

Abundance of the sponge *Hymeniacion* cf. *perlevis* in a stressful environment of Patagonia: relationships with *Ulva lactuca* and physical variables

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Understanding the variables (biotic or abiotic) controlling coastal communities is the main goal of ecology research and it is crucial to predict how communities will evolve under the increasing pressure on coastal systems by human activities. The general aims of this study were to assess the variables affecting the distribution of the fast-growing sponge Hymeniacion cf. perlevis, and to evaluate if physical stressful conditions have an influence in the relationship between Hymeniacion and the sea lettuce Ulva lactuca. Specifically, the aims were to evaluate the abundance patterns of Hymeniacion and Ulva and to assess the relationship of Ulva and physical variables on the abundance of Hymeniacion at both intertidal and subtidal. Hymeniacion and Ulva showed opposite abundance patterns. Hymeniacion was more abundant in sites without Ulva, and negatively correlated with Ulva abundance at both heights. Intertidal Hymeniacion abundance was not correlated with physical variables, but subtidal Hymeniacion was.

Keywords: sponges, macroalgae, negative relationship, physical variables, distribution pattern, intertidal-subtidal heights

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INTRODUCTION

Sponges are important components of low intertidal and subtidal communities from tropical to polar environments (Bell, 2008a). They provide diverse ecosystem services, such as the uptake of nitrogen and carbon dioxide by their symbionts, the production of biologically active metabolites, and an efficient filtering capacity (Reiswig, 1971; Hay, 1996; Pile *et al.*, 1996; Díaz & Ward, 1997). They also perform several ecological roles including the provision of shelter or food for other organisms or as agents of biological disturbance due to the seasonal growth and regression of sponge tissues that create free space for other inferior competitive organisms (Wulff, 2006; Abdo, 2007; Bell, 2008a).

Many sponges show spatial and temporal variation in their abundance pattern that may be related to abiotic factors such as depth, sedimentation, nutrient concentration, solar radiation, salinity, substrate type and inclination (Palacios, 1978; Jokiel, 1980; Wilkinson & Evans, 1989; Bell & Barnes, 2000; Maldonado *et al.*, 2008) as well as biotic factors including competition, predation and food availability (Trussell *et al.*, 2006; Wulff, 2006, 2012). Due to the increasing nutrients load in coastal systems, algae and sponges have increased

their abundance (Valiela *et al.*, 1997; Bell, 2008b) and, consequently, the study of their interaction has grown. While some studies suggest positive interactions between macroalgae and sponges (e.g. Palumbi, 1985; Ávila *et al.*, 2010), others have reported negative interactions such as reduction of the sponge lateral growth due to the contact with algae or due to a shading effect (Freeman & Thacker, 2011; González-Rivero *et al.*, 2012).

Less attention has been paid to the factors affecting growth and abundance of sponges in intertidal and other relatively harsh habitats. Desiccation is one of the most important abiotic factors affecting species distribution and community structure in intertidal habitats (e.g. Bertness *et al.*, 2006; Daleo *et al.*, 2006). In stressful environments, positive interactions may play a significant role in structuring communities, as a consequence of the ability of some species to ameliorate the stress factors of these habitats (Bertness & Callaway, 1994; Bertness *et al.*, 1999; Bruno *et al.*, 2003). For example, in rocky intertidals of the SE Pacific coast, some macroalgae improve water retention under their canopies during low tide, showing positive associations with other macroalgae in the upper intertidal (Molina-Montenegro *et al.*, 2005). Understanding which variables affect coastal community composition and abundances and the relationships of their most conspicuous components, will allow us to predict how these communities will evolve under the increasing anthropogenic impact of coastal systems (e.g. high nutrient loads, pollution, species removal) and to provide specific information

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for implementing conservation measures. Thus, the general aims of this study were to assess the biotic and abiotic variables that affect the distribution of the fast-growing massive sponge *Hymeniacidon* cf. *perlevis* Montagu 1814, and to assess if harsh conditions influence the relationship between *Hymeniacidon* and the fast-growing macroalgae *Ulva lactuca* Linnaeus 1753. Specifically, we evaluated the abundance pattern of *Hymeniacidon* and *Ulva*. We also assessed the relationship between *Ulva* and some physical variables on the abundance of *Hymeniacidon* at both intertidal and shallow subtidal. In this context, we predicted (1) a positive correlation between the cover of *Hymeniacidon* and *Ulva* in the intertidal but negative correlation between them in the relatively more benign subtidal; (2) strong correlations between the intertidal *Hymeniacidon* cover and some physical variables but weak or no correlations between the subtidal *Hymeniacidon* cover and physical variables.

