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Studies of *Cystoseira* assemblages in Northern Atlantic Iberia

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Abstract

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The Iberian Peninsula contains 24 specific and infra-specific taxa of the genus *Cystoseira*, but only 6 inhabit in Northern Iberia: *C. baccata*, *C. foeniculacea*, *C. humilis* var. *myriophylloides*, *C. nodicaulis*, *C. tamariscifolia*, and *C. usneoides*. The *Cystoseira* assemblages exhibit a complex structure and stratification that allows the presence of a large associate biota and a rich epiphytic flora. Although in the Mediterranean Sea several species have been analyzed in depth, the Atlantic ones are less studied. A revision of the literature (1931-2014) and grey information was made to know the diversity of the North Atlantic Iberian *Cystoseira* assemblages. The community of *C. baccata* harbors the biggest number of species (215), followed by *C. tamariscifolia* (162) and *C. usneoides* (126), whereas the community with fewest species was the *C. foeniculacea* one (34). More than 70 species were present in the majority of the *Cystoseira* assemblages. In this article, are revised also environmental issues in the *Cystoseira* assemblages, as pollution and anthropogenic pressures or disturbances that cause regression in their communities, and effects of biological invasions by non-native species. As a conclusion, it will necessary to study the *Cystoseira* assemblage in depth, starting by research of *C. baccata* along Northern Iberia, as it is an exclusive and widely distributed Atlantic species with very scarce information concerning its role in structuring the communities.

Key words: biodiversity, *Cystoseira*, Iberian Peninsula, marine assemblages, seaweeds.

DIVERSITY AND DISTRIBUTION OF THE GENUS *CYSTOSEIRA*

The genus *Cystoseira* C. Agardh was described in 1820, including 37 species, although its taxonomy and nomenclature has suffered many changes since then, because of variability within the genus occurs not only among species but also among individuals of a single species and, seasonally, within a single individual. Moreover, in some species, no holotype was designated in species description, and lectotypes have yet to be chosen (Furnari & al., 1999). To complete the knowledge of *Cystoseira* (taxonomy and evolutionary origin), Draisma & al. (2010) made a phylogenetic analysis of the Sargassaceae and found out that *Bifurcaria*, *Cystoseira*, *Halidrys*, and *Sargassum* (as currently recognized) are polyphyletic and should each be split into two or more genera. The genus *Cystoseira* was originated in the Thetis Sea during the Mesozoic, afterwards, some species stayed in the Indo-Pacific Ocean and others should have entered into the Mediterranean Sea from the Atlantic Ocean during the

Resumen

García-Fernández, A. & Bárbara, I. 2016. Estudios acerca de los agregados de *Cystoseira* de las costas atlánticas del norte de la Península Ibérica. *Anales Jard. Bot. Madrid* 73(1): e035.

La Península Ibérica contiene 24 táxones del género *Cystoseira*, pero sólo 6 habitan en las costas del norte: *C. baccata*, *C. foeniculacea*, *C. humilis* var. *myriophylloides*, *C. nodicaulis*, *C. tamariscifolia* y *C. usneoides*. Las comunidades de *Cystoseira* muestran una estructura compleja debido a su estratificación, lo que permite el desarrollo de una amplia biota asociada y una gran riqueza de flora epífita. Aunque diversas especies mediterráneas han sido analizadas en profundidad, las atlánticas son menos conocidas. Se ha recopilado información bibliográfica (1931-2014) y datos inéditos para conocer la diversidad de las comunidades de *Cystoseira* en las costas atlánticas del norte de la Península Ibérica. Las comunidades de *C. baccata* albergan el mayor número de especies (215), seguido de *C. tamariscifolia* (162) y *C. usneoides* (126), mientras que la comunidad con el menor número de especies fue *C. foeniculacea* (34). Más de 70 especies están presentes en la mayoría de las comunidades de *Cystoseira*. En este artículo, se han revisado también aspectos medioambientales que afectan a las comunidades de *Cystoseira*, como contaminación y perturbaciones antropogénicas que causan la regresión de las poblaciones, así como los efectos de las invasiones biológicas por especies alóctonas. Como conclusión, será necesario el estudio de las comunidades de *Cystoseira* en profundidad, empezando por investigaciones de *C. baccata* en el norte, ya que es una especie exclusiva y ampliamente distribuida en el Atlántico y con escasa información relativa a su papel en la estructuración de comunidades.

Palabras clave: algas, biodiversidad, comunidades marinas, *Cystoseira*, Península Ibérica.

Cenozoic, starting a speciation process that continues nowadays (Oliveras Plá & Gómez Garreta, 1989).

According to the literature (Gómez Garreta & al., 2000; Cormaci & al., 2012) *Cystoseira* species are plants about 1 meter high with a single primary axis or several primary axes in caespitose thalli, attached to the substratum by a conical disc or haptera. Its apex is smooth or spinous and its ramification in branches is abundant, radial or distichous, sometimes with small spine-like or filiform appendages. These branches could exhibit a characteristic greenish-blue iridescence. Some species present conical or ovoid tophules, arranged along the axis or grouped in the apical zone; and aerocysts, isolated or arranged in chains at the apices of the terminal branchlets. Receptacles are developed usually at the upper parts of higher order branchlets, but they are variable in shape, sometimes bifurcate or branched and with spine-like appendages. Conceptacles are generally hermaphrodite, although they can be unisexual at least during some periods of the year. Cryptostomata are present in most species, normally sunk into the branchlets and, only occasionally, pedicellate.

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Table 1. Iberian *Cystoseira* species and their distribution (Ribera & al., 1992; Gómez Garreta & al., 2000; Rodríguez-Prieto & al., 2013).

| Taxa | Mediterranean Iberia | Atlantic Iberia |
|--|----------------------|-----------------|
| <i>C. abies-marina</i> (S.G. Gmelin) C. Agardh | + | |
| <i>C. algeriensis</i> Feldmann | + | |
| <i>C. amentacea</i> var. <i>stricta</i> Montagne | + | |
| <i>C. baccata</i> (S.G. Gmelin) P.C. Silva | | + |
| <i>C. barbata</i> (Stackhouse) C. Agardh | + | |
| <i>C. barbata</i> f. <i>repens</i> A.D. Zinova & Kalugina | + | + |
| <i>C. barbatula</i> Kützinger | + | |
| <i>C. brachycarpa</i> Sauvageau | + | |
| <i>C. brachycarpa</i> var. <i>claudiae</i> (Giaccone) Giaccone | + | |
| <i>C. compressa</i> (Esper) Gerloff & Nizamuddin | + | + |
| <i>C. compressa</i> f. <i>plana</i> (Ercegovic) M. Cormaci & al. | + | |
| <i>C. crinita</i> Duby | + | |
| <i>C. elegans</i> Sauvageau | + | |
| <i>C. foeniculacea</i> (L.L.) Greville | + | + |
| <i>C. foeniculacea</i> f. <i>latiramosa</i> (Ercegovic) A. Gómez Garreta & al. | + | |
| <i>C. foeniculacea</i> f. <i>tenuiramosa</i> (Ercegovic) A. Gómez Garreta & al. | + | |
| <i>C. funkii</i> Schiffner ex Gerloff & Nizamuddin | + | |
| <i>C. humilis</i> Schouboe ex Kützinger | + | + |
| <i>C. humilis</i> var. <i>myriophylloides</i> (Sauvageau) J.H. Price & D.M. John | | + |
| <i>C. mauritanica</i> Sauvageau | + | |
| <i>C. mediterranea</i> Sauvageau | + | |
| <i>C. nodicaulis</i> (Withering) M. Roberts | + | + |
| <i>C. pelagosae</i> Ercegovic | + | |
| <i>C. sauvageauana</i> Hamel | + | + |
| <i>C. sedoides</i> (Desf.) C. Agardh | + | |
| <i>C. spinosa</i> Sauvageau | + | |
| <i>C. spinosa</i> var. <i>compressa</i> (Ercegovic) M. Cormaci & al. | + | + |
| <i>C. spinosa</i> var. <i>tenuior</i> (Ercegovic) M. Cormaci & al. | + | |
| <i>C. squarrosa</i> De Notaris | + | |
| <i>C. tamariscifolia</i> (Hudson) Papenfuss | + | + |
| <i>C. usneoides</i> (L.) M. Roberts | + | + |
| <i>C. zosteroides</i> C. Agardh | + | |

Among the 51 specific and infraspecific taxa of *Cystoseira* (Guiry & Guiry, 2014; Thibaut & al., 2014), 36 are present in the Mediterranean Sea, and 30 are endemic of this Sea. The Iberian Peninsula contains 24 species (31 taxa, table 1) and 14 taxa are exclusive of the Mediterranean Sea, 1 taxa of the Atlantic Ocean, and 9 taxa are present in both, Mediterranean Sea and Atlantic Ocean. In Northern Iberian coasts (table 2, figs. 1-2) inhabit 6 specific and infraspecific taxa: *C. baccata*, *C. foeniculacea*, *C. humilis* var. *myriophylloides*, *C. nodicaulis*, *C. tamariscifolia*, and *C. usneoides*. The diversity of the genus *Cystoseira* is relevant and necessary to protect and manage of their populations, but at present, it has been studied unevenly between regions and issues. Thus, although several species in the Mediterranean Sea have been analyzed in depth (morphology, taxonomy, diversity, assemblages, etc.), the Atlantic ones are less studied, especially in Northern Iberian Peninsula.

THE CYSTOSEIRA ASSEMBLAGES

The assemblages of *Cystoseira* exhibit a complex structure, which allows the presence of a large number of vegetal and animal companion species. Moreover, assemblages dominated by *Cystoseira* species rank amongst the most productive in the Mediterranean and provide habitat for a considerable number of other algae and invertebrate species (Furnari, 1997; Beleggratis & al., 1999; Pardi & al., 2000; Montesanto & Panayotidis, 2001; Sales & Ballesteros, 2007, 2009, 2012; Sales & al., 2012). Following Ballesteros (1989), the benthic production is of great importance in littoral ecosystem dynamics as it represents an input of energy and organic matter that, on a small scale, being higher than the phytoplankton's contribution. Moreover, the production increases from the upper mediolittoral zone to the shallow *Cystoseira* communities and, downwards, it gradually decreases with

Table 2. North Atlantic Iberian species of *Cystoseira* and their features (Roberts, 1967; Ardré, 1970; Bárbara & Cremades, 1987, Bárbara, 1994; Otero-Schmitt & Pérez-Cirera, 1996; Cremades & al., 1998; Gómez Garreta & al., 2000; Otero & al., 2002; Llera González & Álvarez Raboso, 2007).

| | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>C. humilis</i> var. <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> |
|----------------------|--|--|--|---|---|---|
| Attachment | Conical disc | Disc with several axes | Compact disc | Conical disc | Disc or haptera thick and branched | Haptera that usually do not form a disc |
| Axis | Flattened to terete. Axis single (not caespitose) | Terete. Several axes (caespitose). covered with spines | Terete. Several axes (caespitose). Basal appendages | Terete, single (not caespitose). Branched. With tubers at the basis | Terete, single (not caespitose). Often branched | Terete, single (not caespitose). Branched |
| Apex | Smooth. Prominent | Not very prominent | Smooth. Slightly prominent | Smooth. Prominent | Not very prominent. Covered by small spines | Smooth. Not very prominent |
| Branches | Compressed. Distichous | Cylindrical. Alternated and distich | Well-developed | Pinnate. With spinous appendages | Cylindrical. Profusely branched. Covered by numerous spinous appendages | Cylindrical. Highest order covered by small filiform appendage. |
| Foliaceous branches | Frequent, at the base and with midrib | Occasionally, at the base and with midrib | Absent | Absent | Absent | Frequent, at the base and with midrib |
| Tophules | Absent | Absent | Absent | Ovoid or conical, often elongated. Smooth or covered with small tubers | Absent | Rugged or smooth |
| Aerocysts | Elliptical, big and isolated. Present in the axes of higher order branches | Associated with the receptacles | Short (2-4 mm) at the base of receptacles | Occasionally present, narrow and elongated. Isolated or in short chains | Ovoid (5 mm long) isolated or in short chains | Abundant, in chains |
| Iridescence | Absent | Absent | Absent | weak | Profuse, green-bluish | weak |
| Receptacles | Cylindrical (1-5 cm long), with small filiform appendages. | Cylindrical or fusiform, single or branched | Cylindrical or fusiform, branched | Cylindrical. | No compact (1-2 cm long) and surrounded by sort spines | Cylindrical and mucronate, with small spines. |
| Iberian distribution | Atlantic | Atlantic and Mediterranean | Atlantic and Mediterranean | Atlantic and Mediterranean | Atlantic and Mediterranean | Atlantic and Mediterranean |
| Habitat | Lower intertidal to subtidal, from exposed to sheltered coasts | Lower intertidal to subtidal in semiexposed coasts | Upper to middle intertidal rocky pools (with sandy sediments), from exposed to semiexposed coast | Lower intertidal to subtidal in sheltered coasts | Lower intertidal rocky pools to subtidal, from exposed to semiexposed coast | Typically subtidal, from semiexposed to sheltered coasts |

depth (Ballesteros, 1989). Numerous Mediterranean studies (Ballesteros, 1988, 1989, 1990a-b; Pardi & al., 2000; Montesanto & Panayotidis, 2001; Sales & Ballesteros, 2007; 2009, 2012; Sales & al., 2012) described the structure and dynamics of communities characterized by the *Cystoseira* species as they play a key role on hard substrata communities by structuring subtidal photophilic vegetation, and determining the physiognomy of the benthic vegetation. Main parameters analyzed are: community biomass, recovering percentage, specific richness, specific distribution, Molinier's point, specific diversity, pattern-diversity and production.

