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Macroalgal-dominated coastal detritic communities from the Western Mediterranean and the Northeastern Atlantic

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Abstract

This is a qualitative comparison of the distribution of macroalgal-dominated coastal detritic communities from the Western Mediterranean and the Northeastern Atlantic, based on our own data from the Balearic Islands (Western Mediterranean) and available data from the literature. The macroalgal-dominated coastal detritic bottoms in both regions can be distinguished by the presence of a high number of regional exclusive non-carbonated species, and the presence of a high number of maërl-forming species in the Mediterranean. Furthermore, regional differences in the distribution of some exclusive species allowed the distinction of three zones in the Northeastern Atlantic (United Kingdom, French Brittany and Galicia), while no differences were found in the Western Mediterranean. However, the algal communities considered in the selected literature could not be qualitatively distinguished, and all the samples should be considered as maërl beds. *Lithothamnion corallioides* and *Phymatolithon calcareum* were the most widespread maërl forming species in the two regions, while in the Western Mediterranean *Spongites fruticulosus* was also very frequent. According to the differences in the species composition of the basal and erect strata of these beds, and also in their species richness, five different morphologies of macroalgal-dominated detritic bottoms can be distinguished. Their main characteristic species and their biogeographic distribution are detailed.

Keywords: Coastal detritic bottoms, distribution, *Laminaria rodriguezii*, *Lithothamnion corallioides*, macroalgae, maërl, Western Mediterranean, Northeastern Atlantic, *Peyssonnelia* spp., *Phymatolithon calcareum*, *Spongites fruticulosus*.

Introduction

Macroalgal-dominated coastal detritic bottoms constitute major habitats of continental shelves occurring near the shore (Pérès & Picard, 1964; Picard, 1965; Pérès, 1985). The soft bottoms where these coastal detritic bottoms develop are composed of low percentages of silt, sand and gravels, mixed with a large quantity of calcareous skeletons from benthic organisms such as molluscs, bryozoans, corals, echinoderms and macroalgae, with the free-living members of the orders Corallinales and Peyssonneliales being the major constituents of these bottoms (Pérès, 1985; Klein & Verlaque, 2009). Animal skeletons and calcareous algae create a secondary hard substratum that allows the settlement of organisms usually found on rocky bottoms (Bianchi, 2001), contributing to the presence of high species diversity (with taxa typical of both soft and hard bottoms), and high functional diversity (Cabioch, 1969; Ballantine *et al*., 1994; Birkett *et al*., 1998; Foster, 2001; Steller *et al*., 2003).

The bathymetric distribution of macroalgal-dominated coastal detritic bottoms depends mainly on light, water turbulence and current conditions (Jacquotte, 1962; Pérès & Picard, 1964; Ros *et al*., 1985; Ballesteros, 1992; Sciberras *et al*., 2009). Thus, the high light transmittance and the low water turbidity of Mediterranean waters (especially in the Balearic Islands: Ballesteros & Zabala, 1993; Canals & Ballesteros, 1997; Fornós & Ahr, 1997) allows the development of macroalgal-dominated detritic bottoms down to 90 m in this area (Picard, 1965; Augier, 1982; Pérès, 1985; BIOMAERL team, 1999; Bellan-Santini *et al*., 2002; Hall-Spencer *et al.,* 2010), while in the Northeastern Atlantic they are usually present at depths above 30 m (Pérès & Picard, 1964; Birkett *et al*., 1998; BIOMAERL team, 1999; Peña, 2010; Peña *et al*., 2014). However, even if their bathymetric distribution greatly differs, all macroalgal-dominated detritic bottoms of the European coasts (including the Mediterranean and the Northeastern Atlantic), have been considered as analogous habitats (Pérès & Picard, 1964).

European macroalgal-dominated coastal detritic assemblages have been extensively studied. Various categories or facies have been described in the Mediterranean (Pérès & Picard, 1964; Augier, 1982; Giaccone *et al*., 1994; Templado *et al*., 2012), but only maërl beds (e.g. Huvé, 1956; Costa, 1960; Jacquotte, 1962; Gómez *et al*., 1986; Ballesteros, 1988; Joher *et al*., 2015), kelp forests of *Laminaria rodriguezii* (Joher *et al*., 2015), and *Peyssonnelia* beds (e.g. Huvé, 1954; Ballesteros, 1994; Joher *et al*., 2015) have been studied at community lev-

el. In contrast, the majority of studies performed in the Northeastern Atlantic have focused on the study of maërl beds (e.g. Hily *et al*., 1992; Perrins *et al*., 1995; Otero-Schmitt & Pérez-Cirera, 2002; Bárbara *et al*., 2004; Peña & Bárbara, 2006), suggesting that they are the predominant type of detritic bottoms in this region.

