Anales del Jardín Botánico de Madrid 76 (1): e078
https://doi.org/10.3989/ajbm.2502
ISSN-L: 0211-1322

Biodiversity of epiphytic macroalgae *(Chlorophyta, Ochrophyta,* and *Rhodophyta)* on leaves of *Zostera marina* in the northwestern Iberian Peninsula

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Abstract. The composition, abundance, and distribution of epiphytic macroalgae living in meadows of *Zostera marina* L. in the northwestern Iberian Peninsula are here analyzed. We identified 63 species: 40 red algae, 16 brown algae, and 7 green algae. Most of them are classified as filamentous or filiform functional forms, while *Pneophyllum fragile* Kütz. was the only encrusting species. In general, the surface covered by epiphytes on the leaves of *Zostera marina* was low and a 43% of species were only found in juvenile stages. Regarding their frequency, 10 species were collected in the majority of the areas, while others were rare. Most species were found both epiphytic and in other substrata of the meadows, but 9 were exclusively epiphytic. We detected 9 introduced species.

Keywords. *Asperococcus scaber,* biodiversity, epiphytes, Galicia, *Gayliella mazoyerae,* Iberian Atlantic, marine meadows, *Rhodophysema georgei.*

Resumen. Se han analizado la composición, la abundancia y la distribución de macroalgas epifitas que viven en praderas de *Zostera marina* L. del noroeste de la península ibérica. Se han identificado 63 especies: 40 algas rojas, 16 pardas y 7 verdes. La mayoría pertenecen a los grupos funcionales filamentosos o filiformes, excepto *Pneophyllum fragile* Kütz., la única especie costrosa. En general, la cobertura de epifitos en las hojas de *Zostera marina* fue baja y un 43% de las especies solo se encontraron como estadios juveniles. En cuanto a su frecuencia, 10 de ellas se recolectaron en la mayoría de las áreas, mientras que el resto fueron más raras. La mayor parte de las especies se encontraron tanto epifitas como en otros substratos de las praderas, si bien 9 resultaron exclusivamente epifitas. Detectamos 9 especies introducidas.

Palabras clave. *Asperococcus scaber,* Atlántico ibérico, biodiversidad, epifitos, Galicia, *Gayliella mazoyerae,* praderas marinas, *Rhodophysema georgei.*

How to cite this article: García-Redondo V., Bárbara I. & Díaz-Tapia P. 2019. Biodiversity of epiphytic macroalgae *(Chlorophyta, Ochrophyta,* and *Rhodophyta)* on leaves of *Zostera maritima* in the northwestern Iberian Peninsula. *Anales del Jardín Botánico de Madrid* 76 (1): e078. https://doi.org/10.3989/ajbm.2502.

Title in Spanish: Biodiversidad de macroalgas epifitas *(Chlorophyta, Ochrophyta* y *Rhodophyta)* en hojas de *Zostera marina* en el noroeste de la península ibérica.

Received: 22–II–2018; accepted: 4–I–2019; published on-line: 28–II–2019; Associate Editor: A. Flores.

INTRODUCTION

The eelgrass—*Zostera marina* L., *Zosteraceae* Dumort.—meadows represent an important marine ecosystem in the northern temperate region (den Hartog 1970; Homziak & al. 1982; Short & Coles 2001). The protection against predation and the food availability of this habitat are the major traits that attract many organisms to be permanent or temporary residents of seagrass meadows (Hemminga & Duarte 2000). The leaves of *Zostera marina* also provide the substrate to which many benthic organisms attach, such as hydroids, fungi, protozoa, bryozoans or algae. Physical and chemical characteristics of leaf surface vary during growth, onset of reproduction and senescence, and these changes influence the recruitment and distribution of colonists (Michael & al. 2008). Epiphytic algae are the most abundant and diverse group of organisms on *Zostera marina,* which grow especially on its leaves (Borowitzka & al. 2006).

The diversity of epiphytic macroalgae on *Zostera marina* varies with the age of leaves, as they are deciduous and the oldest ones accumulate more epiphytes (Cullinane & al. 1985). Once they shed, they still play an important role as a substrate for algal epiphytes (Novaczek 1987). Epiphytic macroalgae increase biodiversity and total biomass of eelgrass meadows and are a food source for herbivores (Duarte 2002; Orth & al. 2006; Michael & al. 2008). A particular set of species grows exclusively as epiphytes on *Zostera marina,* such as *Rhodophysema georgei* Batters (Saunders & Bird 1989), while a larger number of species can be found epiphytic and on the adjacent substrate. Diversity, distribution, and abundance of seagrasses epiphytes are influenced by abiotic and biotic

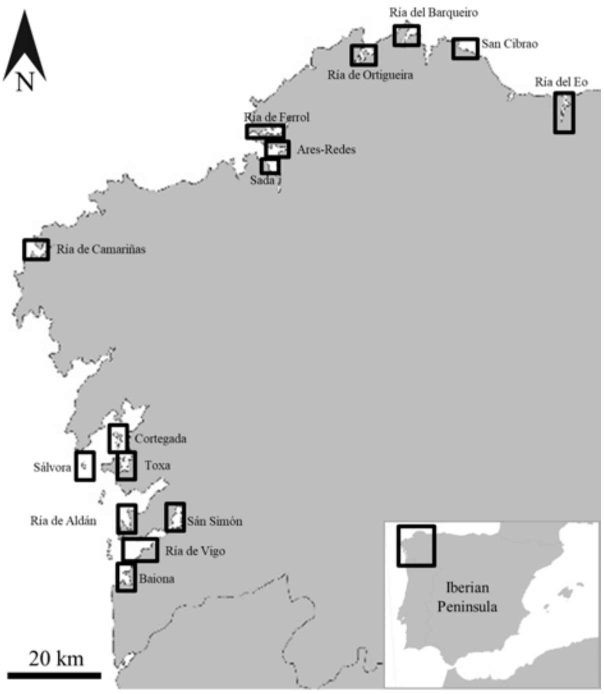

Fig. 1. Sampling areas of meadows of *Zostera marina* L. in the northwestern Iberian Peninsula.

factors (Michael & al. 2008), such as depth, currents, nutrients, light, temperature, season, size, and maturity of leaf (González 1976; Cullinane & al. 1985). Moreover, macroalgal epiphytes on leaves of *Zostera marina* can be used as indicators of anthropogenic environmental impacts in eelgrass meadows (Johnson & al. 2005; Michael & al. 2008).

Despite the ecological relevance of macroalgal epiphytes of *Zostera marina* and their potential application in monitoring programs, they remain poorly studied in the northwestern Iberian Peninsula. A few previous works reported some species as the result of general surveys on macroalgae (Miranda 1934; Bárbara & al. 2014, 2015, 2016; Cacabelos & al. 2015a, 2015b; García-Redondo & al. 2017). However, a specific work on the epiphytic species of *Zostera marina* was not attempted before. The aims of this work are: i) providing a floristic catalogue of the epiphytic macroalgae growing on the leaves of *Zostera marina* along northwest Iberian Peninsula; ii) analyzing their frequency, abundance, and distribution; iii) providing an identification key for the epiphytes of eelgrass meadows.

MATERIAL AND METHODS

This study focuses on the eelgrass meadows of the northwestern Iberian Peninsula, in which we considered fifteen geographical areas: Ares-Redes, Baiona cove, Cortegada, Ría de Aldán, Ría de Camariñas, Ría de Ferrol, Ría de Ortigueira, Ría de Vigo, Ría del Barqueiro, Ría del Eo, Sada, Sálvora, San Cibrao, San Simón cove, and Toxa (fig. 1). These areas include the entire known distribution range of *Zostera marina* in the study area.

Zostera marina grows mainly in the subtidal and, consequently, most collections were carried out by scuba diving (fig. 2). Samplings were performed between April 2014 and April 2017, during spring and summer, which are the most favorable periods from a floristic point of view. In total, 36 eelgrass meadows were sampled and, in each one, five quadrats of 0.0625 m^2 were haphazardly distributed (Duarte & Kirkman 2001). In turn, the six longest leaves of *Zostera marina* were collected in each quadrat to study the macroalgal epiphytes (García-Redondo & al. 2017). Samples were preserved in 4% formalin seawater and kept in darkness at 4ºC. In total, 1,080 leaves of *Zostera marina* were studied.

