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Influence of ambient temperature on the photosynthetic activity and phenolic content of the intertidal *Cystoseira compressa* along the Italian coastline

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Abstract

Understanding the physiological responses of intertidal seaweeds to environmental factors is fundamental to characterize their local physiological adaptation and success in the face of climate change. We measured the photosynthetic activity and the total phenolic content of the intertidal alga *Cystoseira compressa* and explored their relationship with latitude or local ambient air and seawater temperatures. Our results show that, when submerged, the photosynthetic activity of *C. compressa* showed values typical for non-stressed thalli, and the seawater temperatures found across sites explained the variability of these values. We observed a decrease in the photosynthetic activity of *C. compressa* when exposed to air, compared to a submerged condition. This activity remained stationary up to 28 °C and then started to decrease with higher air temperatures. The total phenolic content of *C. compressa* at the end of low tide changed across the study sites from 0.12 to 0.53 % DW. Phenolic variability was explained by the long-term thermal water conditions experienced by the algae, rather than short-term variations encountered during tidal cycles. Overall, our results suggest a crucial role played by temperature in driving the physiological traits of the intertidal *C. compressa*.

Keywords Phaeophyta · *Cystoseira compressa* · Intertidal · Maximum quantum yield · Phenolic content · Seawater and air temperature

Introduction

Temperature acts as the main determinant for the distribution and physiological performance of marine organisms, especially in the intertidal zone where species regularly cope with the alternate influence of aquatic and aerial climatic regimes (Raffaelli and Hawkins 1996; Helmuth et al. 2006). Seaweeds living in this zone experience extreme conditions such as heatwaves, freezing with wide temperature fluctuations in the order of 10–30 °C due to the alternation of emersion and immersion (Davison and Pearson 1996; Helmuth and Hofmann 2001; Becker et al. 2009; Pereira et al. 2015). Although there is ample literature on the effects of temperature on the functional traits (i.e., growth and photosynthesis) of intertidal seaweeds (Colvard et al. 2014; Fernández et al. 2015), understanding the organisms' physiological response to temperature variations remains a fundamental goal in marine ecology.

Temperature is a major factor controlling the growth and photosynthetic rate of intertidal seaweeds (Eggert 2012). Whether seaweeds are submerged or emerged, their photosynthetic rates tend to increase with temperature until they reach a maximum and then decline rapidly near the upper critical temperatures (Bell 1993; Colvard et al. 2014). During low tide the increase of air temperatures can induce a rapid overheating and desiccation of

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macroalgae, affecting their dynamic photoinhibition and their photosynthetic recovery following re-immersion in seawater (Bell 1993; Gómez et al. 2004). These limitations are a direct consequence of high temperatures that decrease or even inactivate enzymatic activities of photosystem II (PSII) and other cellular components (Eggert 2012). Understanding how the photosynthetic activity of intertidal seaweeds responds to ambient temperature fluctuations is crucial to identify their thermal limits and to characterize their local adaptation and their success under the new conditions caused by climate change (Colvard et al. 2014).

High temperatures can also interfere with the photoprotective system of intertidal seaweeds, inhibiting the synthesis of phenolic compounds (Cruces et al. 2013, 2018). Phenolic compounds are primary and secondary metabolites that fulfill a broad range of physiological roles in terrestrial plants and macroalgae (Amsler and Fairhead 2005; Boudet 2007). In brown seaweeds, these compounds, mainly phlorotannins, are accumulated in large quantities (Ragan and Glombitza 1986). Phlorotannins act as herbivore deterrents (Amsler and Fairhead 2005), high PAR and UV screens (Abdala-Díaz et al. 2006; Gómez et al. 2016), and antibacterial agents (Bengtsson et al. 2010; Pérez et al. 2016; Messina et al. 2019). The content of phenolic compounds in brown seaweeds is species-specific (Connan et al. 2004; Mannino et al. 2014, 2017), and they change both spatially (Steinberg 1989; Van Alstyne et al. 1999; Connan et al. 2004; van Hees et al. 2017) and temporally according to environmental factors such as irradiance, UV, temperature, nutrients, and salinity (Arnold et al. 1995; Pavia and Toth 2000; Stiger et al. 2004; Connan et al. 2004, 2007; Abdala-Díaz et al. 2006; Swanson and Fox 2007; Parys et al. 2009; Kamiya et al. 2010; Mannino et al. 2014, 2016; Cruces et al. 2018). Although various studies reported the effects of irradiance on the phenolic content of intertidal seaweeds (Connan et al. 2004; Abdala-Díaz et al. 2006; Mannino et al. 2014), only few studies described the effects of both water (Ragan and Glombitza 1986; Mannino et al. 2014, 2016; Cruces et al. 2018) and air (Connan et al. 2007) temperatures on these compounds.

