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Distribution of epiphytic macroalgae on the thalli of their hosts in Cuba

Yander Luis Diez García[1], Abdiel Jover Capote[2,6], Ana María Suárez Alfonso[3], Liliana María Gómez Luna[4] and Mutue Toyota Fujii[5]

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ABSTRACT

We investigated the distribution of epiphytic macroalgae on the thalli of their hosts at eight localities along the southeastern coast of Cuba between June 2010 and March 2011. We divided he epiphytes in two groups according to their distribution on the host: those at the base of the thallus and those on its surface. We determining the dissimilarity between the zones and the species involved. We identified 102 taxa of epiphytic macroalgae. There were significant differences between the two zones. In 31 hosts, the number of epiphytes was higher on the surface of the thallus, whereas the number of epiphytes was higher at the thallus base in 25 hosts, and the epiphytes were equally distributed between the two zones in five hosts ($R=-0.001$, $p=0.398$). The mean dissimilarity between the two zones, in terms of the species composition of the epiphytic macroalgae, was 96.64%. *Hydrolithon farinosum* and *Polysiphonia atlantica* accounted for 43.76% of the dissimilarity. Among macroalgae, the structure of the thallus seems to be a determinant of their viability as hosts for epiphytes.

Key words: Chlorophyta, epiphytism, distribution, Phaeophyceae, Rhodophyta

Introduction

The structure of intertidal marine communities is determined by a combination of physical factors and biotic interactions (Little & Kitching 1996; Wernberg & Connell 2008). The establishment of marine macroalgae involves a number of complex physical interactions, as well as biological, ecological and chemical processes at the microscale, from the release of propagules by reproductive adults to their migration to appropriate substrates, initial adhesion to a surface, permanent attachment and development (Reed 1990a; Brawley & Johnson 1992; Vreeland & Epstein 1996). Because macroalgae constitute a key component of coastal communities, they are associated with other organisms and processes and have been central to the debate about the nature and scope of the structure and dynamics of those communities (Foster 1990, 1991; Paine 1991; Underwood 2000).

In the intertidal zone, environmental gradients also occur at smaller scales, such as within the host zone of receptivity, where there is a light intensity gradient between the periphery and the interior of the thallus, and along host fronds, where there is a gradient in biomass, which decreases progressively from the holdfast to the frond tip. The investigation of the distribution of epiphytes at different scales is a potentially productive approach. It is important to understand the patterns of abundance of all sympatric epiphytic species along the various gradients, because interspecific relationships could represent one of the factors that explain their distribution (Longtin *et al*. 2009).

The texture and structure of the host thalli are frequently exploited by epiphytes, thus increasing habitat complexity (Hacker & Steneck 1990). The epiphytic macroalgae with a filamentous or branched structure usually present a high degree of structural complexity and might therefore increase the suitability of host algae as habitats for mesoherbivores (Martin-Smith 1993).

In marine communities, the plant substrates that are the most widely colonized by are seagrasses and macroalgae, because they provide the necessary space, shelter and nutrition (Aguilar-Rosas & Galindo 1990). Macroalgae morphology might be related to the density of the community (Reed 1990b; Ang & DeWreede 1992). High densities of adults can help reduce desiccation during low tide due to overlapping thalli, as well as reducing water flow, providing shade and microhabitats below, which can affect the structure of the community (Bruno *et al*. 2003).

The host macroalgae differ considerably in their suitability as substrates for epiphytes. This difference might be

[1] Administración Portuaria Santiago de Cuba, Santiago de Cuba, Cuba
[2] Universidad de Oriente, Departamento de Biología, Santiago de Cuba, Cuba
[3] Universidad de La Habana, Centro de Investigaciones Marinas, Ciudad Habana, Cuba
[4] Universidad de Oriente, Centro Nacional de Electromagnetismo Aplicado, Laboratorio de Ecotoxicología, Santiago de Cuba, Cuba
[5] Instituto de Botânica, Seção de Ficologia, São Paulo, SP, Brazil
[6] Author for correspondence: abdiel@cnt.uo.edu.cu

related to the longevity of the species, which is a determining factor in the process of substrate colonization by epiphytes; in some cases, this phenomenon is more evident in the older parts of the thallus (Aguilar-Rosas & Galindo 1990). In *Zostera noltii*, Lebreton *et al*. (2009) found that the number of diatoms was higher on young leaves than on old leaves.

The suitability of macroalgae as substrates for epiphytes can also vary depending on the morphological characteristics of the base; the degree of branching; the roughness and texture of the surface; the production of allelopathic substances such as mucilage; and the thallus growth rate (Lobban & Harrison 1997). When the thallus surface has little mucilage, it provides favorable conditions for the establishment of epiphytes (Paula & Oliveira-Filho 1980; Széchy *et al*. 2006).

In tropical and subtropical regions, studies have shown reductions in the size of communities that develop on rocky shores, especially communities of macroalgae and epiphytes. Such studies have been limited to identifying epiphytic macroalgae species without studying the basic aspects of their ecology (Aguilar *et al*. 1998; Saad-Navarro & Riosmena-Rodríguez 2005). Understanding the spatial scales at which the rocky intertidal zone communities vary provides the necessary information to initiate the study of the relative importance of the various factors that can affect these communities and how those factors interact (Underwood *et. al*. 2000). Therefore, the objective of the present study was to determine the distribution of epiphytic macroalgae on the thallus of their hosts.

Material and methods

Study area

The study was conducted in the rocky intertidal zone between the municipalities of Aguadores and Baconao, Cuba, within the Baconao Biosphere Reserve (Managed Resource Protected Area), at eight locations (Fig. 1.): Aguadores 1, Aguadores 2; Sardinero; Jutici; Cajobabo; Verraco, Acuario and Baconao. Located east of the city of Santiago de Cuba, the study zone occupies an area of 5635 hectares of sea on the southeastern coast of the country, between Maisí and Cabo Cruz. It is characterized by a rocky intertidal zone with extensive fields of limestone (surface karst formation).

Sampling design

Samples were collected on a quarterly basis between June 2010 and March 2011, although inclement weather precluded sample collection in the month of September. Therefore, with the aim of collecting the greatest number of epiphytic species (Lecha & Chugaev 1989), we performed three samplings: one during the rainy season (in June); and two during the dry season (in December and in March). Samples were collected at low tide in the intertidal zone, which is characterized by short intervals of immersion and emersion.