Each leaf was observed under the stereomicroscope and optical microscope. Epiphytes were identified at the species level using the previously published floristic accounts for the major taxonomic groups, *Chlorophyta* Rchb. emend. Lewis & McCourt, *Ochrophyta* Caval.-Sm., and *Rhodophyta* Wettst. We used specialized literature on macroalgal epiphytes in *Zostera marina* (González 1976; Cullinane & al. 1985; Novaczek 1987; Saunders & Bird 1989; Saunders & McLachlan 1989; Johnson & al. 2005). The observed characters in our material were compared with descriptions available in the literature from the adjacent regions (Cardinal 1964; Dixon & Irvine 1977; Prud'homme van Reine 1982; Irvine 1983; Fletcher 1987; Kim & Lee 1992a, 1992b, 1994; Maggs & Hommersand 1993; Irvine & Chamberlain 1994; Brodie & Irvine 2003; Brodie & al. 2007; Secilla 2012). Likewise, we used floristic studies of the marine flora of the Iberian Atlantic (Peña & Bárbara 2003, 2006; Díaz-Tapia & Bárbara 2013, 2014; Bárbara & al. 2014, 2015, 2016). Representative specimens were deposited in herbarium of the University of Santiago de Compostela (SANT). The species were classified according to nine functional groups—unicellular, thin foliose, intermediated foliose, corticated foliose, filamentous, filiform, corticated filiform, articulated calcareous, and crustose—following García-Fernández & Bárbara (2016), who proposed a classification after the modification of Littler & Littler (1984) and Steneck & Dethier (1994).

We estimated the abundance of each epiphytic species on each studied leaf. As most species had very low values of covering—< 0.03%—, epiphytes were classified into abundance categories according to their percent of covering on the leaves of *Zostera marina.* We calculated the mean and the quartiles, and according to this, we considered five categories: i) mean greater than the minimum and lower than the first quartile; ii) mean greater than or equal to the first quartile and lower than the second quartile; iii) mean greater than or equal to the second quartile and lower than the third quartile; iv) mean greater than or equal to the third quartile and less than the fourth quartile; and v) mean greater than or equal to the fourth quartile and less than the maximum value.

RESULTS AND DISCUSSION

Floristic catalogue

In total, 63 epiphytic macroalgae were found on leaves of *Zostera marina* in the northwestern Iberian Peninsula (Table 1). Diversity was higher than the recorded in other areas of the Iberian Atlantic where eelgrass meadows hosted up to 38 species (Cullinane & al. 1985; Novaczek 1987; Johnson & al. 2005). By contrast, it was higher in Gran Canaria, where up to 79 species were recorded in seagrasses (González 1976).

Red algae—40 species (figs. 3–4)—were much more abundant than brown algae—16 species (fig. 5)—and green algae—7 species (fig. 6)—. The distribution of red, brown, and green algae is similar to the observed in eelgrass meadows from other Iberian regions, and it is proportional to the number of recorded species for these three groups in the northwestern Iberian Peninsula (Bárbara & al. 2005). However, the diversity of epiphytes was lower than the observed in other benthic habitats of the study region, such as maërl beds (Peña Freire 2010) or canopies of species of the genus *Cystoseira* L. (García-Fernández & Bárbara 2016). This is probably related to the short life span of the leaves of *Zostera marina*—88 days (Hemminga &

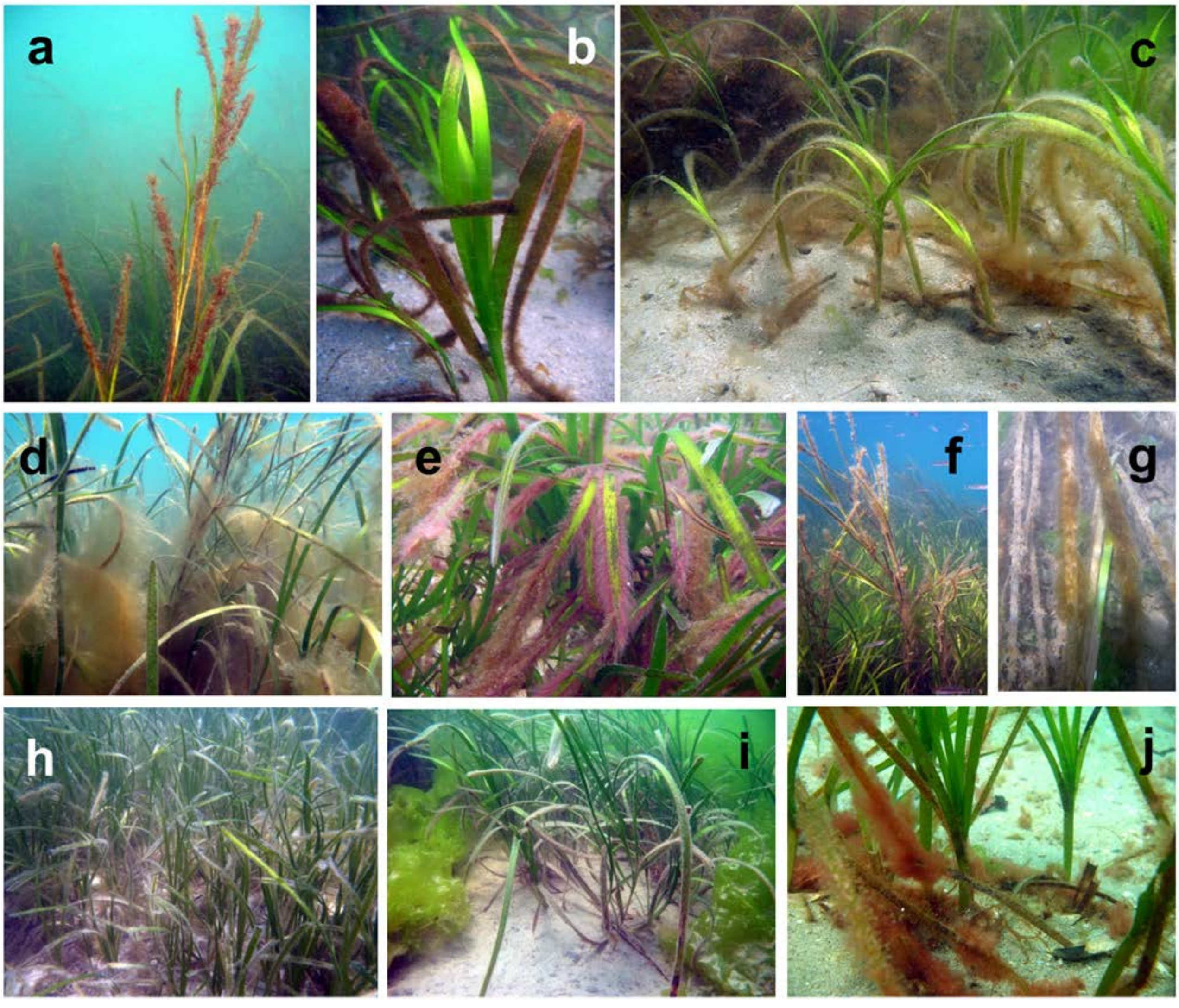

Fig. 2. Macroalgal epiphytes on subtidal meadows of *Zostera marina* L. in the northwestern Iberian Peninsula: **a-c,** Ría de Ferrol; **d,** Ares-Redes; **e, f,** Ría de Camariñas; **g,** Cortegada; **h,** Ría de Aldán; **i,** Ría de Vigo; **j,** Baiona.

Table 1. Distribution and abundance of macroalgal epiphytes on *Zostera marina* L. in the northwestern Iberian Peninsula. [Sampling sites: REO, Ría del Eo; CIB, San Cibrao; BAR, Ría de Barqueiro; ORT, Ría de Ortigueira; FER, Ferrol; ARR, Ares-Redes; SAD, Sada; CAM, Camariñas; SAL, Sálvora; COR, Cortegada; TOX, A Toxa; ALD, Aldán; SIM, San Simón; VIG, Ría de Vigo; BAI, Baiona. Scale of abundance: 1, mean greater than the minimum and lower than the first quartile; 2, mean greater than or equal to the first quartile and lower than the second quartile; 3, mean greater than or equal to the second quartile and lower than the third quartile; 4, mean greater than or equal to the third quartile and less than the fourth quartile; 5, mean greater than or equal to the fourth quartile and less than the maximum value. Morphofunctional groups (MO): 1, unicellular; 2, thin foliose; 3, intermediate foliose; 4, corticated foliose; 5, filamentous; 6, filiform; 7, corticated filiform; 8, articulated calcareous; 9, crustose; according García-Fernández & Bárbara (2016) modified from Littler & Littler (1984) and Steneck & Dethier (1994). The juvenile stages (JUV): +.]