According to Templado & al. (2012), in Spain, the most representative *Cystoseira* communities are the shallow ones that form a dense band, like the *C. mediterranea* in Catalonia,

the *C. amentacea* var. *stricta* in the Balearic Islands and the *C. tamariscifolia* in Alborán and the Canary Islands. In these shallow *Cystoseira* communities can be distinguish different strata with 50 and 300 species of flora and fauna, respectively. The upper canopy is made by the *Cystoseira* species with their epiphytes, like *Jania rubens* and *Ceramium* spp. The middle canopies are formed by algae as *Boergeseniella fruticulosa*, *Polysiphonia mottei* Lauret, *Osmundea truncata*, *Ellisolandia elongata*, *Jania virgata* (Zanardini) Montagne, *Laurencia obtusa* (Hudson) J.V. Lamouroux, *Anadyomene stellata* (Wulfen) C. Agardh, *Hypnea musciformis* (Wulfen) J.V. Lamouroux, and *Feldmannia caespitula* (C. Agardh) Knoepffler-Péguy. The microbiotic stratum is dominated by smaller algae as *Jania rubens*, *Cladophora laetevirens*, *Gelidium* spp. and *Chondracanthus acicularis*. Finally,

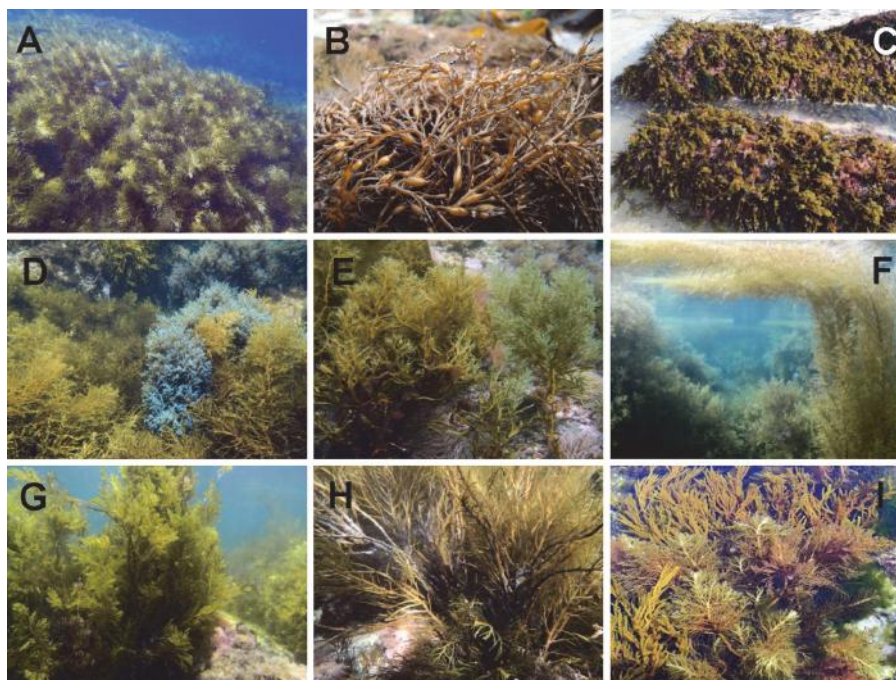


Fig. 1. Northern Atlantic Iberian species of *Cystoseira*: **a**, shallow subtidal community of *C. baccata*; **b**, detail of *C. baccata* and its aerocysts; **c**, lower intertidal community of *C. baccata*; **d-f**, subtidal *C. baccata* assemblages with *C. tamariscifolia* (d), with *C. usneoides* (e) and with *Sargassum muticum* (f); **g**, shallow subtidal *C. foeniculacea* assemblage; **h**, close-up of *C. foeniculacea*; **i**, upper intertidal rocky pool with *C. humilis* var. *myriophylloides* and *Bifurcaria bifurcata*.

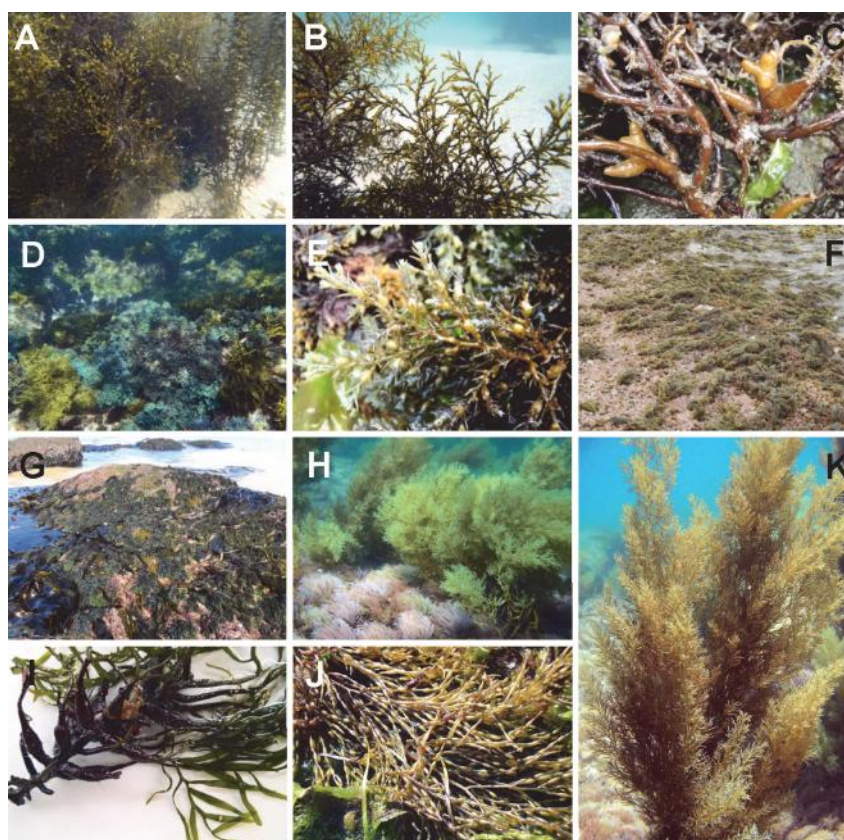


Fig. 2. Northern Atlantic Iberian species of *Cystoseira*: **a**, *C. nodicaulis* with *Sargassum muticum* in sand covered subtidal rocks; **b**, **c**, detail of *C. nodicaulis* with aerocysts (b) and basal tophules (c); **d**, shallow subtidal assemblage of *C. tamariscifolia* with *C. baccata*; **e**, detail of *C. tamariscifolia* and its aerocysts; **f**, **g**, lower intertidal community of *C. tamariscifolia*; **h**, subtidal community of *C. usneoides*; **i**, **j**, detail of *C. usneoides* with tophules (i) and chains of small aerocysts (j); **k**, big subtidal thallus of *C. usneoides*.

there is a calcareous strata *Lithophyllum incrustans*, *Noegoniolithon brassica-florida* (Harvey) Setchell & L.R. Mason, *Hildenbrandia croauaniorum* J. Agardh, *Peyssonnelia polymorpha* (Zanardini) F. Schmitz, *Melobesia membranacea*, and *Valonia utricularis* (Roth) C. Agardh. In the sheltered Mediterranean coast the dominant species is *C. crinita*, although it can be substituted or accompanied by other *Cystoseira* species as *C. caespitosa*, *C. compressa*, *C. foeniculacea*, *C. humilis*, *C. barbata* or *C. brachycarpa* var. *balearica* (Templado & al., 2012).

Following the literature (Barceló i Martí & Seoane Camba, 1984; Cormaci & al., 1990; Ballesteros, 1990b; Ballesteros & al., 1998; Sales & Ballesteros, 2012; Sales & al., 2012; Templado & al., 2012; Thibaut & al., 2014), on the basis of the light intensity and hydrodynamism variations, the Mediterranean marine zonation are divided in five main communities dominated by: (i) *Cystoseira amentacea*, in the infralittoral fringe, (ii) *C. crinita*, in the upper infralittoral, (iii) *C. sauvageauana*, in the mid-infralittoral, (iv) *C. spinosa*, in the lower infralittoral and (v) *C. zosteroides*, in the upper circalittoral zone. However, some ecological factors like temperature, sedimentation and streams can play a fundamental role in the settlement of some other communities, as *C. tamariscifolia*, *C. barbata*, *C. corniculata*, and *C. dubia* (Pardi & al., 2000; Montesanto & Panayotidis, 2001; Sales & Ballesteros, 2007, 2009, 2012; Sales & al., 2012; Templado & al., 2012). Other Mediterranean *Cystoseira* species, as *C. mediterranea* and *C. caespitosa*, were studied by Ballesteros (1988, 1990a) who comment that both species exhibit similar structure and composition to others wave-exposed communities dominated by *Cystoseira*. Apart of all these studies, Pardi & al. (2000) affirmed that little attention has been paid to the demography of the *Cystoseira* genus in the Mediterranean Sea, despite this aspect is relevant for understanding the distribution and abundance of macroalgal species and hence to community structure. Because of that, Pardi & al. (2000) studied a population of *C. humilis* providing the first contribution to the knowledge of its demography, assessing density, growth, reproduction, mortality, and biomass.

Although there is a basic knowledge on the habitat preferences of *Cystoseira* species, there are no much studies about the environmental factors affecting their distribution in the Mediterranean. In this way, Sales & Ballesteros (2009) obtained values of 14 environmental parameters in 103 coves surveyed in Menorca Island, which were added sequentially in a model in order to predict *Cystoseira* assemblages' composition. They detected significant relationships between great part of the factors and *Cystoseira* spp. composition and abundance, what show a high predictability of *Cystoseira* distribution departing from environmental variables.

The Atlantic Iberian *Cystoseira* species typically inhabits in the subtidal forming the canopy of the community, from wave exposed to sheltered areas. Some common subtidal species are *C. baccata* and *C. usneoides*, and other such as *C. humilis* inhabits from upper to middle intertidal rocky pools (Gómez Garreta & al., 2000). In this region, according to Templado & al. (2012) the *Cystoseira* species play an escort role and they could be dominant when the other species are not present. Below the *C. tamariscifolia* band there are present other species as *C. mauritanica*, *C. nodicaulis*, and, deeper, *C. usneoides*. In the Cantabrian coasts, there

is a characteristic community dominated by *Gelidium corneum* in exposed rocks, which could be accompanied by *C. baccata* and other species as *Mesophyllum lichenoides*, *Zanardinia typus*, *Pterosiphonia complanata*, *Corallina officinalis*, *Rhodymenia pseudopalmata*, and *Cryptopleura ramosa* (Gorostiaga & al., 1998; Templado & al., 2012).