We collected all epiphytic macroalgae and their hosts in 15 square metal containers (25 cm × 25 cm × 25 cm) distributed at random (Jover *et al*. 2012). All macroalgae

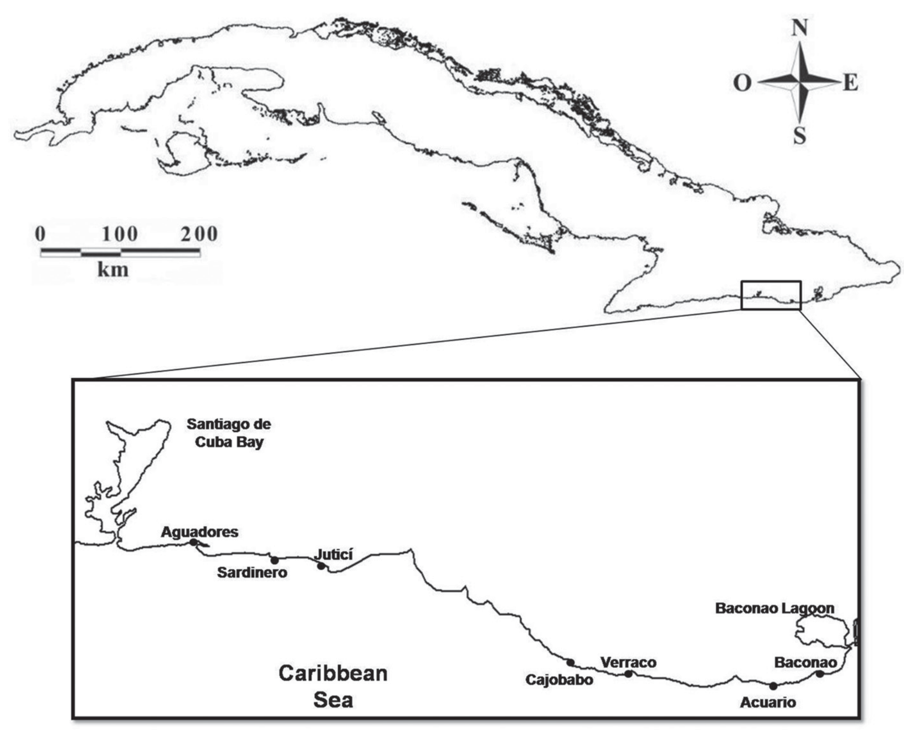

Figure 1. Location of the Aguadores-Baconao coastal sector and of the individual sampling sites.

that were growing on other macroalgae were classified as epiphytes, according to the criteria of Borowitzka *et al.* (2006). In accordance with Montañés *et al.* (2003), the epiphytic macroalgae were separated into two groups by their location on the thallus of the host: at the base or on the surface. The morphofunctional classification of the groups followed the criteria established by Littler & Littler (1984) and Steneck & Dethier (1994).

The macroalgae were identified down to the lowest possible taxonomic level on the basis of the specialized literature (Børgesen 1915-20; Taylor 1960; Littler *et al.* 1989; Littler & Littler 1997, 2000; Castro *et al.* 2008; Dawes & Mathieson 2008; Littler *et al.* 2008). The species list was created according to the taxonomic criteria established by Wynne (2011). For the higher classes (class, division, and kingdom), we followed the criteria established by Guiry & Guiry (2011) in Algaebase (http://www.algaebase.org/).

Data analysis

For each host macroalga and each zone of the thallus, we determined epiphyte species richness on the basis of the number of species observed (Ludwing & Reynolds 1988).

The origin and significance of differences between the zones of the host thalli were determined by analysis of similarity, with 999,999 permutations applied to the similarity matrix (Clarke & Warwick 2001). The similarity matrix was derived from the species presence and absence data using the Jaccard index. The principal species responsible for the dissimilarity were identified by similarity percentage analysis (Clarke 1993). These nonparametric multivariate tests were conducted with the statistical program Primer, version 6 (Clarke & Gorley 2006).

Results

Epiphytic macroalgae and their hosts: flora

The observed number in the rocky intertidal zone of the Aguadores-Baconao sector, we observed 102 taxa of epiphytic macroalgae (18 Phaeophyceae, 53 Rhodophyceae and 31 Chlorophyceae), belonging to 14 orders, 25 families and 52 genera. The most well-represented order was Ceramiales, with 30 species, accounting for 29.4% of the total. Among the Phaeophyceae and Chlorophyceae, respectively, the most well-represented orders were Dictyotales and Cladophorales, with 13 species each.

Among the host macroalgae, we identified 61 taxa: 17 Phaeophyceae, 25 Rhodophyceae and 19 Chlorophyceae, belonging to 14 orders, 23 families and 39 genera. The most well-represented orders were Dictyotales and Ceramiales, with 11 species each. The orders Cladophorales and Siphonocladales presented six species each. The Phaeophyceae genus *Dictyota* presented the greatest number of species, with six.

Systematic list of epiphytic macroalgae (species listed)

Domain: Eukaryota
Kingdom: Chromista
Subkingdom: Chromobiota
Division: Heterokontophyta
Class: Phaeophyceae
Order: Dictyotales
Family: Dictyotaceae
Genus: *Dictyopteris*
1- *Dictyopteris delicatula* J.V.Lamour.
Genus: *Dictyota*
2- *Dictyota bartayresiana* J.V.Lamour.
3- *Dictyota ciliolata* Sonder ex Kützing
4- *Dictyota crenulata* J.Agardh
5- *Dictyota guineensis* (Kützing) P.L.Crouan & H.M.Crouan
6- *Dictyota menstrualis* (Hoyt) Schnetter, Hörning & Weber-Peukert
7- *Dictyota mertensii* (Martius) Kützing
8- *Dictyota pulchella* Hörnig & Schnetter
Genus: *Canistrocrpus*
9- *Canistrocarpus cervicornis* (J.V.Lamour.) DePaula & De Clerck
10- *Canistrocarpus crispatus* (J.V.Lamour.) De Paula & De Clerck
Genus: *Lobophora*
11- *Lobophora variegata* (J.V.Lamour.) Womersley ex E.C.Oliveira
Genus: *Padina*
12- *Padina sanctae-crucis* Børgesen