JUV	MO	Species	REO	CIB	BAR	ORT	FER	ARR	SAD	CAM	SAL	COR	TOX	ALD	SIM	VIG	BAI
		Depth of eelgrass meadows (m)	0	2	1,5	+0.5–+1.5	1–3	0.5–1	0.5–1.5	1.5	2	+0.2–0.3	+0.5–1	2–4	+0.5–2	0–1	1.5–4
		Extension of area (km^2)	8.5	1.8	10	38	21	1.8	0.91	15	1.9	1.9	15	8	23	145	8
		Number of species	7	25	18	10	36	19	18	17	5	18	19	23	13	18	24
		Ochrophyta															
	6	*Asperococcus scaber* Kuck.														1	
	6	*Cladosiphon zosterae* (J. Agardh) Kylin					4	4		4			2	4		3	2
+	3	*Cutleria multifida* (Turner) Grev.		2													
+	3	*Desmarestia ligulata* (Stackh.) J.V. Lamour.								2							
+	3	*Dictyota dichotoma* (Huds.) J.V. Lamour.					2		1					1		1	2
	5	*Ectocarpus fasciculatus* Harv.	4	4	4	3	3			4			3	3	4	4	4
	5	*Ectocarpus siliculosus* (Dillwyn) Lyngb.			2	4	4	4	4	4		5		3	3	3	2
	5	*Feldmannia globifera* (Kütz.) Hamel					4	3	2		2	1	1	2		1	
	5	*Hincksia granulosa* (Smith) P.C. Silva		2	3		2										1
	5	*Hincksia hincksiae* (Harv.) P.C. Silva							2					4		2	
	6	*Litosiphon laminariae* (Lyngb.) Harv.					3										
	6	*Myriotrichia clavaeformis* Harv.				2	1	4	4			1			1	2	3
	6	*Navicula* sp. Bory	5									4			1		
+	7	*Sargassum muticum* (Yendo) Fensholt															1
	6	*Sphacelaria cirrosa* (Roth) C. Agardh			3			2					1				1
+	3	*Taonia atomaria* (Woodw.) J. Agardh															2
		Rhodophyta															
+	2	*Acrosorium ciliolatum* (Harv.) Kylin					1			1							
	5	*Aglaothamnion cordatum* (Børgesen) Feldm.-Maz.															2
	5	*Aglaothamnion hookeri* (Dillwyn) Maggs & Hommers.															1
	5	*Aglaothamnion pseudobyssoides* (P. Crouan & H. Crouan) L'Hardy-Halos		2	2		1							2	1		1
+	5	*Anotrichium furcellatum* (J. Agardh) Baldock		2	2									1			2
	5	*Antithamnion cruciatum* (C. Agardh) Nägeli		1			3						1	2			3
	5	*Antithamnionella ternifolia* (Hook.f. & Harv.) Lyle			2		3							1			3
+	2	*Apoglossum ruscifolium* (Turner) J.Agardh					1										
	5	*Callithamnion corymbosum* (Sm.) Lyngb					3	2									

Table 1. (Continued.)

JUV	MO	Species	REO	CIB	BAR	ORT	FER	ARR	SAD	CAM	SAL	COR	TOX	ALD	SIM	VIG	BAI
		Rhodophyta															
+	5	*Callithamnion tetragonum* (With.) Gray															1
	6	*Ceramium cimbricum* H.E. Petersen		1			4	1						1			
	6	*Ceramium echionotum* J. Agardh		2	1												
+	6	*Ceramium secundatum* Lyngb.	2	2	3	2	4	4	3	2		2	2	1	3	3	2
	6	*Champia parvula* (C. Agardh) Harv.					3										
+	6	*Chondria capillaris* (Hudson) M.J. Wynne						3									
+	6	*Chondria dasyphylla* (Woodw.) C. Agardh					4		1								
+	6	*Chylocladia verticillata* (Lightf.) Bliding		2			4	4	2				1				
	5	*Colaconema daviesii* (Dillwyn) Stegenga	4	4	2	4	4	4	4	2	4	5	4	4	3	4	4
+	5	*Compsothamnion thuyoides* (Sm.) Nägeli		1													
+	2	*Cryptopleura ramosa* (Huds.) L. Newton		2													
	6	*Dasya hutchinsiae* Harv.		2										1			
+	6	*Dasya sessilis* Yamada		2													
+	6	*Dasysiphonia japonica* (Yendo) Hy. S.Kim		1			4										1
	5	*Erythrotrichia bertholdii* Batters	3	3	4	1	4	2	2	2		3		2	1	2	
	5	*Erythrotrichia carnea* (Dillwyn) J. Agardh	3	3			4	4	4	3	2	3	3	3	2	3	
	6	*Gayliella flaccida* (Harv. ex Kütz.) T.O. Cho & L.J. McIvor		4	3	4	4	2	2				1	1		3	2
	6	*Gayliella mazoyerae* T.O. Cho, Fredericq & Hommers.											1				
+	2	*Hypoglossum hypoglossoides* (Stackh.) Collins & Hervey			1												
+	7	*Lomentaria articulata* (Huds.) Lyngb.											1				
+	7	*Lomentaria hakodatensis* Yendo											1				
	6	*Melanothamnus harveyi* (J.W. Bailey) Díaz-Tapia & Maggs					4	3	3			4	2	2		4	3
	9	*Pneophyllum fragile* Kütz.		4	3	4	5		3	4	5	4	4	5	4	5	4
	6	*Polysiphonia fibrillosa* (Dillwyn) Spreng.			3	1	4	4	2			4	2	4		3	2
	2	*Porphyrostromium boryanum* (Mont.) P.C. Silva					3			2							
	6	*Porphyrostromium ciliare* (Carmich.) M.J. Wynne	1	2	4		4	2		4	2	2					
+	2	*Pyropia leucosticta* (Thur.) Neefus & J. Brodie		3			2	2		2							
	2	*Rhodophysema georgei* Batters			2		4			4			4	4		4	3
+	5	*Rhodothamniella floridula* (Dillwyn) Feldmann					2			2							
+	5	*Spermothamnion repens* (Dillwyn) Magnus												1			
	5	*Stylonema alsidii* (Zanardini) K.M. Drew		3			3		3	2		2	2		1		
		Chlorophyta															
	5	*Cladophora albida* (Nees) Kütz.					1										
+	5	*Cladophora hutchinsiae* (Dillwyn) Kütz.										1					
+	5	*Cladophora laetevirens* (Dillwyn) Kütz.							1	2					1		
+	3	*Ulva australis* Aresch.										2		2			
	6	*Ulva clathrata* (Roth) C. Agardh					2					1					
+	3	*Ulva compressa* L.		3			1	1				2					
	6	*Ulva torta* (Mert.) Trevis.		3	2	3			2			4	1		2	3	