Bermejo (2014) studied the genetics of *C. amentacea*, *C. tamariscifolia*, and *C. mediterranea* in the south of the Iberian Peninsula and found that individuals previously identified as *C. amentacea* in Alboran Sea would be closer related to *C. tamariscifolia* from the Atlantic Ocean than to Mediterranean specimens of *C. mediterranea* or *C. amentacea*. Furthermore, the genetic patterns along southern Iberian Peninsula show an important genetic flux between Atlantic and Mediterranean populations in western and central Alboran. Therefore, the results suggest that all specimens of these three species found along Alboran Sea can be considered one specific entity, probably *C. tamariscifolia*, so the morphological differences observed between *C. tamariscifolia* and *C. amentacea* from southern Iberian Peninsula lack a genetic basis. Moreover, Bermejo (2014) results revealed that the highest distances occur between sites instead between groups of populations. The study of the genetic structure of threatened species with reduced dispersion such as *C. tamariscifolia*, which play an important role in the maintaining of the biodiversity and ecosystem functioning in littoral communities of the Mediterranean and the proximate coast of the Lusitanian provinces, could yield important information to favor the resilience of littoral communities or to develop a suitable restoration.

In Asturias, Fernández & Niell (1981, 1982) studied the lower intertidal belt, dominated by *Saccorbiza polyschides*, *Cystoseira baccata*, *Gelidium* spp., and *Mesophyllum lichenoides*. The *Saccorbiza-Cystoseira* belt could also appear with *C. tamariscifolia* and other species like *Chondrus crispus*, *Gymnogongrus crenulatus*, *Pterocladia capillacea*, *Corallina* spp., and *Plocamium cartilagineum*. In rocky intertidal pools of *Bifurcaria bifurcata* and *Gelidium spinosum* Fernández & Niell (1981, 1982) found *Dictyopteris polypodioides*, *C. baccata*, *C. tamariscifolia*, *Gelidium corneum*, *Saccorbiza polyschides*, *Laminaria ochroleuca*, and *M. lichenoides*. Below to the *Saccorbiza-Cystoseira* belt they found a vegetation belt dominated by *C. baccata* accompanied by *Ulva gigantea*, *Gelidium corneum*, and, not so frequently, *Laminaria ochroleuca* and *C. tamariscifolia*.

In the sublittoral seaweed vegetation on the Basque coast (Gorostiaga, 1995; Díez, 1997; Gorostiaga & al., 1998; Díez & al., 1999; Santolaria, 2014), *C. baccata* is a very common species that inhabits in a wide range of depth, exposure and sedimentation conditions. Gorostiaga (1995) compared the vegetation in the shallow zone of the French Basque coast, which is very similar, although with a greater abundance of *Gelidium corneum* and *C. tamariscifolia*. Gorostiaga & al. (1998) explains that, although the macroalgal cover was very homogeneous floristically, *Plocamium cartilagineum*, *Pterosiphonia complanata*, *Asparagopsis armata*, *C. baccata*, *Halopitys incurvus*, and *Corallina officinalis* were the most abundant macrophytes. However, under sedimentation increasing, *Gelidium corneum* cover decreased while the macrophytes *C. baccata* and *Zanardinia typus* become more abundant. The sedimentation was a determining factor in seaweed distribution and the main trends were:

(i) the maximum algal cover corresponded to *Gelidium corneum* beds. At the same time as the sediment increased to moderate levels, the first change detected was the reduction of crustose and epiphytic layers, due to the decrease of *Mesophyllum lichenoides*, *Plocamium cartilagineum*, and *Dictyota dichotoma*. (ii) The most abundant species along the vegetation gradient presented patterns of distribution associated with sedimentation. *Pterosiphonia complanata* and *C. baccata* were well adapted to sedimentation, showing an optimum development at moderate to high levels. In habitats highly exposed to wave action without sediment, *Pterosiphonia complanata* is displaced by *Gelidium corneum*. In contrast, *C. baccata* does not tolerate heavy hydrodynamics and only competes with *Gelidium corneum* in semiexposed conditions.

In the North of Galicia, Anadón & al. (1979) and Gili & al. (1979) found that, below the horizon of *Himanthalia elongata*, the most important vegetation in moderately exposed or protected zones is dominated by *Saccorbiza polyschides* and, going down, appear a *C. tamariscifolia* and *Boergeniella thuyoides* horizon, which is gradually substituted by *Laminaria hyperborea* and *Laminaria ochroleuca* in more exposed zones. Gili & al. (1979) described three strata in the *Laminaria* horizon: (i) arborescent strata, (ii) caespitose strata and (iii) incrusting strata. In deeper zones where *Laminaria* is scarce, they found other brown seaweeds as *C. baccata*, *Desmarestia aculeata*, *Halidrys siliquosa*, *Carpomitra costata*, *Phyllariopsis brevipes*, and a *Dictyota* sp. It could appear some red algae species, like *Rodophyllis divaricata*, *Dilsea carnosa*, and *Palmaria palmata*; and the green algae *Ulva rigida*. In the Central and South Galician coast, Granja & al. (1992), Otero-Schmitt (1993), Bárbara (1994), Bárbara & al. (1995), and Otero-Schmitt & Pérez-Cirera (1996, 2002) studied subtidal populations dominated by laminarials (*Laminaria ochroleuca*, *Laminaria hyperborea*, and *Saccharina saccharina*) and Cystoseiraceae communities (*Cystoseira baccata*, *C. nodicaulis*, and *C. usneoides*), which are also abundant at more sheltered and deeper areas and even on rocky and sandy bottoms. Apart from subtidal, the species of *Cystoseira* inhabit in the lower intertidal (Bárbara & al., 1995, Otero-Schmitt & Pérez-Cirera, 2002; Cremades & al., 2004) where they form erect canopies with other big brown algae like *Laminaria ochroleuca* and *Sargassum muticum*.

The species of *Cystoseira* generally supports a considerable epiphytic flora (Belegratis & al., 1999). The epiphytes in two Mediterranean species (*C. compressa* and *C. spinosa*) were studied by Belegratis & al. (1999) by transplanting plants to different sites. Epiphytic seasonality was generally observed in the sites, what suggests the absence of host-specific epiphytes. Moreover, the distinct zonation pattern of epiphytes covering only certain host areas was not observed. Most floristic and vegetation studies carried out on Northwestern Spain list epiphytic species, but these are not used to characterize differences among communities, as there are not much researches focused on the *Cystoseira* epiphytes. According to Rull Lluç & Gómez Garreta (1989), Morales-Ayala & Viera-Rodríguez (1989), Arrontes (1990), and Otero-Schmitt & Pérez-Cirera (1996), an epiphytic stratification with three strata can be considered: (i) attaching discs, (ii) main axes and branches and (iii) branchlets and phylloids. However, the host plants occur in different

vegetation belts and wave exposure and these factors may be more important in characterizing epiphytism on *Cystoseira* rather than the own structure of the host. In addition, the fall of phylloids and branchlets usually occurs in winter, causing important variations in epiphytic species that can be found in some parts of the hosts, so the perennial axes allow a more stable flora.

Otero-Schmitt & Pérez-Cirera (1996) studied the epiphytism on four species of *Cystoseira* (*C. baccata*, *C. tamariscifolia*, *C. humilis* var. *myriophylloides*, and *C. usneoides*), that develop large and differentiated communities in the Galician coast. According to these authors, the generic specificity is small: of 125 epiphytic species, nearly half were only found on a single *Cystoseira* species. Rodophyta were the most abundant epiphytic group and Cyanophyta were the scarcest. Most epiphytic species were Ephemerophytes or Hypnophytes (Otero-Schmitt & Pérez-Cirera, 1996). The cover of epiphytic species was maximal on *C. tamariscifolia* and *C. humilis* var. *myriophylloides*, whereas *C. usneoides* were much lower. The cover in *C. baccata* was also quite high, but less than in *C. tamariscifolia*. The greater number of epiphytic species on *C. tamariscifolia* could be in part explained because of its position in the littoral zone. On the other hand, the mechanical activity of sand grains among the fronds, mainly in winter, results in a lower abundance of epiphytes in *C. humilis* var. *myriophylloides* (Otero-Schmitt & Pérez-Cirera, 1996). The presence of epiphytes in *C. tamariscifolia* is more or less regular, with a higher abundance in spring and summer, except in *C. humilis* var. *myriophylloides*. By contrast, *C. baccata* and *C. usneoides* presented the lowest variations, probably because of their optimal development in the subtidal, with a maximum in summer and a minimum at the end of autumn (Morales-Ayala & Viera-Rodríguez, 1989; Otero-Schmitt, 1993; Otero-Schmitt & Pérez-Cirera, 1996).

THE NORTH ATLANTIC IBERIAN CYSTOSEIRA ASSEMBLAGES

To study the diversity of the North Atlantic Iberian *Cystoseira* assemblages (*C. baccata*, *C. foeniculacea*, *C. humilis* var. *myriophylloides*, *C. nodicaulis*, and *C. usneoides*), we used information from the literature (Miranda, 1931; Anadón & al., 1979; Gili & al., 1979; Fernández & Niell, 1981, 1982; Otero-Schmitt, 1993; Bárbara, 1994; Gorostiaga, 1995; Gorostiaga & Díez, 1996; Otero-Schmitt & Pérez-Cirera, 1996; 2002; Araújo & al., 2005, 2006; Cremades & al., 2006; Peña & Bárbara, 2006; Díaz Tapia & al., 2011, 2013; Bárbara & al., 2013; Peña & al., 2014) and grey information from herbaria, reports, pictures, unpublished data, etc. In tables 3 and 4, we present the associate flora of the six *Cystoseira* assemblages summarizing the information by species, taxonomic group, morpho-functional group, life form, canopy layers, as well as common species and non-native ones. The assemblage of *C. baccata* harbors the biggest number of species (215), followed by *C. tamariscifolia* (162) and *C. usneoides* (126), whereas the community with fewest species was the *C. foeniculacea* one (34), probably because of the scarcity of studies about this species and probably the small distribution area of it. The numbers of epiphytes, non-native species and common ones follow a similar pattern between the *Cystoseira* communities. The most abundant division

Table 3. Associate flora of *Cystoseira* assemblages in Northern Atlantic Iberian Peninsula (Miranda, 1931; Anadón & al., 1979; Gili & al., 1979; Fernández & Niell, 1981, 1982; Otero-Schmitt, 1993; Bárbara, 1994; Gorostiaga, 1995; Gorostiaga & Díez, 1996; Otero-Schmitt & Pérez-Cirera, 1996; Araújo & al., 2005, 2006; Cremades & al., 2006; Peña & Bárbara, 2006; Bárbara & al., 2013; Díaz Tapia & al., 2011, 2013; Peña & al., 2014) and grey information (from herbaria, reports, pictures, unpublished data, etc.). For each species its position in the assemblage is mentioned: **c** = canopy/substrata, **e** = epiphyte. The canopies were divided in three layers based in Hardy-Halos & al. (1973): **1** = basal layer (<0.10 m, microbiotic and chamaebiotic strata); **2** = medium layer (0.10-0.50 m, meiobiotic strata); and **3** = upper layer (0.50-5 m, megabiobiotic and macrobiobiotic strata). The nine morphofunctional groups (**1** = unicellular; **2** = thin foliose; **3** = intermediated foliose; **4** = corticated foliose; **5** = filamentous; **6** = filiform; **7** = corticated filiform; **8** = articulated calcareous; **9** = crustose) have been modified from Littler & Littler (1984) and Steneck & Dethier (1994). The five life forms (**E** = Ephemerophytes; **H** = Hypnophytes; **P** = Phanerophytes; **C** = Chamaephytes; **Hp** = Hemiphanerophytes) were taken from Garbary (1976) and Fritsch (1981), based on Feldmann (1937).