MATERIALS AND METHODS

Study site

The study was conducted at San Antonio Bay, northern Patagonia ($40^{\circ}46'S$ $64^{\circ}54'W$), an 80 km^2 body of marine water affected by a semidiurnal macrotidal regime (up to 9 m tidal amplitude, see Daleo *et al.*, 2006; Martinetto *et al.*, 2010, 2011). The extensive intertidal is mainly composed of mud, sand and pebble flats (Figure 1) and, given the geomorphology of the bay, the low intertidal remains exposed up to 5 h every low tide (MG personal observation). The bay is a hypersaline system, due to the low average precipitation (250 mm year^{-1}). The mean annual atmospheric temperature is 15.1°C , with extreme temperatures occurring in July (austral winter) and February (austral summer, -7.7 and 41.4°C , respectively). The humidity is 57% and the annual average wind speed is 18 km h^{-1} , reaching an average of 25 km h^{-1} in spring-summer (Lucas *et al.*, 2005; Genchi *et al.*, 2010; González *et al.*, 2010). San Antonio Bay is also subject to high anthropogenic N loading (Teichberg *et al.*, 2010) since the main freshwater input is nitrogen-rich groundwater introduced via the septic system from the nearby city of San Antonio Oeste, which affects an inner channel that runs beside the city (see Martinetto *et al.*, 2010, 2011). In this bay, *Hymeniacidon* cf. *perlevis*, with a cushion-shaped morphology, short papillae, small digitations emerging from its surface, and orange to yellow colour, is a common and abundant sponge that occurs in the intertidal and subtidal. It is able to feed on a wide variety of particulate sources, including microbes such as *Escherichia coli* (Fu *et al.*, 2006; Maldonado *et al.*, 2012). *Ulva lactuca* is the most conspicuous macroalga of this system, which in San Antonio Bay can reach a growth rate up to $20\text{--}25\% \text{ day}^{-1}$ (see Martinetto *et al.*, 2011). Previous observations show that both *Hymeniacidon* and *Ulva* inhabit the intertidal and the entire subtidal of the shallow inner channel that runs beside the city (that reaches a depth of 0.5 m).

Relationship between *Hymeniacidon* and *Ulva*

To describe the seasonal variation in the abundance of *Hymeniacidon* and *Ulva* (per cent cover), we performed seasonal samplings from February 2012 to December 2013, at



Fig. 1. Intertidal zone of San Antonio Bay, northern Patagonia (top). The sponge *Hymeniacidon* cf. *perlevis* and the green alga *Ulva lactuca* occur both in the intertidal and the shallow subtidal (bottom).

two heights: the intertidal, an extensive zone with low slope where the variation in exposure time was minimal between sampling areas; and the subtidal, with 0.5 m depth that is the maximum depth during low tide. The number of samplings varied according to weather conditions. In the intertidal, we performed a total of 29 samplings along the 2-year period (2012: 3 samplings in summer, 3 in autumn, 5 in winter and 4 in spring; 2013: 4 in summer, 3 in autumn, 2 in winter and 4 in spring). Meanwhile at the subtidal we performed a total of 27 samplings along the period (2012: 2 samplings in summer, 3 in autumn, 5 in winter and 4 in spring; 2013: 4 in summer, 3 in autumn, 2 in winter and 4 in spring). At each height, 10 quadrats (0.25 m^2) were randomly placed on the substrate along a transect parallel to the water-line, where *Hymeniacidon* and *Ulva* were both present, and photographed with a Cannon[®] Powershot D20 (75 cm from the bottom approximately). For each quadrat, two photographs were obtained (one of *Ulva* canopy and another of the substrate after removing the *Ulva* canopy). Digital photographs were used to measure the per cent cover of *Ulva* and *Hymeniacidon* with the ImageJ software (Rasband, 1997–2014; <http://rsb.info.nih.gov/ij/download.html>) by manual drawing of the surface area. In addition, to assess *Hymeniacidon* abundance outside *Ulva* canopy, 10 quadrats were placed and photographed at each tidal height, in sites where *Ulva* was absent.