13- *Padina gymnospora* (Kützing) Sonder
Order: Sphacelariales
Family: Sphacelariaceae
Genus: *Sphacelaria*
14- *Sphacelaria novae-hollandiae* Sonder
Order: Ectocarpales
Family: Scytosiphonaceae
Genus: *Chnoospora*
15- *Chnoospora minima* (Hering) Papenfuss
Order: Fucales
Family: Sargassaceae
Genus: *Sargassum*
16- *Saregassum buxifolium* (J.Agardh) M.J.Wynne
17- *Sargassum polyceratium* Montagne
Genus: *Turbinaria*
18- *Turbinaria tricostata* E.S.Barton
Kingdom: Plantae
Subkingdom: Biliphyta
Division: Rhodophyta
Class: Florideophyceae
Order: Corallinales
Family: Hapalidiaceae
Genus: *Mesophyllum*
19- *Mesophyllum* sp.
Family: Corallinaceae
Genus: *Hydrolithon*
20- *Hydrolithon farinosum* (J.V.Lamour.) D.Penrose & Y.M.Chamberlain
Genus: *Jania*
21- *Jania adhaerens* J.V.Lamour.
22- *Jania capillacea* Harvey
23- *Jania cubensis* Montagne ex Kützing
24- *Jania rubens* (Linnaeus) J.V.Lamour.
Genus: *Amphiroa*
25- *Amphiroa beauvoisii* J.V.Lamour.
26- *Amphiroa fragilissima* (Linnaeus) J.V.Lamour.
27- *Amphiroa rigida* J.V.Lamour.
Order: Ceramiales
Family: Ceramiaceae
Genus: *Ceramium*
28- *Ceramium brasiliense* A.B.Joly
29- *Ceramium brevizonatum* var. *caraibicum* H.E.Petersen & Børgesen
30- *Ceramium cimbricum* H.E.Petersen
31- *Ceramium codii* (H.Richards) Mazoyer
32- *Ceramium comptum* Børgesen
33- *Ceramium corniculatum* Montagne
34- *Ceramium dawsonii* A.B.Joly
35- *Ceramium* sp.
Genus: *Gayliella*
36- *Gayliella transversalis* (Collins & Hervey) T.O.Cho & Fredericq
Genus: *Centroceras*
37- *Centroceras clavulatum* (C.Agardh) Montagne
Family: Wrangeliaceae
Genus: *Griffithsia*
38- *Griffithsia globulifera* Harvey ex Kützing
Genus: *Ptilothamnion*

39- *Ptilothamnion speluncarum* (Collins & Hervey) D.L.Ballantine & M.J.Wynne
Family: Dasyadaceae
Genus: *Dasya*
40- *Dasya* sp.
Genus: *Heterosiphonia*
41- *Heterosiphonia crispella* (C.Agardh) M.J.Wynne
Family: Rhodomelaceae
Genus: *Chondrophycus*
42- *Chondrophycus iridescens* (M.J. Wynne & D.L. Ballantine) Garbary & Harper
Genus: *Palisada*
43- *Palisada perforata* (Bory) K.W.Nam
Genus: *Laurencia*
44- *Laurencia caraibica* P.C.Silva
45- *Laurencia obtusa* (Hudson) J.V.Lamour.
46- *Laurencia* sp.
Genus: *Digenia*
47- *Digenea simplex* (Wulfen) C.Agardh
Genus: *Lophosiphonia*
48- *Lophosiphonia cristata* Falkenberg
Genus: *Herposiphonia*
49- *Herposiphonia bipinnata* M.Howe
50- *Herposiphonia secunda* (C.Agardh) Ambronn
Genus: *Neosiphonia*
51- *Neosiphonia sphaerocarpa* (Børgesen) M.S.Kim & I.K.Lee
52- *Neosiphonia howei* (Hollenberg) Skelton & G.R. South
Genus: *Polysiphonia*
53- *Polysiphonia atlantica* Kapraun & J.N.Norris
54- *Polysiphonia havanensis* Montagne
55- *Polysiphonia schneideri* Stuercke & Freshwater
56- *Polysiphonia scopulorum* Harvey
57- *Polysiphonia scopulorum* var. *villum* (J.Agardh) Hollenberg
Order: Gelidiales
Family: Gelidiaceae
Genus: *Gelidium*
58- *Gelidium americanum* (W.R.Taylor) Santelices
59- *Gelidium pusillum* (Stackhouse) Le Jolis
Family: Gelidiellaceae
Genus: *Gelidiella*
60- *Gelidiella acerosa* (Forsskål) Feldmann & G.Hamel
Genus: *Parviphycus*
61- *Parviphycus setaceus* (Feldmann) Afonso-Carrillo, Sansón, Sangril & Díaz-Villa
62- *Parviphycus trinitatensis* (W.Rtaylor) M.J.Wynne
Order: Gigartinales
Family: Cystocloniaceae
Genus: *Hypnea*
63- *Hypnea musciformis* (Wulfen) J.V.Lamour.
64- *Hypnea spinella* (C.Agardh) Kützing
65- *Hypnea valentiae* (Turner) Montagne
Order: Rhodymeniales
Family: Rhodymeniales
Genus: *Botryocladia*
66- *Botryocladia pyriformis* (Børgesen) Kylin
Family: Champiaceae
Genus: *Champia*
67- *Champia parvula* (C.Agardh) Harvey

