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## Temporal dynamics of algal epiphytes on *Leathesia marina* and *Colpomenia sinuosa* macrothalli (Phaeophyceae)

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### ABSTRACT

This is the first study on the temporal dynamics of the epiphyte communities of *Leathesia marina* and *Colpomenia sinuosa*, in terms of richness, diversity and abundance, and their relationships between the hosts and the environmental factors. A total of 31 epiphyte taxa were recorded, with the two hosts sharing 64.5% of the epiphytic species found. The red algal epiphytic group had the highest abundance on both hosts and the diatoms presented the highest species richness. The epiphyte species on *L. marina* showed a progressive increase in abundance during the warm seasons that was related to the end of the macroscopic life stage of the host. They also showed a greater specific richness on *L. marina* than on *C. sinuosa*, but a lower diversity and evenness, and a clear dominance of the species *Urospora penicilliformis* and *Erythrotrichia carnea*. Low abundance of epiphytes was found on *C. sinuosa*, without temporal variation, but high diversity and evenness and without any dominant species. In addition, a clear zonation was observed on this host, where epiphytic abundance decreased on the lateral and upper part of the thallus.

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### Introduction

In marine environments a wide variety of epiphytic algae grow on seaweeds and seagrasses, especially in the rocky intertidal zones; hence, epiphytism is considered a widespread phenomenon in these environments (Rindi & Guiry 2004). Epiphytic algae compete for substrate, proximity to light and dissolved nutrients (Edwards & Connell 2012). Although most epiphyte–host relationships are essentially facultative (not obligate) without a specific association with the host (Wahl & Mark 1999), some epiphytes are known to be specific and obligate on certain hosts (Harlin 1980; Pearson & Evans 1990). Because epiphytic algae have well-developed chloroplasts, they are considered as casual intruders, being carbon independent of their hosts. Several studies have revealed that most epiphytic algae are able to grow in isolation from their hosts, which confirms the above assertion (Garbary 1979; Correa 1994; Eggert et al. 2010).

The establishment and development of an algal epiphyte community is related to biotic factors, such as abundance, diversity and germination success of algal propagules, as well as the degree of herbivory. These factors together with the abiotic factors, such

as light, dissolved nutrients, seawater temperature and motion, influence the recruitment and colonization of epiphytes (Lavery et al. 2007; Lee et al. 2007).

Epiphytes normally represent most of the existing species of algae in benthic environments, increasing the heterogeneity of a particular habitat (Cardoso et al. 2004). Studies on epiphyte communities have also revealed that epiphytic primary productivity may often exceed the annual productivity of macrophytes (Moncreiff & Sullivan 2001). Therefore, variations in the epiphytic biomass are regarded as natural and sensitive indicators of environmental variations (Richardson 2006; Martínez-Crego et al. 2010) since the increase of epiphytes is closely associated with nutrient level increase (Frankovich et al. 2003; Hays 2005; Peterson et al. 2007).

At the ecological level, epiphytic algae may decrease host fitness due to increased shading, altered water flow, reduced diffusion rates of nutrients and CO<sub>2</sub>, increased drag force and vulnerability of the host to dislodgement (Sand-Jensen 1977). However, some beneficial effects to the host are also known; epiphytic algae can protect their hosts from desiccation and excessive light during low tides (Richardson 1980).

Concerning the host, different species of macroalgae do not host epiphytic organisms in the same way, as epiphytism depends on surface availability, morphological architecture, host life cycle and the presence of chemical defences (Michael et al. 2008). In many cases, the degree of epiphytism is high when the algal host has both the greatest colonization surface and biomass (Ortuño-Aguirre & Riosmena-Rodríguez 2007).

The saccate brown seaweeds *Leathesia* and *Colpomenia* are conspicuous components of rocky intertidal communities with a cosmopolitan distribution. *Leathesia marina* (Lyngbye) Decaisne and *Colpomenia sinuosa* (Mertens ex Roth) Derbès & Solier are primarily epiphytic macroalgae distributed in rocky intertidal communities from temperate to cold climates around the world (Oates 1989). They exhibit an annual life cycle consisting of an alternation of microscopic filamentous microthalli and macroscopic macrothalli (Dangeard 1965). In *L. marina*, the microthalli represent the gametophytic phase (n), and the macrothalli the sporophytic phase (2n), whereas the gametophyte of *C. sinuosa* is macroscopic and the sporophyte is microscopic.

On the Patagonian Atlantic coast, both species inhabit lower intertidal zones. *Leathesia marina* is reported as a species typical of hot-temperate periods, whereas *C. sinuosa* is a typical species of temperate and cold periods. Because of their analogous morphology these two species have a similar ecological role in the intertidal zone, giving rise to the following questions: do both species have the same assemblage of epiphytes? Do epiphytic species occur on different hosts during warm-temperate to temperate-cold periods? Do the differences in the sexual phases of both hosts affect the composition and abundance of the epiphytic community? This study aims to analyse the temporal dynamics of the algal epiphyte community on the sporophytic macrothalli of *L. marina* and the gametophytic macrothalli of *C. sinuosa* that inhabit the Patagonian Atlantic coasts, in terms of richness, diversity and abundance and their relationships with the environmental factors and host abundance.

## Material and methods

### Study site

This study was carried out on the Patagonian Atlantic coast (42°46'32.57"S, 62°59'23.49"W).

Climatologically, the region is characterized by the predominance of strong westerly winds and year-round low humidity. Therefore, this area is considered

an arid region (Paruelo et al. 1998) with an average annual precipitation around 239 mm.