Here, we measured the photosynthetic activity and the total phenolic concentration of *Cystoseira compressa* (Esper) Gerloff and Nizamuddin (Fucales, Phaeophyceae) in the intertidal zone in eight sites around the Italian coastline and investigated their relationship with local temperatures along a latitudinal gradient. Specifically, we aimed to understand the variability of maximum quantum yield and total phenolic concentrations of *C. compressa* among the investigated sites. Then, we used a multiple linear regression analysis to asses if the variability observed was related to the latitudinal gradient or the local air and water temperatures collected at each site.

Materials and methods

Species and experimental design

We sampled *Cystoseria compressa* from the lower intertidal zone (from the mean sea level to shallow water of spring tides, ≈ 30 cm) at 8 study sites around the Italian coast between June and July 2013 (Fig. 1, Table S1). All sites were gently sloping to sub-vertical rocky platforms, typically suitable for the growth of *Cystoseira* spp. (Lasinio et al. 2017), and covered a broad latitudinal gradient where *C. compressa* could be found (Mancuso et al. 2018). *Cystoseira compressa* is one of the most widespread habitat-forming species of *Cystoseira* in the Mediterranean Sea, able to colonize the rocky shore from the infralittoral (max 40 m depth) to the intertidal zone in both exposed and sheltered places (Gómez-Garreta et al. 2002). In the intertidal zone, *C. compressa* remains one of the relatively common *Cystoseira* spp. along the shallow Italian coasts, where its ecological status explained by co-occurring anthropogenic and environmental stressors (Mancuso et al. 2018). Knowing the physiological responses of *C. compressa* to ambient air and water temperatures is crucial to understand how this alga could cope with novel environmental conditions.

At each site, during high tide, 6 individual thalli of *C. compressa* were collected and acclimated for 1 h in opaque plastic boxes ($40 \times 90 \times 30$ cm) opened on the top and filled with natural seawater. Water temperature was measured (±0.1 °C). After acclimation, we simulated the low tide by removing seawater from the plastic boxes. The plastic boxes were placed under stands provided with GreenPower LED lights supplying a constant light intensity (PAR) of 200 μmol quanta m^{-2} s^{-1}. This was necessary because variations in weather conditions (light intensity, clouds) among sites could interfere with the measurement of the effect of temperature on the fluorescence of *C. compressa*. The thalli of *C. compressa* were left at the ambient air temperature of each site for 3 h to simulate the condition of maximum air exposure typical of a day with high atmospheric pressure. The air temperature was monitored with thermometers (±0.1 °C) placed near the algal surfaces. Average temperature values were used in subsequent statistical analyses. After 3 h of air exposure, apical tissues of *C. compressa* (∼0.25 g wet weight, $n = 6$) were collected and stored (−20 °C) until phenolic compound concentration analyses were conducted. Thalli used in the experiment were labeled and stored (−20 °C) to measure wet (FW) and dry (DW) weight (±0.00001 g). Dry weight was measured after placing the thalli at 60 °C for 48 h. FW and DW were used to estimate phenolic concertation as a percentage of dry weight (see the "Total phenolic content" paragraph below for details).