8- *Champia vieillardii* Kützing
Family: Lomentariaceae
Genus: *Ceratodictyon*
69- *Ceratodictyon intricatum* (C.Agardh) R.E.Norris
70- *Ceratodictyon scoparium* (Montagne & Millardet) R.E.Norris
71- *Ceratdictyon variable* (Grefville ex J.Agardh) R.E.Norris
Kingdom: Plantae
Subkingdom: Viridaeplantae
Division: Chlorophyta
Class: Ulvophyceae
Order: Ulvales
Family: Ulvaceae
Genus: *Pringsheimiella*
72- *Pringsheimiella scutata* (Reinke) Marchewianka
Genus: *Ulva*
73- *Ulva fasciata* S.F.Gray
74- *Ulva flexuosa* Wulfen
75- *Ulva flexuosa* subsp. *paradoxa* (C.Agardh) M.J.Wynne
76- *Ulva lactuca* Linnaeus
77- *Ulva rigida* C.Agardh
Order: Cladophorales
Family: Anadyomenaceae
Genus: *Anadyomene*
78- *Anadyomene stellata* (Wulfen) C.Agardh
Family: Cladophoraceae
Genus: *Cladophora*
79- *Cladophora albida* (Nees) Kutzing
80- *Cladophora brasiliana* G.Martens
81- *Cladophora* cf. *liniformis* Kützing
82- *Cladophora prolifera* (Roth) Kützing
83- *Cladophora vagabunda* (Linnaeus) C.Hoek
84- *Cladophora* sp.
Genus: *Chaetomorpha*
85- *Chaetomorpha aerea* (Dillwyn) Kützing
86- *Chaetomorpha antennina* (Bory) Kützing
87- *Chaetomorpha clavata* Kützing
88- *Chaetomorpha gracilis* Kützing
89- *Chaetomorpha vieillardii* (Kützing) M.J.Wynne
Genus: *Bryobesia*
90- *Bryobesia johannae* Weber-van Bosse
Order: Siphonocladales
Family: Boodleaceae
Genus: *Cladophoropsis*
91- *Cladophoropsis macromeres* W.R.Taylor
92- *Cladophoropsis membranacea* (Bang ex C.Agardh) Børgesen
Genus: *Boodlea*
93- *Boodlea struveoides* M.A. Howe
Genus: *Phyllodictyon*
94- *Phyllodictyon anastomosans* (Harvey) Kraft & M.J.Wynne
Family: Siphonocladaceae
Genus: *Dictyosphaeria*
95- *Dictyosphaeria ocellata* (M.Howe) J.L.Olsen-Stojkovich
Family: Valoniaceae
Genus: *Valoniopsis*
96- *Valoniopsis pachynema* (G.Martens) Børgesen
Genus: *Valonia*

97- *Valonia ventricosa* J.Agardh
Class: Bryopsidophyceae
Order: Bryopsidales
Family: Bryopsidaceae
Genus: *Bryopsis*
98- *Bryopsis plumosa* (Hudson) C.Agardh
Family: Udoeaceae
Genus: *Boodleopsis*
99- *Boodleopsis pusilla* (F.S.Collins) W.R.Taylor, A.B.Joly & Bernatowicz
Family: Halimedaceae
Genus: *Halimeda*
100- *Halimeda* sp.
Class: Dasycladophyceae
Order: Dasycladales
Family: Polyphysaceae
Genus: *Acetabularia*
101- *Acetabularia crenulata* J.V.Lamour.
Genus: *Parvocaulis*
102- *Parvocaulis polyphysoides* (P.Crouan & H.Crouan) S. Berger, U. Fettweiss, S. Gleissberg, L. B. Liddle, U. Richter, H. Sawitsky, H. & G. C. Zuccarello

Distribution of epiphytic macroalgae on the host thalli

The distribution of epiphytes on the host thalli varied considerably. In 31 host species, the number epiphyte species was higher on the surface of the thallus than at its base, whereas the inverse was observed in 25, and the number epiphyte species was comparable between the two zones in five host species. Epiphytes were located only on the surface of the thallus in nine host species and only at its base in three. The cumulative species richness (both zones) was 89 species. The greatest epiphyte species richness was recorded for macroalgae with thalli that were more complex, belonging to the corticated, leathery, leafy and globose morphofunctional groups (Tab. 1).

The total R value for the comparison between the two areas was −0.001 (p=0.398). The mean dissimilarity between the surface and the base of the host thallus, in terms of the species composition of epiphytic macroalgae, was 96.64%. The species *Hydrolithon farinosum* (J.V.Lamouroux) D.Penrose & Y.M.Chamberlain and *Polysiphonia atlantica* Kapraun & J.N.Norris accounted for 43.76% of the dissimilarity.

The species that accounted for the majority of the mean similarity among epiphytic macroalgae at the base of the host thallus (2.99%) was *Hydrolithon farinosum*, which accounted for 59.36%. In addition, *H. farinosum* accounted for 92.37% of the mean similarity among epiphytic macroalgae on the surface of the host thallus (4.51%).

Among the species occurring at the base of the thallus, the following were the most common: *Dictyosphaeria ocellata* (M.Howe) J.L.Olsen-Stojkovich (n = 11); *Cladophora albida* (Nees) Kutzing (n = 13); *Valoniopsis pachynema* (G.Martens) Børgesen (n = 19); *Hypnea spinella* (C.Agardh) Kützing (n = 19); *Palisada perforata* (Bory) K.W.Nam (n = 10); *Centroceras clavulatum* (C.Agardh) Montagne (n = 11); *Amphiroa rigida* J.V.Lamouroux (n = 18); *Amphiroa fragilissima* (Linnaeus) J.V.Lamouroux (n = 12); *Jania adhaerens* J.V.Lamouroux (n = 21); *Hydrolithon farinosum* (n = 39); and *Dictyota menstrualis* (Hoyt) Schnetter, Hörning & Weber-Peukert (n = 10). There were 20 host species that showed no epiphytes at the base of the thallus.

The following were the most common species occurring on the surface of the thallus: *Padina sanctae-crucis* Børgesen (n = 12); *Hydrolithon farinosum* (n = 40); *Centroceras clavulatum* (n = 15); *Ceramium brasiliense* A.B.Joly (n = 11); *Neosiphonia sphaerocarpa* (Børgesen) M.S.Kim & I.K.Lee (n = 10); *Polysiphonia atlantica* (n = 18); and *Cladophora albida* (n = 10). There were only three host species that showed no epiphytes on the surface of the thallus (Tab. 1): *Gelidium americanum* (W.R.Taylor) Santelices; *Ulva flexuosa* Wulfen; and *Bryopsis plumosa* (Hudson) C.Agardh.

