Epiphytism in a subtidal natural bed of *Gracilaria gracilis* of southwestern Atlantic coast (Chubut, Argentina)

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Abstract The diversity of epiphytes, their temporal abundance variation and the anatomical structure of host–epiphyte interfaces were studied in the agarophyte *Gracilaria gracilis* from a natural bed in Bahía Bustamante, Chubut Province, Argentina. Twenty-nine algal species were recorded as epiphytes during 2 years of monthly sampling (March 2006–February 2008). Total epiphyte density ranged between 0.037 ind. cm^{-2} (November 2006) and 39.37 ind. cm^{-2} (April 2007), with higher density values throughout the second sampling year. Ceramiales species were the most abundant epiphytes. The density of *Ceramium rubrum* ranged from 0.09 ind. cm^{-2} (52 % of the total amount) in September 2006 to 17.4 ind. cm^{-2} (44.18 % of the total amount) in April 2007. Epiphyte infection was more dependent on spore recruitment and sporeling development, especially on thalli derived from fragmentation, than on seasonal environmental variations.

The different infections were analysed, taking into account the epiphytic attachment strength and invasiveness and the degree of damage inflicted on the host. *Calothrix confervicola* was one of the most abundant species. This epiphyte, weakly attached to the host surface, generated no host tissue damage. In contrast, *C. rubrum*, *Polysiphonia abscissa* and other Ceramiales were the species that caused more damage to the host because their rhizoids penetrated the cortical portion of the host thallus, sometimes reaching the medullary tissue. Some generalisations and characterisations of the different epiphyte groups in relation to their consequences to *Gracilaria* spp. are presented.

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Introduction

Gracilaria gracilis (Stackhouse) Steentoft, Irvine and Farnham is one of the main agarophyte species. Its distribution in Argentina is limited to some Patagonian bays in the coast of Chubut Province. Among these, the natural bed in Bahía Bustamante is particularly interesting as it has been the most productive since the end of the 1960s.

In Chubut, *Gracilaria* harvesting has always been restricted to wave-cast drift material. Despite this sustainable procedure, the annual *Gracilaria* production dropped from 3,000–4,000 dry tonnes in the 1970s (Boraso de Zaixso 1995) to barely 66.1 dry tonnes in 2003 (Boraso de Zaixso et al. 2006). Taking into account that the algal harvesting method has remained unaltered since the 1960s and that no major environmental changes have been registered for the area, a possible explanation for this notable yield decrease could be attributed to epiphyte-imposed stress. Epiphytes negatively affect host production either by competitively

removing nutrients and inorganic carbon from the water column (Sand-Jensen 1977), by shading (Kuschel and Buschmann 1991; Buschmann and Gómez 1993) or by increasing drag effect with subsequent breakage or detachment of the thalli (Kuschel and Buschmann 1991; Buschmann and Gómez 1993; González et al. 1993). Moreover, the entry of bacteria and pathogens is facilitated by the damage in the host tissue generated by epiphyte attachment (Vairappan 2006; Vairappan et al. 2008). Concerning commercial aspects, a high epiphytic load reduces raw material value (Buschmann et al. 2001; Vairappan 2009).

In subtidal and intertidal natural beds of *Gracilaria* species, epiphytism has been observed by Brawley and Xiugeng (1988) and González et al. (1993). But these investigations focused on subtidal and intertidal open cultures (Kuschel and Buschmann 1991; Buschmann et al. 1997, 2001; Leonardi et al. 2006), as well as on tank and pond cultures (Edding et al. 1987; Friedlander 1992; Pickering et al. 1993; Svirski et al. 1993; Friedlander et al. 1996, 2001). In turn, Fletcher (1995) reviewed epiphytism in *Gracilaria* farms and Muñoz and Fotedar (2010) updated the list of epiphytes reported on *Gracilaria* spp. Experimental research on this subject (Buschmann and Gómez 1993; Buschmann et al. 1997) is restricted to the chemical relationships between epiphytes and *Gracilaria* species, as well as to host defence responses (Santelices and Varela 1993; Friedlander et al. 1996, 2001; Weinberger and Friedlander 2000). Regarding the anatomical relationships between *Gracilaria* species and its epiphytes, Dawes et al. (2000) reported *Ulva lactuca* penetration into *G. tikvahiae* and *G. cornea*. However, the only comprehensive studies on the characterisation of diverse epiphyte–*Gracilaria* interactions were performed with *Gracilaria chilensis* and *Gracilaria cliftonii* (Leonardi et al. 2006; Muñoz and Fotedar 2010).

In this study, we report the temporal variation of whole epiphyte groups growing on *G. gracilis* in the natural population of Bahía Bustamante. The anatomical relationships between the host and the identified epiphyte species were characterised at ultrustructural level. With the background of our previous knowledge on the characteristics of the algal bed, together with environmental variables of the area (Martín et al. 2011), this study aims to relate the particular features of the host that affect epiphyte development as well as those of the epiphytes that modify the growth of *G. gracilis*.

Materials and methods

Bahía Bustamante (45°08′ S, 66°32′ W) is located in the north of Golfo San Jorge (Department of Escalante, Chubut province). The bed of *G. gracilis* grows at the south of the bay, between 0 and 8 m below the mean low water level. Field sampling was performed monthly over 2 years,

between March 2006 and February 2008 (totalling 20 samples in all). *G. gracilis* samples were collected by scuba diving. Each sample consisted of 20 sampling units of 0.25 m^2 each. The sampling units were placed on four transects parallel to the shore laid 100 m from each other and beginning 100 m away from the shore. On each transect, five sampling units were located at 100-m intervals. For each sampling unit, drained wet biomass of larger size epiphytes was determined. For each sample, 100 *G. gracilis* whole thalli were randomly selected for examination, except for samplings consisting of less than 100 individuals, which were totally examined.

The epiphyte density was evaluated by observation with a binocular microscope, and expressed as epiphyte number per square centimetre on *G. gracilis*. Differences among samples were studied by one-way analysis of variance (ANOVA) performed with InfoStat Professional 2012 software (Di Rienzo et al. 2012). Cube root transformation of data was used for homoscedasticity (Levene's test, $\alpha = 0.05$).