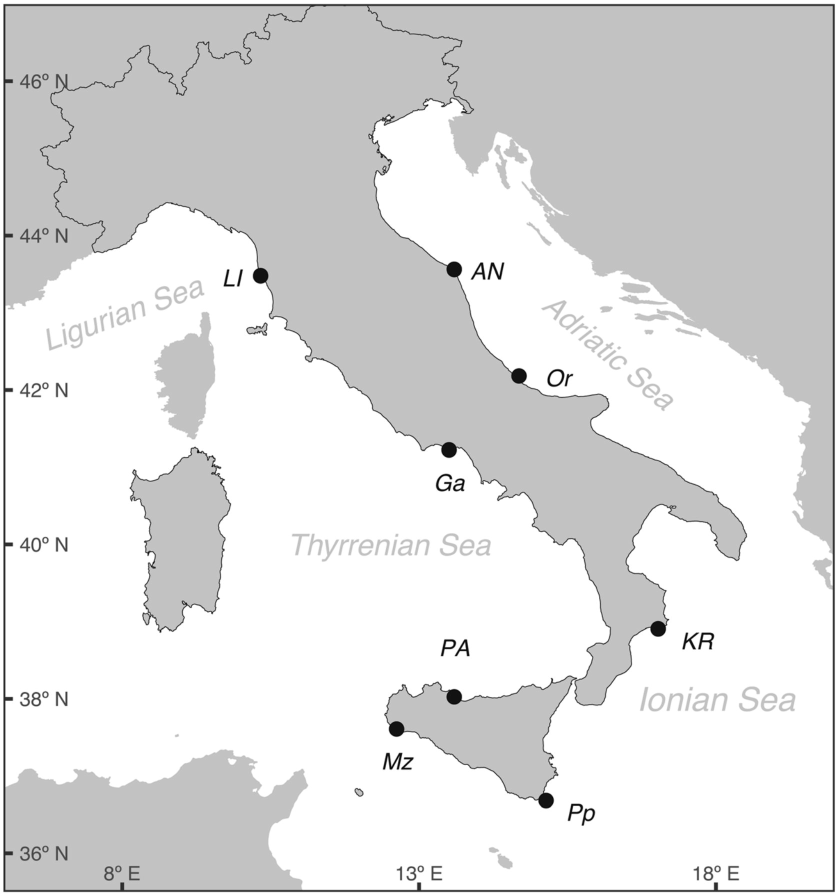

Fig. 1 Map of the 8 study sites (black dots) along the Italian coastline. AN, Ancona; LI, Livorno; Or, Ortona; Ga, Gaeta; KR, Crotone; PA, Palermo; Mz, Mazara del Vallo; Pp, Portopalo. Geographical coordinates reported in Table S1

In vivo chlorophyll fluorescence

The photosynthetic activity of *C. compressa* was quantified measuring in vivo chlorophyll *a* fluorescence of photosystem II (PSII) with a portable pulse amplitude modulation fluorometer (Diving-PAM, Waltz). We estimated the maximum quantum yield (F_v/F_m) before and at the end of air exposure. This parameter is a valuable indicator of physiological stress (Murchie and Lawson 2013), widely used to monitor temperature-induced changes of photosynthetic activity and tends to decrease with increasing temperatures (Bruhn and Gerard 1996; Eggert 2012; Pereira et al. 2015). Thalli of *C. compressa* were dark adapted for 30 min and the minimum (basal) fluorescence (F_o) was measured. Then, maximum fluorescence (F_m) was measured applying a saturation pulse (9000 μmol quanta m^{-2} s^{-1}, 800 ms) of actinic light and maximal quantum yield was calculated as $F_v/F_m = F_m{-}F_o/F_m$ (Murchie and Lawson 2013). For each thallus, three measures of F_v/F_m were taken randomly from the surface of *C. compressa*. The mean of the three values was used for the subsequent statistical analyses.