Discussion

Epiphytic macroalgae and their hosts: typical flora

The 102 taxa of epiphytic macroalgae observed here correspond to 21% of those identified for the waters of Cuba, whereas the host species correspond to 12.5% (Suárez 2005). The level of species richness observed here was high in comparison with those previously reported for Cuban waters. That might be due, in part, to the community approach taken in our study of the hosts, given that the majority of investigations of the hosts of epiphytic macroalgae have been conducted at the population level.

In an estuarine ecosystem, Cabrera *et al*. (2005) identified only 25 epiphytes on *Palisada perforata*. In contrast,

Table 1. Characteristics of the macroalgae hosting epiphytic macroalgae, including morphofunctional group, thallus zone in which the epiphytes were found, and epiphyte species composition, in a rocky intertidal zone in the Baconao Biosphere Reserve, in Cuba.

Hosts Division Species	MG	Thallus zone	Epiphyte species*
HETEROKONTOPHYTA			
Dictyopteris delicatula	LG	B	19, 20, 59, 63, 64, 65, 70, 76, 86, 96, 98
		S	20
Dictyota bartayresiana	LG	B	20
		S	20, 28, 34, 57
Dictyota cervicornis	LG	B	20, 21, 26, 37, 63, 64
		S	20
Dictyota ciliolata	LG	B	12, 20
		S	20, 53
Dictyota guineensis	LG	B	20, 53
		S	20
Dictyota menstrualis	LG	B	12, 20, 21, 22, 31, 32, 33, 43, 45, 51, 64, 96, 80
		S	20
Dictyota mertensii	LG	B	6, 11, 20, 21, 26, 43, 50, 52, 78, 79, 84
		S	20, 53
Dictyota pulchella	LG	B	20
		S	20, 53
Lobophora variegata	Lthy	S	69
Padina gymnospora	Lthy	B	21, 27, 37, 64, 73, 74, 76, 80, 91, 97
		S	74
Padina sanctae-crucis	Lthy	B	5, 6, 7, 8, 20, 21, 22, 26, 27, 28, 30, 31, 32, 34, 37, 38, 39, 40, 41, 43, 44, 45, 46, 47, 50, 51, 53, 55, 56, 63, 64, 78, 79, 81, 82, 84, 87, 89, 91, 92, 93, 95, 96, 97, 100
		S	20, 28, 36, 37, 38, 39, 40, 41, 49, 50, 51, 55, 56, 57, 64, 67, 79, 88
Chnoospora minima	Cort	B	20, 96
		S	20
Sargassum buxifolium	Lthy	B	2, 5, 6, 7, 9, 11, 12, 18, 20, 21, 23, 25, 26, 27, 32, 42, 43, 44, 45, 51, 52, 53, 63, 67, 68, 69, 71, 78, 80, 84, 88, 95, 96
		S	7, 20, 51, 53, 89, 91
Sargassum fluitans	Lthy	B	20, 25, 27, 50, 60, 64, 95
		S	20, 95
Sargassum polyceratium	Lthy	B	2, 11, 12, 17, 25, 27, 28, 29, 30, 37, 43, 44, 45, 51, 60, 63, 64, 70, 76, 79, 88, 95, 96
		S	1, 7, 17, 19, 20, 35, 36, 45, 52, 51, 53, 98
Turbinaria tricostata	Lthy	B	2, 6, 7, 11, 12, 20, 21, 23, 25, 26, 27, 37, 29, 31, 35, 38, 39, 40, 43, 44, 45, 53, 63, 64, 66, 69, 71, 78, 79, 84, 95, 96
		S	20, 27, 41, 49, 50, 52, 54, 96
Turbinaria turbinata	Lthy	B	2, 6, 20, 27, 45, 53, 64, 79, 90, 96
		S	20
RHODOPHYTA			
Jania cubensis	AC	S	32
Amphiroa rigida	AC	S	78
Tricleocarpa cilindrica	AC	S	32, 53, 68, 90
Centroceras sp.	Fila	B	20
		S	20, 50
Acanthophora muscoides	Cort	B	21, 27, 64, 96
		S	98
Chondrophycus iridiscens	Cort	B	20, 95
		S	6, 7, 20, 21, 53, 64, 93
Yuzurua poiteaui	Cort	B	20, 51, 79
		S	20, 32, 53

Continues

Table 1. Continuation.

Hosts Division Species	MG	Thallus zone	Epiphyte species*
Palisada perforata	Cort	B	2, 6, 7, 11, 12, 19, 20, 21, 25, 26, 27, 28, 31, 32, 38, 41, 44, 45, 46, 49, 51, 60, 61, 62, 63, 67, 78, 84, 89, 95,96, 97, 101
		S	2, 3, 6, 8, 12, 15, 17, 20, 23, 25, 26, 27, 28, 30, 31, 34, 35, 37, 44, 49, 50, 51, 52, 53, 54, 60, 63, 64, 69, 70, 78, 79, 91, 92, 95, 96, 99, 101
Digenea simplex	Cort	B	20, 21, 25, 26, 43, 44, 64, 79, 95, 99
		S	6, 7, 10, 12, 14, 16, 19, 20, 22, 28, 37, 43, 45, 46, 48, 49, 51, 53, 54, 56, 47, 62, 79, 82, 83, 85, 88, 91, 93, 96
Herposiphonia bipinnata	Fila	S	11
Laurencia caraibica	Cort	B	6, 20, 51, 79
		S	6, 20, 21, 29, 50, 53, 70
Laurencia obtusa	Cort	B	2, 6, 12, 20, 27, 53, 55, 57, 69, 70, 91
		S	4, 11, 20, 28, 32, 37, 50, 51, 53, 81
Laurencia sp.	Cort	B	12, 20, 21, 96
		S	8, 12, 15, 20, 23, 53, 79, 80, 91
Neosiphonia sphaerocarpa	Fila	B	6, 20, 33, 79
		S	12, 20, 79
Polysiphonia scopolorum	Fila	B	20
		S	20, 37, 79, 84
Gelidium americanum	Fila	B	21
Gelidium pusillum	Fila	B	21, 27, 58, 64, 86, 91, 95, 96, 98
		S	19, 28
Gelidiella acerosa	Cort	B	20, 25
		S	20, 37, 92
Hypnea musciformis	Cort	B	20, 21, 26, 27, 53, 96
		S	1, 20, 28, 37, 51, 54, 56, 57, 74, 75, 76, 83, 96, 98
Hypnea spinella	Cort	B	2, 12, 20, 21, 26, 30, 37, 43, 79, 86, 95, 96
		S	1, 6, 11, 12, 13, 20, 37, 43, 45, 51, 56, 59, 74, 76, 77, 82, 83, 88, 89, 91, 98
Hypnea valentiae	Cort	B	21, 74, 96
		S	1, 37, 76, 98
Ochtodes secundiramea	Fila	S	98
Champia parvula	Fila	B	20
		S	20
Ceratodyction intricatum	Cort	B	20
		S	12, 20
Ceratodyction scoparia	Cort	B	1, 21, 27, 37, 63, 64, 74, 76, 77, 79, 86, 91, 98
		S	1
CHLOROPHYTA			
Ulva flexuosa	LG	B	37
Ulva lactuca	LG	B	1, 13, 19, 21, 22, 26, 27, 37, 59, 65, 74, 80, 86, 89, 91, 94, 96, 98
		S	20
Anadyomene stellata	LG	B	11, 20, 27, 43, 44, 45, 56
		S	11, 20, 53
Valoniopsis pachynema	Fila	B	20, 24, 25, 26, 27, 32, 43, 44, 46, 53, 56, 62, 64, 78, 83, 95
		S	2, 5, 6, 8, 9, 11, 12, 14, 20, 26, 27, 35, 43, 45, 47, 53, 55, 57, 58, 63, 64, 73, 73, 75, 76, 77, 77, 78, 79, 80, 88, 89, 91, 95, 98
Chaetomorpha antennina	Fila	B	21, 32, 37, 51, 59, 76, 78, 80
		S	37, 64, 74, 76
Chaetomorpha vieillardii	Fila	B	2, 59, 64, 73, 76
		S	98