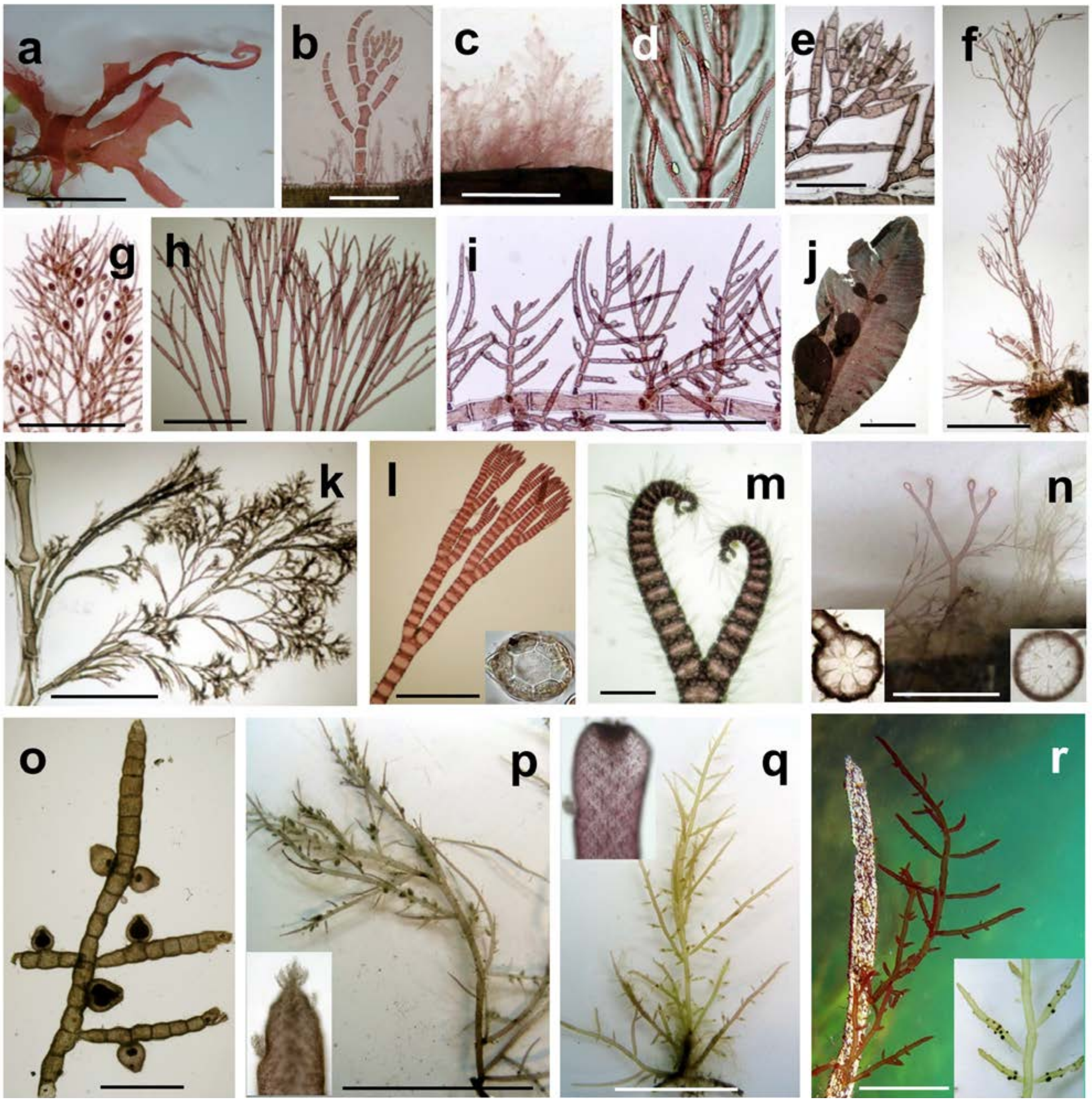

Fig. 3. Red algae on leaves of *Zostera marina* L. in the NW Iberian Peninsula: **a,** *Acrosorium ciliolatum* (Harv.) Kylin, with apical hooks; **b,** *Aglaothamnion hookeri* (Dillwyn) Maggs & Hommers., juvenile thallus with *Colaconema daviesii* (Dillwyn) Stegenga at the base; **c,** *Antithamnionella ternifolia* (Hook.f. & Harv.) Lyle, habit; **d,** *Antithamnionella ternifolia* filament with 3 whorled-branches and gland cells; **e,** *Callithamnion tetragonum* (With.) Gray with minute conical cells; **f,** *Aglaothamnion cordatum* (Børgesen) Feldm.-Maz.; **g,** *Aglaothamnion pseudobyssoides* (P.Crouan & H.Crouan) L'Hardy-Halos with terasporangia; **h,** *Anotrichium furcellatum* (J.Agardh) Baldock, filaments dichotomously branched; **i,** *Antithamnion cruciatum* (C.Agardh) Nägeli, filaments bearing opposite branches; **j,** *Apoglossum ruscifolium* (Turner) J.Agardh; **k,** *Callithamnion corymbosum* (Sm.) Lyngb.; **l,** *Ceramium cimbricum* H.E.Petersen, axis in cross section with 6 periaxial cells; **m,** *Ceramium echionotum* J.Agardh, with abundant spines single-celled; **n,** *Ceramium secundatum* Lyngb., habit and axes in cross section with 7 and 8 periaxial cells; **o,** *Champia parvula* (C.Agardh) Harv. bearing conical cystocarp with pore; **p,** *Chondria capillaris* (Hudson) M.J.Wynne, habit and detail of attenuate apex; **q,** *Chondria dasyphylla* (Woodw.) C.Agardh, habit and detail of obtuse apex; **r,** *Chylocladia verticillata* (Lightf.) Bliding, habit and detail of sphaerical cystocarps. [Scale bars: a, c, p-r, 1 cm; b, e, g, i, 500 µm; d, 100 µm; f, h, j-l, 1 mm; m, 200 µm; n, 5 mm; o, 2 mm.]