Total phenolic content

The total phenolic concentration (TPC) in the tissue of *C. compressa* was evaluated using a modified Abdala-Díaz protocol (Abdala-Díaz et al. 2006). Samples mass were homogenized for 3 min in Ultra-Turrax with 80% (*v*/*v*) methanol (1:5). The mixture was centrifuged (1000× *g* for 30 min at 4 °C) and the supernatant was collected and stored at − 20 °C. The residual matrix was extracted incubating the samples with another volume of 80% (*v*/*v*) methanol overnight at room temperature, continuously agitated. This second fraction was centrifuged (1000× *g* for 30 min at 4 °C), the supernatant added back to the first fraction and stored at − 20 °C. Total phenolic compounds were determined according to the Folin-Ciolcateau method (Folin and Ciocalteau 1927). Briefly, 50 μL of extract, 500 μL of ethanol (VWR chemicals), and 250 μL of the Folin-Ciocalteu reagent (VWR chemicals, diluted 1:1 with ethanol) were diluted to 3 mL with ultrapure distilled water (Simpak2, Millipore). The solutions were mixed and incubated for 5 min at room temperature in the dark. The reaction was stopped adding 500 μL of 5% Na_2CO_3 to each tube; samples were again incubated for 1 h at room temperature, in the dark. The absorbance was recorded at 725 nm using a UV/Vis spectrophotometer (Varian Cary 50 Scan). Total phenolic compounds were quantified using the standard curve of gallic acid (Sigma Aldrich) and expressed as milligram of gallic acid equivalents per gram of dry weight of algal tissue (mg GAE g^{-1} DW) after the determination of the wet to dry ratio in the tissue for each collected thallus. These values were converted to a percentage of dry weight (% DW) dividing values by 10.

Statistical analysis

Multiple linear regression (MLR) analysis was applied to assess the importance of latitude, water, and air temperatures on the F_v/F_m and TPC of *C. compressa*. We performed a partial *F* test to select the most parsimonious model that could explain the variability of the F_v/F_m and TPC in *C. compressa* comparing a full model (with all terms) with reduced models (obtained dropping one different term of the model each iteration). Diagnostic plots and formal tests were used to check the MLR assumptions. Data were graphically explored for outliers and we applied Shapiro-Wilk and Breusch-Pagan tests to check the assumptions of normality and homoscedasticity, respectively. If a non-linear relationship between response and depended variables were detected, we examined the significance of applying a quadratic term in the model (but report both the linear and non-linear interactions in Supplementary Materials). All analyses were performed with R software 3.5.1 (R Core Team 2018). See "Data availability and reproducible research" section below for further details.

Data availability and reproducible research The repository with all the data and the scripts used to reproduce the research in this paper is available at https://doi.org/10.17632/xfvykctgp6.1.

Results

The 8 study sites spanned 7° of latitude representing a variety of environmental conditions around the Italian peninsula (Fig. 1, Table S1). Air and water temperatures varied across the study sites (Table S1). Seawater temperatures measured across the sites ranged from 22 °C in *LI* and *Mz* to 27.7 °C in *Or*, while average air temperature during low tide varied from 24.5 °C in *Ga* to 31.5 °C in *KR* (Table S1). There was no significant correlation between latitude and water temperature (Pearson cor. = − 0.12, $p > 0.05$), although temperature tended to decrease at higher latitudes (Fig. S1a), while air temperature decreased significantly (Pearson cor. = − 0.49, $p < 0.05$) with latitude (Fig. S1b).

In vivo chlorophyll fluorescence

When *C. compressa* was submerged, maximum quantum yield (F_v/F_m) ranged from 0.56 ± 0.02 at *PA* to 0.73 ± 0.01 at *Or*, with the majority of the sites above 0.64 (Table S2, Fig. 2). Model selection revealed that these values were significantly explained by the increasing water temperature across the sites, with higher F_v/F_m values at 28 °C. However, the correlation was a very week to support any kind of trend (Linear regression, adj. $r^2 = 0.06$, $F_{(1,44)} = 4.044$, $p < 0.05$, Fig. 3).