The substrate of the intertidal zone is composed of a consolidated limestone platform, locally known as 'tosca' (Casal 1946). The tidal regime is semidiurnal, with a maximum amplitude of 5.86 m and an annual average of 4.13 m (Servicio de Hidrología Naval 2014).

The environmental parameters, such as day length, solar radiation and rainfall, were provided for this study by the Automatic Weather Station of CENPAT-CONICET. The seawater temperature was measured *in situ*.

### Host populations: *L. marina* and *C. sinuosa*

Fronds of both hosts were randomly taken monthly from December 2013 to November 2014 in the low intertidal zone. The lower intertidal zone in the sampling area is a small surface ~12 m long and 5 m wide. *Leathesia marina* macrothalli were present for two periods (December 2013–April 2014 and October 2014–November 2014) corresponding to the temperate-warm season along the Patagonian coast and *C. sinuosa* macrothalli only from April–October 2014, corresponding to the temperate-cold season.

During these periods, 20 macrothalli of each species were collected randomly each month. Samples were stored in plastic bags overnight at 5°C and each specimen was carefully washed with seawater to remove any adhering sand. The thalli were fixed in FAA (formaldehyde-glacial acetic acid-ethanol solution, 8:1:1 proportion). Two morphological variables of the host, the maximum diameter and wet weight, were recorded for each individual. To evaluate the abundance of *L. marina* and *C. sinuosa*, six quadrats (25 cm × 25 cm) were randomly placed in the lower intertidal zone and photographed every 15 days throughout the year from December 2013 to November 2014.

### Identification and quantification of the epiphyte community

To study the epiphyte community 20 fronds of *L. marina* and *C. sinuosa* were randomly collected each month in the lower intertidal zone from December 2013 to November 2014. Each macrothallus was divided into three distinct regions (upper, lateral and basal); in each region, one subsample of 35 mm<sup>2</sup> was randomly selected. The total area observed was 105 mm<sup>2</sup> for each frond and 2100 mm<sup>2</sup> per month for each host. Epiphyte organisms were identified at both genus and species levels and quantified using a Nikon Eclipse TE 300 microscope (Tokyo, Japan) equipped with a Nikon

FDX 35 camera. Counts were normally conducted at 400× magnification. Cyanobacterial filaments and non-filamentous colonies were counted as individuals, along with brown algae and single-celled green algae.

To record the epiphytic incidence on *L. marina* and *C. sinuosa* macrothalli, four epiphytic groups were recognized: (i) very abundant (present on more than 100 host thalli), (ii) abundant (50–100 host thalli), (iii) rare (24–50 host thalli) and (iv) occasional (fewer than 24 host thalli) (Gauna et al. 2016).

### Epiphyte isolation under culture conditions

In order to identify some epiphyte species correctly, *in vitro* cultures were needed to generate reproductive structures. Epiphytic species such as *Erythrotrichia carnea* (Dillwyn) J.Agardh, *Urospora penicilliformis* (Roth) Areschoug and *Ectocarpus siliculosus* (Dillwyn) Lyngbye were cultured for four weeks. For this purpose, small portions of host thalli were sectioned and gently rinsed three times in sterile seawater. They were then placed in Petri dishes containing seawater enriched with modified Provasoli medium (PES) (Provasoli 1968), at 17°C with a light/dark regime of 12:12 h, with light irradiance of 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  provided by cool white fluorescent tubes and monitored using a Quantum Flux meter (Apogee MQ-200, USA). Under these conditions, different reproductive stages of the epiphyte organisms were obtained, which were subsequently transferred and maintained under the same culture conditions.

### SEM methods

For scanning electron microscopy (SEM), macrothalli fragments of *Leathesia marina* and *Colpomenia sinuosa* were fixed in 2.5% glutaraldehyde, containing 0.01 M sodium cacodylate buffer (pH 7.2), at 5°C for 2 h. Subsequently, three washes in sodium cacodylate buffer (0.005 M) were carried out for 10 min each. The fixed portions were dehydrated in a series of acetone, following the protocol by Cáceres (1995). Finally, the samples were critical-point dried for 1 h, and were coated with gold in a 9100 mod. 3 sputter coater (Pelco, Clovis, CA, USA), according to Sorrivás de Lozano & Morales (1986). Samples were observed with a Leo Evo 40 SEM (Jena, Germany).

### Statistical analyses

Each data set was examined for homogeneity of variances using Bartlett's test and normality using the Shapiro–Wilk test. To evaluate differences in

macrothalli abundance, maximum diameter and wet weight of *C. sinuosa* and *L. marina*, analyses of variance (ANOVA) were conducted to establish the differences between the species. Analysis of variance (ANOVA) was conducted to determine the differences between epiphyte abundance on the host macrothalli regions (upper, lateral and basal), over the months. The epiphyte abundance data on *L. marina* were log-transformed ( $\ln$ ) to obtain homoscedasticity. In addition, multivariate analyses were performed with the purpose of describing variability in epiphyte assemblages over the months for both species. Data were previously standardized and transformed using  $\log_{10}x + 1$  and non-metric multidimensional scaling (nMDS) was run using the Bray–Curtis similarity index with 999 permutations (Bray & Curtis 1957; Clarke & Gorley 2006).

Shannon–Wiener diversity index ( $H'$ ) (Shannon & Weaver 1949), Pielou's evenness index ( $J'$ ) (Pielou 1975), Simpson dominance ( $\lambda$ ) (Simpson 1960) and epiphyte richness were calculated.