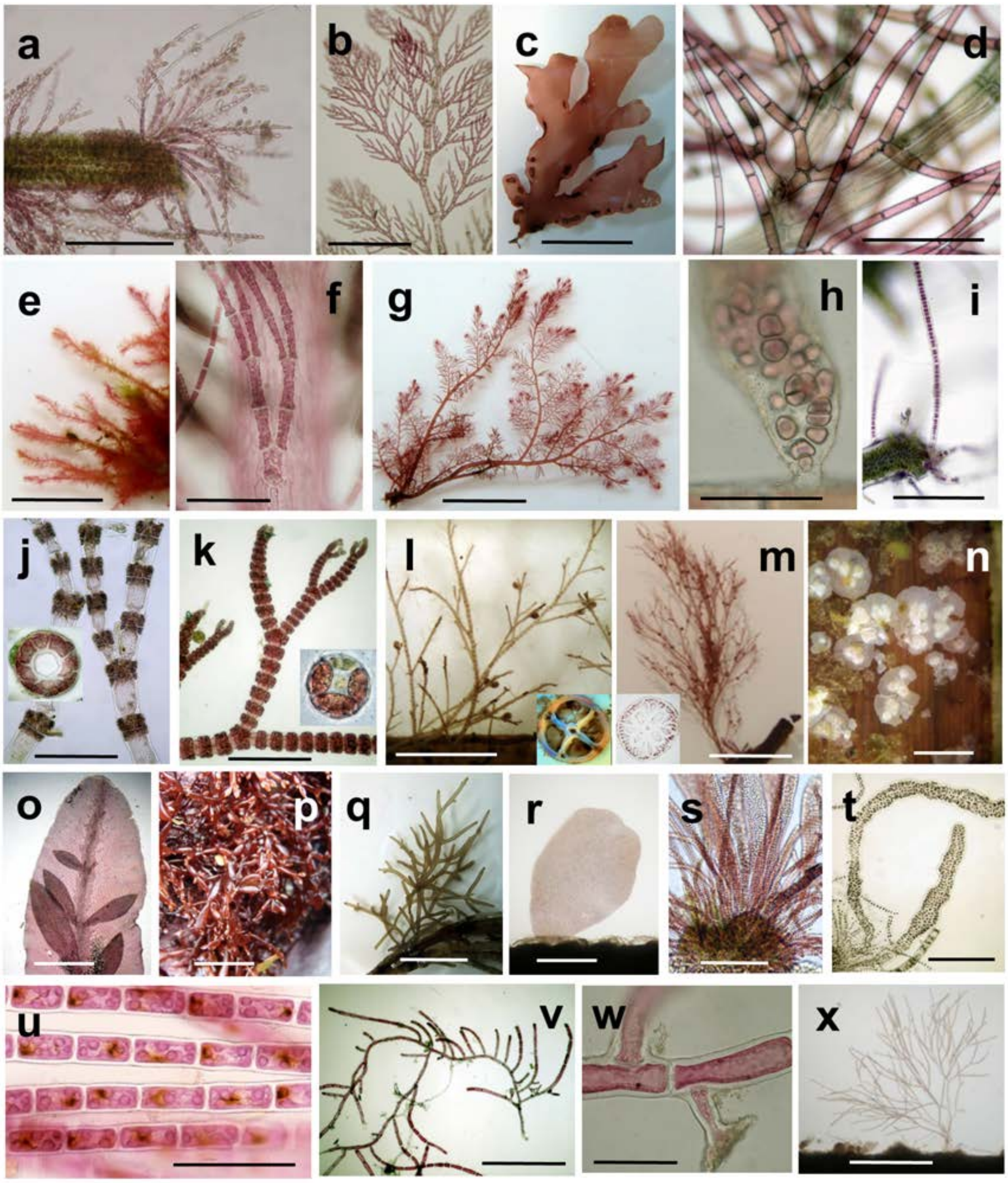

Fig. 4. Red algae on leaves of *Zostera marina* L. in the NW Iberian Peninsula: **a,** *Colaconema daviesii* (Dillwyn) Stegenga; **b,** *Compsothamnion thuyoides* (Sm.) Nägeli, regular alternate-distichous branches; **c,** *Cryptopleura ramosa* (Huds.) L.Newton; **d,** *Dasya hutchinsiae* Harv., detail of axis and pseudolaterals; **e,** *Dasya sessilis* Yamada; **f,** *Dasya sessilis,* detail of pseudolaterals; **g,** *Dasysiphonia japonica* (Yendo) Hy.S.Kim, habit; **h,** *Erythrotrichia bertholdii* Batters; **i,** *Erythrotrichia carnea* (Dillwyn) J.Agardh; **j,** *Gayliella flaccida* (Harv. ex Kütz.) T.O.Cho & L.J.McIvor, axis in cross section with 6 periaxial cells; **k,** *Gayliella mazoyerae* T.O.Cho, Fredericq & Hommers., axis in cross section with 4 periaxial cells; **l,** *Melanothamnus harveyi* (J.W.Bailey) Díaz-Tapia & Maggs, axis in cross section with 4 pericentral cells; **m,** *Polysiphonia fibrillosa* (Dillwyn) Spreng., axis in cross section with 4 pericentral cells; **n,** *Pneophyllum fragile* Kütz., discoidal thallus; **o,** *Hypoglossum hypoglossoides* (Stackh.) Collins & Hervey; **p,** *Lomentaria articulata* (Huds.) Lyngb.; **q,** *Lomentaria hakodatensis* Yendo, branching opposite; **r,** *Pyropia leucosticta* (Thur.) Neefus & J.Brodie; **s,** *Porphyrostromium boryanum* (Mont.) P.C.Silva; **t,** *Porphyrostromium ciliare* (Carmich.) M.J.Wynne; **u,** *Rhodothamniella floridula* (Dillwyn) Feldmann, cell with 3-8 plastids; **v, w,** *Spermothamnion repens* (Dillwyn) Magnus, prostrate axes bearing rhizoids in basal position (w); **x,** *Stylonema alsidii* (Zanardini) K.M.Drew. [Scale bars: a, f, i, j, s, 200 µm; b, d, t, 500 µm; c, e, g, l, m, p, q, 1 cm; h, 50 µm; n, o, v, x, 1 mm; r, 2 mm; u, w, 100 µm.]

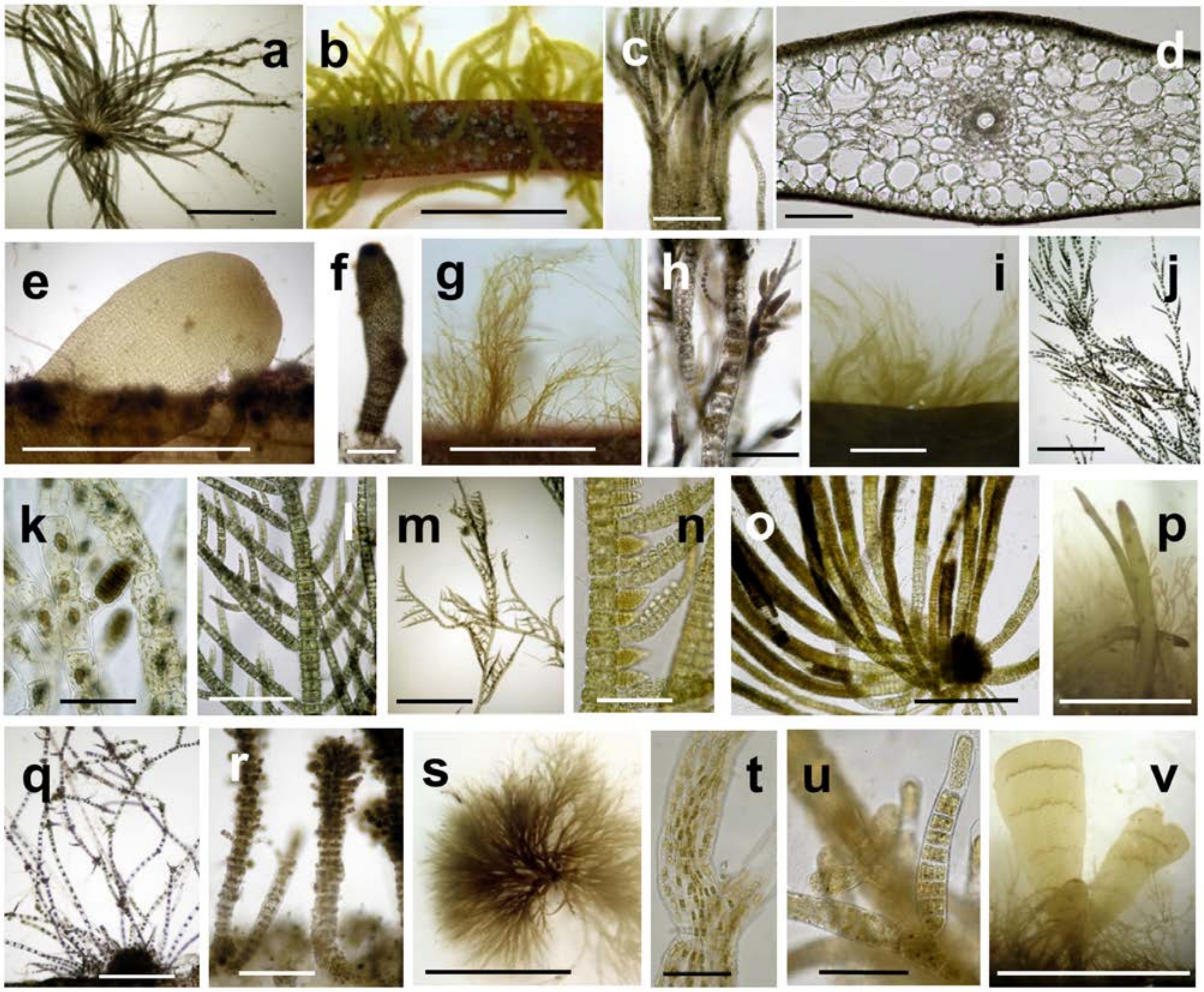

Fig. 5. Brown algae on leaves of *Zostera marina* L. in the NW Iberian Peninsula: **a,** *Asperococcus scaber* Kuck.; **b,** *Cladosiphon zosterae* (J.Agardh) Kylin, with crusts of *Pneophyllum fragile* Kütz.; **c,** *Cutleria multifida* (Turner) Grev., apex with marginal hairs; **d,** *Desmarestia ligulata* (Stackh.) J.V.Lamour., uniaxial structure in cross section; **e, f,** *Dictyota dichotoma* (Huds.) J.V.Lamour., thallus ribbon-like and cylindrical, respectively; **g, h,** *Ectocarpus fasciculatus* Harv., with plurilocular sporangia (h); **i, j,** *Ectocarpus siliculosus* (Dillwyn) Lyngb., with plurilocular sporangia (j); **k,** *Feldmannia globifera* (Kütz.) Hamel, with pedicellate plurilocular sporangia; **l,** *Hincksia granulosa* (Smith) P.C.Silva, with opposite branches; **m, n,** *Hincksia hincksiae* (Harv.) P.C.Silva, with series of unilateral branches (m) and plurilocular sporangia densely arranged (n); **o,** *Litosiphon laminariae* (Lyngb.) Harv., tuft; **p,** *Sargassum muticum* (Yendo) Fensholt, juvenile; **q, r,** *Myriotrichia clavaeformis* Harv., juvenile (q) and mature axis (r); **s, t,** *Navicula* sp., macroscopic aggregation (s) containing bacillar diatom cells (t); **u,** *Sphacelaria cirrosa* (Roth) C.Agardh, propagule with arms basally constricted and apical cells; **v,** *Taonia atomaria* (Woodw.) J.Agardh, banded in surface view. [Scale bars: a, b, e, g, i, p, s, v, 1 cm; c, d, f, h, l, r, 200 µm; j, o, q, 400 µm; k, n, t, u, 100 µm; m, 1 mm.]

Duarte 2000)—, the physical and chemical changes that occur in the leaves during their growth or the stressful environmental conditions of eelgrass meadows—v. gr., influence of sediments or emersion time—. Interestingly, the diversity of epiphytes varies among seagrass species and the studied regions. *Posidonia oceanica* (L.) Delile has a longer life span than *Zostera marina*—170 days (Hemminga & Duarte 2000)—but the diversity recorded on its leaves in the Mediterranean is even smaller—51 spp. (Nesti & al. 2009)—. By contrast, in the Canary Islands *Cymodocea nodosa* (Ucria) Asch. has a similar diversity of epiphytes—53 spp.—than *Posidonia oceanica,* despite the life span of the former species is shorter—68 vs. 170 days (Reyes & al. 1995; Reyes & Sansón 1996).

