated that low pH limits growth and photosynthesis (Chen and Zou, 2014; Gutow et al., 2014) and can cause damage at tissue level (Israel and Hophy, 2002). Moreover, the ongoing decrease of ocean pH which modifies the equilibrium of inorganic carbon (DIC) dissolved species, could have a strong impact on photosynthesis that may be considered a useful indicator of environmental changes (Ashraf and Harris, 2013). In this framework, the ongoing decrease in ocean pH is modifying the equilibrium of inorganic carbon (DIC) dissolved species thus affecting photosynthesis. At current seawater pH, CO_2 is the less abundant compound among DIC species but forecasts of future conditions reveal that it will increase by at least 250% by 2100 (Koch et al., 2013), whereas the current most abundant DIC, HCO_3^-, will only increase by 24% (Fabry et al., 2008; Longphuirt et al., 2010).

At present, most of the knowledge on the physiological consequences of OA on macroalgae comes from short-term (i.e. days) or mid-term (i.e. weeks) laboratory- or mesocosm-based experiments focused on one or a few species (Riebesell and Gattuso, 2015; Widdicombe et al., 2010). Despite the great amount of studies investigating this issue, it is not easy to define an univocal growth and photosynthesis response of macroalgal species to OA (Egilsdottir et al., 2013; Gao et al., 1993; Gao and Zheng, 2010; Hall-Spencer et al., 2008; Israel and Hophy, 2002; Kuffner et al., 2008; Roleda et al., 2012; Zou and Gao, 2009). The species-specific response (Fabry et al., 2008; Harley et al., 2012; Koch et al., 2013; Xiao et al., 2015) as well as the different strategies of adaptation to local environmental conditions (e.g. light, temperature, wave motion) also contribute to this great variability. In addition, short-term experiments have limitations, where the stressful conditions for the tested organism s, may alter the final response (Widdicombe et al., 2010). In order to overcome many experimental constraints, natural high pCO_2/low pH vent sites are precious "natural facilities" to assess long-term responses (Munday et al., 2013) and physiological tolerances due to plasticity (Sunday et al., 2014) or adaptation (Hofmann et al., 2014).

Organisms in their own environment evolve a synergy of strategies in order to optimize the resources utilized and/or overcome unfavourable conditions. These mechanisms involve photochemical as well as biochemical strategies. In this paper we investigated long-term (decades) effects of OA on physiological traits of a natural population of the brown macroalga *Sargassum vulgare* (Phaeophyceae, Fucales) living in the high density CO_2 vent system of the Castello Aragonese off the Island of Ischia (Gulf of Naples, Italy) (Porzio et al., 2011). As *S. vulgare* is widespread in the most acidified zone (Porzio et al., 2011), in this location it represents a good model to assess the physiological mechanisms in a potential adaptation to decreased pH. In particular, we focused the attention on the partitioning of the absorbed light energy in photochemical and non-photochemical processes, the photosynthetic pigment content and the Rubisco expression. In addition, the occurrence of any oxidative stress induced by pH variation has been also evaluated analysing, for the first time in a macroalgal species, the expression and activity of the poly(ADP-ribose) polymerases (PARP) enzyme. Generally, PARP enzymes are indicators of DNA damage since they are involved in DNA repair (Amé et al., 2004; Hassa and Hottiger, 2008); it has been demonstrated in higher plants that PARP activity is finely modulated under oxidative stress (i.e. reactive oxygen species, ROS), cold, ionizing radiation and heavy metal stresses (Hassa and Hottiger, 2008; Arena et al., 2011, 2013, 2014).

In summary, the aims of the present study are: i) to assess the physiological performance and ii) the stress response of *S. vulgare* to chronic low pH exposure compared to current pH; iii) to discuss the different physiological response, if any, in relation to the presence/absence of the species along the gradient of acidification. We expect a higher photosynthetic performance of *S. vulgare* at low pH compared to current pH since higher pCO_2 may facilitate photochemistry and carbon fixation as found in other studies of brown algae (Betancor et al., 2014; Celis-Plá et al., 2015). On the other hand, we do not expect a stress response of *S. vulgare* at low pH since the population has lived at that conditions for decades. The different distribution of this species along the pH gradient (Porzio et al., 2011) has been discussed in the light of our results and hypothesis for relative short-term (i.e. decades) adaptation to OA.

This study will give new insights on mechanisms used in physiological plasticity/local adaptation and stress management of the habitat-forming *Sargassum vulgare*, and will contribute to our understanding of the ecological impacts driven by OA (Harley et al., 2012).

2. Material and methods

2.1. Study area

The study area is located around the Castello Aragonese (Island of Ischia, Italy) (40° 043.84′ N; 13° 57.08′ E). The site (a shallow coastal stretch line of 300 m long) is characterized by natural underwater CO_2 vents that produce a natural pH gradient (300 m long) from current (pH ~8.01) to lower (pH 6.7) values. The brown alga *Sargassum vulgare* occurs only at the lowest pH conditions, where it forms a conspicuous population (Porzio et al., 2011). Distribution and abundance of *Sargassum vulgare* in the study area were analysed from reworked data available from Porzio et al. (2011). Diversity index (H′) and evenness (E) were calculated for macroalgal communities at each pH conditions according to Boudouresque (1971).

2.2. Physico-chemical features

Physico-chemical characteristics as well as carbon chemistry of the study area have been assessed during summer 2009 (Rodolfo-Metalpa et al., 2011) and are summarized in Table A.1 in Appendices.