Physical variables

Atmospheric and seawater temperatures ($^{\circ}\text{C}$), wind speed (km h^{-1}), rainfall (mm), solar ultraviolet radiation (UV, 400–280 nm, expressed as $\text{kJ m}^{-2} \text{day}^{-1}$) and photosynthetically active radiation (PAR, 700–400 nm, expressed as $\text{kJ m}^{-2} \text{day}^{-1}$) were used as physical variables to correlate with the cover of *Hymeniacidon* in sites without *Ulva*. Physical variables were measured every 3 h and then averaged for 1 week. Data for the 2-year study period were obtained from the weather stations of the National Meteorological Service (<http://www.smn.gov.ar/>) and the Photobiological Station of Playa Unión (<http://www.efpu.org.ar/>). Seawater temperature was measured every 90 min with three dataloggers (Thermo Button) permanently submerged in different points of the inner channel of San Antonio Bay.

To examine differences in desiccation we placed water-saturated artificial sponges (3 cm side squared pieces of plastic foam) inside and outside the *Ulva* canopy ($N = 20$ per treatment) in the intertidal during the low tide (*sensu* Bertness *et al.*, 1999). Artificial sponges were collected just before the incoming tide and desiccation was calculated as the difference in initial and final water masses divided by the time the sponges remained deployed (g min^{-1}). Inside the canopy, artificial sponges were placed below a plastic frame (a small ring of 5 cm in diameter with 3 legs of 4 cm height) to avoid water transfer from *Ulva* to the artificial sponges. These frames were assumed not to affect the temperature surrounding the artificial sponges. The same experiment was replicated twice for each season in 2012.

Data analyses

Per cent cover data of *Hymeniacidon* obtained for each tidal height was grouped by season for further analyses. Differences in mean per cent cover of *Hymeniacidon* were

tested with a factorial two-way ANOVA (Zar, 1999), with season and presence of *Ulva* as main factors. Cover data were fourth root transformed to meet the assumptions of parametric statistics. Post hoc comparisons were performed using LSD test. To analyse the relationships between covers of *Hymeniacidon* and *Ulva*, and between *Hymeniacidon* cover and the physical variables, Spearman correlation tests (r_s) were used (non-parametric tests were used since assumptions were not met for *Ulva* cover after data transformation). Mean desiccation rates were compared with a two-way ANOVA (Zar, 1999), with seasons and presence of *Ulva* as main factors. LSD test was used for post hoc comparisons.

RESULTS

Relationship between *Hymeniacidon* and *Ulva*

Hymeniacidon cf. perlevis and *Ulva lactuca* showed seasonal variation at both tidal heights over the 2-year period (Figure 2). During cover peaks, *Ulva* always had higher cover than *Hymeniacidon*. Cover of *Hymeniacidon* differed between tidal heights with maximum cover approximately double in the subtidal that in the intertidal ($t = -17.86$, $df = 558$, $P < 0.01$).

Cover patterns of *Hymeniacidon* and *Ulva* were opposite. For example at the intertidal (Figure 2 top panel), while *Hymeniacidon* reached the highest cover in autumn (201 ± 113 and $103 \pm 75 \text{ cm}^2$ in 2012 and 2013, respectively), *Ulva* presented the lowest cover (274 ± 165 and $885 \pm 374 \text{ cm}^2$, respectively), then *Hymeniacidon* decreased up to spring when *Ulva* peaked (28 ± 36 and $37 \pm 39 \text{ cm}^2$ and 2301 ± 156 and $2320 \pm 348 \text{ cm}^2$, for *Hymeniacidon* and *Ulva*, respectively). Similarly, at the subtidal (Figure 2 bottom panel) *Hymeniacidon* cover peaked in autumn and persisted during the winter (550 ± 366 and $218 \pm 206 \text{ cm}^2$ and