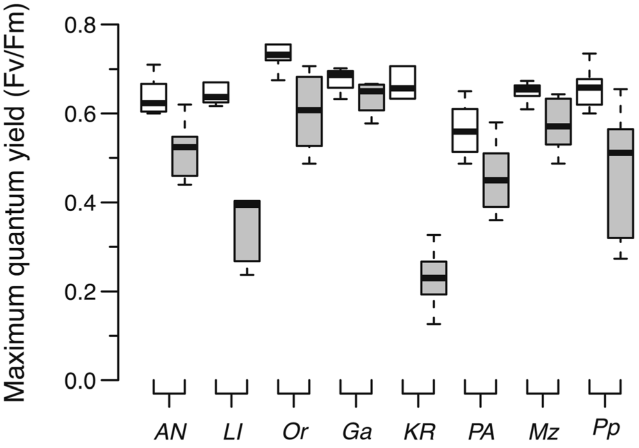

Fig. 2 Maximum quantum yield (F_v/F_m) of *C. compressa* before (white boxes) and after 3 h of air exposure (gray boxes) across the 8 study sites. Site acronyms as in Fig. 1. Boxplots show extreme and lower whisker (dashed line), lower and upper quartile (box), and median (black line)

After exposure to air, *C. compressa* showed a decrease of F_v/F_m with values ranging from 0.23 at KR to 0.64 at Ga, corresponding to a percentage decrease in photosynthetic activity ranged from 6 (Ga) to 66% (KR) compared to submerged condition (Fig. 2, Table S2). The decrease of F_v/F_m in *C. compressa* was related to the increasing average air temperatures experienced during the 3-h emersion (Linear regression, adj. $r^2 = 0.42$, $F_{(2,43)} = 17.298$, $p < 0.01$, Table S4, Fig. 4). In particular, F_v/F_m remained stationary until 28 °C and then started to decrease with higher air temperatures (Fig. 4).

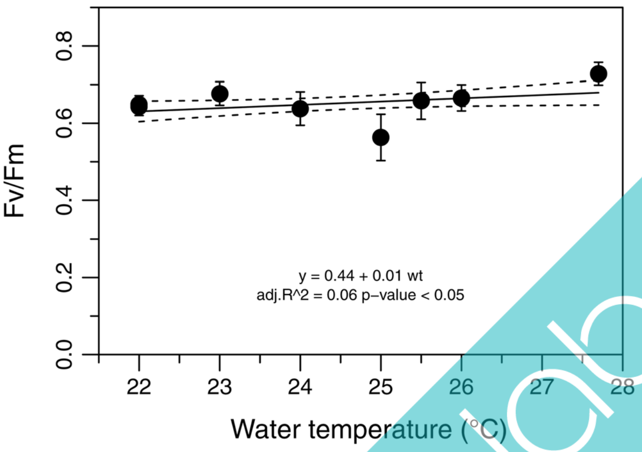

Fig. 3 Relationship between maximum quantum yield (F_v/F_m) of *C. compressa* and average seawater temperatures before the emersion phase. Values are mean ± 1 SD ($n = 4$–6). Solid and dashed black lines are respectively linear model fits across all sites and confidence interval (95%)

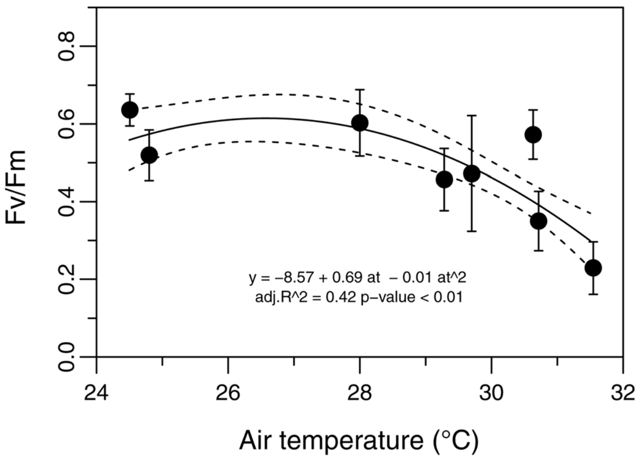

Fig. 4 Relationship between maximum quantum yield (F_v/F_m) of *C. compressa* and the average ambient air temperatures experienced during 3-h emersion. Values are mean ± 1SD ($n = 4$–6). Solid and dashed black lines are respectively quadratic model fits across all sites and confidence interval (95%)