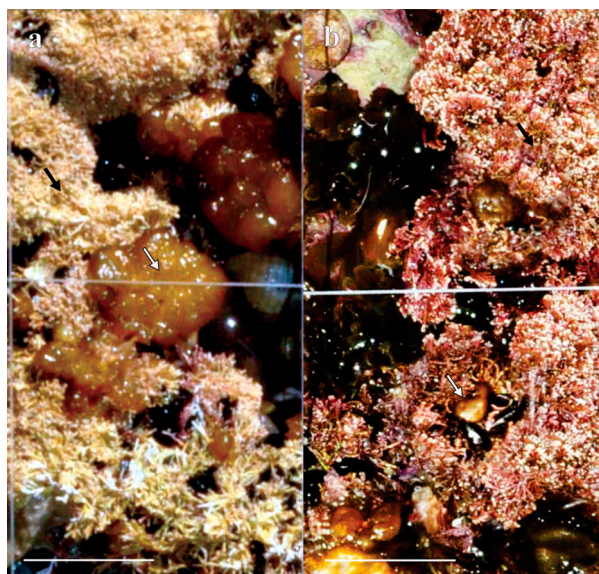
To analyse the relationships of the epiphytes with the hosts and the environmental variables over the months, we performed canonical correspondence analyses (CCA) (Ter Braak 1994) based on abundance data for the epiphytic taxa and the means of the environmental variables, such as seawater temperature, day length and solar radiation, and abundance of *L. marina* and *C. sinuosa*.

The statistical program R Studio (R Core Team 2014) and the PRIMER (Plymouth Routines in Multivariate Ecological Research) package (Clarke & Gorley 2006) were used to perform analyses with a significance level of 0.05.

## Results

### Host populations: *L. marina* and *C. sinuosa*

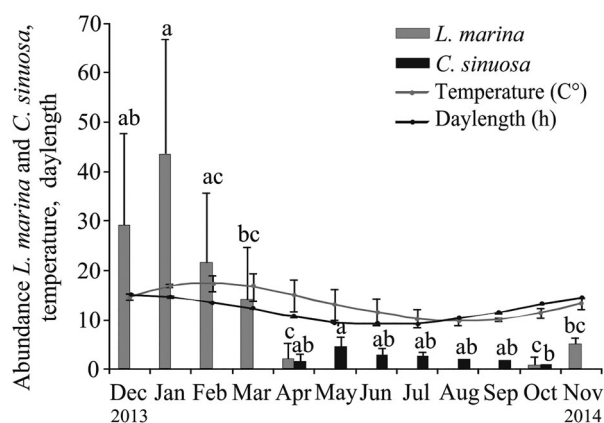
The sporophytes of *L. marina* had hemispherical to irregular cushion-shaped thalli with many interstices. On the other hand, gametophytes of *C. sinuosa* had a globular to irregular form with a smooth surface. Both brown macroalgae, *L. marina* and *C. sinuosa*, were settled predominantly in the low intertidal zone. This was also colonized by *Brachidontes rodriguezii* (d'Orbigny 1842) and *Perumytilus purpuratus* (Lamarck 1819), and associated with a macroalgal community of *Corallina officinalis* Linnaeus, *Undaria pinnatifida* (Harvey) Suringar, *Myriogloea major* Asensi, *Ralfsia verrucosa* (Areschoug) Areschoug, and occasionally of *Adenocystis utricularis* (Bory de Saint-Vincent) Skottsberg.



**Figure 1.** *Leathesia marina* and *Colpomenia sinuosa* in nature. (a) Sporophyte of *L. marina* (white arrow) epiphytic on *C. officinalis* (black arrow). (b) Gametophyte of *C. sinuosa* (white arrow) epiphytic on *C. officinalis* (black arrow). Scale bars represent 2.5 cm.

Both macrothalli were often found as epiphytes on *C. officinalis* thalli (Figure 1a,b).

In the period studied, the seawater temperature ranged from  $17.5 \pm 0.5^\circ\text{C}$  to  $9.8 \pm 1.5^\circ\text{C}$  (mean  $\pm$  SE), being maximal during February and minimal in August (Figure 2). Day length varied between  $15.15 \pm 0.05$  h and  $9.05 \pm 0.06$  h, maximal in December and minimal in June. The average solar radiation ranged between  $8341 \pm 1182 \text{ W m}^{-2}$  and  $2060 \pm 1033 \text{ W m}^{-2}$ , with maximum values during January and minimum in June.



**Figure 2.** Abundance of *Leathesia marina* and *Colpomenia sinuosa* (no. 625 cm<sup>2</sup>; mean  $\pm$  SE). Environmental parameters (mean  $\pm$  SE): seawater temperature ( $^\circ\text{C}$ ), day length (h). Significant differences ( $\alpha < 0.05$ ) are indicated by different letters using Tukey's Honestly Significant Difference (HSD).

The *L. marina* abundance ( $19 \pm 16 \text{ ind./625 cm}^2$ ) was significantly higher than that of *C. sinuosa* ( $3 \pm 1 \text{ ind./625 cm}^2$ ) (ANOVA:  $F(1, 84) = 21.4$ ,  $P < 0.001$ ) (Figure 2). The highest abundance of *L. marina* was recorded during January and of *C. sinuosa* in May.

The wet weight of macrothalli of *L. marina* was significantly higher than of *C. sinuosa* (ANOVA:  $F(1, 280) = 16.2$ ,  $P < 0.001$ ). The macrothalli of *L. marina* had a weight of  $1.3 \pm 1 \text{ g}$  and *C. sinuosa* of  $0.7 \pm 0.6 \text{ g}$ . The maximum diameter was similar in both species (ANOVA:  $F(1, 280) = 0.6$ ,  $P = 0.42$ ). *Leathesia marina* had a diameter of  $2.36 \pm 0.8 \text{ cm}$  and *C. sinuosa* of  $2.44 \pm 0.8 \text{ cm}$ .