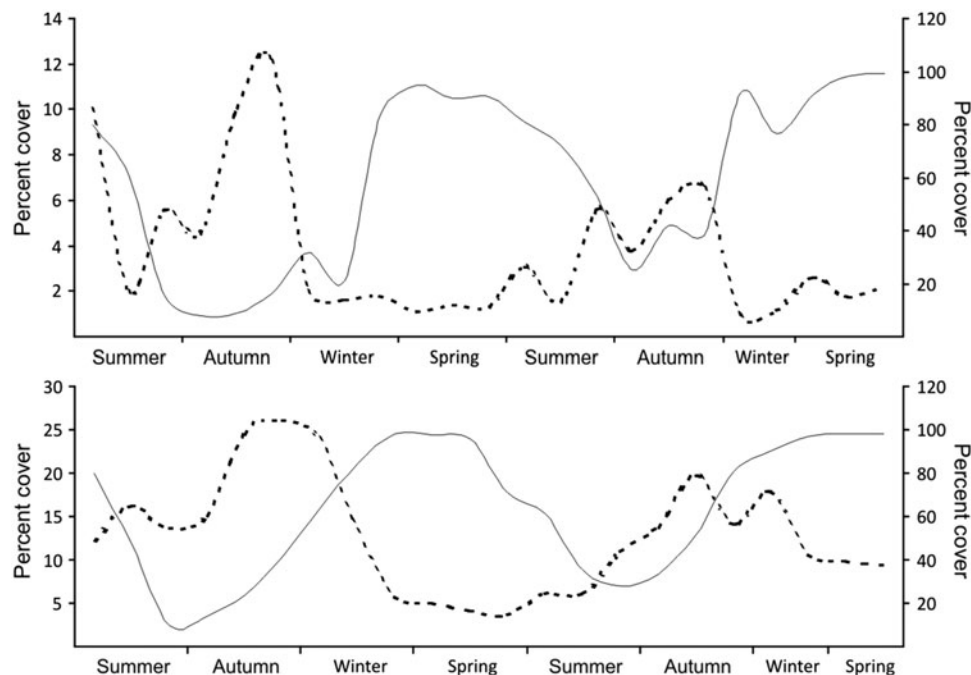


Fig. 2. Per cent cover of *Hymeniacidon cf. perlevis* (dashed line, left axis) and *U. lactuca* (solid line, right axis) during 2 year in the intertidal (top panel) and the subtidal (bottom panel). Note the different scale of y-axes.

395 ± 320 and 132 ± 133 cm², for both in 2012 and 2013, respectively) when *Ulva* cover was scarce (395 ± 245 and 939 ± 403 cm², respectively), and reached the lowest cover when *Ulva* cover peaked, in spring (72 ± 65 and 89 ± 95 cm² and 2424 ± 73 and 2410 ± 115 cm², for *Hymeniacion* and *Ulva*, respectively).

In sites without *Ulva*, *Hymeniacion* cover peaked in autumn at the intertidal (223 ± 131 cm² in 2012 and 135 ± 97 cm² in 2013) and in autumn and winter at the subtidal (445 ± 245 and 370 ± 320 cm² and 524 ± 352 and 399 ± 238 cm², for the both seasons in 2012 and 2013, respectively). The lowest cover was observed in spring both in the intertidal (36 ± 31 and 42 ± 47 cm² for both years, respectively) and the subtidal (115 ± 103 and 254 ± 195 cm², respectively).

At the intertidal, *Hymeniacion* cover differed between seasons and sites. *Hymeniacion* cover was the highest in autumn ($F_{3, 572} = 81.9$, $P < 0.01$, LSD test) and in sites without *Ulva* ($F_{1, 572} = 16.9$, $P < 0.01$, LSD test; Figure 3A). At the subtidal, an interaction between seasons and sites was found ($F_{3, 572} = 1.2$, $P < 0.01$, Figure 3B). *Hymeniacion* cover was lower in sites with *Ulva* in winter and spring, and

did not differ between sites for the remaining seasons (LSD test). The Spearman (r_s) coefficient showed a relatively strong and negative correlation between *Ulva* and *Hymeniacion* in sites with *Ulva* at both tidal heights ($r_s = -0.66$, $P < 0.01$ and $r_s = -0.78$, $P < 0.01$, respectively).