The host–epiphyte interfaces were studied with light microscopy and transmission electron microscopy (TEM). Five fragments of each infected thallus were fixed in 3 % glutaraldehyde in 0.1 M Na–cacodylate buffer (pH 7.4) containing 0.25 M sucrose. Then, fragments were trimmed and transferred to a fresh fixative solution containing 1.5 % paraformaldehyde. Fixation was followed by a series of rinses in cold 0.1 M Na–cacodylate buffer with gradually decreasing sucrose concentrations. Then, the samples were subjected to post-fixation in 2 % OsO$_4$ in 0.1 M Na–cacodylate buffer, dehydration in acetone and infiltration in Spurr's resin. For light microscopy, semithin sections (0.5–1 μm) were stained with toluidine blue. For TEM, ultrathin sections were stained with aqueous uranyl acetate followed by lead citrate and observed in a JEOL 100CX-II TEM operated at 80 kV. On the basis of these analyses and taking into account a previous study in *G. chilensis*, the infections were classified in five types, in accordance with epiphytic attachment strength and invasiveness and with the degree of damage that the infection causes in the host (Leonardi et al. 2006).

Results

Epiphytic diversity and density

Twenty-nine algal species were recorded as *G. gracilis* epiphytes between March 2006 and February 2008 (Table 1). These included seventeen Rhodophyta, nine Heterokontophyta (class Phaeophyceae), two Chlorophyta and one Cyanophyta species.

Although no clear seasonality was observed in the total epiphytic density, lower relative values for both years were registered in spring. Total epiphyte density ranged from

Table 1 Epiphyte species on *G. gracilis*

	Infection type	Occurrence
Rhodophyta		
O. Compsopogonales		
Sahlingia subintegra (Rosenvinge) Kornmann	II	R
O. Acrochaetiales		
Acrochaetium sp. Nägeli	II	F
Rhodocorton sp. Nägeli	II	R
O. Ceramiales		
Anotrichium furcellatum (J. Agardh) Baldock	II	R
Antithamnion densum (Suhr) Howe	II	R
Antithamnionella sp. Lyle	II	R
Callithamnion gaudichaudi C. Agardh	II	R
Callithamnion montagnei Hooker and Harvey	II	R
F. Ceramiaceae		
Ceramium rubrum (Hudson) C. Agardh	V	A
Ceramium strictum Greville ex Harvey	V	R
F. Rhodomelaceae		
Heterosiphonia merenia Falkenberg	V	R
Neosiphonia harveyi (J.Bailey) Kim, Choi, Guiry and Saunders	V	F
Polysiphonia abscissa Hooker and Harvey	V	A
Steblocladia camptoclada (Mont.) Falkenberg	II	R
O. Rhodymeniales		
Lomentaria clavellosa (Turner) Gaillon	II	R
O. Corallinales		
Corallina officinalis L.	IV	R
Titanoderma sp. Nägeli	IV	F
Phaeophyceae		
O. Ectocarpales		
Acinetospora crinita (Carmichael) Kornman	I	R
Ectocarpus constanciae Hariot	I	F
Hincksia mitchelliae (Harvey) Silva	I	F
Leathesia difformis (L.) Areschoug	I	R
Punctaria latifolia Greville	II	R
O. Dictyotales		
Dictyota dichotoma (Hudson) Lamouroux	II	R
O. Sphacelariales		
Sphacelaria fusca (Hudson) S.F. Gray	II	A
Petalonia fascia (O. F. Müller) O. Kuntze	II	R
Halopteris sp. Kützing	II	A
Chlorophyta		
O. Ulvales		
Sporocladopsis novae-zelandiae Chapman	II	R
Chaetomorpha sp. Kützing	II	R
Cyanophyta		
Calothrix confervicola (Dillwyn) C. Agardh	I	A

Infection types (I, II, IV, V) and occurrence

A abundant, *F* frequent, *R* rare

0.037 ind. cm^{-2} (November 2006) to 39.37 ind. cm^{-2} (April 2007). At least a tenfold increase in the ephiphyte density values were measured for the second sampling year. Significant differences (ANOVA, 18 *df*, *F*=22.38, *P*<0.01) between the first sampling year and second sampling year were found. The maximum epiphytic biomass was recorded on May 2007 (1.17 kg m^{-2}), a month after the maximum density value appeared (Fig. 1).

Ceramiales, Acrochaetiales, Sphacelariales, and *Calothrix confervicola* were the most frequent and abundant epiphytes (Fig. 2). The dominant epiphytes during most of the sampling period were Ceramialian algae (Fig. 2), *Ceramium rubrum* yielding the highest density (Fig. 3a). The values ranged from 0.09 ind. cm^{-2} (52 % of the total amount) in September 2006 to 17.4 ind. cm^{-2} (44.18 % of the total amount) in April 2007. In August 2006, *C. rubrum* density represented 73.92 % of the epiphytes. The Rhodomelaceae (Ceramiales) reached lower densities than *C. rubrum*, their maxima appearing in summer, with 2.17 ind. cm^{-2} in January 2007 (Fig. 3b). The considerable increase in epiphyte density in the summer and early autumn could be attributed to the presence of microscopic stages of Ceramiales, whose length was less than 1 mm (Fig. 3a, b). *C. confervicola* was the main epiphyte in February 2007, May 2007, November 2007 and February 2008. In February 2007, *C. confervicola* comprised 57.12 % of the total epiphytes, achieving its highest density in April 2007 (15.8 ind. cm^{-2}; 40.11 % of the total amount) (Fig. 2).

Anatomical relationships between *G. gracilis* and its epiphytes

The healthy *G. gracilis* thallus has two layers of cortical cells and several layers of medullary cells in cross section. The epidermal cell wall consisted of the outermost decklamella and the outer and the inner wall layers (Fig. 4). Each cortical cell has a central nucleus, surrounded by floridean starch granules and numerous parietal chloroplasts that occupied most of the cytoplasm (Fig. 5).