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>C. humilis</i> var. <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> |
|--|----------|--------|------------------------|-----------|-------------|------------|-------------------|------------------------|---|----------------------|--------------------------|---------------------|
| CYANOPHYTA | | | | | | | | | | | | |
| <i>Cyanocystis olivacea</i> (Reinsch) Komárek & Anagnostidis | e | | 1 | E | | A | | | | | + | |
| <i>Dermocarpella prasina</i> (Reinsch) Komárek & anagnostidis | e | | 1 | E | | A | + | | | | + | + |
| <i>Oscillatoria tenuis</i> C. Agardh ex Gomont | e | | 1 | E | | A | | + | | | | |
| <i>Phormidium baculum</i> (Gomont ex Gomont) Anagnostidis | e | | 1 | E | | A | | | | | | + |
| <i>Spirulina subsalsa</i> Oersted ex Gomont | c/e | 1 | 1 | E | | A | + | | | | | + |
| OCHROPHYTA | | | | | | | | | | | | |
| <i>Bifurcaria bifurcata</i> R. Ross | c | 2 | 7 | P | | A | + | | + | | + | |
| <i>Carpomitra costata</i> (Stackhouse) Batters | c | 2 | 7 | P | | A | | | | + | | |
| <i>Cladostephus spongiosus</i> (Hudson) C. Agardh | c | 2 | 7 | P | | A | + | | + | | + | |
| <i>Colpomenia peregrina</i> Sauvageau | c/e | 1 | 3 | E | + | I | + | | + | + | + | + |
| <i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier | c/e | 1 | 3 | E | | A | | | | | + | |
| <i>Cutleria adspersa</i> (Mertens ex Roth) De Notaris | c/e | 1 | 3 | H | | A | | | | | + | |
| <i>Cutleria multifida</i> (Turner) Greville | c/e | 2 | 3 | H | | A | + | | | | + | + |
| <i>Cutleria multifida stadium "Aglaozonia parvula"</i> (Greville) Zanardini | c | 2 | 9 | C | | A | + | | | | + | + |
| <i>Cystoseira baccata</i> (S.G. Gmelin) P.C. Silva | c | 3 | 7 | Hp | | A | + | + | | + | + | + |
| <i>Cystoseira foeniculacea</i> (L.) Greville | c | 3 | 7 | Hp | + | A | + | + | | + | + | |
| <i>Cystoseira humilis</i> var. <i>myriophylloides</i> (Sauvageau) J.H. Price & D.M. John | c | 3 | 7 | Hp | | A | | | + | | + | |
| <i>Cystoseira nodicaulis</i> (Withering) M. Roberts | c | 3 | 7 | Hp | + | A | + | + | | + | + | |
| <i>Cystoseira tamariscifolia</i> (Hudson) Papenfuss | c | 3 | 7 | Hp | | A | + | + | + | + | + | |
| <i>Cystoseira usneoides</i> (L.) M. Roberts | c | 3 | 7 | Hp | | A | + | | | | | + |
| <i>Desmarestia aculeata</i> (L.) J.V. Lamouroux | c | 3 | 7 | P | + | A | + | | | | + | + |
| <i>Desmarestia ligulata</i> (Stackhouse) J.V. Lamouroux | c | 3 | 3 | P | + | A | + | + | + | | + | + |
| <i>Dictyopteris polypodioides</i> (A.P. DC.) J.V. Lamouroux | c/e | 2 | 3 | P | + | A | + | + | + | + | + | |
| <i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux | c/e | 2 | 3 | E | + | A | + | + | + | + | + | + |
| <i>Dictyota dichotoma</i> var. <i>intricata</i> (C. Agardh) Greville | c | 2 | 3 | E | | A | + | | | | + | + |

Table 3. (Continued)

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>C. humilis</i> var. <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> |
|---|----------|--------|------------------------|-----------|-------------|------------|-------------------|------------------------|---|----------------------|--------------------------|---------------------|
| <i>Ectocarpus fasciculatus</i> Harvey | e | | 5 | E | | A | + | | | | + | + |
| <i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye | c/e | 1 | 5 | E | | A | + | | | | + | + |
| <i>Elachista flaccida</i> (Dillwyn) Fries | e | | 5 | E | + | A | + | | | | + | + |
| <i>Elachista intermedia</i> P.L. Crouan & H.M. Crouan | e | | 5 | E | | A | + | | | | | |
| <i>Feldmannia lebelii</i> (Areschoug ex P.L. Crouan & H.M. Crouan) G. Hamel | e | | 5 | E | | A | | | | | + | |
| <i>Feldmannia mitchelliae</i> (Harvey) H.S. Kim | c/e | 1 | 5 | E | | A | + | | | | + | |
| <i>Feldmannia simplex</i> (P.L. Crouan & H.M. Crouan) G. Hamel | e | | 5 | E | | A | | | | | + | |
| <i>Fucus serratus</i> L. | c | | 4 | P | | A | + | | | + | | + |
| <i>Halidrys siliquosa</i> (L.) Lyngbye | c | 3 | 7 | P | + | A | + | | + | + | | + |
| <i>Halopteris filicina</i> (Grateloup) Kützing | c/e | 1 | 6 | P | + | A | + | | + | + | | |
| <i>Halopteris scoparia</i> (L.) Sauvageau | c/e | 2 | 7 | P | + | A | + | | + | | + | + |
| <i>Herponema valianteri</i> (Bornet ex Sauvageau) G. Hamel | e | | 5 | H | | A | | | | | + | |
| <i>Himanthalia elongata</i> (L.) S.F. Gray | c | 3 | 4 | P | | A | + | | | | + | |
| <i>Hincksia granulosa</i> (Smith) P.C. Silva | c/e | 1 | 5 | E | + | A | + | | | | + | + |
| <i>Hincksia hincksiae</i> (Harvey) P.C. Silva | e | | 5 | E | + | A | + | | | | + | + |
| <i>Hincksia sandriana</i> (Zanardini) P.C. Silva | c/e | 1 | 5 | H | | A | + | | | | + | + |
| <i>Hincksia secunda</i> (Kützing) P.C. Silva | e | | 5 | E | | A | + | | | | + | + |
| <i>Kuckuckia spinosa</i> (Kützing) Kornmann | e | | 5 | E | | A | + | | | | | |
| <i>Laminaria hyperborea</i> (Gunnerus) Foslie | c/e | 3 | 4 | Hp | + | A | + | | + | | + | + |
| <i>Laminaria ochroleuca</i> Bachelot de la Pylaie | c | 3 | 4 | P | + | A | + | | | + | + | + |
| <i>Leathesia marina</i> (Lyngbye) Decaisne | c | 1 | 3 | E | | A | | | | | + | |
| <i>Litosiphon laminariae</i> (Lyngbye) Harvey | e | | 6 | H | | A | + | | | | | |
| <i>Myriactula rivulariae</i> (Suhr ex Areschoug) Feldmann | e | | 5 | E | | A | | + | | | + | |
| <i>Myrionema strangulans</i> Greville | e | | 2 | E | | A | + | | | | | + |
| <i>Petalonia fascia</i> (O.F. Müller) Kuntze | c/e | 1 | 3 | H | | A | + | | | | + | |
| <i>Phyllariopsis brevipes</i> subsp. <i>pseudopurpurascens</i> Pérez-Cirera & al. | c/e | 2 | 4 | H | | A | + | | | | | + |
| <i>Phyllariopsis purpurascens</i> (C. Agardh) E.C. Henry & G.R. South | c | 2 | 4 | H | | A | + | | | | | |
| <i>Ralfsia verrucosa</i> (Areschoug) Areschoug | e | | 9 | C | | A | + | | | | | |
| <i>Saccharina latissima</i> (L.) C.E. Lane, C. Mayes, Druehl & G.W. Saunders | c/e | 3 | 4 | P | | A | + | | | | + | + |
| <i>Saccorhiza polyschides</i> (Lightfoot) Batters | c/e | 3 | 4 | H | + | A | + | | + | | + | + |
| <i>Sargassum muticum</i> (Yendo) Fensholt | c | 3 | 7 | Hp | + | I | + | | + | | + | + |
| <i>Sphacelaria cirrosa</i> (Roth) C. Agardh | c/e | 1 | 6 | E | + | A | + | | + | | + | + |
| <i>Sphacelaria rigidula</i> Kützing | e | | 6 | E | | A | + | | | | + | |

Table 3. (Continued)

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>C. humilis</i> var. <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> |
|---|----------|--------|------------------------|-----------|-------------|------------|-------------------|------------------------|---|----------------------|--------------------------|---------------------|
| <i>Spongonema tomentosum</i> (Hudson) Kützing | e | | 5 | E | | A | | | | | + | |
| <i>Stilophora tenella</i> (Esper) P.C. Silva | c | 2 | 6 | H | | A | | | | | | + |
| <i>Taonia atomaria</i> (Woodward) J. Agardh | c | 2 | 3 | E | | A | + | + | | | | |
| <i>Undaria pinnatifida</i> C. Agardh | c | 3 | 4 | H | | I | + | | | | | + |
| <i>Zanardinia typus</i> (Nardo) P.C. Silva | c | 2 | 3 | C | | A | + | | | | | |
| RHODOPHYTA | | | | | | | | | | | | |
| <i>Acrochaetium secundatum</i> (Lyngbye) Nägeli | c/e | 1 | 5 | E | | A | + | | + | | + | + |
| <i>Acrosorium ciliolatum</i> (Harvey) Kylin | e | | 2 | E | | A | + | | + | | + | + |
| <i>Aglaothamnion hookeri</i> (Dillwyn) Maggs & Hommersand | c/e | 1 | 5 | E | | A | + | | | | + | + |
| <i>Aglaothamnion pseudobyssoides</i> (P.L. Crouan & H.M. Crouan) L'Hardy-Halos | e | | 5 | E | | A | | | | | | + |
| <i>Aglaothamnion tenuissimum</i> (Bonnemaison) Feldmann-Mazoyer | e | | 5 | E | | A | + | | | + | + | + |
| <i>Ahnfeltia plicata</i> (Hudson) Fries | c | 2 | 7 | P | | A | + | | | | | |
| <i>Ahnfeltiopsis devoniensis</i> (Greville) P.C. Silva & De Cew | c | 1 | 4 | P | | A | + | | | | + | + |
| <i>Amphiroa vanbosseae</i> Me. Lemoine | c/e | 1 | 8 | P | | A | | | + | | | |
| <i>Anotrichium furcellatum</i> (J. Agardh) Baldock | e | | 5 | E | | I | + | | | | | + |
| <i>Antithamnion cruciatum</i> (C. Agardh) Nägeli | c/e | 1 | 5 | E | + | A | + | | + | | + | + |
| <i>Antithamnion densum</i> (Suhr) M.A. Howe | e | | 5 | E | | A | | | | | | + |
| <i>Antithamnionella elegans</i> (Berthold) J.H. Price & D.M. John | e | | 5 | E | | A | | | | | + | |
| <i>Antithamnionella spirographidis</i> (Schiffner) E.M. Wollaston | e | | 5 | E | | I | + | | + | | + | + |
| <i>Antithamnionella ternifolia</i> (J.D. Hooker & Harvey) Lyle | e | | 5 | E | | I | + | | | | | + |
| <i>Apoglossum ruscifolium</i> (Turner) J. Agardh | c/e | 1 | 2 | E | + | A | + | | | + | + | + |
| <i>Asparagopsis armata</i> Harvey | c/e | 2 | 6 | E | + | I | + | | + | | + | + |
| <i>Asparagopsis armata</i> Harvey stadium "Falkenbergia rufolanosa" (Harvey) F. Schmitz | e | | 5 | E | | I | + | | + | | + | + |
| <i>Boergesenella fruticulosa</i> (Wulfen) Kylin | e | | 6 | P | + | A | + | | + | + | + | + |
| <i>Boergesenella thuyoides</i> (Harvey) Kylin | c/e | 1 | 6 | E | | A | + | | + | | + | |
| <i>Bonnemaisonia asparagoides</i> (Woodward) C. Agardh | c/e | 1 | 6 | H | | A | + | | | | + | |
| <i>Bonnemaisonia hamifera</i> Hariot | e | | 6 | H | | A | + | | | | | |
| <i>Bonnemaisonia hamifera</i> stadium "Trailiella intricata" Batters | e | | 5 | E | | A | + | | | | | |
| <i>Bornetia secundiflora</i> (J. Agardh) Thuret | e | | 5 | E | | A | + | | | | + | |
| <i>Brongniartella byssoides</i> (Goodenough & Woodward) F. Schmitz | c/e | 2 | 6 | H | | A | | | | | | + |

Table 3. (Continued)