Relationships between *Hymeniacion* and physical variables

Striking seasonal variations were found in the physical variables over the study period (Figure 4). UV and PAR radiations showed a seasonal pattern, peaking in spring-summer (from 994 to 1162 kJ m⁻² day⁻¹ for UV and from 6748 to 9105 kJ m⁻² day⁻¹ for PAR, Figure 4A). Atmospheric and seawater temperatures showed a similar pattern, varying over seasons, with higher values in midsummer (February, up to 38.5 and 28°C for atmospheric and seawater temperatures, respectively) and lower in winter (August, up to 5°C, Figure 4B). Rainfalls were higher in summer and lower in spring (32 and 4 mm, respectively; Figure 4C). Summer and spring were the windiest seasons over the whole study period with peaks over 63 km h⁻¹. Overall, all seasons showed relatively strong winds (Figure 4D).

In the intertidal, *Hymeniacion* cover was not correlated with any of the physical variables considered (UV: $r_s = -0.31$; PAR: $r_s = -0.33$; atmospheric temperature: $r_s = 0.06$; seawater temperature: $r_s = 0.05$; rainfall: $r_s = 0.11$; wind: $r_s = -0.13$, $P > 0.05$ for all). At the subtidal, *Hymeniacion* cover showed negative correlations with UV radiation ($r_s = -0.832$, $P < 0.05$), PAR radiation ($r_s = -0.831$, $P < 0.05$) and water temperature ($r_s = -0.68$, $P < 0.05$).

An interaction between factors was found for desiccation in the intertidal ($F_{3,232} = 4.2$, $P < 0.05$). The highest desiccation was observed in U- in summer, followed by U- in spring, autumn and winter. Desiccation at U- in winter was similar to that at U+ in summer, and then U+ in spring, autumn and winter (Figure 5).

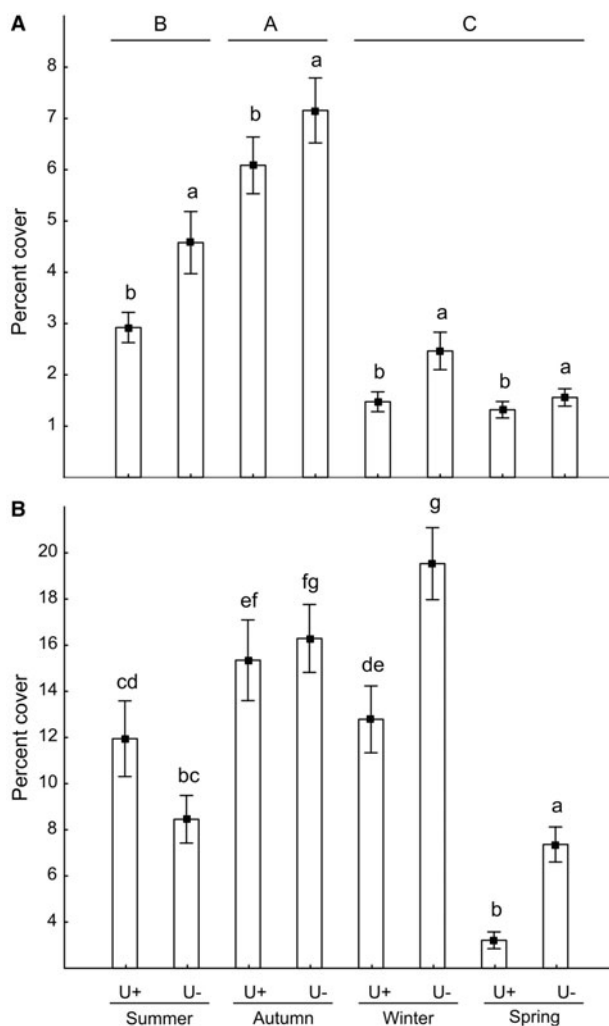


Fig. 3. Per cent cover of *Hymeniacion* cf. *perlevis* (mean ± SE) with and without *U. lactuca* (U+ and U-, respectively) in the intertidal (A) and the subtidal (B). Different lower case and upper case letters indicate differences between treatments and among seasons. Note the different scale of y-axes.