Despite the amount of descriptive literature focusing on algal detritic communities from the Mediterranean and the Northeastern Atlantic coasts, a quantitative comparison is not easy to perform because most of the available data are presented either as checklists for wide geographic zones (e.g. Peña & Bárbara, 2013; Peña *et al*., 2014), or as semi-quantitative data at phytosociological scale (e.g. Otero-Schmitt & Pérez-Cirera, 2002). Furthermore, although maërl beds and their associated flora have been qualitatively compared at European level (BIOMAERL team, 1999; Peña & Bárbara, 2008; Peña *et al*., 2014), we are not aware of any attempt to compare the species composition and distribution of all macroalgal-dominated coastal detritic communities. For these reasons, the aim of this article is to compare the species composition and the distribution of macroalgal-dominated coastal detritic communities described so far in the Western Mediterranean Sea and the Northeastern Atlantic Ocean.

Material and Methods

Data used in this paper was derived from our own samples and from the literature. Our samples were collected in the Menorca Channel and Southern Menorca (Balearic Islands, Spain) during the MEDITS_ES05_09 sampling survey by means of Box-Corer dredging and beam trawling, as detailed in Joher *et al*. (2015). Literature data were compiled from studies performed in the Western Mediterranean (in the Spanish areas of the Costa Brava and the Balearic Islands) and in the Northeastern Atlantic (United Kingdom, French Brittany, and Galicia, Spain). Literature providing checklists concerning wide areas, different sampling stations and probably different communities compiled into a single list (e.g. Blunden *et al*., 1977; Soto, 1990; BIOMAERL team, 1999; Peña & Bárbara, 2013; Peña *et al*., 2014), works focused only on maërl epiflora (e.g. Cabioch, 1969; Augier & Boudouresque, 1978), or old studies that shed doubts on species identification (e.g. Huvé, 1954, 1956; Jacquotte, 1962), were disregarded.

Taking into account these criteria, nine studies and 224 inventories of macroalgal detritic communities were selected from published references (Table 1): 4 articles with 38 inventories from the Western Mediterranean, and 5 studies with 186 inventories from the Northeastern Atlantic.

As the majority of studies did not provide quantitative data, a qualitative approach was adopted for the comparison of the macroalgal communities developed in the coastal detritic bottoms of the Western Mediterranean and the Northeastern Atlantic. Therefore, a similarity matrix was constructed based on the Sørensen similarity index, including only the taxa identified to genus and

Table 1. Main features of the samples from the Western Mediterranean and the Northeastern Atlantic, including geographic area (regions in bold, and zones), locality, depth, type of detritic bottom, code used in nMDS figures, and bibliographic references.

Area	Locality	Depth (m)	Type of detritic bottom	Code	References
Western Mediterranean Sea					
Costa Brava, Spain	Tossa de Mar	40-51	Maërl beds	1-7	Ballesteros, 1988
Balearic Is., Spain	Palma Bay	40-50	Maërl beds	8-16	Gómez *et al*., 1986
	Cabrera Channel	40-54	Maërl beds	17	Ballesteros, 1994
	Several locations	40-54	*Peyssonnelia* beds	18-23	Ballesteros, 1994
	Menorca Channel	50-65	*Laminaria rodriguezii* forests	24-27	Joher *et al*., 2015
	Menorca Channel	50-65	Maërl beds	28-34	Joher *et al*., 2015
	South Menorca	50-65	*Peyssonnelia* beds	35-38	Joher *et al*., 2015
Northeastern Atlantic Ocean					
United Kingdom	Fal Estuary	Unknown	Maërl beds	39-112	Perrins *et al*., 1995
	Fal Estuary	2.4-7.5	Maërl beds	113-183	Perrins *et al*., 1995
	Fal Estuary	2.4-7.5	*Saccharina latissima* forests	184	Perrins *et al*., 1995
Brittany, France	Brest	0-3	Maërl beds	185-205	Hily *et al*., 1992
Galicia, Spain	Several locations	4-26	Maërl beds	206-211	Peña & Bárbara, 2006
	Muros	10-20	Maërl beds	212-219	Otero-Schmitt & Pérez-Cirera, 2002
	Arousa	10-16	Maërl beds	220-224	Bárbara *et al*., 2004