Two functional forms, filamentous—23 spp.—and filiform—23 spp.—, accounted most of the functional diversity of the epiphytic flora of *Zostera marina.* Foliose species, both thin and intermediate, were also common—seven and six species, respectively—, while the corticated filiform and crustose species were rare—three and one species, respectively—. Unicellular, corticated foliose and articulated calcareous functional groups included in García-Fernández & Bárbara (2016) were never observed among epiphytes. This pattern is the expected considering the short life span that the leaves of *Zostera marina* provide for epiphytes, as mentioned above. Consequently, species with high growth rates thrive better in this particular habitat, while perennial species cannot persist. Filiform, filamentous, and foliose are the functional forms characterized by having the highest growth rates (Littler & Littler 1984). *Pneophyllum fragile* Kütz. is the only crustose species that occur on the leaves. It is a thin calcareous coralline algae with only a few cell layers (Irvine & Chamberlain 1994), so it can grow quickly and is adapted to eelgrass habitat. It is also a common epiphyte on the seagrass *Cymodocea nodosa,* in which *Pneophyllum fragile* is one of the first epiphytic species colonizing the young leaves (Reyes & Sansón 1996). Probably, the pioneer character of this species also applies in *Zostera marina.* Mean covering of epiphytic macroalgae on the leaves of *Zostera marina* is low. Table 1 shows that the category 2—0.007–0.033%—is the most common, while category 5—10–73% cover—is rare. Some species were occasionally observed covering a high percentage of leaves, such as *Pneophyllum fragile*—up to 73%—, *Colaconema daviesii* (Dillwyn) Stegenga—up to

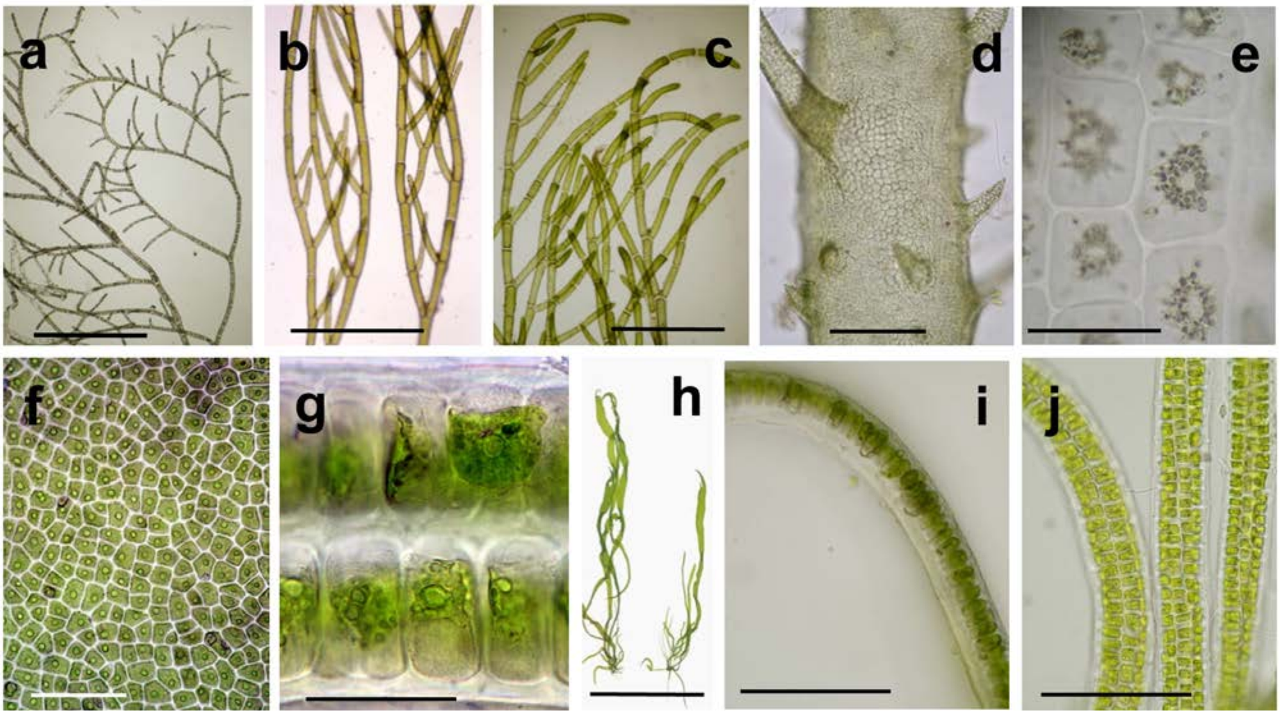

Fig. 6. Green algae on leaves of *Zostera marina* L. in the NW Iberian Peninsula: **a,** *Cladophora albida* (Nees) Kütz.; **b,** *Cladophora hutchinsiae* (Dillwyn) Kütz.; **c,** *Cladophora laetevirens* (Dillwyn) Kütz., branches falcate; **d, e,** *Ulva clathrata* (Roth) C.Agardh, spine like projections (d) and plastids with several pyrenoids (e); **f, g,** *Ulva australis* Aresch., surface view and cross section, cells mainly with 1 pyrenoid; **h, i,** *Ulva compressa* L., habit (h) and cross section (i); **j,** *Ulva torta* (Mert.) Trevis., thallus tubular up to 8 cells around. [Scale bars: a-c, 1 mm; d, f, i, j, 100 µm; e, g, 50 µm; h, 1 cm; n, 500 µm.]

16.23%—, *Ectocarpus siliculosus* (Dillwyn) Lyngb.—up to 29.60%—or *Rhodophysema georgei*—up to 5.23%.

Ten species were more abundant and common, as were found in practically all the sampling dates and sites. Among them, *Colaconema daviesii, Porphyrostromium ciliare* (Carmich.) M.J.Wynne, *Erythrotrichia bertholdii* Batters, and *Erythrotrichia carnea* (Dillwyn) J.Agardh are small—< 5 mm—red algae with filamentous or foliose morphologies. *Ceramium secundatum* Lyngb., *Gayliella flaccida* (Harv. ex Kütz.) T.O.Cho & L.J.McIvor, and *Polysiphonia fibrillosa* (Dillwyn) Spreng. are filiform red algae whose thallus can be up to 1 cm in length. The brown algae *Ectocarpus fasciculatus* Kütz. and *Ectocarpus siliculosus* are filamentous species that can be up to 2 cm in length.

The diversity of epiphytes greatly varied among sampling sites (Table 1). Ferrol—FER—had the highest diversity and Sálvora—SAL—the lowest, 36 and five species, respectively. Interestingly, the low diversity found in Sálvora contrasts with the highest covering observed in this study—73%, *Pneophyllum fragile*—. Some of the species here recorded were only found in one of the areas (Table 1), and, for example, *Litosiphon laminariae* (Lyngb.) Harv., *Apoglossum ruscifolium* (Turner) J.Agardh, *Champia parvula* (C.Agardh) Harv., and *Cladophora albida* (Nees) Kütz. were only observed in Ferrol. Thus, it is important to study several meadows in order to achieve a comprehensive view of the epiphytic flora at a regional scale.

The present work, focused on the epiphytic macroalgae, was developed in the framework of a broader study on the flora associated with *Zostera marina.* This allows us to establish comparisons among the flora associated to the different habitats within the meadows. Nine species have been found in *Zostera marina* exclusively as epiphytes on leaves: *Cladosiphon zosterae* (J.Agardh) Kylin, *Ectocarpus fasciculatus, Ectocarpus siliculosus, Feldmannia globifera* (Kütz.) Hamel, *Litosiphon laminariae, Myriotrichia clavaeformis* Harv., *Pneophyllum fragile, Polysiphonia fibrillosa,* and *Rhodophysema georgei.* However, other epiphytic species can be found also growing on the adjacent sedimentary substrate of meadows—V. García-Redondo, pers. comm.—, such as *Cutleria multifida* (Turner) Grev., *Hincksia* spp., *Sargassum muticum* (Yendo) Fensholt, *Aglaothamnion* spp., *Ceramium* spp., *Dasya* spp. or *Ulva* spp. Most of the species here recorded were only found as juvenile stages—43%—. For example, specimens of the brown algae—*Cutleria multifida, Desmarestia ligulata* (Stackh.) J.V.Lamour., *Dictyota dichotoma* (Huds.) J.V.Lamour., *Taonia atomaria* (Woodw.) J.Agardh, *Sargassum muticum*—as well as red algae—*Apoglossum ruscifolium, Callithamnion tetragonum* (With.) Gray, *Compsothamnion thuyoides* (Sm.) Nägeli, *Dasya sessilis* Yamada, *Dasysiphonia japonica* (Yendo) Hy.S.Kim, *Hypoglossum hypoglossoides* (Stackh.) Collins & Hervey—and green algae—*Cladophora hutchinsiae* (Dillwyn) Kütz. and *Ulva australis* Aresch.—were found on leaves of *Zostera marina,* but they were less than 1.5 cm in length and lack reproductive structures.