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | C. baccata | C. foeniculacea | C. humilis var. myriophylloides | C. nodicaulis | C. tamariscifolia | C. usneoides |
|--|----------|--------|------------------------|-----------|-------------|------------|------------|-----------------|---------------------------------|---------------|-------------------|--------------|
| <i>Calliblepharis ciliata</i> (Hudson) Kützing | c/e | 2 | 4 | P | | A | + | | | | | + |
| <i>Calliblepharis jubata</i> (Goodenough & Woodward) Kützing | c/e | 2 | 4 | H | + | A | + | + | | + | + | + |
| <i>Callithamnion corymbosum</i> (Smith) Lyngbye | c/e | 1 | 5 | E | | A | + | | | | + | |
| <i>Callithamnion granulatum</i> (Ducluzeau) C. Agardh | c/e | 1 | 5 | E | | A | + | | | | + | + |
| <i>Callithamnion tetragonum</i> (Withering) S.F. Gray | e | | 5 | E | + | A | + | | + | | + | + |
| <i>Callithamnion tetricum</i> (Dillwyn) S.F. Gray | e | | 5 | E | | A | + | | | | + | |
| <i>Callocolax neglectus</i> F. Schmitz ex Batters | e | | 3 | E | | A | | | | | | + |
| <i>Callophyllis laciniata</i> (Hudson) Kützing | c/e | 2 | 4 | P | + | A | + | | | + | + | + |
| <i>Ceramium botryocarpum</i> A.W. Griffiths ex Harvey | e | | 6 | H | | A | | | | | + | |
| <i>Ceramium ciliatum</i> (J. Ellis) Ducluzeau | c/e | 1 | 6 | H | + | A | + | | + | | + | + |
| <i>Ceramium diaphanum</i> (Lightfoot) Roth | e | | 5 | H | + | A | + | | + | + | + | + |
| <i>Ceramium echionotum</i> J. Agardh | e | | 5 | H | | A | + | | | | + | |
| <i>Ceramium gaditanum</i> (Clemente) Cremades | c | 1 | 6 | E | | A | + | | | | + | |
| <i>Ceramium pallidum</i> (Nägeli ex Kützing) Maggs & Hommersand | e | | 6 | E | | A | + | | | | + | |
| <i>Ceramium secundatum</i> Lyngbye | e | | 6 | E | + | A | + | | | | + | + |
| <i>Ceramium shuttleworthianum</i> (Kützing) Rabenhorst | c/e | 1 | 5 | H | | A | + | | + | | + | |
| <i>Ceramium tenuicorne</i> (Kützing) Waern | e | | 5 | E | | A | | | + | | | + |
| <i>Ceramium virgatum</i> Roth | c/e | 1 | 6 | E | + | A | + | | + | + | + | + |
| <i>Champia parvula</i> (C. Agardh) Harvey | e | | 6 | E | + | A | + | | + | + | + | + |
| <i>Chondracanthus acicularis</i> (Roth) Fredericq | c/e | 1 | 7 | P | + | A | + | | + | | + | + |
| <i>Chondracanthus teedei</i> (Mertens ex Roth) Kützing | c/e | 2 | 7 | P | + | A | + | | + | + | + | + |
| <i>Chondria coerulescens</i> (J. Agardh) Falkenberg | c | 1 | 6 | E | | A | + | | | | + | |
| <i>Chondria dasyphylla</i> (Woodward) C. Agardh | c | 2 | 6 | E | | A | + | | | | | |
| <i>Chondria scintillans</i> Feldmann-Mazoyer | c | 2 | 6 | P | | A | + | | | | | |
| <i>Chondrus crispus</i> Stackhouse | c | 2 | 4 | P | + | A | + | + | + | + | + | + |
| <i>Chylocladia verticillata</i> (Lightfoot) Bliding | e | | 6 | E | + | A | + | | | + | + | + |
| <i>Colaconema daviesii</i> (Dillwyn) Stegenga | e | | 5 | E | + | A | + | | + | | + | + |
| <i>Colaconema endophyticum</i> (Batters) J.T. Harper & G.W. Saunders | e | | 2 | E | | A | | | | | + | |
| <i>Colaconema infestans</i> (M.A. Howe & Hoyt) Woelkerling | e | | 2 | E | | A | | | | | | + |
| <i>Compothamnion thuyoides</i> (Smith) Nägeli | e | | 5 | E | | A | + | | | | | |
| <i>Corallina officinalis</i> L. | c | 1 | 8 | P | + | A | + | + | | + | + | |

Table 3. (Continued)

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>C. humilis</i> var. <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> |
|--|----------|--------|------------------------|-----------|-------------|------------|-------------------|------------------------|---|----------------------|--------------------------|---------------------|
| <i>Cordylecladia erecta</i> (Greville) J. Agardh | c | 1 | 7 | P | | A | + | | | | | |
| <i>Cruoria pellita</i> (Lyngbye) Fries | c | 1 | 9 | C | | A | + | | | | | |
| <i>Cryptonemia lomation</i> (Bertoloni) J. Agardh | c | 2 | 4 | Hp | + | A | + | | | + | | + |
| <i>Cryptopleura ramosa</i> (Hudson) L. Newton | c/e | 1 | 2 | E | + | A | + | + | + | + | + | + |
| <i>Dasya hutchinsiae</i> Harvey | c/e | 1 | 6 | E | | A | + | | | | + | |
| <i>Dasya ocellata</i> (Grateloup) Harvey | c/e | 1 | 5 | E | | A | + | | | | + | |
| <i>Dasya sessilis</i> Yamada | e | | 6 | E | | I | | | | | | + |
| <i>Dasysiphonia japonica</i> (Yendo) H.S. Kim | e | | 6 | E | + | I | + | | | | + | + |
| <i>Delesseria sanguinea</i> (Hudson) J.V. Lamouroux | c | 1 | 3 | Hp | + | A | + | + | | + | | |
| <i>Dilsea carnosa</i> (Schmidel) Kuntze | c | 2 | 4 | P | | A | + | | | + | | |
| <i>Dudresnaya verticillata</i> (Withering) Le Jolis | c/e | 1 | 5 | E | | A | + | | | | | + |
| <i>Dumontia contorta</i> (S.G. Gmelin) Ruprecht | c/e | 1 | 6 | H | | A | + | | | | + | + |
| <i>Ellisolandia elongata</i> (J. Ellis & Solander) K.R. Hind & G.W. Saunders | c/e | 1 | 8 | P | + | A | + | | + | + | + | + |
| <i>Erythrogloussum laciniatum</i> (Lightfoot) Maggs & Hommersand | e | | 2 | E | | A | | | | | | + |
| <i>Erythrogloussum lusitanicum</i> Ardré | c | 1 | 2 | P | | A | + | | | | | |
| <i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh | e | | 5 | E | + | A | + | | + | | + | + |
| <i>Furcellaria lumbricalis</i> (Hudson) J.V. Lamouroux | c | 2 | 7 | P | | A | + | + | | + | + | |
| <i>Gastroclonium ovatum</i> (Hudson) Papenfuss | c/e | 1 | 7 | P | | A | + | | | | + | |
| <i>Gayliella flaccida</i> (Harvey ex Kützing) T.O. Cho & L.J. McIvor | e | | 5 | E | | A | + | | | | | |
| <i>Gelidium attenuatum</i> (Turner) Thuret | c | 2 | 6 | P | | A | + | | | | + | |
| <i>Gelidium corneum</i> (Hudson) J.V. Lamouroux | c/e | 2 | 7 | P | + | A | + | + | | | + | |
| <i>Gelidium pulchellum</i> (Turner) Kützing | c/e | 1 | 6 | P | | A | + | | + | + | + | |
| <i>Gelidium pusillum</i> (Stackhouse) Le Jolis | c | 1 | 6 | P | | A | + | | | | + | + |
| <i>Gelidium spinosum</i> (S.G. Gmelin) P.C. Silva | c/e | 1 | 7 | P | | A | + | | | | + | |
| <i>Gigartina pistillata</i> (S.G. Gmelin) Stackhouse | c/e | 2 | 7 | P | | A | + | | | | + | |
| <i>Gracilaria multipartita</i> (Clemente) Harvey | c | 2 | 4 | P | + | A | + | | | + | + | + |
| <i>Gracilariopsis longissima</i> (S.G. Gmelin) M. Steentoft & al. | c | 2 | 7 | P | | A | + | | | | | + |
| <i>Grateloupia filicina</i> (J.V. Lamouroux) C. Agardh | c | 1 | 6 | P | | A | + | | | + | | |
| <i>Grateloupia turuturu</i> Yamada | c | 2 | 3 | P | | I | | | | | | + |
| <i>Griffithsia schousboei</i> Montagne | e | | 5 | E | | A | + | | | | | + |
| <i>Gymnogongrus crenulatus</i> (Turner) J. Agardh | c | 1 | 4 | P | + | A | + | | | | + | + |

Table 3. (Continued)

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>C. humilis</i> var. <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> |
|--|----------|--------|------------------------|-----------|-------------|------------|-------------------|------------------------|---|----------------------|--------------------------|---------------------|
| <i>Gymnogongrus griffithsiae</i> (Turner) Martius | c | 1 | 7 | P | | A | + | | | | | |
| <i>Halarachnion ligulatum</i> (Woodward) Kützing | c | 2 | 3 | H | | A | + | | | | | + |
| <i>Halopithys incurva</i> (Hudson) Batters | c | 2 | 7 | P | | A | + | | | | | |
| <i>Halurus equisetifolius</i> (Lightfoot) Kützing | c/e | 1 | 6 | E | | A | + | + | | | + | |
| <i>Halymenia latifolia</i> P.L. Crouan & H.M. Crouan ex Kützing | c | 2 | 3 | H | | A | + | | | | | + |
| <i>Haraldiophyllum bonnemaisonii</i> (Kylin) A.D. Zinova | e | | 2 | E | | A | + | | | | | + |
| <i>Herposiphonia tenella</i> (C. Agardh) Ambronn | e | | 5 | H | | A | | | | | + | + |
| <i>Heterosiphonia plumosa</i> (J. Ellis) Batters | c/e | 2 | 5 | P | + | A | + | + | + | + | + | + |
| <i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini | c | 1 | 9 | C | | A | + | | | | | |
| <i>Hypoglossum hypoglossoides</i> (Stackhouse) F.S. Collins & hervey | c/e | 1 | 2 | E | | A | + | | | | + | + |
| <i>Jania longifurca</i> Zanardini | c/e | 1 | 8 | P | | A | + | | | | + | |
| <i>Jania rubens</i> (L.) J.V. Lamouroux | e | | 8 | P | + | A | + | + | + | + | + | + |
| <i>Jania squamata</i> (L.) J.H. Kim & al. | e | | 8 | P | + | A | + | + | | | + | |
| <i>Kallymenia reniformis</i> (Turner) J. Agardh | c/e | 2 | 4 | P | + | A | + | + | | | | + |
| <i>Laurencia pyramidalis</i> Bory de Saint-Vincent ex Kützing | c/e | 1 | 7 | H | | A | + | | | | | |
| <i>Leptosiphonia schousboei</i> (Thuret) Kylin | c/e | 1 | 6 | H | | A | | | + | | + | |
| <i>Lithophyllum incrustans</i> Philippi | c | 1 | 9 | C | + | A | + | + | + | + | + | + |
| <i>Lomentaria articulata</i> (Hudson) Lyngbye | c/e | 1 | 6 | P | + | A | + | + | + | + | + | + |
| <i>Lomentaria clavellosa</i> (Lightfoot ex Turner) Gaillon | c/e | 1 | 6 | E | | A | + | | | | + | + |
| <i>Lomentaria hakodatensis</i> Yendo | c | 1 | 6 | P | | I | | | | | + | |
| <i>Lophosiphonia reptabunda</i> (Suhr) Kylin | e | | 5 | E | | A | | | | | + | |
| <i>Mastocarpus stellatus</i> (Stackhouse) Guiry | c | 1 | 4 | P | | A | + | | | | + | + |
| <i>Mastocarpus stellatus</i> stadium "Petrocelis cruenta" J. Agardh | c | 1 | 9 | C | | A | + | | | | + | + |
| <i>Melobesia membranacea</i> (Esper) J.V. Lamouroux | e | | 9 | C | + | A | + | | | | + | + |
| <i>Meredithia microphylla</i> (J. Agardh) J. Agardh | c | 1 | 4 | P | | A | + | | | | | |
| <i>Mesophyllum lichenoides</i> (J. Ellis) M. Lemoine | c/e | 1 | 9 | C | + | A | + | | + | + | + | |
| <i>Monosporus pedicellatus</i> (Smith) Solier | e | | 5 | E | | A | | | | | | + |
| <i>Neosiphonia collabens</i> (C. Agardh) Díaz-Tapia & Bárbara | e | | 6 | E | | A | + | | | | + | + |
| <i>Neosiphonia ferulacea</i> (Suhr ex J. Agardh) S.M. Guimaraes & M.T. Fujii | e | | 6 | E | | A | + | | | | + | + |
| <i>Neosiphonia harveyi</i> (Bailey) M.S. Kim & al. | e | | 6 | E | | I | + | | | | | |