C. confervicola (Figs. 6 and 7) and Ectocarpales species, such as *Ectocarpus constanciae* and *Hincksia mitchelliae*, developed type I infection (i.e., epiphytes weakly attached to the host surface without host tissue damage).

Type II infection (i.e., epiphytes strongly attached to the host surface, but without host tissue damage) was caused by some red algae, such as *Antithamnion densum* (Fig. 8) and *Acrochaetium* sp., by the green algae *Chaetomorpha* sp. (Fig. 9) and *Sporocladopsis novae-zelandiae* and by several Phaeophyceae. *Dictyota dichotoma* was mostly represented by thallus fragments attached to the host by hyaline rhizoids (Fig. 10) and also by young thalli (Fig. 11). *Punctaria latifolia* showed a similar pattern of infection (Fig. 12), but, in this case, the components in outer wall layer of *G. gracilis* exhibited a laxer arrangement (Fig. 13) when compared to
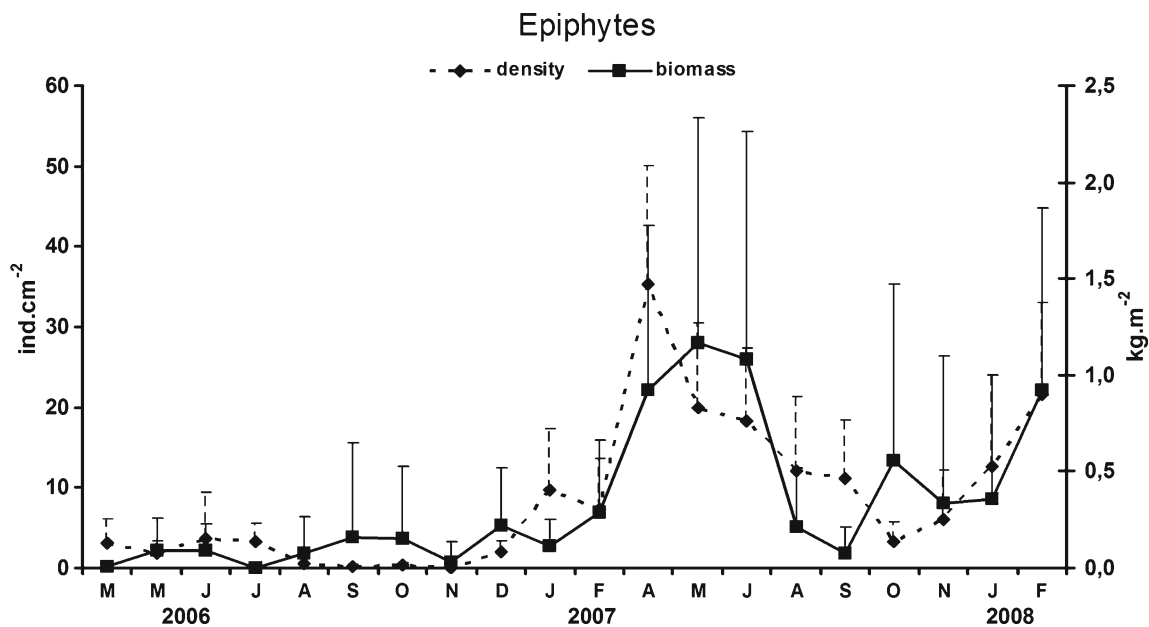
Fig. 1 Mean epiphytic density and biomass (wet weight). *Bars* indicate standard deviation

control cells (Fig. 4). *Sphacelaria fusca* was an exception within type II infection because it brought about conspicuous vacuolization in the host cortical cells even though the cell walls in *G. gracilis* remained intact (Figs. 14 and 15).

Epiphytes developing type III infection (i.e., epiphytes that breach the deck-lamella and penetrate the outer layer of the host cell wall without damaging its cortical tissue) were not observed in *G. gracilis*.

Type IV infection (i.e., epiphytes that penetrate the deck-lamella and the outer layer of the host cell wall disorganizing its cortical tissue) was represented by young thalli of the calcareous red alga *Corallina officinalis*. Its rhizoids

penetrated the host cell wall, which lost its deck-lamella in the area in contact with the epiphyte. Changes were observed in cortical cells of *G. gracilis*, namely the number of cortical cell layers increased from two to four, the outer layer of cortical cells was vacuolated and their external walls considerably thickened (Fig. 16). A similar type of infection was recorded for the calcareous crustose red alga *Titanoderma* sp. (Fig. 17). However, in this species, there was no rhizoid penetration, and the host cell wall appeared so compressed that it was impossible to discern the outer from the inner layer (Fig. 18).

Type V infection (i.e., epiphytes that penetrate deeply the host cortex and reach the medullary tissue) was exemplified by
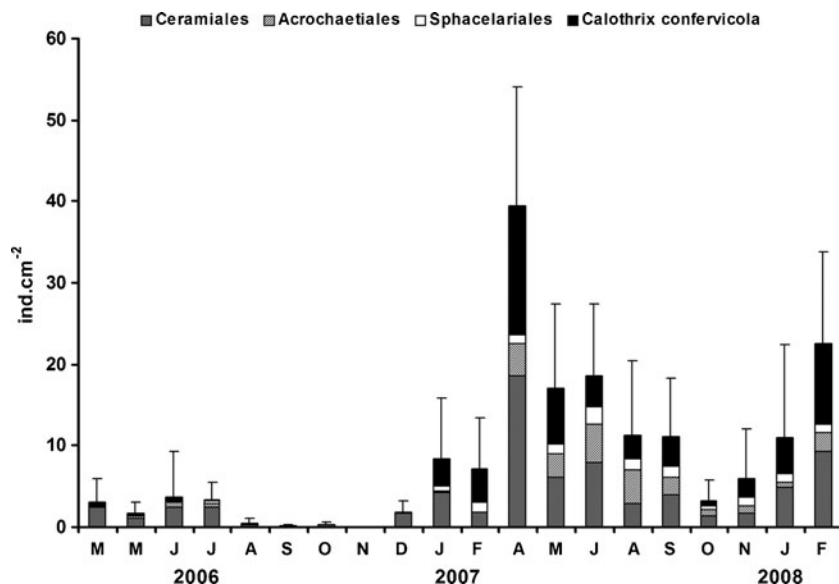