Regarding non-native seaweeds, nine species have been recorded: *Sargassum muticum, Anotrichium furcellatum* (J.Agardh) Baldock, *Antithamnionella ternifolia* (Hook.f. & Harv.) Lyle, *Dasya sessilis, Dasysiphonia japonica, Lomentaria hakodatensis* Yendo, *Melanothamnus harveyi* (J.W.Bailey) Díaz-Tapia & Maggs, *Pyropia leucosticta* (Thur.) Neefus & J.Brodie, and *Ulva australis.* The high diversity of introduced species might be facilitated by the placement of most of the eelgrass meadows in sheltered areas, which are subjected to a high incidence of the most relevant vectors for introduction and spread of non-native seaweeds, i.e., harbors or aquaculture facilities (Williams & Smith 2007).

Some of the species here recorded are unusual or scarcely known in the northwestern Iberian Peninsula. *Rhodophysema georgei* (fig. 7) had been only recorded before by Miranda (1934) and remained unnoticed up to now. The lack of information on this species is probably explained because it is an obligate epiphyte on *Zostera marina* and its flora has been scarcely studied in the Iberian Peninsula. Morphological characters of *Rhodophysema georgei* from the northwestern Iberian Peninsula agree with the descriptions for other regions (Saunders & Bird 1989; Saunders & McLachlan 1989). Other scarcely known species are *Asperococcus scaber* Kuck., which is here recorded for the second time in the Iberian Atlantic—first report in Bárbara & al. (2015)—and for the first time in the province of Pontevedra—Ría de Vigo—; and *Gayliella mazoyerae* T.O.Cho, Fredericq & Hommers.that is recorded for the first and second time in Pontevedra—A Toxa—and Galicia, respectively—first report in Bárbara & al. (2016).

In sum, our study shows that the epiphytic flora on the leaves of *Zostera marina* is a diverse assemblage, considering the continuous environmental variations associated with this habitat. The composition of the flora was highly variable in frequency and abundance among the studied regions, as it depends on the interaction of several factors and processes that operate at different spatial and temporal scales (Borowitzka & al. 2006). The supply of propagules is a key process that influences the epiphytic assemblage (Borowitzka & al. 2006). They can come from the meadows or from adjacent communities, which explain the high number of species that were observed only as juvenile stages because leaves are an unsuitable substrate for mature stages.

Key to the NW Iberian Peninsula epiphytic macroalgae on Zostera marina

Identification of epiphytes is sometime challenging because most part of specimens were found as juvenile and immature stages. Thus, some of the key vegetative and reproductive characters needed for morphological identifications were not properly developed. In order to facilitate the identification of epiphytic macroalgae of the leaves of *Zostera marina,* we provide the following identification key that can be successfully used independently of the maturity of specimens. Pictures showing the main characters of these species are provided in figs. 3–7.

1. Green algae; thallus filamentous, laminar or tubular 2
– Brown algae; thallus filamentous, filiform or laminar 5
– Red algae; thallus filamentous, filiform or laminar 12
2. Thallus laminar distromatic and cells mainly with one pyrenoid .... *Ulva australis* Aresch.
– Thallus tubular 3
– Thallus filamentous, typically branched several times 4
3. Thallus entirely tubular, 30–50 µm in diameter, unbranched and composed by up to 8 cells around ....… *Ulva torta* (Mert.) Trevis.
– Thallus entirely tubular, > 100 µm in diameter, branched, usually with spine-like projections; plastids filling cells and containing 5–15 pyrenoids …..... *Ulva clathrata* (Roth) C.Agardh
– Thallus tubular, branched or unbranched, occasionally compressed at upper parts; cells arranged in short to long rows; plastids hood-shaped with one pyrenoid …............. *Ulva compressa* L.
4. Apical cell 10–20 µm in diameter; slightly acropetal growth only in young plants .... *Cladophora albida* (Nees) Kütz.
– Apical cell < 90 µm in diameter; main axes pseudodichotomously branched; ultimate branch-system acropetally organized; branches generally falcate .... *Cladophora laetevirens* (Dillwyn) Kütz.
– Apical cell > 90 µm in diameter. Slightly acropetal growth only in young plants .... *Cladophora hutchinsiae* (Dillwyn) Kütz.
5. Thallus mainly ribbon-like 6
– Thallus filamentous, branched several times 7
– Thallus filiform or terete 10
6. Branching pinnate and opposite; apex attenuate, with marginal hairs; uniaxial growth ...… *Desmarestia ligulata* (Stackh.) J.V.Lamour.
– Branching dichotomous, regular; apex obtuse, without marginal hairs; some juvenile plants are cylindrical ….................................. .... *Dictyota dichotoma* (Huds.) J.V.Lamour.
– Branching dichotomous, irregular; apex blunt, with marginal hairs ….. *Cutleria multifida* (Turner) Grev.
– Branching dichotomous, irregular; apex blunt, without marginal hairs; blade mainly banded in surface view …................................ .... *Taonia atomaria* (Woodw.) J.Agardh
7. Plastids ribbon-like, 2–3 per cell, each with several pyrenoids 8
– Plastids discoid, >10 per cell, each with one pyrenoid 9
8. Main axis wider than secondary axes; plurilocular sporangia < 100 µm long, 2–4 times longer than wide .... *Ectocarpus fasciculatus* Harv.
– Main and secondary axes similar in diameter. Plurilocular sporangia 100–200 µm long, 7–8 times longer than wide .... *Ectocarpus siliculosus* (Dillwyn) Lyngb.
9. Filaments 70–100 µm in diameter, usually oppositely branched; plurilocular sporangia globose, sessile, and usually isolated ....… *Hincksia granulosa* (Smith) P.C.Silva
– Filaments 35–60 µm in diameter, plurilocular sporangia pedicellate .... *Feldmannia globifera* (Kütz.) Hamel
10. Axes and branches pliable, containing numerous bacillar diatom cells .... *Navicula* sp.
– Juvenile plants terete and rigid, < 1 cm long and 1 mm wide .... *Sargassum muticum* (Yendo) Fensholt
– Thallus filiform, transverse and longitudinal cell divisions conspicuous in surface view, growing from a dark apical cell; propagules frequent .... *Sphacelaria cirrosa* (Roth) C.Agardh
– Thallus different 11
11. Thallus < 5 mm long, terete, growing in groups and bearing apical and lateral hairs; sorus of plurilocular sporangia protruding .... *Asperococcus scaber* Kuck.
– Thallus > 5 mm long, terete, isolated or in groups; only lateral hairs; plurilocular sporangia not protruding .... *Litosiphon laminariae* (Lyngb.) Harv.

Fig. 7. *Rhodophysema georgei* Batters in the NW Iberian Peninsula: **a, b,** subspherical cushions on *Zostera marina* L., surface view and cross section; **c-d,** tetrasporangial sorus. [Scale bars: a, 2 mm; b-d, 200 µm; e, 50 µm.]