Table 3. (Continued)

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>C. humilis</i> var. <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> |
|---|----------|--------|------------------------|-----------|-------------|------------|-------------------|------------------------|---|----------------------|--------------------------|---------------------|
| <i>Nitophyllum punctatum</i> (Stackhouse) Greville | c/e | 1 | 2 | E | + | A | + | | + | + | + | + |
| <i>Ophiodocladus simpliciusculus</i> (P.L. Crouan & H.M. Crouan) Falkenberg | c | 1 | 6 | P | | A | + | | | | + | |
| <i>Osmundea hybrida</i> (A.P. de Candolle) K.W. Nam | c | 1 | 7 | H | | A | | | | | + | |
| <i>Osmundea osmunda</i> (S.G. Gmelin) K.W. Nam & Maggs | c | 2 | 7 | P | | A | + | | | | + | |
| <i>Osmundea pinnatifida</i> (Hudson) Stackhouse | c/e | 1 | 7 | H | + | A | + | | + | | + | |
| <i>Osmundea truncata</i> (Kützing) K.W. Nam & Maggs | e | | 7 | P | | A | + | | | | | |
| <i>Palmaria palmata</i> (L.) Wber & Mohr | c/e | 2 | 4 | P | | A | + | + | | | + | |
| <i>Peyssonnelia atropurpurea</i> P.L. Crouan & H.M. Crouan | c | 1 | 9 | C | + | A | + | | | + | + | + |
| <i>Peyssonnelia dubyi</i> P.L. Crouan & H.M. Crouan | c | 1 | 9 | C | | A | + | | | | | + |
| <i>Peyssonnelia squamaria</i> (S.G. Gmelin) Decaisne | c | 1 | 9 | C | | A | + | | | | | |
| <i>Phyllophora crispa</i> (Hudson) P.S. Dixon | c | 1 | 4 | P | | A | + | | | | | |
| <i>Phyllophora sicula</i> (Kützing) Guiry & L.M. Irvine | c | 1 | 3 | P | | A | + | | | | | |
| <i>Phymatolithon lenormandii</i> (Areschoug) Adey | c | 1 | 9 | C | | A | + | | | + | | |
| <i>Pleonosporium borneri</i> (Smith) Nägeli | c/e | 1 | 5 | E | | A | + | | | + | + | + |
| <i>Plocamium cartilagineum</i> (L.) P.S. Dixon | c/e | 2 | 7 | P | + | A | + | + | + | + | + | + |
| <i>Plocamium raphelisianum</i> P.J.L. Dangeard | c/e | | 7 | P | | A | + | | | | | |
| <i>Polyides rotundus</i> (Hudson) Gaillon | c | 1 | 7 | P | | A | + | | | | | |
| <i>Polyneura bonnemaisonii</i> (C. Agardh) Maggs & Hommersand | c/e | 1 | 2 | E | | A | + | | | + | | + |
| <i>Polysiphonia atlantica</i> Kapraun & J.N. Norris | c/e | 1 | 5 | E | | A | + | | | | | |
| <i>Polysiphonia brodiaei</i> (Dillwyn) Sprengel | c/e | 1 | 6 | E | | A | + | | + | | + | + |
| <i>Polysiphonia caespitosa</i> (M.A. Pocock) Hollenberg | c | 1 | 5 | E | | A | + | | | | + | |
| <i>Polysiphonia denudata</i> (Dillwyn) Greville ex Harvey | e | | 6 | E | | A | + | | | | | |
| <i>Polysiphonia elongata</i> (Hudson) Sprengel | c/e | 1 | 6 | E | | A | | | | | + | |
| <i>Polysiphonia fibrillosa</i> (Dillwyn) Sprengel | e | | 5 | E | | A | + | | | | + | + |
| <i>Polysiphonia fucooides</i> (Hudson) Greville | c | 1 | 6 | P | | A | + | | | | | |
| <i>Polysiphonia stricta</i> (Dillwyn) Greville | e | | 5 | E | | A | | | | + | | |
| <i>Polysiphonia subulata</i> (Ducluzeau) Kützing | e | | 5 | E | | A | | | | | + | |
| <i>Porphyra umbilicalis</i> Kützing | c/e | 1 | 2 | E | | A | + | | | | + | + |
| <i>Porphyrostromium boryanum</i> (Montagne) P.C. Silva | e | | 2 | E | | A | + | | | | + | |
| <i>Pseudopolyides furcellarioides</i> Gallardo & al. | c | 2 | 7 | P | + | A | + | + | | + | + | |

Table 3. (Continued)

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | C. baccata | C. foeniculacea | C. humilis var. myriophylloides | C. nodicaulis | C. tamariscifolia | C. usneoides |
|---|----------|--------|------------------------|-----------|-------------|------------|------------|-----------------|---------------------------------|---------------|-------------------|--------------|
| <i>Pterosiphonia ardreana</i> Maggs & Hommersand | c/e | 1 | 6 | P | | A | + | | | | + | |
| <i>Pterosiphonia complanata</i> (Clemente) Falkenberg | c/e | 1 | 7 | P | + | A | + | + | + | | + | + |
| <i>Pterosiphonia parasitica</i> (Hudson) Falkenberg | c/e | 1 | 6 | E | | A | + | + | | | | + |
| <i>Pterosiphonia pennata</i> (C. Agardh) Sauvageau | c/e | 1 | 6 | E | + | A | + | | + | | + | |
| <i>Pterothamnion crispum</i> (Ducluzeau) Nägeli | e | | 5 | E | | A | + | | | + | + | + |
| <i>Pterothamnion plumula</i> (J. Ellis) Nägeli | c/e | 1 | 5 | E | | A | + | + | | | | + |
| <i>Ptilothamnion pluma</i> (Dillwyn) Thuret | e | | 5 | E | | A | | | | | | + |
| <i>Ptilothamnion sphaericum</i> (P.L. Crouan & H.M. Crouan ex J. Agardh) Maggs & Hommersand | c | 1 | 5 | E | | A | + | | | | | |
| <i>Pyropia leucosticta</i> (Thuret) Neefus & J. Brodie | e | | 2 | H | + | A | + | | | | + | + |
| <i>Rhodophyllis divaricata</i> (Stackhouse) Papenfuss | c/e | 1 | 2 | E | + | A | + | + | + | | + | + |
| <i>Rhodothamniella floridula</i> (Dillwyn) Feldmann | c/e | 1 | 5 | E | | A | + | | | | + | |
| <i>Rhodymenia coespitosella</i> L'Hardy-Halos | c | 1 | 3 | E | | A | + | | | | | |
| <i>Rhodymenia holmesii</i> Ardissonne | c/e | 1 | 3 | P | | A | + | | | | | + |
| <i>Rhodymenia pseudopalmata</i> (J.V. Lamouroux) P.C. Silva | c/e | 2 | 4 | P | + | A | + | + | + | + | | + |
| <i>Sahlingia subintegra</i> (Rosenvinge) Kornmann | e | | 2 | E | | A | + | | | | + | |
| <i>Schizymenia dubyi</i> (Chauvin ex Duby) J. Agardh | c/e | 2 | 4 | H | + | A | + | + | | | + | |
| <i>Schizymenia dubyi</i> stadium " <i>Haematocelis rubens</i> " J. Agardh | c/e | 1 | 9 | C | | A | + | | | | | |
| <i>Schottera nicaeensis</i> (J.V. lamouroux ex Duby) Guiry & Hollenberg | c | 1 | 3 | P | | A | + | | | + | | |
| <i>Scinaia furcellata</i> (Turner) J. Agardh | e | | 6 | E | | A | | | | | + | |
| <i>Spermothamnion repens</i> (Dillwyn) Rosenvinge | e | | 5 | E | | A | + | | | | + | |
| <i>Sphaerococcus coronopifolius</i> Stackhouse | c | 2 | 7 | P | + | A | + | + | | + | | + |
| <i>Sphondylothamnion multifidum</i> (Hudson) Nägeli | c | 1 | 5 | E | | A | + | | | | | |
| <i>Stenogramme interruptum</i> (C. Agardh) Montagne | c | 2 | 3 | P | | A | + | | | | | |
| <i>Stylonema alsidii</i> (Zanardini) K.M. Drew | e | | 5 | E | | A | + | | + | + | | + |
| <i>Tiffaniella capitata</i> (Schousboe ex Bornet) Doty & Meñez | c | 1 | 5 | E | | A | | | | | | + |
| <i>Titanoderma pustulatum</i> (J.V. Lamouroux) Nägeli | e | | 9 | C | + | A | + | | + | | + | |
| CHLOROPHYTA | | | | | | | | | | | | |
| <i>Bryopsidella neglecta</i> (Berthold) G. Furnari & M. Cormaci | c | 1 | 5 | E | | A | + | | | | | |
| <i>Bryopsis plumosa</i> (Hudson) C. Agardh | c/e | 1 | 5 | H | | A | + | | | | + | |

Table 3. (Continued)

| | Position | Canopy | Morphofunctional group | Life Form | Common spp. | Non-Native | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>C. humilis</i> var. <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> |
|--|----------|--------|------------------------|-----------|-------------|------------|-------------------|------------------------|---|----------------------|--------------------------|---------------------|
| <i>Chaetomorpha aerea</i> (Dillwyn) Kützing | c/e | 1 | 5 | E | + | A | + | | + | | + | |
| <i>Chaetomorpha mediterranea</i> (Kützing) Kützing | c | 1 | 5 | E | | A | + | | | | | |
| <i>Cladophora albida</i> (Nees) Kützing | c/e | 1 | 5 | E | | A | + | | | | + | + |
| <i>Cladophora hutchinsiae</i> (Dillwyn) Kützing | c/e | 1 | 5 | E | | A | | | | | + | + |
| <i>Cladophora laetevirens</i> (Dillwyn) Kützing | c/e | 1 | 5 | E | | A | + | | | | + | |
| <i>Cladophora lehmanniana</i> (Lindenberg) Kützing | c | 1 | 5 | E | | A | + | | | | | |
| <i>Cladophora prolifera</i> (Roth) Kützing | c | 1 | 5 | P | | A | + | | | | | |
| <i>Cladophora rupestris</i> (L.) Kützing | c | 1 | 5 | E | | A | + | | | | | |
| <i>Codium fragile</i> (Surinagar) Hariot | c | 2 | 6 | P | | A | + | | | | + | + |
| <i>Codium tomentosum</i> Stackhouse | c | 2 | 6 | P | + | A | + | + | + | | + | |
| <i>Codium vermilara</i> (Olivi) Delle Chiaje | c | 2 | 6 | P | | A | + | | | | | + |
| <i>Spongomorpha arcta</i> (Dillwyn) Kützing | c | 1 | 5 | H | | A | | | | | + | |
| <i>Ulva ardrea</i> M. Cormaci & al. | e | | 2 | E | | A | + | | | | | |
| <i>Ulva clathrata</i> (Roth) C. Agardh | e | | 2 | E | + | A | + | | + | | + | + |
| <i>Ulva compressa</i> L. | c/e | 1 | 2 | E | | A | + | | | | + | + |
| <i>Ulva gigantea</i> (Kützing) Bliding | c | 2 | 2 | E | | A | + | | | | + | |
| <i>Ulva prolifera</i> O.F. Müller | c/e | 1 | 2 | E | | A | + | | + | | + | |
| <i>Ulva rigida</i> C. Agardh | c/e | 2 | 2 | E | + | A | + | | + | + | + | + |
| <i>Ulvaria obscura</i> (Kützing) P. Gayral ex C. Bliding | c/e | 1 | 2 | E | | A | | | | | + | |
| <i>Ulvella viridis</i> (Reinke) R. Nielsen & al. | e | | 2 | E | | A | + | | | | | |

in the *Cystoseira* communities was Rhodophyta (24-148 species), followed by Ochrophyta (9-46) and Chlorophyta (1-19). Cyanophyta (up to 3 species) is a not well studied group due to the difficulty to find and determinate them. This distribution of the species among the divisions is very similar to the number of algal species recorded on subtidal Atlantic maerl beds (Peña & al., 2014), although it seems to be more similar to the France Atlantic region than to the Spain Atlantic region.