Fig. 2 Mean epiphytic density of Ceramiales, Achrochaetiales, Sphacelariales and *C. confervicola* from March 2006 to February 2008. *Bars* indicate standard deviation
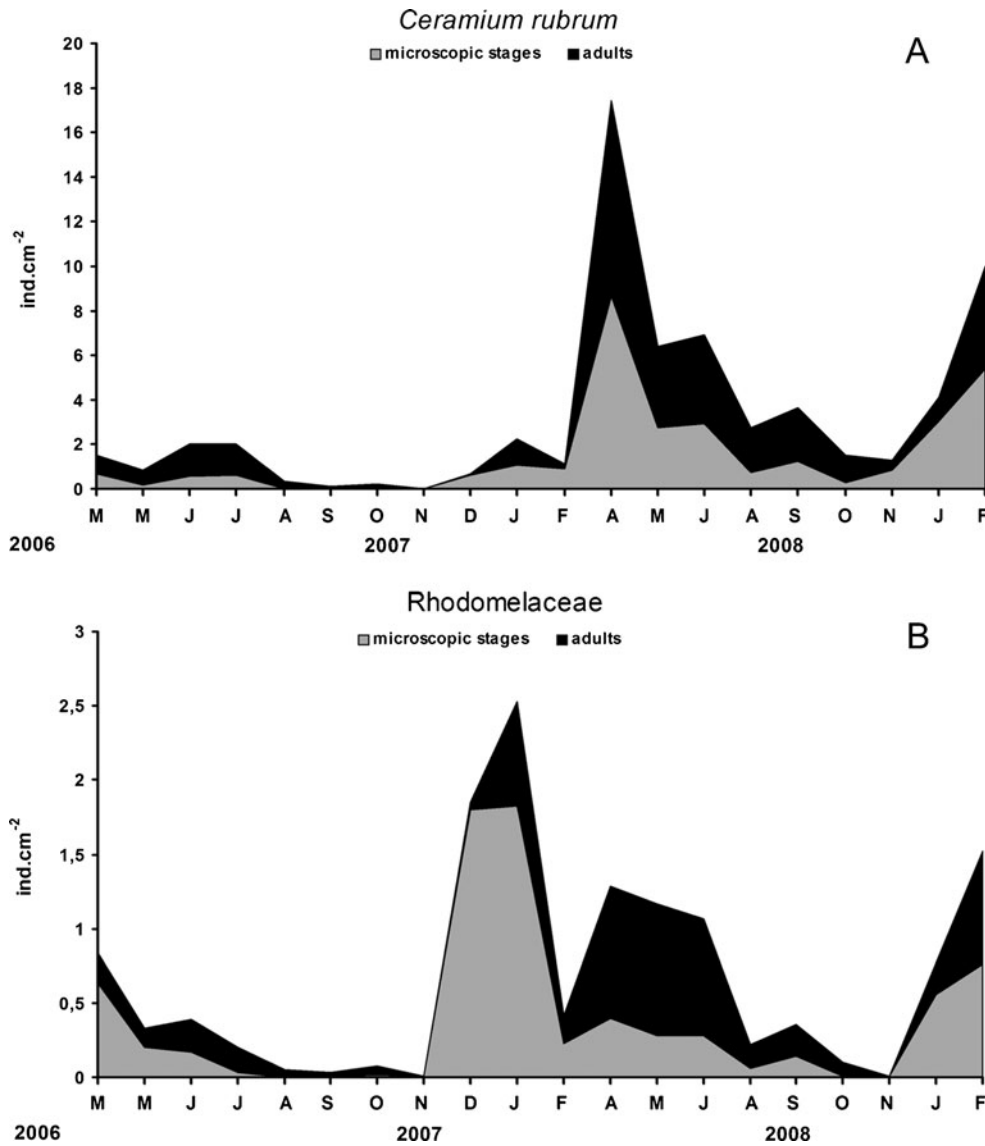
Fig. 3 Mean density of microscopic and adult Ceramiales stages from March 2006 to February 2008. **a** *C. rubrum* density. **b** Rhodomelaceae density

Ceramiales species, such as *C. rubrum*, *Ceramium strictum*, *Polysiphonia abscissa*, *Neosiphonia harveyi* and *Heterosiphonia merenia* (Figs. 19, 20, 21, 22, 23, and 24). Their rhizoids penetrated the host intercellularly (Figs. 19, 20, and 22) and in some cases they traversed perpendicularly through the epidermal cell wall (Fig. 21). In the infected thalli, areas compromised by the epiphyte's penetrating rhizoids, the host cells presented vacuolization (Fig. 23) or wavy profiles of the plasmalemma and the inner wall (Figs. 22 and 24). A severe cellular compression could also be observed, mainly in the infection produced by *P. abscisa* (Figs. 19 and 22).

Discussion

The *G. gracilis* population at Bahía Bustamante is the substratum for several epiphytes displaying various degrees of

infection and/or attachment. Having been reported for other macroalgal hosts in Argentina (Boraso de Zaixso and Zaixso 2007; Miravalles 2009), the epiphytic species do not exhibit host specificity for *G. gracilis*. Moreover, some of them have been cited as free-living species (Eyras and Sar 2003; Casas et al. 2004; Boraso de Zaixso and Akselman 2005). Regarding epiphytes on *G. gracilis* (as *Gracilaria verrucosa*) populations in Golfo Nuevo (42°42′0″ S, 64°36′0″ W), Boraso de Zaixso (1983) also identified *Antithamnionella* sp., *Ceramium rubrum*, *Hincksia mitchelliae*, *D. dichotoma* and *Chaetomorpha* sp. Most of the ceramialean epiphytes coincide to a good extent with the ones cited for other *Gracilaria* species worldwide (Brawley and Xiugeng 1988; Fletcher 1995; Leonardi et al. 2006; Muñoz and Fotedar 2010).