Total phenolic compounds

The TPC in *C. compressa* at the end of low tide ranged, on average, from 0.12 ± 0.02% DW at *PA* to 0.53 ± 0.05% DW at *Or* (Table S3, Fig. 5). Sites showed low variability in the TPC values between replicates, apart from some outliers at AN, LI, Mz, and Pp (Fig. 5). The variability of the TPC in *C. compressa* after 3 h of air exposure was explained by increasing water temperatures across sites (linear regression, adj. $r^2 = 0.66$, $F_{(2,39)} = 40.459$, $p < 0.01$, Table S5, Fig. 6), with the higher TPC values at 28 °C (Fig. 6).

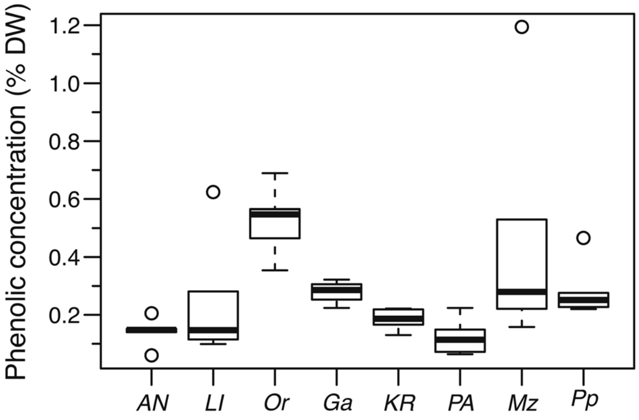

Fig. 5 Total phenolic content as % dry weight (TPC % DW) of *C. compressa* across the 8 study locations. Sites are ordered by high to low latitude from left to right. Site acronyms as in Fig. 1. Boxplots show extreme and lower whisker (dashed line), lower and upper quartile (box), median (black line), and outliers (white circles)

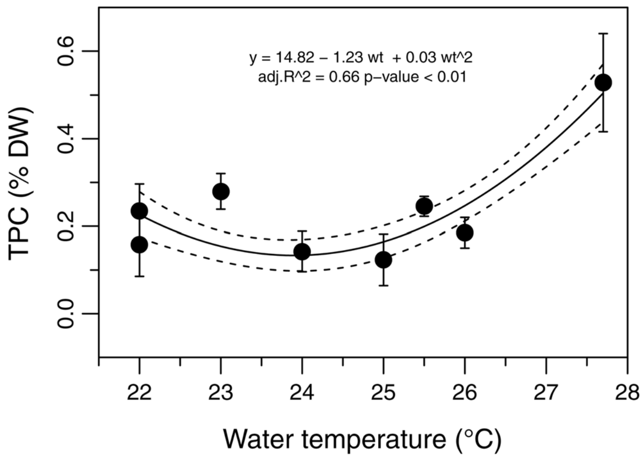

Fig. 6 Relationship between the total phenolic content as % dry weight (TPC % DW) of *C. compressa* and the seawater temperature found across sites. Values are mean ± 1 SD ($n = 4$–6). Solid and dashed black lines are respectively quadratic model fits across all sites and confidence interval (95%)

Discussion

We measured the maximum quantum yield and the total phenolic content of intertidal *C. compressa* in eight sites around the Italian coastline and explored their relationships with latitude and both water and air temperatures. We observed that the F_v/F_m of *C. compressa* was lower when the thalli were exposed to air compared to the submerged condition. The variability in F_v/F_m of *C. compressa* was explained by seawater temperature when the thalli were submerged and to air temperature when exposed to air. We also found that the phenolic content in *C. compressa* was related to increasing seawater temperature, rather than the air temperature experienced during low tide.