The predominant morphofunctional groups (Table 4) were those of filamentous and filiform, followed by the three foliose groups. Among morphological groups, the most abundant varies between the communities. Thus, in the *C. baccata*, *C. tamariscifolia*, and *C. usneoides* communities the filamentous morphological group which includes most species was the thin filamentous (55, 47, and 37 species, respectively), while *C. foeniculacea* community was the corticated filiform (10). In contrast, in the *C. humilis* var. *myriophylloides* and *C. nodicaulis*, the three filamentous morphological groups were very similar (7-13). On the other hand, the three foliose morphological groups (thin to corticated) were similar

among the *C. baccata*, *C. tamariscifolia*, and *C. usneoides* assemblages. Concerning the life forms of the associate flora to *C. baccata*, *C. tamariscifolia*, and *C. usneoides* (Table 4), the predominant group was the ephemerophytes (97, 82 and 69 species) and phanerophytes (71, 44 and 32 species). This means that *Cystoseira* assemblages exhibit a constant number of species throughout the year, both by perennial plants (phanerophytes) or constant renewing of individuals by non-perennial plants (ephemerophytes).

More than 70 species were present in the majority of the *Cystoseira* assemblages (Table 3), the most of them appearing in the *C. baccata* community. The erect canopy were made by brown algae like *Desmarestia aculeata*, *Desmarestia ligulata*, *Halidrys siliquosa*, *Laminaria hyperborea*, *Laminaria ochroleuca*, *Saccorbhiza polyschides*, *Sargassum muticum* living together to *Cystoseira* species. Other species (mainly red and brown seaweeds) formed a basal canopy, as *Callophyllis laciniata*, *Calliblepharis jubata*, *Codium tomentosum*, *Corallina officinalis*, *Chondrus crispus*, *Delesseria sanguinea*, *Dictyota dichotoma*, *Dictyopteris polypodioides*, *Ellisolandia elongata*, *Lithophyllum incrustans*, *Gelidium corneum*, *Heterosiphonia*

Table 4. Summary of the associate flora of *Cystoseira* assemblages in the Northern Atlantic Iberian Peninsula.

| | <i>C. humilis</i> var. | | | | | | |
|------------------------|-------------------------------|------------------------|------------------------|----------------------|--------------------------|---------------------|----|
| | <i>C. baccata</i> | <i>C. foeniculacea</i> | <i>myriophylloides</i> | <i>C. nodicaulis</i> | <i>C. tamariscifolia</i> | <i>C. usneoides</i> | |
| TOTAL | 215 | 34 | 61 | 52 | 162 | 126 | |
| Ochrophyta | 46 | 9 | 15 | 12 | 41 | 29 | |
| Chlorophyta | 19 | 1 | 5 | 1 | 14 | 7 | |
| Rhodophyta | 148 | 24 | 40 | 39 | 105 | 87 | |
| Cyanophyta | 2 | 0 | 1 | 0 | 2 | 3 | |
| Morphofunctional group | Unicellular (1) | 2 | 0 | 1 | 0 | 2 | 3 |
| | Thin foliose (2) | 21 | 2 | 7 | 5 | 17 | 16 |
| | Intermediated foliose (3) | 17 | 5 | 4 | 5 | 10 | 10 |
| | Corticated foliose (4) | 25 | 6 | 4 | 9 | 14 | 18 |
| | Thin filamentous (5) | 55 | 3 | 13 | 7 | 47 | 37 |
| | Intermediated filamentous (6) | 42 | 4 | 14 | 8 | 36 | 22 |
| | Corticated filamentous (7) | 34 | 10 | 12 | 11 | 24 | 12 |
| | Articulated calcareous (8) | 5 | 3 | 3 | 3 | 5 | 2 |
| | Crustose calcareous (9) | 14 | 1 | 3 | 4 | 7 | 6 |
| | Ephemerophytes (E) | 97 | 8 | 27 | 15 | 82 | 68 |
| Life form | Hypnophytes (H) | 23 | 2 | 6 | 2 | 22 | 15 |
| | Phanerophytes (P) | 71 | 18 | 21 | 25 | 44 | 32 |
| | Chamaephytes (C) | 15 | 1 | 3 | 4 | 7 | 6 |
| | Hemiphanerophytes (Hp) | 9 | 5 | 4 | 6 | 7 | 5 |
| Epiphytes | Epiphytes | 139 | 20 | 51 | 31 | 123 | 96 |
| | Basal Layer (1) | 95 | 10 | 26 | 19 | 71 | 43 |
| | Middle Layer (2) | 48 | 16 | 13 | 17 | 29 | 28 |
| Canopy | Upper Layer (3) | 15 | 5 | 7 | 6 | 13 | 11 |
| | Non-native species | 10 | 0 | 5 | 1 | 7 | 11 |
| Common species | 70 | 25 | 43 | 36 | 63 | 54 | |
| Typical species | 15 | 0 | 1 | 0 | 1 | 1 | |

plumosa, *Lomentaria articulata*, *Mesophyllum lichenoides*, *Plocamium cartilagineum*, *Pseudopolyides furcellarioides*, *Pterosiphonia complanata*, *Rhodymenia pseudopalmata*, *Sphaerococcus coronopifolius*, and *Ulva rigida*. There were also some epiphytes common in the most of the *Cystoseira* assemblages, as *Antithamnion cruciatum*, *Boergeseniella fruticulosa*, *Champia parvula*, *Colaconema daviesii*, *Colpomenia peregrina*, *Cryptopleura ramosa*, *Elachista flaccida*, *Rhodophyllis divaricata*, *Hinckesia hincksiae*, *Jania rubens*, *J. squamata*, *Melobesia membranacea*, *Pyropia leucosticta*, *Titanoderma pustulatum*, and *Ulva clathrata* (Tab. 3, Fig. 3). Other species found as typical epiphytes but not present in all the *Cystoseira* assemblages were brown seaweeds (*Ectocarpus fasciculatus*, *Elachista intermedia*, *Hinckesia granulosa*, *Litosiphon laminariae*, and *Myriactula rivularia* spp.) and red algae (*Callithamnion tetragonum*, *Chylocladia verticillata*, *Compsobamnion thuyoides*, *Mesophyllum lichenoides*, *Nitophyllum punctatum*, *Polyneura bonnemaisonii*, *Rhodophyllis divaricata*, *Schizymenia dubyi*, and *Spermothamnion repens*).

The number of exclusive species by *Cystoseira* assemblages varies between communities. Neither species were exclusive

of the *C. foeniculacea* and the *C. nodicaulis* communities, whereas the *C. humilis* var. *myriophylloides* and the *C. tamariscifolia* communities exhibit *Amphiroa vanbosseae* and *Jania longifurca* as typical species, respectively. The *C. usneoides* community contained two species (*Erythrogllossum laciniatum* and *Brongniartella byssoides*) not present in other *Cystoseira* assemblages. *Cystoseira baccata* community comprises great number of species (Table 3) that are absent or scarce in other *Cystoseira* assemblages, such as *Phyllariopsis brevipes* subsp. *pseudopurpurascens*, *Abnfeltia plicata*, *Chondria dasyphylla*, *C. scintillans*, *Cordylecladia erecta*, *Cruoria pellita*, *Elachista flaccida*, *Erythrogllossum lusitanicum*, *Halopithys incurva*, *Laurencia pyramidalis*, *Meredithia microphylla*, *Neurocaulon foliosum*, *Phyllophora crispa*, *P. sicula*, *Plocamium raphelisia-num*, and *Polysiphonia fucoides*.

Regarding the non-native algae in the *Cystoseira* communities (Tables 3 and 4), up to twelve species have been reported in the literature, as canopy over rocks (*Codium fragile*, *Lomentaria bakodatensis*, *Sargassum muticum*, and *Undaria pinnatifida*) and epiphytes *Anotrichium furcellatum*, *Antithamnionella spirographidis*, *A. ternifolia*, *Asparagopsis armata*, and its stadium "*Falkenbergia rufolanosa*",

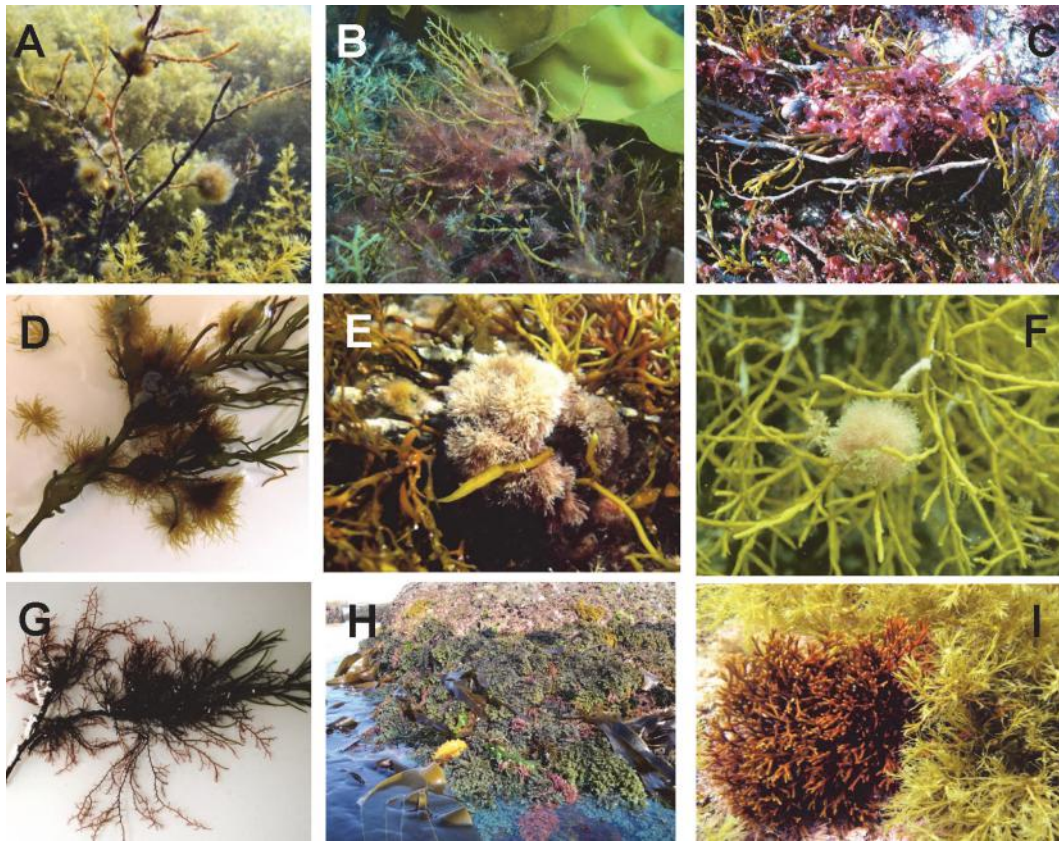


Fig. 3. Epiphytes and associate species of the Northern Atlantic Iberian *Cystoseira* assemblages: **a**, *Sphacelaria cirrhosa*; **b**, *Antithamnionella ternifolia*; **c**, *Cryptopleura ramosa*; **d**, *Elachista flaccida*; **e**, *Jania rubens*; **f**, *Asparagopsis armata* as tetrasporangial stadium (*Falkenbergia rufolanosa*); **g**, *Boergeseniella fruticulosa*; **h**, *C. tamariscifolia* with *Saccorhiza polyschides*, *Asparagopsis armata*, and *Ulva rigida*; **i**, *Pseudopolyides furcellaroides* with *C. baccata*.