species levels and avoiding the unidentified taxa referring to family and order levels. nMDS ordination was used to visualize patterns of similarities between samples (Kruskal & Wish, 1978) and cluster analysis, using single linkage, was performed to obtain the groups of samples. Identification of the sample groups was performed by selecting the percentage of similarity that presented the best fit with the pattern shown in the nMDS. The SIMPER test allowed the identification of the main characteristic species for each group of samples. Following Joher *et al*. (2012, 2015), the species that contributed up to the 70% of similarity between the samples of each group were identified as characteristic species.

To elucidate the importance of the basal and erect stratums in the differentiation of the macroalgal-dominated coastal detritic communities from European coasts, statistical analyses (nMDS, cluster analysis and SIMPER test) were also performed taking into account, separately, non maërl-forming (non-MFS) and maërl-forming species (MFS) (the species considered as MFS are listed in Appendix 1).

All statistical analyses were performed with PRIMER, version 6, software (Clarke & Warwick, 2001).

Results

Four different macroalgal detritic communities were represented in the inventories: maërl beds characterized mainly by *Lithothamnion corallioides* and *Phymatolithon calcareum* in both regions; kelp forests of *Laminaria rodriguezii* and *Peyssonnelia* beds with different characteristic *Peyssonnelia* species in the Western Mediterranean; and kelp forests of *Saccharina latissima* in the Northeastern Atlantic (Table 1).

A total of 322 taxa found in the inventories were taken into account, of which 252 were Rhodophyta, 42 Phaeophyceae, 26 Chlorophyta and 2 Tracheophyta (Fig. 1). The Western Mediterranean was the richest zone with 200 species, including 149 exclusive species (= species that were only present on the detritic bottoms of this area), while the Northeastern Atlantic harboured 173 species, of which 122 were exclusive. The exclusive species were usually non-MFS, although some exclusive MFS were also present in the Western Mediterranean. Besides, exclusive species were mostly endemic and subtropical in the Western Mediterranean, whereas they were boreal and North-Atlantic temperate in the Northeastern Atlantic. Furthermore, the two regions had 51 species (15.8%) in common (see Appendix 1 for a complete list of taxa). All regions and zones presented maërl-forming species (up to 13 different species), the Western Mediterranean being the region with the highest number of MFS (Fig. 1).

Analyses involving all the species

Seven groups of sample were distinguished at 45.2% of similarity, taking into account all taxa (Fig. 2). Samples from the Western Mediterranean were mainly assembled in four clusters (A, B, C and D), while three groups (E, F and G) were identified for the samples from the Northeastern Atlantic. Thus, for the Western Mediterranean, all the samples from the Costa Brava were gathered in group A, and those from the Balearic Islands were found in groups B, C and D. Only one sample from the Balearic Islands (sample 8) did not follow this pattern