### Identification and quantification of the epiphyte community on *L. marina* and *C. sinuosa*

A total of 31 epiphyte taxa were recorded on *L. marina* and *C. sinuosa*, of which 20 taxa were observed on both hosts, sharing 64.5% of epiphytic species found (Table I).

In *L. marina*, the epiphyte taxa were from five different taxonomic classes: Cyanophyceae represented by one species, Rhodophyceae by four taxa, Bacillariophyceae by 17 taxa, Phaeophyceae by two species and Chlorophyceae by two species. In *C. sinuosa*, the Cyanophyceae were represented by the only species recorded, Rhodophyceae by four taxa, Bacillariophyceae by 14 taxa, Phaeophyceae by three species and Chlorophyceae by three epiphytic taxa. The diatoms showed the highest species richness in both hosts.

The epiphyte abundance showed significant differences between the two hosts (ANOVA,  $F(6, 21) = 24$ ,  $P < 0.001$ ). *Leathesia marina* showed higher epiphyte abundance, with  $1276 \pm 1123 \text{ ind./month}$  and *C. sinuosa* had an epiphyte abundance of  $154 \pm 86 \text{ ind./month}$ , which was seven times lower than the abundance of *L. marina*.

The surface of the macrothalli of *L. marina* had a rough texture colonized by epiphytes (Figure 3a,b,c), whereas the morphology of *C. sinuosa* was smoother with a morphologically distinct cuticle of neutral polysaccharides, showing a lower epiphyte abundance (Figure 3d,e,f).

Rhodophyceae was the group with highest abundance on both hosts;  $3392 \pm 2920 \text{ ind./month}$  were observed on *L. marina* and  $216 \pm 191 \text{ ind./month}$  on *C. sinuosa* (Figure 4). Phaeophyceae epiphytes were considerably less abundant with  $220 \pm 200 \text{ ind./month}$  observed on *L. marina* and  $177 \pm 149 \text{ ind./month}$  on *C. sinuosa*. Bacillariophyceae were equally abundant on both *L. marina* and *C. sinuosa*. The mean abundance of Bacillariophyceae on *L. marina*

**Table I.** Algal epiphytes from Patagonia.

Epiphytic taxa	On <i>Leathesia marina</i>		On <i>Colpomenia sinuosa</i>	
	No. of epiphytized fronds	Incidence	No. of epiphytized fronds	Incidence
Cyanophyceae				
<i>Oscillatoria corallinae</i> Gomont ex Gomont	17	occasional	15	occasional
Rhodophyceae				
<i>Anotrichium furcellatum</i> (J.Agardh) Baldock	–		1	occasional
<i>Colaconema daviesii</i> (Dillwyn) Stegenga	3	occasional	41	occasional
<i>Erythrotrichia carnea</i> (Dillwyn) J.Agardh	108	very abundant	68	abundant
<i>Polysiphonia</i> spp.	83	abundant	6	occasional
<i>Stylonema alsidii</i> (Zanardini) K.M.Drew	3	occasional	–	occasional
Bacillariophyceae				
<i>Achnanthes</i> sp.	2	occasional	–	
<i>Bacillaria</i> sp.	1	occasional	1	occasional
<i>Cocconeis</i> spp.	26	rare	12	occasional
<i>Cymbella</i> sp.	1	occasional	–	
<i>Fragilaria</i> sp.	2	occasional	5	occasional
<i>Grammatophora oceanica</i> Ehrenberg	7	occasional	35	rare
<i>Gyrosigma</i> sp.	3	occasional	14	occasional
<i>Licmophora</i> sp.	17	occasional	15	occasional
<i>Navicula</i> spp.	45	rare	39	rare
<i>Nitzschia</i> sp.	1	occasional	26	rare
<i>Parlibelus</i> sp.	4	occasional	–	
<i>Pinnularia</i> spp.	27	rare	22	occasional
<i>Pleurosigma</i> sp.	2	occasional	1	occasional
<i>Rhabdonema</i> sp.	9	occasional	5	occasional
<i>Rhoicosphenia</i> sp.	–		21	occasional
<i>Surirella</i> sp.	2	occasional	1	occasional
<i>Synedra</i> sp.	1	occasional	1	occasional
<i>Tubularia</i> sp.	14	occasional	–	
Phaeophyceae				
<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	71	abundant	37	rare
<i>Pylaiella littoralis</i> (Linnaeus) Kjellman	–		37	rare
<i>Sphacelaria cirrosa</i> (Roth) C.Agardh	2	occasional	1	occasional
Chlorophyceae				
<i>Ulvela leptochaete</i> (Huber) R.Nielsen, C.J.O'Kelly & B.Wysor	1	occasional	25	rare
<i>Epicladia</i> sp.	–		23	occasional
<i>Ulvela lens</i> P.Crouan & H.Crouan	–		5	occasional
<i>Urospora penicilliformis</i> (Roth) Areschoug	18	occasional	–	

Note: The number of *Leathesia marina* and *Colpomenia sinuosa* fronds epiphytized ( $n = 140$  for each host) from December 2013 to November 2014 and the incidence (very abundant: present on more than 100 host thalli; abundant: 50–100 host thalli; rare: 24–50 host thalli; and occasional: less than 24 host thalli) are reported.