DISCUSSION

This study suggests that the abundance pattern of *Hymeniacion* may be driven by biotic relationships at the intertidal while a more complex interaction between variables (combining biotic and abiotic stressors) may influence its abundance pattern at the subtidal. Negative relationships between *Hymeniacion* and *Ulva* were observed at both tidal heights. Environmental conditions (e.g. desiccation) are harsher outside the *Ulva* canopy at the intertidal, but only subtidal sponges seem to be affected by the physical variables considered in this study. Thus, seawater temperature as well as UV and PAR solar radiation was negatively correlated with subtidal *Hymeniacion* abundance.

Both positive and negative relationships between sponges and macroalgae have already been reported for different habitats (Palumbi, 1985; Bell, 2002; Ávila et al., 2010; Cárdenas et al., 2012). Our results suggest a negative relationship between *Hymeniacion* and *Ulva*, since *Hymeniacion* was more abundant in sites and seasons when *Ulva* was scarce. Some authors suggest that sponge assemblages are more influenced by substrate inclination than by algae abundance and

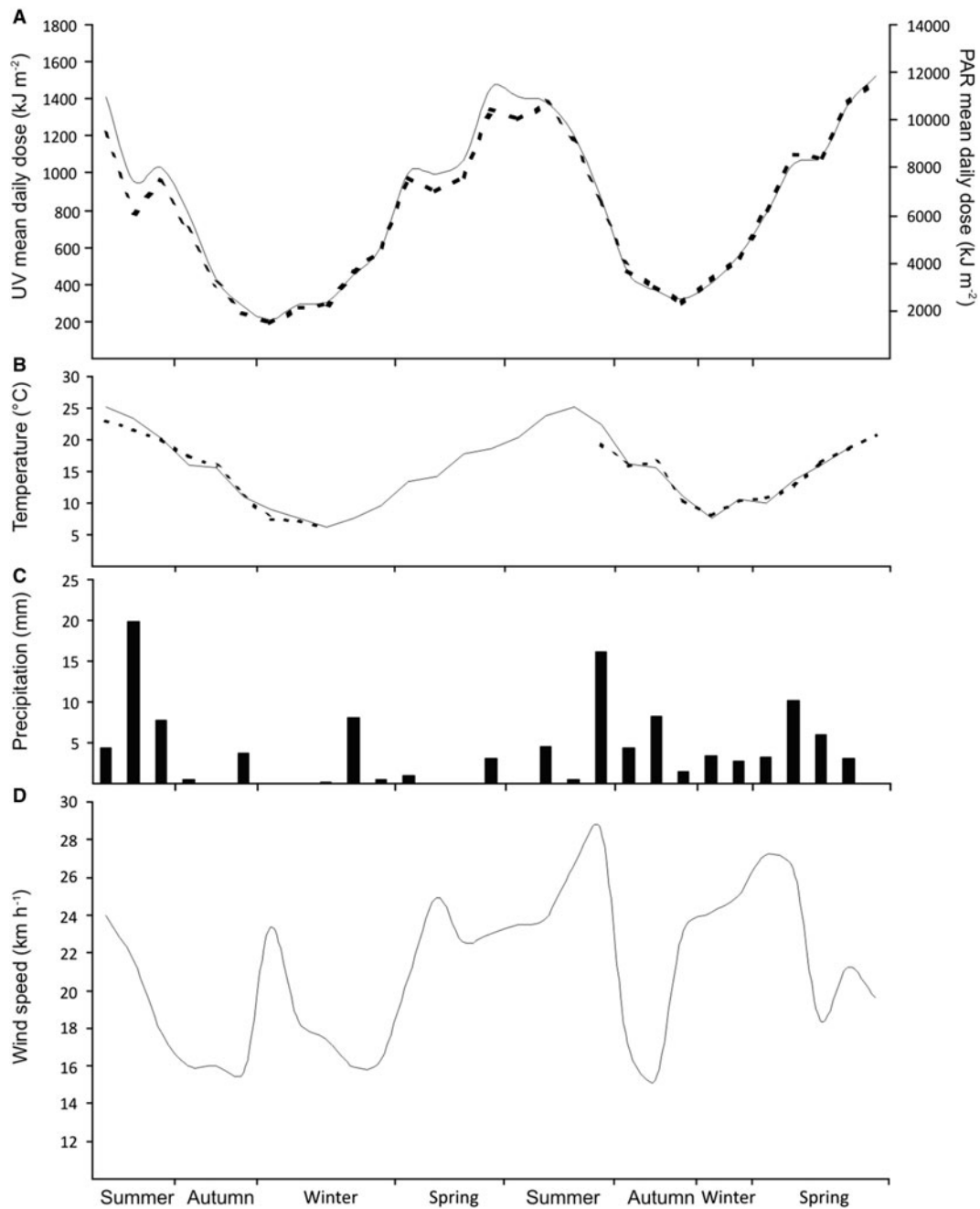


Fig. 4. UV and PAR daily dose (A, solid and dashed line respectively), air and water temperature (B, solid and dashed line respectively), precipitation (C) and wind speed (D) during 2 years in the study area.