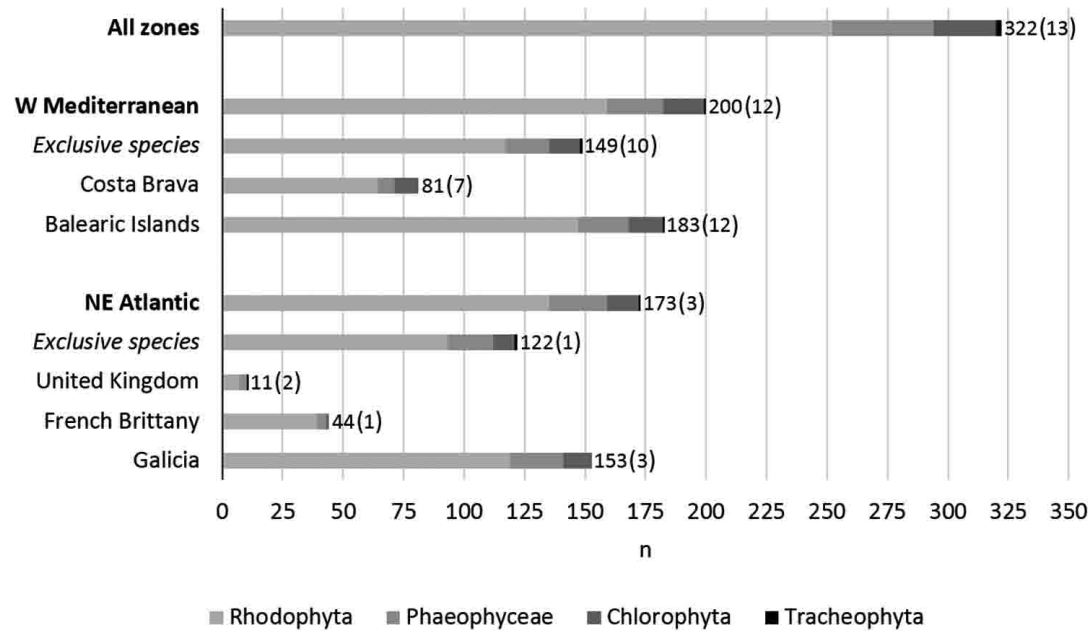

Fig. 1: Number of taxa (n) found in the studies used for the comparison of the detritic algal beds of the Western Mediterranean and the Northeastern Atlantic. We provide global, regional and site-specific data as well as the number of exclusive species for the corresponding regions and the number of maërl-forming species for each one of the geographic areas (in brackets).

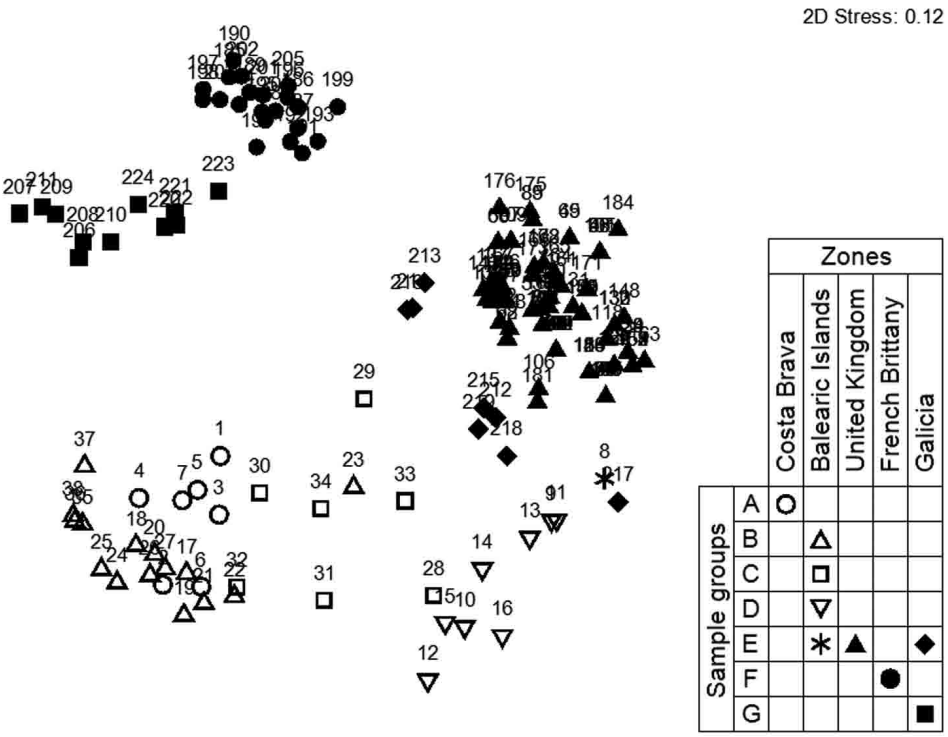

Fig. 2: nMDS ordination based on qualitative data for all the inventories including all the species. The sample groups corresponding to 45.2% of similarity between samples, and the geographic zones are distinguished by symbols. Sample codes correspond to studies in Table 1.

and grouped with samples from the Northeastern Atlantic (group E). For the Northeastern Atlantic, all samples from the United Kingdom were found inside group E, while those from French Brittany in group F, and the ones from Galicia assembled in groups E and G.