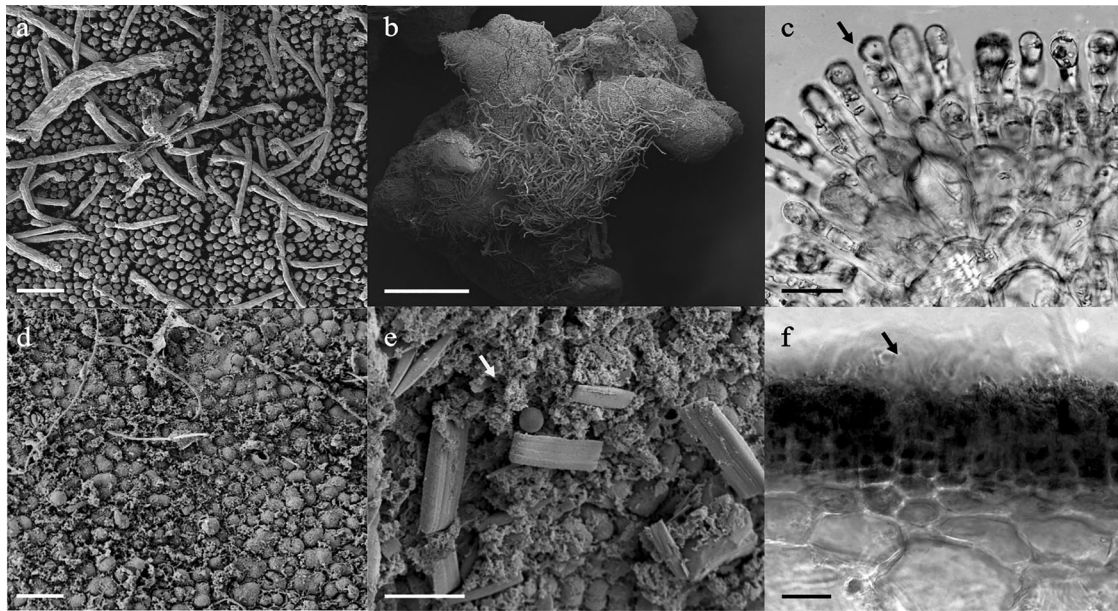
was  $171 \pm 64$  ind./month and on *C. sinuosa* it was  $154 \pm 139$  ind./month. Cyanophyceae and Chlorophyceae epiphytes were the least abundant on both *L. marina* and *C. sinuosa*. The mean abundance of Cyanophyceae on *L. marina* was  $50 \pm 36$  ind./month and on *C. sinuosa* it was  $3 \pm 1$  ind./month. The mean abundance of Chlorophyceae on *L. marina* was only  $1 \pm 1$  ind./month and  $22 \pm 2$  ind./month on *C. sinuosa*.

The red algae *Erythrotrichia carnea* (Dillwyn) J.Agardh was the most abundant epiphyte on *L. marina*, with the highest incidence (Table I). *Polysiphonia* spp. and *Ectocarpus siliculosus* (Dillwyn) Lyngbye were the unique abundant species on the same host. The diatoms *Cocconeis* spp., *Pinnularia* spp. and *Navicula* spp. were rare species and the 20 remaining taxa recorded were occasional epiphytes. The diatoms *Navicula* spp., *Grammatophora oceanica* Ehrenberg and *Nitzschia* spp., the brown algae *E. siliculosus* and *Pylaiella littoralis* (Linnaeus) Kjellman, and the green algae *Ulvela leptochaete* (Huber) R.Nielsen, C.J.O'Kelly & B.Wysor were rare epiphytes

on *C. sinuosa* and the 19 remaining taxa recorded were occasional epiphytes. Very abundant epiphytes on the thalli of *C. sinuosa* were not observed.

The epiphyte abundance on *L. marina* showed significant differences among the months examined (ANOVA,  $F(6, 21) = 24$ ,  $P < 0.001$ ) (Figure 5). The highest abundance was recorded in April, with  $3064 \pm 771$  ind. observed and the lowest in the periods December–January and October–November, with  $49 \pm 18$ ,  $296 \pm 43$ ,  $132 \pm 26$  and  $87 \pm 10$  ind., respectively. No significant differences were found in the epiphyte abundance on the different host thallus regions (upper, lateral and basal) of *L. marina* (ANOVA,  $F(2, 21) = 0.202$ ,  $P = 0.8175$ ).

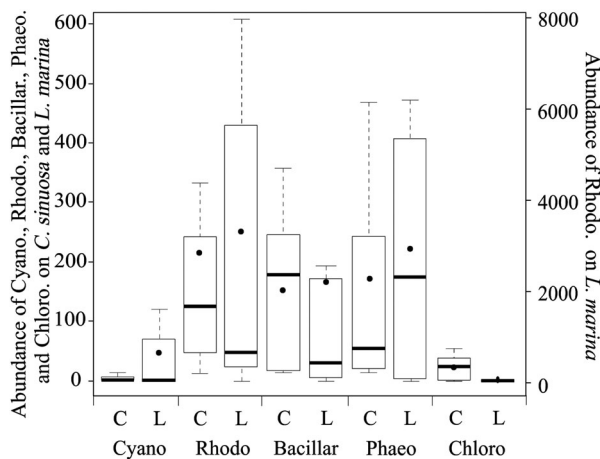
On *C. sinuosa*, the epiphyte abundance was similar among months (ANOVA,  $F(6, 21) = 1.14$ ,  $P = 0.38$ ) (Figure 5). However, the epiphyte abundances on the different host thallus regions were significantly different (ANOVA,  $F(2, 21) = 4.51$ ,  $P = 0.02$ ). The highest abundance was recorded in basal regions of the host thallus, with  $222 \pm 84$  ind., and the lowest in the