Throughout this 2-year sampling period, the most remarkable variation in infection intensity was a tenfold
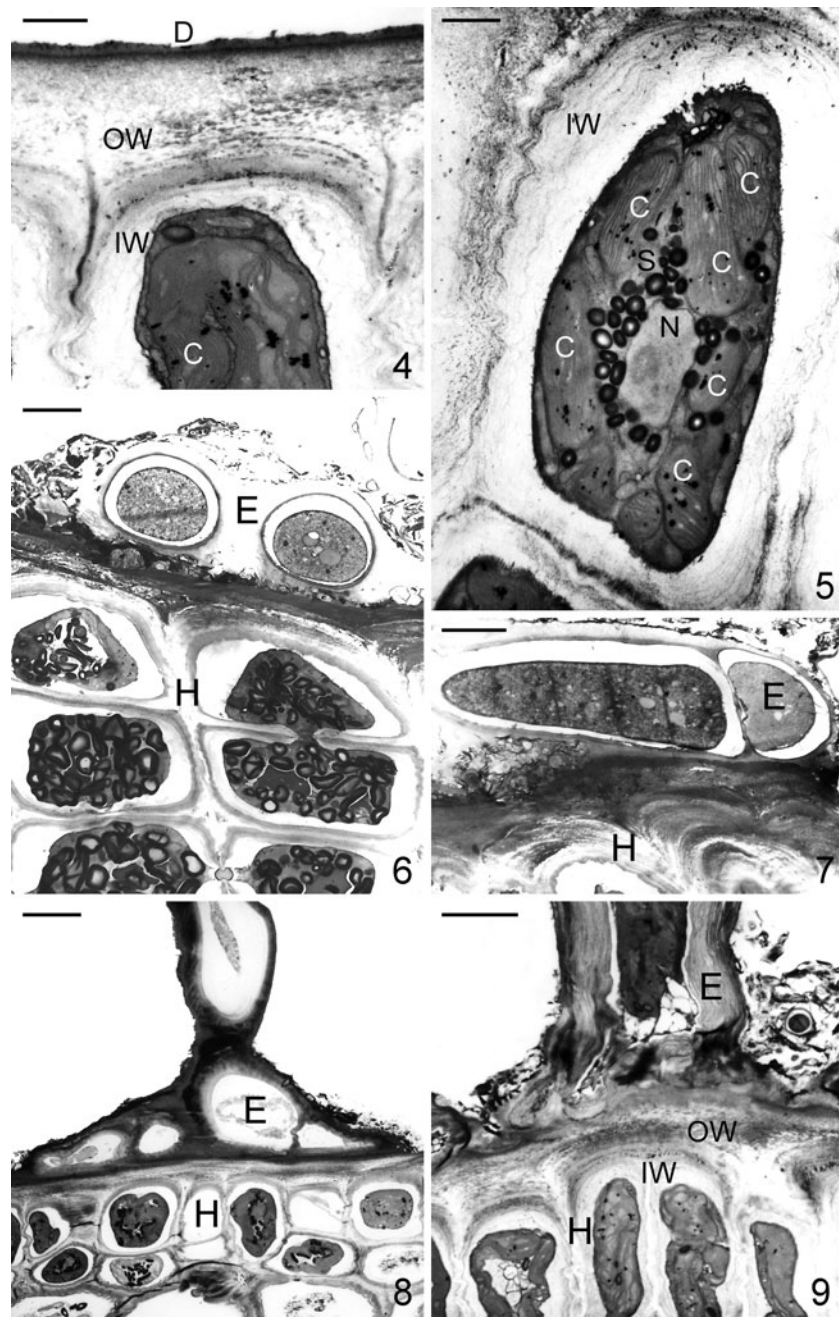
Figs. 4–9 Fine structure of *G. gracilis* healthy cells and thalli infected with different epiphytes. *4–5* Healthy cells. *4* Detail of epidermal cell wall. *5* Detail of a cortical cell. *6–7* Type I infection. *C. confervicola* growing on the host surface. Transversal and longitudinal sections through the epiphytic filaments, respectively. *8–9* Type II infection. *8 A. densum* basal portion attached to the host. *9 Chaetomorpha* sp. attached to the host. *Scale bars*: 1.5 μm (*4–5*), 5 μm (*6–8*), 10 μm (*9*). Abbreviations: *C*, chloroplast; *D*, deck-lamella; *E*, epiphyte; *H*, host; *IW*, inner wall; *N*, nucleus; *OW*, outer wall; *S*, floridean starch