In the Western Mediterranean, samples from the Costa Brava (group A) were described as maërl beds of *Spongites fruticulosus* with *Phymatolithon calcareum*, while those from the Balearic Islands corresponded to *Laminaria rodriguezii* forests and *Peyssonnelia* beds (group B), maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* and *Lithothamnion valens* (group C), and maërl of *Phymatolithon calcareum* (group D) (Table 2). The samples from the macroalgal detritic communities of the Balearic Islands included a higher number of species compared to those of the Costa Brava (Fig. 1). All Western Mediterranean groups were characterized by a number of Mediterranean exclusive species (e.g. *Cryptonemia tuniformis, Flabellia petiolata* or *Peyssonnelia harveyana*) (Table 2).

Almost all samples from the Northeastern Atlantic were described as maërl beds, with the exception of one sample from the United Kingdom, which corresponded to a *Saccharina latissima* kelp forest (Table 1). The samples from the United Kingdom and some of those from Galicia (group E) were identified as maërl beds dominated by *Lithothamnion corallioides*, *Phymatolithon calcareum* or both species; those from French Brittany (group F) corresponded to maërl beds dominated by *Lithothamnion corallioides*; and the majority of samples from Galicia (group G) were described as maërl beds with both *Lithothamnion corallioides* and *Phymatolithon calcareum* (Table 2). These maërl beds were distinguished by the number of species mainly, which decreases with latitude, being higher in Galicia and very low in the United Kingdom (Fig. 1). The three sample groups were characterized by a number of exclusive soft algae (e.g. *Cutleria multifida, Polysiphonia flexella* or *Stenogramma interruptum*) as well as other species with a wider distribution (Table 3).

Analyses involving non-MFS only

In the statistical analyses performed with non-MFS only (Fig. 3), a smaller number of groups than in the analysis performed with all the species were identified at 41% of similarity. This is due to the fact that the samples from the Western Mediterranean, which grouped in four groups in the previous analysis, were gathered here in a single group (group A). The sample from the Balearic Islands that previously joined the Atlantic samples (sample 8), corresponded here to a one-sample group (group B). Moreover, in the Northeastern Atlantic, the samples formed exactly the same groups as in the previous analysis.

The samples from the Costa Brava and the Balearic Islands (group A) were characterized by a high number of species, including a high number of exclusive Mediterranean species (Table 4). These samples corresponded

Table 2. Western Mediterranean sample groups obtained by comparison of all species with 45.2% similarity: characteristic species (SIMPER test, 70% cumulative similarity), described communities according to literature source, distribution and number of samples. [m], exclusive species from the Western Mediterranean.

	Group A	**Group B**	**Group C**	**Group D**
Characteristic species	*Contarinia peyssonneliaeformis*[m] *Cryptonemia tuniformis*[m] *Dictyota dichotoma* *Eupogodon planus*[m] *Falkenbergia rufolanosa* *Kallymenia requienii*[m] *Lithophyllum* sp.[m] *Mesophyllum expansum*[m] *Peyssonnelia rosa-marina*[m] *Phymatolithon calcareum* *Plocamium cartilagineum* *Rhodymenia delicatula*[m] *Spongites fruticulosus*[m] *Bonnemaisonia asparagoides* *Hydrolithon farinosum*[m] *Ulvella scutata*[m] *Gloiocladia furcata*[m]	*Cryptonemia tuniformis*[m] *Peyssonnelia rosa-marina*[m] *Dictyota dichotoma* *Polysiphonia subulifera*[m] *Leptofauchea coralligena*[m] *Peyssonnelia harveyana*[m] *Phyllophora crispa*[m] *Osmundaria volubilis*[m] *Irvinea boergeseni*[m] *Hydrolithon farinosum*[m] *Phymatolithon calcareum* *Peyssonnelia rubra*[m] *Flabellia petiolata*[m] *Kallymenia requienii*[m] *Hypoglossum hypoglossoides* *Peyssonnelia* sp.[m] *Gloiocladia furcata*[m] *Gracilaria corallicola*[m] *Rhodymenia* sp.[m] *Myriogramme tristromatica*[m] *Lithothamnion corallioides* *Ceramium codii*[m] *Eupogodon planus*[m] *Polysiphonia* sp.[m] *Rytiphlaea tinctoria*[m] *Derbesia tenuissima* *Lithothamnion valens*[m] *Spongites fruticulosus*[m] *Halopteris filicina* *Peyssonnelia inamoena*[m]	*Kallymenia requienii*[m] *Phymatolithon calcareum* *Spongites fruticulosus*[m] *Lithothamnion valens*[m] *Cryptonemia tuniformis*[m] *Dictyota dichotoma*	*Peyssonnelia rosa-marina*[m] *Phymatolithon calcareum* *Osmundaria volubilis*[m] *Hydrolithon farinosum*[m] *Peyssonnelia rubra*[m]
Described communities	Maërl of *Spongites fruticulosus* with *Phymatolithon calcareum*	*Laminaria rodriguezii* forests *Peyssonnelia* beds	Maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* and *Lithothamnion valens*	Maërl of *Phymatolithon calcareum*
Distribution (number of samples)	Costa Brava (7)	Balearic Islands (15)	Balearic Islands (7)	Balearic Islands (8)