**Figure 3.** Morphology of *Leathesia marina* and *Colpomenia sinuosa* macrothalli. (a) SEM photograph of macrothalli of *L. marina* showing detail of the cortical layer with hyaline hairs. (b) SEM photograph of epiphytes on *L. marina*. (c) Cross-section of *L. marina* showing medullary cells and cortical layer. Arrow indicates assimilating filaments. (d) SEM photograph of macrothalli of *C. sinuosa* showing detail of the cortical layer with a cuticle. (e) SEM photograph of epiphytes on *C. sinuosa*. Arrow indicates cuticle. (f) Cross-section of *C. sinuosa* showing medullary cells and cortical layer. Arrow indicates cuticle. Scale bars represent: a, 40 µm; b, 1 mm; c, d, e, f, 20 µm.

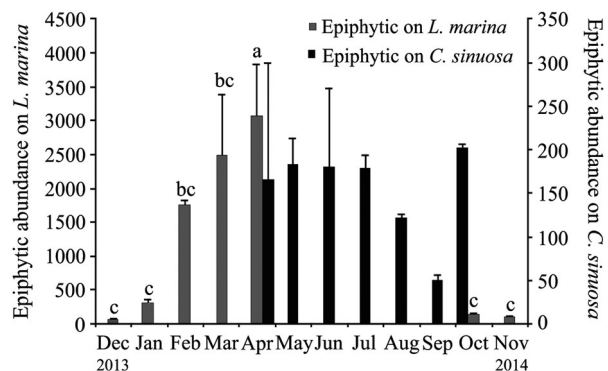
lateral and upper regions, with  $112 \pm 67$  and  $127 \pm 65$  ind. respectively.

Analyses of nMDS and SIMPER showed a clear differentiation in epiphytic composition and abundance over the months in both hosts (Figure 6). A marked

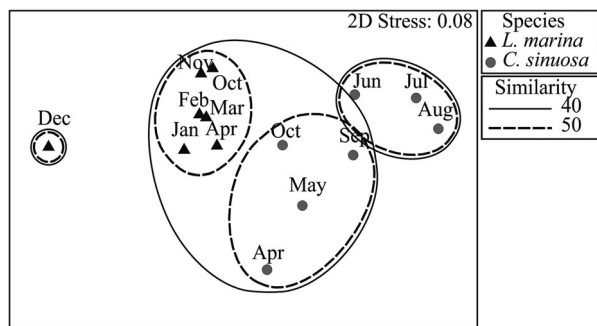


**Figure 4.** Abundance of Cyanophyceae (*Cyano*), Rhodophyceae (*Rhodo*), Bacillariophyceae (*Bacillar*), Phaeophyceae (*Phaeo*) and Chlorophyceae (*Chloro*) taxa on *Colpomenia sinuosa* (C) and *Leathesia marina* (L) during sampling period. Boxes encompass the 25 and 75% quartiles of all abundance data. The central line represents the median and average values were marked with a dot. The length of the bars represents 25% of the upper and lower data.

separation between December and the other months was observed in the epiphyte community on *L. marina*. This differentiation was due to the high abundance of the green alga *Urospora penicilliformis* (Roth) Areschoug. A second monthly group in the epiphyte community on *C. sinuosa* was observed in June, July and August. This group integrated samples with a high abundance of diatoms, such as *Navicula* spp., *G. oceanica* and *Nitzschia* spp. A common group integrated by epiphytes observed on both *L. marina* and *C. sinuosa* included high abundances of *E. carnea*, *E. siliculosus* and *Polysiphonia* spp.



**Figure 5.** Monthly epiphyte abundance on *Leathesia marina* and *Colpomenia sinuosa* by month (no. 2100 mm<sup>2</sup>; mean  $\pm$  SE).



**Figure 6.** Non-metric multidimensional scaling (nMDS) plot showing variability separating epiphytic groups in regard to abundance and composition on *Leathesia marina* and *Colpomenia sinuosa*. Superimposed cluster analysis at similarity levels of 40–50%.

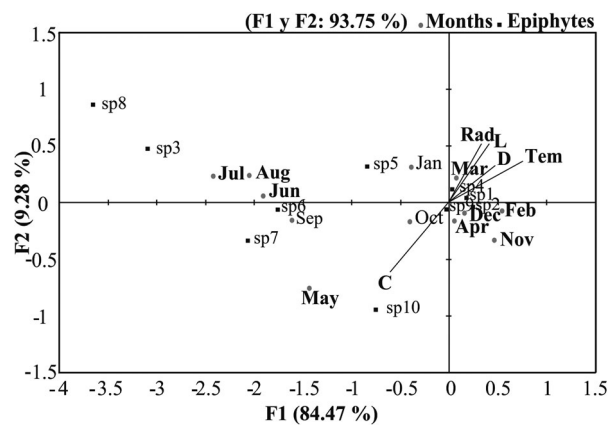
### Richness, diversity, evenness and dominance of the epiphyte assemblage

The species richness was homogeneous in both hosts (ANOVA,  $F(1, 42) = 0.99$ ,  $P = 0.32$ ). There were 27 epiphytic taxa recorded in *L. marina* and 25 epiphytic taxa in *C. sinuosa*. The epiphyte diversity indices showed significant differences in both hosts (ANOVA,  $F(1, 42) = 18.81$ ,  $P < 0.001$ ). The highest diversity was recorded on *C. sinuosa*, noting an index of  $H' = 2.29 \pm 0.31$ , and the lowest on *L. marina* with an index of  $H' = 0.73 \pm 0.29$ . In addition, the epiphyte evenness indices showed significant differences in both hosts (ANOVA,  $F(1, 42) = 91.2$ ,  $P < 0.001$ ). The highest evenness was also recorded on *C. sinuosa* ( $J' = 0.71 \pm 0.14$ ) and the lowest on *L. marina* ( $J' = 0.31 \pm 0.17$ ).