In vivo chlorophyll fluorescence

In this study, when submerged, the photosynthetic activity of *C. compressa* across sites was comparable to that of non-stressed tissue of other intertidal *Cystoseira* (Abdala-Díaz et al. 2006; Celis-Plá et al. 2014). The variability of F_v/F_m when submerged was related to the seawater temperature found across sites with higher values found at 28 °C. This result is consistent with what observed by Baghdadli et al. (1990) on *Cystoseira barbata*, who found maximum net photosynthesis between 20 and 30 °C of water temperature. Moreover, Mannino et al. (2016) reported no evident signals of suffering on *Cystoseira amentacea* when exposed at a water temperature of 25 or 30 °C. Then, our results led to the hypothesis that the thalli of *C. compressa* investigated in this study were adapted to the local water temperatures measured at each site. We also found that the photosynthetic activity of

C. compressa exposed to air was lower than when submerged and this was supported by other studies (Williams and Dethier 2005). At the end of low tide, the F_v/F_m of *C. compressa* remained constant until 28 °C, beyond which it began to decrease. We were not able to find other studies analyzing the effect of air temperature on intertidal *Cystoseira* to directly compare our results. However, Bell (1993) reported a similar response on the net photosynthesis of the intertidal red alga *Mastocarpus papillatus* that was strongly dependent on air temperature during emersion, generally increasing from 15 to 30 °C, and then sharply dropping at 35 °C. The author also reported the relevant role of desiccation, highlighting that emerged photosynthesis appeared to be depressed when thalli were fully hydrated (Bell 1993). However, our study lacks data about the desiccation rate of *C. compressa*.

Total phenolic content

The TPC of *C. compressa* found across our study sites was comparable with those reported in previous studies for intertidal *Cystoseira* species (Abdala-Díaz et al. 2006; Mannino et al. 2014, 2016, 2017). Phenolic content in brown algae has been observed to change across multiple spatial scales (Connan et al. 2007; van Hees et al. 2017). Concentrations of phenolic compounds produced by macroalgae changed along a latitudinal gradient or among different geographical regions (Steinberg 1989; Van Alstyne et al. 1999; van Hees et al. 2017). At a smaller scale, as in the intertidal zone, the phenolic contents appeared to be related to the location of the algae, with higher values found closer to the upper margin of this zone (Connan et al. 2007). In our study, the variability in the TPC of *C. compressa* was not related to latitude, probably because the latitudinal range investigated was too small to detect significant variations in the TPC of the alga. In fact, studies reporting a significant effect of latitude investigated larger latitudinal gradients covering temperate and tropical regions (Steinberg 1989; Van Alstyne et al. 1999; van Hees et al. 2017). We observed that water temperature, rather than air temperature experienced during 3 h of emersion, explained the variability in the TPC of *C. compressa* across sites. The synthesis of phenolic compounds in intertidal seaweeds has been related with increasing seawater or air temperatures (Ragan and Glombitza 1986; Connan et al. 2007; Mannino et al. 2014), although the results were controversial. For example, Mannino et al. (2014) showed that the phenolic content of the intertidal *C. amentacea* increased with increasing seawater temperature, with lower values observed in winter. However, the same authors reported a complete opposite relationship of TPC for the same species, with higher values in winter-spring and lower in summer-autumn (Mannino et al. 2016). Short-term variation in the TPC of intertidal seaweeds has also shown a positive relationship with increasing air temperature during low tide (Connan et al. 2007). Our results led to the hypothesis that the TPC in *C. compressa* was affected by the long-term thermal seawater conditions experienced by the algae, rather than short-term variations encountered during tidal cycles.

Conclusions

Overall, our results suggest a crucial role played by temperature in driving physiological responses of the intertidal *C. compressa*. Knowing how seaweeds respond to ambient temperature variations can help our understanding on how these algae could cope with novel environmental conditions (Colvard et al. 2014), especially in the intertidal zone where they face multiple human and environmental stressors (Sarà et al. 2014). Although our study provides information about some physiological responses of the intertidal *C. compressa* to ambient air and water temperatures, we were unable to compare our results with others due to the lack of published peer-reviewed literature. There is a need to determine the physiological temperature-response curves of *C. compressa* in water and air conditions. These physiological responses should not only include the photosynthetic rates but also other relevant responses such as TPC or the heat-shock proteins of the algae. Further experiments are also necessary to gain insight into the relationship between the TPC of *C. compressa* and temperature as well as the interaction with other abiotic factors such as irradiation and UV.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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