Continues

Table 1. Continuation.

Hosts Division Species	MG	Thallus zone	Epiphyte species*
Cladophora albida	Fila	B	20
		S	20, 21, 29, 31, 51, 53, 56
Cladophora liniforme	Fila	S	12, 27
Cladophora prolifera	Fila	B	20
		S	20
Phyllodictyon anastomosans	LG	S	20, 79, 83
Cladophoropsis macromeres	Fila	B	11, 21, 27, 53, 64
		S	12, 26, 68, 30, 32, 37, 51, 56, 57, 59, 64, 67, 60,74, 76, 79, 81, 96
Cladophoropsis membranacea	Fila	B	20
		S	20
Dictyosphaeria cavernosa	LG	B	20
		S	20, 25, 96
Dictyosphaeria ocellata	LG	B	20, 22, 25, 26, 47, 69, 96
		S	2, 3, 4, 6, 7, 8, 9, 11, 12, 14, 15, 17, 19, 20, 21, 26, 27, 28, 31, 32, 37, 38, 42, 43, 44, 45, 46, 49, 50, 51, 52, 53, 54, 55, 56, 57, 60, 63, 64, 67, 69, 70, 72, 79, 81, 84, 91, 96, 99, 102
Valonia ventricosa	LG	B	20, 21, 96
		S	20, 21, 28, 91
Bryopsis plumosa	Fila	B	1, 20, 37, 59, 64, 73, 76
Halimeda sp.	AC	S	12, 53
Boodleopsis pusilla	Fila	S	12, 21, 37, 43, 91
Parvocaulis polyphysoides	AC	B	20
		S	20, 53

MG – morphofunctional group; LG – leafy, globose; Lthy – leathery; Cort – corticate; AC – articulated calcareous; Fila –filamentous.
*For the names of the species corresponding to the numbers shown, see the taxonomic list in the Results section.

Suárez *et al*. (1989) identified 98 species of epiphytic macroalgae on *Stypopodium zonale* (Lamouroux) Papenfuss in a rocky subtidal ecosystem. That discrepancy can be explained by the differences between the two host species, in terms of the complexity of the thallus (greater in *S. zonale*) and in terms of habitat (species richness is typically greater in rocky subtidal ecosystems than in estuarine ecosystems).

Zayas *et al*. (2006) found only 13 species of epiphytic macroalgae within the community of macroalgae in the reef lagoon at Guardalavaca Beach. That low level of species richness could be attributed to the fact that epiphytic macroalgae more adhere to Thalassia testudinum Banks & Sol. ex K.D.Koenig, in algal beds, or to angiosperms (Borowitzka *et al.* 2006).

The greater epiphyte richness observed among hosts belonging to the morphofunctional groups with higher thallus complexity is due to the fact that those groups present morphological differences among their component species, which makes them responsible for increasing the spatial heterogeneity of the community. In addition, species with differentiated blades and thalli have greater morphological complexity, are more resistant to adverse conditions and confer greater stability upon the community (Littler & Littler 1980; 1984).

Distribution of epiphytic macroalgae on the host thallus

Greater epiphyte species richness on the surface of the thallus might be determined by the protection that provides against the extreme conditions in the intertidal zone, such as desiccation and wave exposure, as well as avoiding the competition for light that could lead to the overlapping of host thalli. In turn, macroalgae hosts with more epiphytes at the thallus base could better withstand those adversities and tolerate competition for light. The various structures that give rise to the thalli differ in terms of desiccation and solar irradiation. Longtin *et al.* (2009) found that these two factors were more intense in the distal segments of the thallus than at its base.

The variation in the accumulated epiphyte species richness in the rocky intertidal zone at the Aguadores-Baconao site is related to the complexity, rather than the zonation, of the host thalli. Montañés *et al*. (2003) argued that not only the habits but also the organizational type of epiphytes directly conditions their adhesion sites and preference for different parts of the host. The morphology of the host thallus is also crucial, it is expected that structurally complex thalli favor colonization by a greater number of epiphytes, because they create a greater number of niches and shelters (Ayala & Martín 2003). Apparently morphologically complex thalli, such as those of leathery corticate algae, create protected microhabitats (Kendrick & Burt 1997; Lavery & Vanderklift 2002). In addition, the texture and structure of the thalli are frequently used by epiphytes, increasing the complexity of the habitat (Hacker & Steneck 1990).