interannual increase in epiphyte density between the first and the second year. According to Pizarro and Santelices (1993), long-term recording of the most significant abiotic factors might allow the correlation of environmental variations with changes in *Gracilaria* productivity and with epiphyte pressure. The relation between blooms of different *G. chilensis* epiphyte species and variations in the surface water temperature and light intensity were analysed (Pizarro and Santelices 1993). Epiphyte density changes have also been ascribed to variables such as salinity (Vairappan 2006), as well as increases in irradiance and water temperature (Westermeier et al. 1991; Ugarte and Santelices 1992; González et al. 1993; Buschmann et al. 1997). However, as was previously noted by Martín et al. (2011), changes in
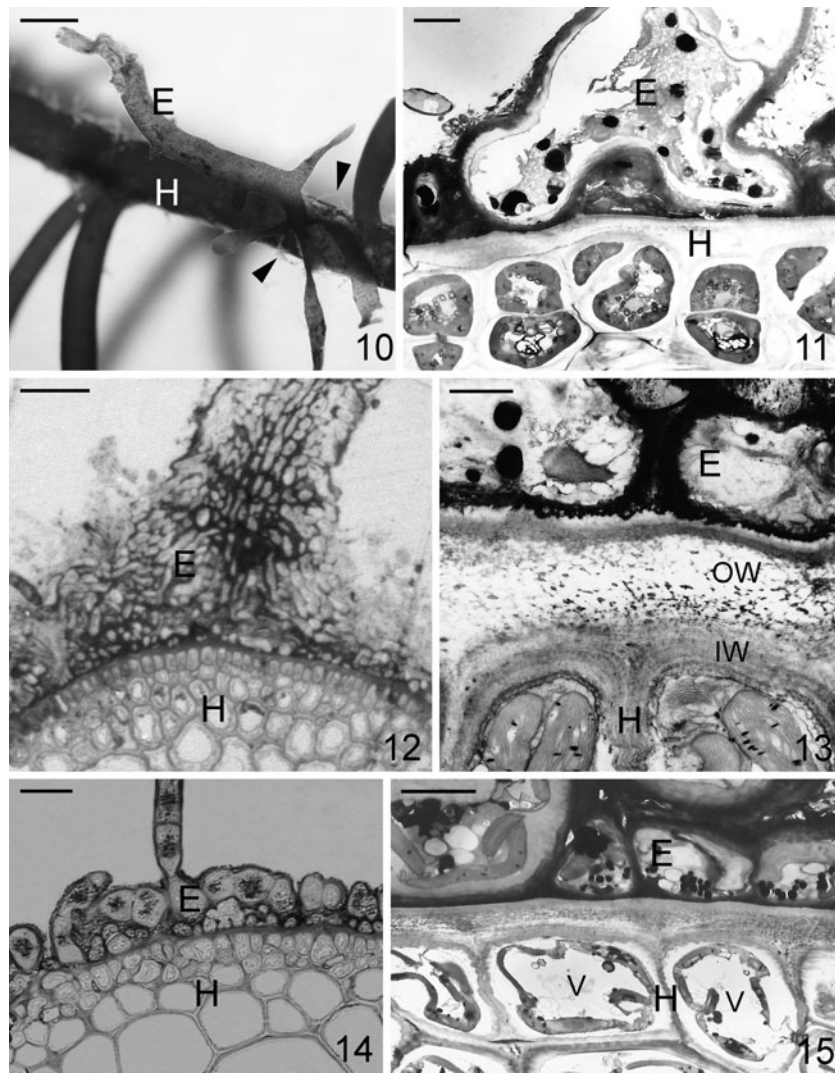
Figs. 10–15 Type II infection in *G. gracilis*. *10–11 D. dichotoma. 10* Fragment of *D. dichotoma* attached to the host. *Arrowheads* indicate hyaline rhizoids. *11* Detail of epiphytic rizhoid and the host interface. *12–13 P. latifolia. 12* Interaction between host and epiphyte. *13* Detail of the interface. Note the lax disposition of the *G. gracilis* outer wall layer. *14–15 S. fusca. 14* Interaction between host and epiphyte. *15* Detail of the interface. Note the *G. gracilis* vacuolated cortical cells. *10* Stereoscopic micrograph. *11, 13, 15* TEM micrographs. *12, 14* Light micrographs. *Scale bars*: 2 mm (*10*), 5 μm (*11, 13, 15*), 40 μm (*12*), 20 μm (*14*). Abbreviations: *E*, epiphyte; *H*, host; *IW*, inner wall; *OW*, outer wall; *V*, vacuole

epiphyte density in Bahía Bustamante could not be attributed to variations in either temperature or salinity or nutrients. Conclusions could not be drawn in respect with light intensity, since these measurements were not carried out.

Instead, an inverse relationship between epiphyte density and *G. gracilis* biomass and thallus size was found (Martín et al. 2011). During the first year, large *G. gracilis* biomass, big thallus size and a high proportion of reproductive thalli were observed. In contrast, during the second year, the host population was characterised by low biomass, small thallus size and a high proportion of vegetative thalli (Martín et al. 2011). Epiphyte spore recruitment and settlement limit epiphyte abundance. The settlement of epiphytes necessarily depends on the availability of suitable substrata. Expectedly,

larger host thalli would favour the attachment of epiphytes, especially where there is a sandy bottom. This does not seem to be the case for this population of *G. gracilis*, since a lower load of infection is noted for larger-sized thalli. An explanation can be found in the rubbing effect of larger thalli leading to host self-cleaning through thallus movement, as suggested by Lobban and Baxter (1983), Pizarro (1986), Lignell et al. (1987) and Dawes (1992).

During the second year, the smaller average host thallus size observed could be a consequence of both recruitment from spores and thallus fragmentation (Martín et al. 2011). Damaged tissues in fragmented thalli of the host favour the colonisation by epiphyte spores (Lobban and Baxter 1983). This behaviour is consistent with the large *C. rubrum* and
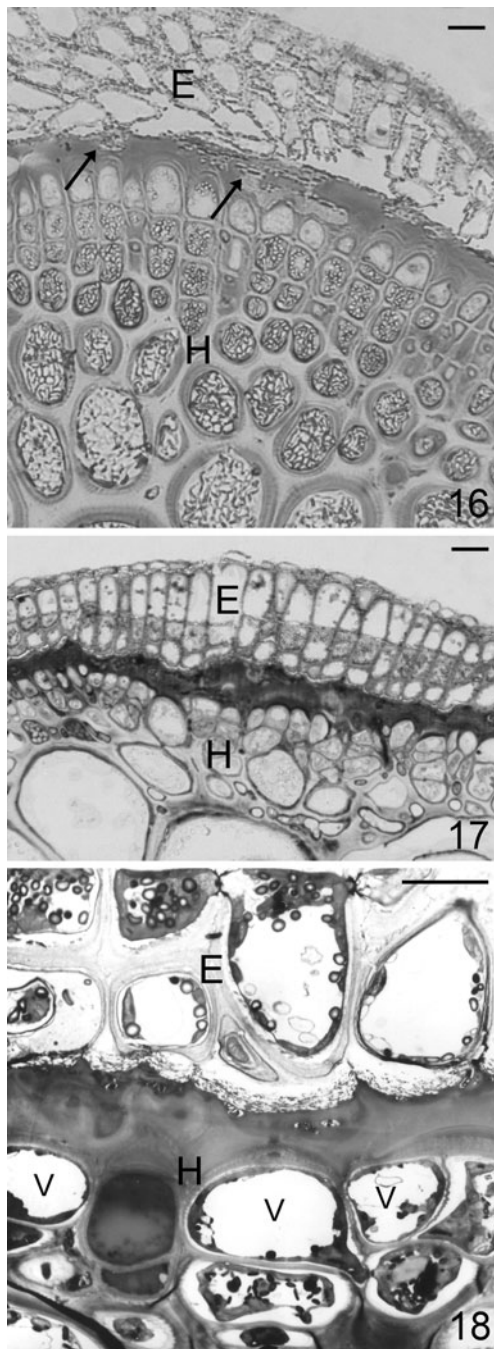
Figs. 16–18 Type IV infection in *G. gracilis*. *16 C. officinalis* disrupting *G. gracilis* deck-lamella and penetrating the wall. The *arrows* indicate the epiphytic rhizoids. *17–18*. *Titanoderma* sp. *17* General view of the interface. *18* Detail of the interface. Outer and inner layers of the host wall appear fused in the attachment site. Note the *G. gracilis* vacuolated cortical cells. *16–17* Light micrographs. *18* TEM micrograph. *Scale bars*: 5 μm (*16–18*). Abbreviations: *E*, epiphyte; *H*, host; *V*, vacuole