that the negative correlation between them is due to their different spatial distribution (algae dominate horizontal substrates while sponges dominate more vertical ones; Preciado & Maldonado, 2005). Though we do not measure substrate inclination, our study area is an intertidal flat with a homogenous and smooth slope, without crevices or vertical walls. In subtidal systems a negative relationship between sponge community and turf-forming algae was suggested since sponge community decrease and turf-forming algae increase when the canopy of a foundation species, a canopy-forming alga, was removed (Cárdenas *et al.*, 2015). Also, the lateral growth rate of clionoids decrease when they are in contact with macroalgae (Lopez-Victoria *et al.*, 2006; González-Rivero *et al.*, 2012) and the physiology of the

sponge *Aplysina cauliformis* is affected in contact with a green macroalga, though without affecting its biomass (Easson *et al.*, 2014).

The stress-gradient hypothesis predicts that community structuring processes are context dependent of the environmental conditions (either biotic or abiotic). Thus, the importance of negative biotic effects is higher under benign environmental conditions, while positive facilitative effects become more important as environmental stress increases (Bertness & Callaway, 1994). Under such benign conditions, the dominance of foundation species may result in competitive exclusion of other organisms that overlap in terms of resources requirements (Paine, 1966; Power *et al.*, 1996), whereas in stressful environments foundation species are

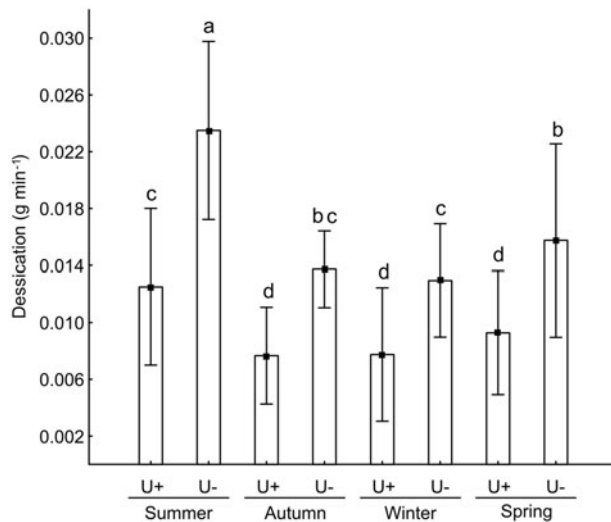


Fig. 5. Desiccation (mean \pm SE) with and without *U. lactuca* (U+ and U-, respectively). Different lower case letters indicate differences between treatments and among seasons.