The fact that the similarity in overall shape was near zero indicates no difference in the distribution of epiphytic macroalgae, which might be attributable to the similarity between the base of the thallus and its surface, in terms of epiphyte species richness. However, the dissimilarity values are very high, given the existence of quite significant differences in epiphyte species composition and in the proportional contributions of individual species.

Species such as *Hydrolithon farinosum*, *Centroceras clavulatum* and *Cladophora albida* showed no preference for any specific area of the host thallus, presenting high values of frequency of appearance at its base and on its surface. This behavior could be determined by the low complexity of the host thalli, given the possibility that the developmental requirements of those species might not be as specific as are those of other epiphytes.

The hosts that did not have epiphytes adhering to the thallus base were typically the simpler forms, with few occurrences during the sampling periods. Macroalgae that host a great number of epiphytes in general or at the thallus base might have greater viability in the ecosystem, as has been suggested by various authors (Davis *et al*. 1989; Wahl 1989). The significantly low number of species hosting epiphytes of the thallus surface might be attributable to the epiphytes having a preference for zones that provide more light and more nutrients (Pedersen & Borum 1996; Lobban & Harrison 1997; Kraberg & Norton 2007). *Ulva flexuosa* and *Bryopsis plumosa* both present thalli that are structurally simple, with very smooth blade surfaces.

We conclude that the development of epiphytes can be influenced not only by the extreme physical conditions in the rocky intertidal zone but also by the structural characteristics of the host thalli and of the epiphytes, their ability to adhere to other macroalgae thalli or allow their own thalli to be adhered to by others.

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References

Aguilar, M.; Aguilar-Rosa L. & Aguilar-Rosas R. 1998. Algas marinas de la región central del Estado de Quintana Roo, México. **Polibotánica 7**: 15-32.

Aguilar-Rosas, R. & Galindo A. 1990. Ecological aspects of *Sargassum muticum* (Fucales, Phaeophyta) in Baja California: reproductive phenology and epiphytes. **Hydrobiologia 204/205**: 185-190.

Ang, P. & DeWreede R. 1992. Density-dependence in a population of *Fucus distichus*. **Marine Ecology Progress Series 90**: 169-181.

Ayala, Y. & A. Martin. 2003. Relaciones entre la comunidad de anfípodos y las macroalgas a las que están asociados, en una plataforma rocosa del litoral central de Venezuela. **Boletino Del Instituto Espanol De Oceanografia 19**: 171.184.

Børgesen, F. 1915-20. II. Rhodophyceæ, with addenda to the Chlorophyceæ, Phæophyceæ and Rhodophyceæ. **Dansk Botanisk Arkiv 3**: 1-504.

Borowitzka, M.A.; Lavery, P.S. & van Keulen, M. (2006) Epiphytes of seagrasses, Pp. 441-461. In: Larkum, A.W.D.; Orth, P.J. & Duarte, C.M. (Eds.). **Seagrasses: Biology, Ecology and Conservation**. Berlín, Springer.

Brawley, S. & Johnson L. 1992. Gametogenesis, gametes and zygotes: an ecological perspective on sexual reproduction in the algae. **British Phycological Journal 27**: 233-252.

Bruno, J.; Stachowicz J. & Bertness M. 2003. Inclusion of facilitation into ecological theory. **Trends in Ecology and Evolution 18**(3): 119-125.

Cabrera, R.; Moreira, Á.; Primelles, J. & Suárez, A. 2005. Variación de la Biomasa de *Chondrophycus papillosus* (C. Agardh) Garvary et Harper (Ceramiales: Rhodophyta) y su epifitismo en la Bahía de Nuevitas, Cuba. **Revista de Investigaciones Marinas 26**(1): 15-20.

Castro, J. de; Barros-Barreto, M. & Pita, S. 2008. A família Ceramiaceae (Ceramiales, Rhodophyta) no estado da Bahia, Brasil. Pp. 75-159. En: A. Santíes y K. Dreckmann (Eds.). **Monografías Ficológicas 3**. Universidad Autónoma de México.

Clarke, K. 1993. Non-parametric multivariate analyses of changes in community structure. **Australian Journal of Ecology 18**: 117-143.

Clarke, K. & Gorley, R. 2006. **PRIMER v 6: User manual/tutorial, PRIMER-E**. United Kingdom, Plymouth.

Clarke, K. & Warwick, R. 2001. **Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E**. United Kingdom, Plymouth.

Davis, A.; Targett, N.; McConnell, O. & Young, C. 1989. Epibiosis of marine algae and benthic invertebrates: natural product chemistry and other mechanisms inhibiting settlement and overgrowth. Pp. 85-114. In: Scheuer, P. (Ed.). **Bioorganic Marine Chemistry**. V. 3. Berlin, Springer-Verlag.

Dawes, C. & Mathieson, A. 2008. **The Saeweeds of Florida**. Florida, University of Florida Press.

Foster, M. 1990. Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. **Hydrobiologia 192**: 21-34.

Foster, M. 1991. Rammed by the Exxon Valdez: a reply to Paine. **Oikos 62**: 93-96.

Guiry, M. & Guiry, G. 2011. **AlgaeBase.** World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org. (Consultado: 16 mayo 2011).

Hacker, S. & Steneck R. 1990. Habitat architecture and body- size-dependent habitat selection of a phytal amphipod. **Ecology 71**: 2269-2285.

Jover, A.; Reyes, L.; Gómez, L. & Suárez, A. 2012. Variación espacial y temporal de las macroalgas del mesolitoral rocoso en Aguadores-Baconao, Cuba I: Composición. R**evista de Investigaciones Marinas 32**: 38-49.

Kraberg, A. & Norton, T. 2007. Effect of epiphytism on reproductive and vegetative lateral formation in the brown, intertidal seaweed *Ascophyllum nodosum* (Phaeophyceae). **Phycological Research 55**: 17-24.

Kendrick G. & Burt, J. 1997. Seasonal changes in epiphytic macro-algae assemblages between offshore exposed and inshore protected *Posidonia sinuosa* Cambridge et Kuo seagrass meadows, Western Australia. **Botanica Marina 40**: 77-85

Lavery P. & Vanderklift, M. 2002. A comparison of spatial and temporal patterns in epiphytic algae assemblages of the seagrasses *Amphibolis griffithii* and *Posidonia coriacea*. **Marine Ecology Progress Series 236**: 99-112

Lebreton, B.; Richard P.; Radenac G.; Bordes M.; Bréret M.; Arnaud C.; Mornet F. & Blanchard G. 2009. Are epiphytes a significant component of intertidal *Zostera noltii* beds? **Aquatic Botany 91**: 82-90.