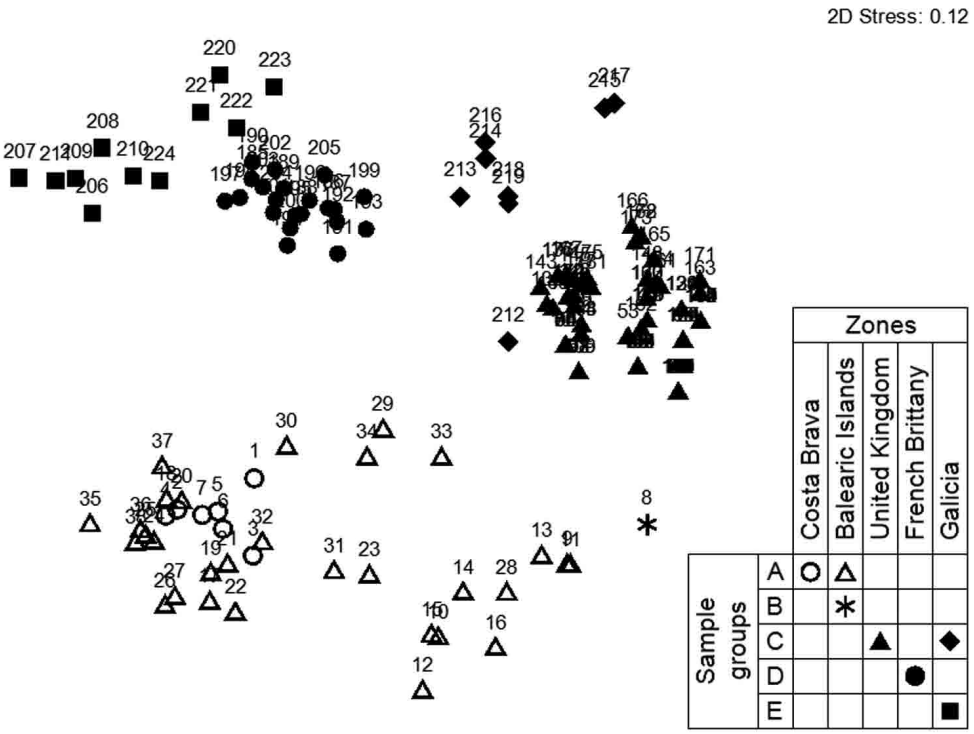

Fig. 3: nMDS ordination based on qualitative data for all the inventories taking into account only non maërl-forming species. The sample groups corresponding to 41% of similarity between samples, and the geographic zones are distinguished by symbols. Sample codes correspond to studies in Table 1.

to *Laminaria rodriguezii* forests, *Peyssonnelia* beds, maërl of *Phymatolithon calcareum*, maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* and *Lithothamnion valens*, and maërl of *Phymatolithon calcareum* (Table 4). Lastly, the single-sample group B was identified as a sample from a Balearic *Peyssonnelia* bed, which presented a low number of species compared with the other samples collected at the same locality.

The identified communities of the Northeastern Atlantic groups were the same as the grouping obtained when considering all the species (Tables 2 and 4).

Analyses involving MFS only

In the analysis performed using MFS only (Fig. 4), only four sample groups were distinguished at 80% of similarity. The obtained groups did not show a clear geographic pattern because of the widespread distribution of the maërl-forming species *Lithothamnion corallioides* and *Phymatolithon calcareum*. Thus, group A included the highest number of samples from both the Western Mediterranean and the Northeastern Atlantic, and was characterized by *Phymatolithon calcareum* and *Lithothamnion corallioides*, although samples from the Western Mediterranean in this group also included *Spongites fruticulosus*. On the other hand, group B was restricted to the Western Mediterranean and had up to four characteristic MFS (*Phymatolithon calcareum*, *Spongites fruticulosus*, *Mesophyllum expansum* and *Lithophyllum* sp.), while group C, that grouped Western Mediterranean samples too, was characterized by *Lithophyllum* sp. and *Lithophyllum stictaeforme*.