expected to play a critical role in structuring communities (Silliman *et al.*, 2011). Patagonian shores present higher desiccation rates than other previously studied intertidals and this is known to be the main factor structuring the shore communities (Bertness *et al.*, 2006; Silliman *et al.*, 2011). We expected to find a positive correlation between *Hymeniacidon* and *Ulva* in a harsher site (low intertidal) and a negative correlation in a more benign site (shallow subtidal). However, we observed negative associations at both heights, suggesting that competition may play an important role at both heights. Hence, three alternative explanations arise: (1) we considered both tidal heights as contrasting environments of the stress gradient at San Antonio Bay, since while the subtidal was permanently submerged; the intertidal was subjected to air exposure during 10 h per day (considering both low tides). During emersion intertidal sponges are subjected to loss of oxygen and food supply, increased salinity and exposure to solar radiation and, eventually, loss of cellular water upon draining and drying of the internal cavity and aquiferous system (Rützler, 1995). However, these two environments would not be contrasting enough for *Ulva* and *Hymeniacidon*. (2) Predation and reproduction seem to have large effects on sponges' abundance (Stone, 1970; Tanaka, 2002; Wulff, 2006; Bell, 2008a; Gaino *et al.*, 2010). However, during the first year of sampling no recruitment was observed on settlement plates deployed in the subtidal (MG, unpublished data). On the other hand, predation on *Hymeniacidon perlevis* has not been reported yet (Bell, 2008a) and no evident predator of *Hymeniacidon* could be identified at San Antonio Bay. Nevertheless, these biotic processes, not considered in this study, may be playing an important role in determining *Hymeniacidon* abundance pattern, overwhelming the effect of the physical variables. (3) Both species *Hymeniacidon* and *Ulva* may have different optimal environmental requirements. In San Antonio Bay *Ulva* abundance is strongly driven by seasonal environmental factors, such as the availability of nutrients and temperature (Martinetto *et al.*, 2011). On the other hand, studies about the environmental requirements of *Hymeniacidon* are scarce, but growth of *Hymeniacidon*

cover occur between 17–20°C on controlled temperature aquarium (Stone, 1970). Here only subtidal *Hymeniacidon* cover was correlated with seawater temperature and radiation, and while *Ulva* showed similar abundances at both heights, *Hymeniacidon* doubled the abundance at the subtidal. The pattern observed for *Ulva* suggests that none of the heights are limiting environments for its growth, agreeing with previous studies which demonstrate that *Ulva* has a great capacity to thrive in the harsh intertidal, maintaining or even enhancing photosynthesis during air exposure and high levels of desiccation, and showing a fast adaptation of growth under different light conditions (Henley *et al.*, 1992; Altamirano *et al.*, 2000; Gao *et al.*, 2011). Even though *Hymeniacidon* is an intertidal sponge that seems to resist high desiccation rates, the observed pattern of *Hymeniacidon* suggests that the subtidal would be a more suitable environment. This may be explained by the supply of food particles which is continuous in the subtidal and restricted to high tide in the intertidal (see also Reiswig, 1971; Steindler *et al.*, 2002). The latter may explain the opposite abundance pattern showed by *Ulva* and *Hymeniacidon*, the seasonal variation of abundances in both species and the differences in abundance between heights. However, none of these three explanations satisfactorily elucidate why *Hymeniacidon* is more abundant in sites where *Ulva* is absent. Macroalgae can exert several negative effects on survivorship of sponges by releasing allelochemical compounds (González-Rivero *et al.*, 2012), shading (Freeman & Thacker, 2011), and/or the enhancement of sedimentation (Maldonado *et al.*, 2008). None of these negative chemical or physical effects have been reported on *Hymeniacidon*, however it seems unlikely that *Ulva* may affect *Hymeniacidon* by enhancing sedimentation since, as already observed (Stone, 1970), in San Antonio Bay, *Hymeniacidon* is able to grow on muddy gravel and soft mud. However, to understand the mechanisms underlying such interactions, disentangling the physical from chemical effects of *Ulva* on *Hymeniacidon*, manipulative experiments are needed.

Under a scenario of climate change, with increasing human activities, nutrient loads and rising water temperatures, it is essential to enhance our knowledge of the factors controlling intertidal and shallow subtidal communities in stressful environments to predict how natural communities will perform. However, further studies are needed to determine the role of other potential stressors, such as food availability and reproduction events on the abundance pattern of *Hymeniacidon*.

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