Dasya sessilis, *Dasyisiphonia japonica*, *Neosiphonia harveyi*, *Colpomenia peregrina*. *Cystoseira baccata* and *C. usneoides* harbor most of the non-native species (10 and 11 species) followed by *C. tamariscifolia* (7 species). Some small and epiphytic species like *A. ternifolia*, *Colpomenia peregrina*, *Falkenbergia rufolanosa* or *Neosiphonia harveyi* can be mixture with typical epiphytes of *Cystoseira* spp., but other big and invasive species (*Sargassum muticum*) can disturb the habitat by occupying the substrata and shading the *Cystoseira* canopy as it was observed in Arenas & al. (1995) and Sánchez & Fernández (2005). Similar number of non-native species were found the revision of the European maerl beds (Peña & al., 2014) so the non-native species represent an important part of the associate flora of both maerl and *Cystoseira* assemblages, but more important is that the non-native species can cover more extensive part of substrata more than the native ones.

DISTURBANCES IN THE CYSTOSEIRA ASSEMBLAGES

In the literature (Belegratis & al., 1999; Sales & al., 2011; Sales & Ballesteros, 2012; Templado & al., 2012) is reported that assemblages of *Cystoseira* have regressed considerably during the last decades in several Mediterranean localities, a fact attributed mainly to the negative impact of pollution and other anthropogenic pressures in the most of species of the genus *Cystoseira*. Moreover, five *Cystoseira* taxa

(*C. amentacea*, *C. mediterranea*, *C. sedoides*, *C. spinosa*, and *C. zosteroides*) are currently listed as species strictly protected under the Berne Convention (Annex I, 1979) and all the Mediterranean species of the genus *Cystoseira*, except *C. compressa*, have been listed under Annex II of the Barcelona convention (2010). Moreover, all the Mediterranean *Cystoseira* species are under surveillance by international organizations such as the IUCN, the RAC/ASP and MedPan (Thibaut & al., 2014). Monitoring studies generally suggest pollution as the main factor influencing the disappearance of *Cystoseira* spp., however, there are not much studies providing experimental evidences for the disappearance of *Cystoseira* species related to pollution. Belegratis & al. (1999) pointed out that one of the most negative effects is the eutrophication, as high nutrient levels trigger growth of epiphytes and phytoplankton, that concurrently inhibiting host growth through shading and, as a consequence, host-epiphyte complexes ultimately decline and are replaced by phytoplankton dominated systems. However, other factors like inorganic chemical pollution increased turbidity levels, overgrazing and climate change could be other possible causes (Sales & Ballesteros, 2009). In addition, their data shows a positive relationship of rich and well developed *Cystoseira* assemblages to urbanization distance and low levels of nutrient concentration (Sales & Ballesteros, 2009) and the results of the study of Sales & al. (2011) suggest that heavy metal pollution could be negatively affecting survival and growth of *Cystoseira* species with species-specific responses.

In their study, individuals of three *Cystoseira* species were transplanted from non-polluted to slightly polluted and heavily polluted areas, in places known to have *Cystoseira* spp. populations before pollution increased one century ago. Effects of pollution were species-specific: negative effects in survival of *C. barbata* and growth of *C. crinita* were detected in specimens transplanted to the high polluted area. The pollution could have been the cause that led to the disappearance of *Cystoseira* species in the past; however, neither survival nor growth of any of the *Cystoseira* species was negatively affected at the slightly polluted area, and growth was favored for *C. barbata* (Sales & al., 2011).

Although great efforts are directed in the EU to improve water quality by the implementation of the Water Framework Directive and *Cystoseira* species are used as indicators of good water quality, no recovery of *Cystoseira* populations after improvement of water quality has been detected. Therefore, some authors (Belegratis & al., 1999; Sales & al., 2011; Bermejo & al., 2012; Sales & Ballesteros, 2012; Templado & al., 2012) claim for alternative management of measures that facilitates the re-establishment of *Cystoseira* populations in areas where water quality has improved. In the Balearic Island, Sales & Ballesteros (2007) found nine taxa of *Cystoseira*, some of them widely distributed around the island but other ones scarcely spread. Although these differences are probably due to physical causes more than pollution or anthropogenic disturbances, as sheltered *Cystoseira* assemblages are strongly determined by geomorphological features of the coast, Sales & Ballesteros (2007) proposed to use *Cystoseira* assemblages as ecological indicators in biological monitoring for water quality assessment according to the EEC Water Framework Directive since they are very good indicators.

Because of the sedentary condition of attached microalgae that integrates the effects of long-term exposure to nutrients and/or other pollutants, the use of these benthic organisms as bioindicators to assess pollution values in the marine environment was proved successful in many ecological studies (Gorostiaga & Díez, 1996; Díez & al., 1999; Bermejo & al., 2012; Santolaria, 2014). As macroalgal communities provide habitat and harbor for a wide variety of organisms, changes in these communities will have significant effects on shore ecosystems (Bermejo & al., 2012). Hernández & al. (2011) studied the vegetation in the intertidal zone of the port of Tarifa, (South Iberia). Some of the species were found in the catalogue of endangered species and can be used as bioindicators and should have a special attention, so recently the *Cystoseira* species have been included in the list of endangered species of the Mediterranean (Hernández & al., 2011).

In Northeastern Atlantic Iberia was detected regression of the *Cystoseira* assemblages (Gorostiaga & Díez, 1996; Díez, 1997; Díez & al., 2009; Santolaria, 2014) pointed out that, the *Cystoseira* species are sensitive to contamination, as *C. baccata* and *C. tamariscifolia* were not present in polluted areas. Gorostiaga & Díez (1996) found that in these unstable environments the community responds by simplifying its structure: reducing the number of layers, reducing vegetal cover and allowing a proliferation of opportunistic species with simple morphology, especially ceramiacous algae. There is also proliferation of sciaphilous and sedimentation-resistant species. The crustose layer, made up of species having these characteristics, shows strong

development in polluted environments. Díez & al. (2009) found that only the most degraded assemblages experienced a significant increase in algal cover, revealing that this structural community parameter is not relevant in distinguishing between moderately degraded and unaltered vegetation. These results suggest that a significant reduction in algal cover takes place when a threshold of pollution intensity is exceeded. Likewise, the degree of water motion, depth, salinity and the nature of the pollution discharged seem to play major roles in algal cover response. The conclusion of this study is that following pollution abatement there was a partial recovery of intertidal phytobenthic assemblages. Intertidal vegetation at the degraded sites has become progressively more similar to that of the reference site, characterizing five succession stages. The *Cystoseira* species only appears in the last recovery stages, the reference stage, so the first sign of degradation of natural communities is the loss of large perennial macrophytes as *Cystoseira*. In this way, Santolaria (2014) pointed out that where the contamination were worse, the macrophytes as *Cystoseira* spp. were absent and replaced by caespitose algae as *Gelidium pusillum* and *Caulacanthus ustulatus*; however, with the progressive recovery of the water quality, the *Cystoseira* species appear again, so it would indicate the full biological recuperation of the station.

The biological invasions is another disturbance in the *Cystoseira* assemblages, as in marine ecosystems they have been increasing all around the world, mainly due to human activities such as international shipping, aquaculture and aquarium activity. The brown macroalgae *Sargassum muticum*, native to East Asia, is considered an invasive species around the world, being distributed mainly in sheltered or semi-exposed rocky shores, and regularly invades the habitats of algal species from the genus *Cystoseira* (Vaz-Pinto & al., 2014). Previous studies (Sánchez & Fernández, 2005; Olabarria & al., 2009) showed the impact of the invasive *Sargassum muticum* on native assemblages, with a limited impact on native assemblages in northern Spain. Native species of *Cystoseira* can be displaced by *Sargassum muticum* (Critchley & al., 1986; Viejo, 1997; Engelen & Santos, 2009) and it causes changes in the structure of the native communities (Britton-Simmons, 2014). This could be explained because, although *Sargassum muticum* has a small basal disc, its bigger branches outshine the basal strata and compete for light and nutrients (Critchley & al., 1986; Viejo, 1997; Britton-Simmons, 2004; Sánchez & Fernández, 2005). Furthermore, the normal growth of *Sargassum* results in higher growth rates during shorter periods of time than those of *Cystoseira* (Rico & Fernández, 1997) and the productivity is higher than in native species as *C. baccata* or *Saccorbiza polyschides* (Fernández & al., 1990). In southwestern Portugal, Engel & Santos (2009) found out that the progression of the *Sargassum muticum* invasion modulates the environment to its own requirements and the combination of K-selected traits and an increase in population growth rate when *Sargassum muticum* became more dominant suggested that competition with the native species *C. humilis* was an important biotic filter for the establishment phase of *Sargassum muticum* invasion. However, Arenas & al. (1995) suggested that reproductive investment was higher in *C. nodicaulis*, so the successful colonization of *Sargassum muticum* in northern Spain shores is likely to be

due to the large production of embryos. In addition, Vaz-Pinto & al. (2014) suggested a better nutritional strategy of *C. humilis* than *Sargassum muticum* to cope with limiting nutrient conditions of intertidal rocky pools, contrary to the expectations. In conclusion, *Sargassum muticum* has little effect in the native communities that are poorly invaded (Viejo, 1997; Sánchez & Fernández, 2005) but exhibits an important effect under high density and size of the non-native species (Britton-Simmons, 2004).

Undaria pinnatifida, another non-native species, quickly colonizes the substrata and in some geographic areas is the dominant species, triggering decreasing in abundance of the native species. It is an opportunistic species with a high capacity to colonize new substrata, but, as it appears in empty spaces, it is not very competitive in natural and stable conditions (Eno & al., 1997). In Galicia it appears in the *C. baccata* assemblage, having not important impact in the community (Cremades & al., 2006).

The non-native species *Codium fragile* affects the native species as *Codium tomentosum* because it is very competitive and aggressive. An empty space in the substrata due to exploitation or the damage of the habitats, make easier that *Codium fragile* colonizes the substrata, making changes in the benthic communities and affecting the sedimentation process (Harris & Tyrrel, 2001; Levin & al., 2002).

Apart from these invasive species, other non-native ones have been reported in the literature as canopy over rocks (*Lomentaria bakodatensis*) and epiphytes (*Anotrichium furcellatum*, *Antithamnionella spirographidis*, *A. ternifolia*, *Asparagopsis armata* (gametophyte and sporophyte), *Dasya sessilis*, *Dasydiphonia japonica*, *Neosiphonia harveyi*, and *Colpomenia peregrina*) in the *Cystoseira* assemblages.

FUTURE RESEARCHES FOR THE CYSTOSEIRA ASSEMBLAGES IN THE NORTH ATLANTIC IBERIA

Taking into account that there is not much known about *Cystoseira* communities in the Atlantic Iberian coast, especially in the North coasts, it will be necessary to study their assemblages in depth concerning the habitat, the structure, the diversity, the seasonally changes, disturbing effects, non-native and invasive species, long term changes, protected areas, etc. At the present, the more urgent study will be making an extensive research about *C. baccata* in Northern Iberia, as it is an exclusive Atlantic species that is widely distributed along the coast it is very little known about how its communities work, although it plays a key role structuring the communities. Furthermore, it is accompanied by the highest number of species and it has the highest number of epiphytes. In addition, *C. baccata* inhabits together with other four *Cystoseira* species so while studying the *C. baccata* communities we will obtain information of more species of *Cystoseira*. The necessity of making a study the *Cystoseira* communities in the North Atlantic Iberian coasts could be noticed reading Templado & al. (2012), since they establish that, in general, the *Cystoseira* species play an accompanied role, while in the literature the *Cystoseira* assemblages exhibit an important role in the North Atlantic Iberian coasts communities, more than only escort species. What is more, Templado & al. (2012) only mentioned *C. baccata* in a sole paragraph as a species that sometimes appear in the *Gelidium corneum* communities. However, *C. baccata* is

one of the most important species and widely distributed one in the North Atlantic Iberian coasts, developing their own communities, which have the highest diversity in the *Cystoseira* communities in these coasts. In addition, there are several biological invasions that disturb the habitat by occupying the substrata and shading the *Cystoseira* canopy (Arenas & al., 1995; Sánchez & Fernández, 2005), so it is important to know the distribution of non-native species and their impacts, especially in Galicia as some rías are important hotspot of introduced marine species (Bárbara & al., 2008).

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