Lecha, L. & Chugaev, A. 1989. **La bioclimatología y algunas de sus aplicaciones en condiciones de clima tropical húmedo**. La Habana, Editorial Academia, Cuba.

Little, C. & Kitching J. 1996. **The biology of rocky shores**. Oxford, Oxford University Press.

Littler, M.M. & D.S. Littler. 1980. The evolutions of thallus form and survival strategies in benthic marine macroalgae: field and laboratory test of and functional: forms model. **American Naturalist 116(1)**: 25-44.

Littler, D.S. & M.S. Littler. 1984. Relationships between macoalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. **Journal of Experimental Marine Biology and Ecology 74**: 13-34.

Littler, D. & Littler, M. 1997. An illustrated marine flora of the Pelican Cays, Belize. **Boletim de Botânica 9**: 1-149.

Littler, D. & Littler, M. 2000. **Caribbean Reef Plants. An identification to tha reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico**. Florida, Offshore Graphics, Inc.

Littler, D.; Littler, M. & Dennis, M. 2008. **Submersed Plants of the Indian River Logoon**. Florida, Offshore Graphics, Inc.

Littler, D.; Littler, M.; Rucher, K. & Noris, J. 1989. **Marine Plants of the Caribbean. A fiel guide from Florida to Brazil**. New York, Smithosonian Institution Press.

Lobban, C. & Harrison P. 1997. **Seaweed ecology and physiology**. Cambridge, Cambridge University Press.

Longtin, C. & Scrosati, R. 2009. Role of surface wounds and brown algal epiphytes in the colonization of *Ascophyllum nodosum* (Phaeophyceae) fronds by *Vertebrata lanosa* (Rhodophyta). **Journal of Phycolgy 45**: 535-539.

Longtin, C.; Scrosati, R.; Whalen, G. & Garbary, D. 2009. Distribution of algal epiphytes across environmental gradients at different scales: intertidal elevation, host canopies and host fronds. **Journal of Phycolgy 45**: 820-827.

Ludwig, J. & Reynolds, J. 1988. **Statistical Ecology**. Nueva York, John Wiley and Sons.

Martin-Smith, K. 1993. Abundante of mobile epifauna: the role of habitat complexity and predation by fishes. **Journal of Experimental Marine Biology and Ecology 174**: 243-260.

Montañes, M.; Reyes, J. & Senzón, M. 2003. La comunidad de epífitos de *Zonaria tournefortiien* el norte de Tenerife (islas Canarias): análisis florístico y comentarios sobre su epifauna. **Vieraea 31**: 121-132.

Paine, R. 1991. Between Scylla and Charybdis: do some kinds of criticism merit a response? **Oikos 62**: 90-92.

Paula, E. & Oliveira-Filho E. 1980. Phenology of two populations of *Sargassum cymosum* (Phaeophyta- Fucales) of São Paulo State coast, Brazil. **Boletim de Botânica 8**: 21-39.

Pedersen, M. & Borum, J. 1996. Nutrient control of algal growth in estuarinen waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. **Marine Ecology Progress Series 142**: 261-272.

Reed, D. 1990a. The effects of variable settlement and early competition on patterns of kelp recruitment. **Ecology 71**(2): 776-787.

Reed, D. 1990b. An experimental evaluation of density dependence in a subtidal algal population. **Ecology 71**: 2286-2296.

Saad-Navarro, G. & Riosmena-Rodrígez R. 2005. Variación espacial y temporal de la riqueza florística de macroalgas en la zona rocosa de Bahía de Muertos, B.C.S. México. **Ciencia y Mar IX (26)**: 19-32.

Steneck, R.S. & M.N. Dethier. 1994. A functional group approach to the structure of algal dominated communities. **Oikos 69**: 476-498.

Suárez, A. 2005. Lista de las macroalgas marinas cubanas. **Revista de Investigaciones Mararinas 26**(2): 93-148.

Suárez, A.; Gil, L. & Poseck R. 1989. Variación del epifitismo en *Stypopodium zonale* (Lamouroux) Papenfuss a lo largo de un año. **Revista de Investigaciones Mararinas 10**(1): 3-20.

Széchy, M.; Galliez M. & Marconi M. 2006. Quantitative variables applied to phenological studies on *Sargassum vulgare* C. Agardh (Phaeophyceae, Fucales) from Ilha Grande Bay, state of Rio de Janeiro. **Revista Brasileira de Botânica 29**: 27-37.

Taylor, W. 1960. **Marine algae of the Eastern Tropical and Subtropical coast of the Americans.** Michigan, The University of Michigan Press.

Underwood, A. 2000. Experimental ecology of rocky intertidal habitats: what are we learning? **Journal of Experimental Marine Biology and Ecology 250**: 51-76.

Underwood, A; Chapman M. & Connell S. 2000. Observations in ecology: You can´t make progress on processes without understanding the patterns. **Journal of Experimental Marine Biology and Ecology 250**: 97-115.

Vreeland, V. & Epstein L. 1996. Analysis of plant-substratum adhesives. Pp. 95-116. In: Linskens & Jackson, J. (Eds.). **Modern Methods of Plant Analysis. Plant Cell Wall Analysis**. v. 17. Berlin, Springer-Verlag.

Wahl, M. 1989. Marine epibiosis: I. Fouling and antifouling: some basic aspects. **Marine Ecology Progress Series 58**: 175-189.

Wernberg, T. & Connell S. 2008. Physical disturbance and subtidal habitat structure on open coasts: effects of wave exposure, extent and intensity. **Journal of Sea Research 59**: 237-248.

Wynne, M. 2011. A checklist of benthic marine algae of the tropical and subtropical western Atlantic: third revision. **Beiheft Nova Hedwigia. 140**: 1-166.

Zayas, C.; Ocaña, F.; Suárez, A. & La O, J. 2006. Variación estacional del epifitismo del fitobentos marino de Playa Guardalavaca, Cuba. **Revista de Investigaciones Marinas 27**: 95-101.