rhodomelaceaen recruitment in early 2007. Moreover, the damage caused by epiphytes, mainly Ceramiales, in *G. gracilis* thalli, can enhance their fragmentation (Kuschel and Buschmann 1991; Buschmann and Gómez 1993;

González et al. 1993), contributing to reduce the biomass and the thallus size of the host. The considerable increase in microscopic stages for the major epiphytic species (*C. rubrum* and Rhodomelaceae) seems to be an important factor in this interannual variation in epiphyte density. In fact, Santelices et al. (1995) and Buschmann et al. (1997) have suggested that the bank of microscopic propagules is important for the survival of Ceramiales and other perennial species.

Representatives of Ceramiales have been also been described as dominant and inflicting a negative impact on *G. chilensis* (Westermeier et al. 1991; González et al. 1993; Buschmann et al. 1997; Leonardi et al. 2006), *Chondracanthus chamissoi* (Vásquez and Vega 2001) and on *Kappaphycus alvarezii* (Hurtado et al. 2006; Vairappan 2006; Vairappan et al. 2008). Even though seasonal epiphytism pattern may differ in intensity and time of occurrence between different hosts and areas (Buschmann et al. 1995), Ceramialean epiphytism abundance patterns seem to be common for different hosts, latitudes and environments.

It is difficult to establish a periodicity for epiphyte abundance peaks in Bahía Bustamante, partly because a longer sampling period is lacking. Yet, in this biannual period, a bimodal abundance distribution is suggested, even when no clear seasonality is evident, except for a tendency for minima in spring. This bimodal pattern in epiphyte abundance has also been reported for *G. chilensis* (Westermeier et al. 1993) and *K. alvarezii* (Vairappan 2006). Buschmann et al. (1997) reported a decrease in epiphytes in spring due to a renewed *G. chilensis* growth. Then, the host had a competitive advantage in this case, which could explain the decrease in *G. gracilis* epiphyte density at Bahía Bustamante in spring. Instead, epiphyte abundance is related to spore recruitment, as discussed above. In short, a combination between epiphyte recruitment throughout the year and the status of the host population favouring or deterring the development of epiphyte sporelings might be the key to the seasonal and also interannual variations of the epiphytic density.

In this work, *C. confervicola* is described for the first time as an epiphyte on *Gracilaria*. This species was one of the most abundant. According to its type of infection, no host severe tissue damage is provoked. The small size of this cyanophyte is insufficient to produce a significant shading effect (except perhaps at very high densities) and to contribute to *G. gracilis* meaningful weight. The latter can be deduced by the differences in biomass and density of epiphytes found in April and May 2007. In April 2007, high density of total epiphytes and, in particular, of *C. confervicola* was observed, but epiphytic biomass was lower than in May 2007.