The lowest diversity and evenness noted on macrothalli of *L. marina* was related to a high dominance of the green alga *Urospora penicilliformis* ( $\lambda = 0.82 \pm 0.02$ ) observed during December and the red alga *Erythrotrichia carnea* ( $\lambda = 0.74 \pm 0.14$ ) during the remaining months. In *C. sinuosa* there were no dominant epiphyte taxa during the period analysed.

### Epiphytism associated with host abundances, and environmental parameters

Canonical correspondence analyses (CCA) showed that the first two axes explained 93.75% of the joint variation in the environmental (seawater temperature, day length and radiation, abundance of *L. marina* and of *C. sinuosa*) and biological variables (epiphyte species) (Figure 7). The epiphytes, such as *Erythrotrichia carnea*, *Polysiphonia* spp., *Cocconeis* spp. and *Pinnularia* spp., were associated with a high abundance on the *L. marina* macrothalli and the hotter and warmer months characterized by high seawater temperature,



**Figure 7.** Canonical correspondence analysis (CCA) plot showing temporal relationship between epiphytes with abundant and rare incidence: *Erythrotrichia carnea* (sp. 1), *Polysiphonia* spp. (sp. 2), *Colaconema daviesii* (sp. 3), *Cocconeis* spp. (sp. 4), *Pinnularia* spp. (sp. 5), *Navicula* spp. (sp. 6), *Grammatophora oceanica* (sp. 7), *Nitzschia* spp. (sp. 8), *Ectocarpus siliculosus* (sp. 9), *Pylaiella littoralis* (sp. 10); and environmental parameters: seawater temperature (Tem), day length (D), radiation (Rad), and abundance of *Leathesia marina* (L) and *Colpomenia sinuosa* (C).

long day length and high solar radiation. The diatoms *Navicula* spp., *G. oceanica*, *Nitzschia* spp. and the red alga *Colaconema daviesii* (Dillwyn) Stegenga were associated with the colder months characterized by low seawater temperature, short day length and low radiation. The brown alga *Ectocarpus siliculosus* was associated with the high abundance of *C. sinuosa* reported in October.

### Discussion

Sporophytic macrothalli of *L. marina* were present during the warm and hot seasons, whereas during the colder months this species was resting as microscopic filamentous gametophytic microthalli. On the other hand, the gametophytic macrothalli of *C. sinuosa* were present during the temperate and cold seasons and in the other months this species was observed as microscopic sporophytic microthalli. A well-marked succession between the two brown macroalgae was observed, with overlapping in only two months (April and October). This successional distribution of the brown macroalgae species indicates a clear seasonality associated with the environmental conditions.

In an ecological sense, both hosts presented an ephemeral nature, with a short life cycle span, simple thallus form, susceptibility to seasonal changes, forming patches only during its normal seasonal



occurrence, and characterized by high surface-area/volume (Eriksson et al. 2002; Piazzini et al. 2012).

Both macroalgal hosts occupied the same ecological niche, but were separated by time. The individuals of both the brown macroalgae analysed in this study were distributed in the lower intertidal area in Patagonia, mainly growing as epiphytes on *C. officinalis*. Similarly, on the southern coasts of California, species of *Leathesia* and *Colpomenia* were mostly observed on *Corallina* sp. (Oates 1989). In addition, previous studies in this area revealed the presence of sporophytic macrothalli of *L. marina* as epizoids on mussels (Quartino & Boraso de Zaixso 1996).

Epiphytic algae found on sporophytes of *L. marina* thalli and gametophytes of *C. sinuosa* have also often been mentioned as epiphytes on different macroalgae and seagrasses (Ortuño-Aguirre & Riosmena-Rodríguez 2007). Most of these epiphytic taxa were uncorticated filamentous algae with marked fluctuations with time. Also, the algal epiphytes identified and quantified in this study were mainly observed as immature individuals without any reproductive structure development. This fact may be due to the ephemeral nature of the macrothalli of both *L. marina* and *C. sinuosa*. The ephemeral nature of both species has been discussed by Vandermeulen & Dewreede (1986), Somsueb et al. (2001) and Eriksson et al. (2002), and is characterized by a highly dynamic population with conspicuous peaks of seasonal abundance and a high proportion of reproductive structures throughout the season.

Variation in the seasonal abundance in an epiphyte community may be related to variation in the physical environment, seasonality, grazing pressure or the needs and preferences of epiphytic algae per host substrate (Michael et al. 2008). According to González & Goff (1989), the relationship between the epiphyte and the host is established on chemical, physical and ecological bases. The algal host supports epiphytes according to the resources they provide, such as the availability of space, shelter, trapping of sediment and nutrients (Jones & Thornber 2010). Both the hosts analysed, *L. marina* and *C. sinuosa*, shared 64.5% of the assemblage of epiphytes found. This result indicated that the epiphytic assemblage was not associated with a particular host. However, marked differences in epiphytic abundance were observed between hosts, being higher on the sporophyte of *L. marina* during warm and hot seasons in comparison with a lower epiphytic abundance on the gametophyte of *C. sinuosa* during the cold season. In previous studies on the Patagonian Atlantic coast, a similar epiphytic assemblage was found on *Ulva* sp. growing in the lower intertidal zone. A greater