– Young thallus filamentous, becoming nodose and filiform at maturity, > 5 mm long; unilocular and plurilocular sporangia growing at the same time .... *Myriotrichia clavaeformis* Harv.
– Thallus filiform multiaxial; unilocular sporangia on the thallus surface and plurilocular sporangia terminal on short filaments .... *Cladosiphon zosterae* (J.Agardh) Kylin
12. Thallus calcified, crustose, discoidal, up to 1 cm; reproductive structures housed into protruding conceptacles; tetrasporangia zonate .... *Pneophyllum fragile* Kütz.
– Thallus forming subspherical cushions up to 1 mm in diameter; tetrasporangia cruciate …............ *Rhodophysema georgei* Batters
– Thallus with branches constricted at intervals …........................ 13
– Thallus with a different morphology …...................................... 14
13. Branches whorled; segments of axis and branches longer than wide; cystocarp sphaerical and without a pore .... *Chylocladia verticillata* (Lightf.) Bliding
– Branches alternate or irregular, rarely whorled; segments slightly constricted and shorter than wide; cystocarp conical with pore .... *Champia parvula* (C.Agardh) Harv.
– Apical branching often dichotomous; segments longer than wide; cystocarp with prominent pore .... *Lomentaria articulata* (Huds.) Lyngb.
– Branching opposite; contiguous branches welded .... *Lomentaria hakodatensis* Yendo
14. Thallus filamentous, filiform, laminar or ribbon-like, monostromatic, membranous, and translucent throughout; structure simple, without cortication; pit connections not observed under optical microscope 15
– Thallus laminar or ribbon-like, membranous, and translucent, generally monostromatic; pit connections observed under optical microscope 19
– Thallus filamentous, filiform or terete; pit connections observed under optical microscope 22
15. Thallus laminar or ribbon-like ....… 16
– Thallus filamentous …... 17
– Thallus filiform ….. 18
16. Thallus laminar, monostromatic and orbicular; at the base, multicellular disc with abundant rhizoidal cells; male sorus arranged in radial rows ..... *Pyropia leucosticta* (Thur.) Neefus & J.Brodie
– Thallus laminar, monostromatic and elongate, < 5 mm wide; at the base, multicellular disc without rhizoidal cells .... *Porphyrostromium boryanum* (Mont.) P.C. Silva
17. Thallus filamentous, unbranched, with a basal cell .... *Erythrotrichia carnea* (Dillwyn) J.Agardh
– Thallus filamentous, branched, with a basal cell .... *Stylonema alsidii* (Zanardini) K.M.Drew
18. Thallus filiform unbranched, with a basal multicellular disc .... *Porphyrostromium ciliare* (Carmich.) M.J.Wynne
– Thallus filiform unbranched, with a basal cell …............................. .... *Erythrotrichia bertholdii* Batters
19. Midrib conspicuous, running from base to apex 20
– Midrib absent, but veins or thickenings may be present 21
20. Tips rounded; blade cells small, < 20 µm; microscopic lateral veins present .... *Apoglossum ruscifolium* (Turner) J.Agardh
– Tips attenuate; blade cells large, > 60 µm; microscopic lateral veins absent .... *Hypoglossum hypoglossoides* (Stackh.) Collins & Hervey
21. Blade red to brownish-red, ruffled and membranous, generally with lobed margin; macroscopic veins conspicuous, at least near base of blade ....… *Cryptopleura ramosa* (Huds.) L.Newton
– Blade rose-pink, crisp and membranous, generally with apical hooks; macroscopic veins absent, only microscopic veins present …............. .... *Acrosorium ciliolatum* (Harv.) Kylin
22. Thallus filamentous throughout; cortication generally absent 23
– Thallus filamentous or filiform, composed by uniaxial axes—internodes—and axes surrounded by periaxial cell—nodes—and external cortical cells 28
– Thallus filiform or terete, with inner polysiphonous structure that can be covered by cortical cells 30
23. Thallus composed by prostate and erect axes, < 150 µm in diameter, bearing paired or whorled-branches 24
– Thallus composed by prostate and erect axes, < 150 µm in diameter, irregularly branched 25
– Erect filaments without extensive prostate axes 26
24. Erect filaments, 40–60 µm in diameter, bearing 3 whorled-branches; gland cells lying alongside one cell of short branchlets ....… *Antithamnionella ternifolia* (Hook.f. & Harv.) Lyle
– Erect filaments, 100–120 µm in diameter, bearing opposite branches; gland cells lying alongside 2–3 cells of short branchlets …............ .... *Antithamnion cruciatum* (C.Agardh) Nägeli
– Erect filaments, 40–70 µm in diameter, bearing opposite branches; prostrate axes bearing rhizoids ventrally and erect axes dorsally …. .... *Spermothamnion repens* (Dillwyn) Magnus
25. Erect filaments, 40–100 µm in diameter, irregularly branched; cell with 3–8 plastids, each with one pyrenoid .... *Rhodothamniella floridula* (Dillwyn) Feldmann
– Erect filaments, 30–55 µm in diameter, irregularly branched but usually in one plane; cell with one parietal plastid with an obvious pyrenoid .... *Colaconema daviesii* (Dillwyn) Stegenga
26. Erect filaments, 170–260 µm in diameter, dichotomously branched without extensive prostate axes .... *Anotrichium furcellatum* (J.Agardh) Baldock
– Main axes, 100–150 µm in diameter; every cell of first and second-order branches bears branchlets in a perfectly regular alternate-distichous arrangement .... *Compsothamnion thuyoides* (Sm.) Nägeli
– Thallus and branching different 27
27. Main axes 20–80 µm in diameter, branching alternate-distichous; apex of the main axis conspicuous ....… *Aglaothamnion hookeri* (Dillwyn) Maggs & Hommers.
– Main axes 30–85 µm in diameter, spirally branched, alternately branched at upper parts; basal cells of the main axes longer than wide …................... *Aglaothamnion pseudobyssoides* (P.Crouan & H.Crouan) L'Hardy-Halos
– Main axes 45–100 µm in diameter, spirally branched, dichotomously branched at upper parts; basal cells of the main axes longer than wide ….. .... *Aglaothamnion cordatum* (Børgesen) Feldm.-Maz.
– Main axes 50–200 µm in diameter, composed by cells 6–12 diameters long; upper branches dichotomously divided …............ .... *Callithamnion corymbosum* (Sm.) Lyngb.
– Main axes 150–300 µm in diameter, composed by cells < 6 diameters long; terminal lateral branchlets > 6 cells long, ending by a minute—6–8 µm—conical cell …... .... *Callithamnion tetragonum* (With.) Gray
28. Axis and branches entirely corticate; axes branching every 10–18 segments; periaxial cells typically 8 .... *Ceramium secundatum* Lyngb.
– Thallus incompletely corticated; spines single-celled bearing on cortical bands .... *Ceramium echionotum* J.Agardh
– Thallus incompletely corticated; axes branching < 10 segments; spines absent 29
29. Axis 50–120 µm in diameter, with 5–6 periaxial cells and unicellular rhizoids; gland cells at the nodes .... *Gayliella flaccida* (Harv. ex Kütz.) T.O.Cho & L.J.McIvor
– Axis 60 µm in diameter, with 4 periaxial cells and unicellular rhizoids; gland cells among cortical cells .... *Gayliella mazoyerae* T.O.Cho, Fredericq & Hommers.
– Axis 150–200 µm in diameter, with 5–8 periaxial cells and multicellular rhizoids; gland cells absent; tetrasporangia covered by cortical cells .... *Ceramium cimbricum* H.E.Petersen
30. Axis and branches corticate; inner polysiphonous structure, but bearing outer monosiphonous pseudolateral branches ....… 31
– Cylindrical axis densely corticated; inner structure polysiphonous with 5 pericentral cells ….. 32
– Cylindrical axis weakly corticated; inner structure polysiphonous with 4 pericentral cells ….. 33

31. Axes with by 5 pericentral cells; branching spiral; pseudolaterals in narrow angle—< 45 .... *Dasya sessilis* Yamada
– Axes with 5 pericentrals cells; branching spiral; pseudolaterals in wide angle—80–100 .... *Dasya hutchinsiae* Harv.
– Axes with 4 pericentrals cells; branching distichous; pseudolaterals in wide angle—80–100 .... *Dasysiphonia japonica* (Yendo) Hy.S.Kim
32. Apex attenuate .... *Chondria capillaris* (Hudson) M.J.Wynne
– Apex obtuse, ending in a shallow depression .... *Chondria dasyphylla* (Woodw.) C. Agardh
33. Cortication present near base; plastids on all walls of pericentral cells .... *Polysiphonia fibrillosa* (Dillwyn) Spreng.
– Cortication absent; plastids only on radial walls of pericentral cells .... *Melanothamnus harveyi* (J.W.Bailey) Díaz-Tapia & Maggs

ACKNOWLEDGEMENTS

We thank Xunta de Galicia for providing founding through the programme "Axudas para a consolidación e estruturación de unidades de investigación competitivas" (GPC2015/025). PDT acknowledges support by the postdoctoral programmes "Axudas de apoio á etapa de formación posdoutoral" (Xunta de Galicia). We thank the Galician Atlantic Islands maritime-terrestrial National Park their kindness in the management of sampling permits. We thank Alicia García-Fernández for her collaboration in the fieldwork.

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