Sahlingia subintegra is described as type II infection in *G. gracilis*, while it was characterised as type III infection in
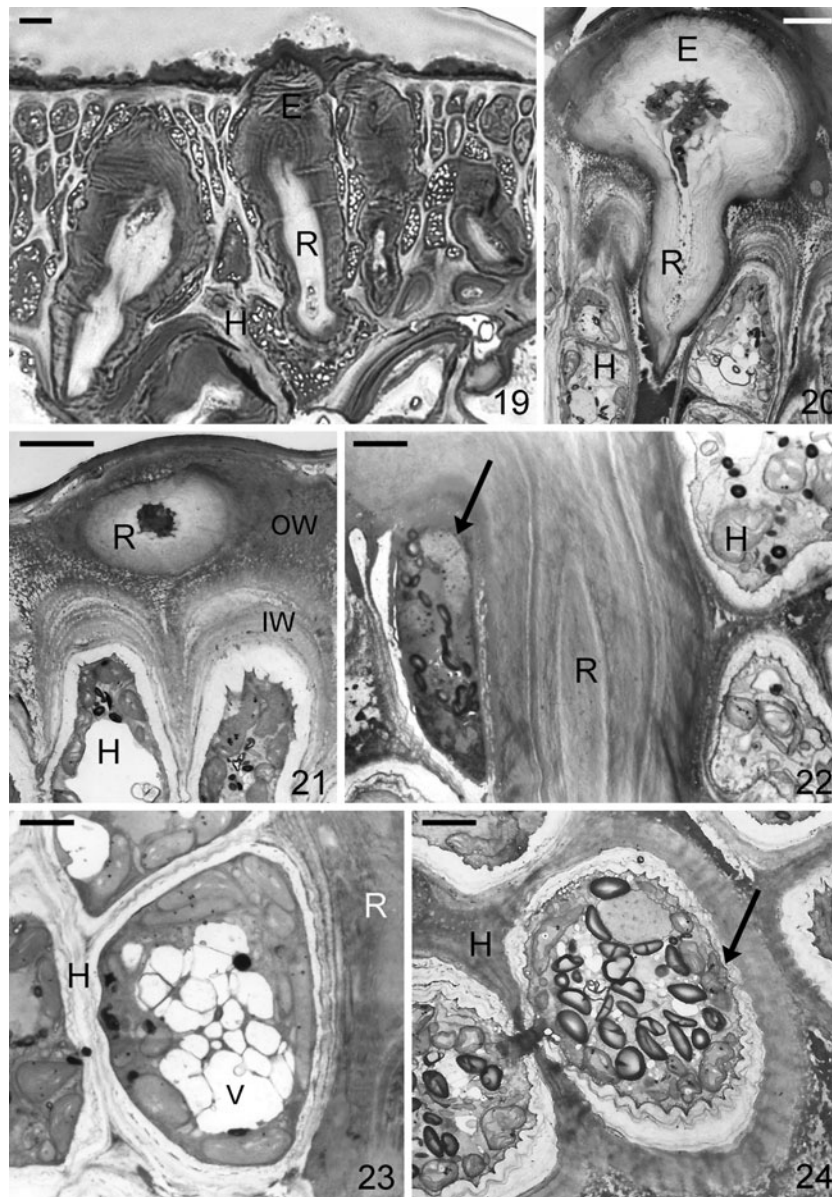
Figs. 19–24 Type V infection in *G. gracilis*. *19, 22 P. abscissa*. *20, 21, 23, 24. C. rubrum*. *19* General view of epiphytic rhizoids penetrating the host tissue. Note that numerous *G. gracilis* cells are severely compressed. *20* Detail of epiphytic rhizoid penetrating intercellularly. *21* Detail of epiphytic rhizoid perpendicularly penetrating the host's epidermal wall. *22–24* Different damages caused by rhizoid penetration into the host. *22* Very compressed host cell adjacent to the rhizoid (*arrow*). *23* Host cell highly vacuolated. *24* Host cells with wavy profiles of the plasmalemma and the inner wall (*arrow*). *19* Light micrograph. *20–24* TEM micrographs. *Scale bars*: 10 μm (*19*), 4 μm (*20–21*), 2 μm (*22–23*), 3 μm (*24*). Abbreviations: *E*, epiphyte; *H*, host; *IW*, inner wall; *OW*, outer wall; *R*, rhizoid; *V*, vacuole

G. chilensis (Leonardi et al. 2006). This difference in infection type may be due to the smaller *S. subintegra* thalli found on *G. gracilis*. Being less developed, they were unable to breach the deck-lamella. This difference may also be due to unlike texture or thickness of the *G. gracilis* deck-lamella (Dawes et al. 2000). Regarding type IV infection, it was only represented by *C. officinalis* and *Titanoderma* sp. Calcareous red algae are recorded for the first time as epiphytes on *Gracilaria*.

Not only due to their abundance did Ceramiales species cause a deleterious effect on *G. gracilis* but also because of their type V infection pattern, which implies considerable host tissue damage. According to the stress imposed by Ceramialean epiphytic invasion, *G. gracilis* thallus fragmentation may be enhanced or thalli completely obliterated (Poblete and Inostroza 1987), notwithstanding a higher susceptibility to bacterial attack derived from host cell-wall breakage (Vairappan 2006).

Waving of *G. gracilis* plasmalemma and inner wall layer, accompanied by its cell compression, indicates a mechanical action of the rhizoids inside the host tissue. Unlike the behaviour of *N. harveyi* (as *Polysiphonia harveyi*) on *G. chilensis* (Leonardi et al. 2006), no evidence was found in *G. gracilis* about the enzymatic digestion of its tissue. This disparity in epiphytic performance may be due to the more aggressive *N. harveyi*'s behaviour or to differences in the host wall structure (Dawes et al. 2000), as was previously indicated. However, further studies are required to draw a conclusion.

The degree of interaction between epiphyte–*Gracilaria* spp. depends on (1) the epiphyte species and its stage of development and (2) the host's stage and the structure and composition of its cell wall. However, some generalisations and characterisations of the different epiphyte groups can be made in relation to their consequences to their hosts. The anatomical interactions observed in *G. gracilis* and other *Gracilaria* spp. so far indicate that phaeophyceaen epiphyte species are restricted to the surface of the host (Leonardi et al. 2006). Regarding green algae epiphytes, two types of attachment are observed: (a) species strongly attached to the host surface without penetration, like some filamentous ulvalean, ulotrichalean and cladophoralean epiphytes; and (b) species that provoke alteration of the cellular structure at the attachment site, like the ulvophycean *Ulva* and *Bryopsis* (Dawes et al. 2000; Leonardi et al. 2006; Muñoz and Fotedar 2010). Red algae, the most dominant group in all *Gracilaria* spp. studied, present diverse types of interactions: (a) different *Ceramium*, *Polysiphonia* and *Neosiphonia* species showed the most aggressive interaction, where epiphyte rhizoids penetrated deeply into the host; (b) other species of Ceramiales, Acrochaetiales, Compsopogonales, Rhodymeniales and Batrachospermales were observed strongly attached to the *Gracilaria* deck-lamella, without damaging the host; and (c) Corallinalean epiphyte species showed a deeper invasion of the host (Leonardi et al. 2006; Muñoz and Fotedar 2010). Only a few studies record cyanobacteria epiphytes on *Gracilaria* spp. (Fletcher 1995; Leonardi et al. 2006). In this group, two types of anatomical interactions were observed: (a) a weak attachment represented by the filamentous Oscillatorialean *Calothrix* and (b) a superficial host penetration caused by the Chamaesiphonalean *Xenococcus* (Leonardi et al. 2006).

This is the first report on epiphytic diversity and abundance and the anatomical relationships between the host and its epiphytes in a *G. gracilis* population of southwestern Atlantic coast. This research provides important basic information to be considered when designing a management plan for sustainable exploitation of *G. gracilis* beds, as well as useful information for future mariculture development.

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