epiphytic abundance was also observed on this green macroalga during the temperate and hot seasons and a lower abundance during the cold season (Gauna et al. 2017). This observation indicates that the abundance of epiphytes on both species analysed in this study was associated with the environmental conditions. The gradual increase in epiphyte abundance towards the end of the occurrence of *L. marina* in nature was observed. This phenomenon could be due to facilitated colonization when the host thallus is in a senescent state with a decline in its defence mechanisms against epiphytes and an increased residence time of the host in the area. This was also observed by Ortuño-Aguirre & Riosmena-Rodríguez (2007) for the brown macroalga *Padina concrescens* Thivy in which the epiphytic abundance was highest when the host was senescent. In addition, Steinberg & De Nys (2002) and Lane & Kubanek (2008) explained that some species are only heavily epiphyted during certain periods of the year, which can be correlated with apparent metabolic changes in the algal host.

A clear temporality in the composition of epiphytes was observed on *L. marina*. This assumption was based on both low diversity and evenness, and the clear dominance of *Urospora penicilliformis* and *Erythrotrichia carnea*. Also *U. penicilliformis* was noted on the sporophyte of *L. marina*. However, temporality of epiphytes on *C. sinuosa* was not observed. Greater evenness and low abundance of epiphytes was noted on the gametophytic macrothalli of this brown alga and no dominance of species.

With respect to the epiphyte algal classes, the Bacillariophyceae was the group with the highest species richness on both hosts. The diatoms are usually the most abundant components of epiphyte communities and primary colonizers of marine surfaces and hence they play a crucial part in the structure of algal communities (Hernández-Almeida & Siqueiros-Beltrones 2008; Kumar et al. 2011). The diatoms, *Navicula* spp., showed the highest incidence on both *L. marina* and *C. sinuosa*, whereas *G. oceanica* and *Nitzschia* spp. were the most abundant epiphytes on *C. sinuosa*. These taxa are likely to be released by the water current, allowing occasional colonization, as they are not firmly attached to the substrate (Hudon & Legendre 1987).

In this study, epiphyte abundance on different host thallus regions was homogeneous on the sporophytes of *L. marina*. However, a clear zonation pattern was observed on *C. sinuosa*, indicating that the epiphyte abundance was decreasing towards the lateral and upper parts. Segregation of epiphytes on different parts of the host has also been reported by previous authors. Arrontes (1990) reported differential locations

of epiphytes on different parts of the host, such as the apices of the host thallus, inner or intermediate parts of the host thallus, stipes and holdfasts. The most persistent epiphytes tended to be those that grew on the lower parts of the macroalgal thallus. The cause for unequal distribution of epiphytes on hosts may again be due to many factors, such as variable environmental conditions (e.g. light and water motion) on different parts of the host, including shading effects underneath a canopy (Dayton 1975); uneven distribution of compounds in the host which might act as epiphyte deterrents (Bjærke & Fredriksen 2003); different age of cells and therefore different amounts of time available for developing an epiphytic community (Ballantine 1979; Krumhansl et al. 2015); and differences in surface tension and roughness of the host thallus (Dodds & Biggs 2002).

In macroalgae with apical meristematic zones, the epiphytes usually show clear zonation patterns, and the number of species usually decreases towards the younger parts (Bjærke & Fredriksen 2003; Krumhansl et al. 2015). However, in cerebroid species such as *Leathesia* and *Colpomenia*, where the multiaxial axis is reduced to tissues lining the inside of the crust (Boraso 2013), the epiphyte distribution is not related to the age of the macrothallus.

Under a morphological concept, the smoother texture in lateral and upper regions of *C. sinuosa* provided a more exposed area to the environmental microconditions, avoiding colonization by several epiphyte organisms. In addition, the extruded polysaccharide cuticle on the surface of *C. sinuosa* undoubtedly affects colonization by other algae, either providing substrates for the pioneer growth of bacteria and small diatoms or hindering the establishment of sporelings as Round (1984) and Weber & Schagerl (2007) pointed out.

A different situation is observed on *L. marina*, which has a rough texture with more interstices, favouring the recruitment and colonization of epiphyte taxa. This same phenomenon was observed by Arrontes (1990), Reyes & Afonso-Carrillo (1995), Kanamori et al. (2004) and Ortuño-Aguirre & Riosmena-Rodríguez (2007) on *Padina concrescens*, *Cystoseira* sp., *Gelidium* sp. and *Cymodocea nodosa* (Ucria) Ascherson, observing that the greater surface area to colonize with highest algal host biomass presented the highest epiphyte abundance.

In conclusion, on the Northern Patagonian coasts of Argentina, *L. marina* and *C. sinuosa* inhabit the same spatial niche but occur at different time frames, under different environmental conditions, to which both species are adapted. Despite this difference in

their temporal occurrence, the hosts shared most of the epiphyte assemblage. Our findings indicate that this temporal variability does not play a key role in explaining the epiphyte assemblage in lower intertidal systems. Nevertheless, the different morphological structure of each host could explain the higher epiphytic abundance on *L. marina* macrothalli. The factors studied, such as host morphology and temporality, contributed significantly to the variability of the species abundance and dominance of the structure of epiphytes on *L. marina* and *C. sinuosa*. This is the first comprehensive study on the temporal variability of the epiphytic communities of a *L. marina* and *C. sinuosa* population, aiming to understand the interactions between the dynamics of the epiphytic community with the environmental parameters and the host algae population dynamics.

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