Finally, no MFS were found in group D, which included only one sample from the United Kingdom corresponding to a forest of *Saccharina latissima.*

Discussion

The algal communities from the detritic bottoms studied here presented large qualitative differences. Thus, as regards the number of species, the samples from the Western Mediterranean were richer, both in MFS and non-MFS, than those from the Northeastern Atlantic. The higher MFS richness of the Mediterranean coastal detritic bottoms compared to that of the Northeastern Atlantic found in this study has also been pointed in the past by Birkett *et al*. (1998), the BIOMAERL team (1999) and Peña & Bárbara (2008). Besides, the analyses showed that the number of species increased from North to South in the two studied regions (Fig. 1). This increase might be due to an increased stability of the environmental conditions that would enable the development of a higher number of species. However, although similar results have been obtained previously in the Northeastern Atlantic (BIOMAERL team, 1999; Peña & Bárbara, 2008; Pardo *et al*., 2014; Peña *et al*., 2014), this increase could be due to differences in sampling effort, as highlighted previously by and Peña *et al*. (2014).

Table 3. Northeastern Atlantic sample groups obtained by the comparison of all species with 45.2% similarity: characteristic species (SIMPER test, 70% cumulative similarity), described communities according to literature source, distribution and number of samples.[a], exclusive species from the Northeastern Atlantic.

	Group E	Group F	Group G
Characteristic species	*Phymatolithon calcareum* *Lithothamnion corallioides*	*Dictyota dichotoma* *Halarachnion ligulatum*[a] *Lithothamnion corallioides* *Polysiphonia flexella*[a] *Stenogramma interruptum*[a] *Cryptopleura ramosa* *Hypoglossum hypoglossoides* *Nitophyllum punctatum* *Brongniartella byssoides* *Rhodophyllis divaricata* *Ulva* sp.[a] *Chondria dasyphylla*[a] *Polysiphonia stricta* *Ceramium echionotum*[a]	*Cruoria cruoriiformis* *Cutleria multifida*[a] *Dasysiphonia japonica*[a] *Gelidiella calcicola*[a] *Lithothamnion corallioides* *Phymatolithon calcareum* *Plocamium cartilagineum* *Acrosorium ciliolatum* *Pterothamnion plumula* *Ulva rigida*[a] *Cryptopleura ramosa* *Erythroglossum laciniatum*[a] *Dictyota dichotoma* *Stenogramma interruptum*[a] *Kallymenia reniformis*[a] *Ahnfeltiopsis devoniensis*[a] *Spermothamnion repens*[a] *Halarachnion ligulatum*[a] *Callophyllis laciniata* *Compsothamnion thuyoides*[a] *Brongniartella byssoides* *Antithamnionella ternifolia*[a] *Apoglossum ruscifolium* *Halurus flosculosus*[a] *Hypoglossum hypoglossoides* *Myriogramme minuta*[a] *Callithamnion tetragonum*[a] *Trailliella intricata*[a]
Described communities	Maërl of *Lithothamnion corallioides* Maërl of *Phymatolithon calcareum* Maërl of *Lithothamnion corallioides* and *Phymatolithon calcareum* *Saccharina latissima* forests	Maërl of *Lithothamnion corallioides*	Maërl of *Lithothamnion corallioides* and *Phymatolithon calcareum*
Distribution (number of samples)	United Kingdom (146) Galicia (8) Costa Brava (1)	French Brittany (21)	Galicia (11)

The species composition of the samples from the Western Mediterranean and the Northeastern Atlantic significantly differed, mainly because both regions had a high number of exclusive species (representing 74.5% and 70.5% of total species, respectively). As exclusive species were mainly non-MFS, these contributed to a great extent to the distinction of the two regions (see Appendix 1 for a detailed list of exclusive species). However, in this regard it is important to highlight that we were unable to provide a complete list of exclusive species, as some of the literature concerning these bottoms were excluded from the current study because they did not provide data at community level.

In the Western Mediterranean, all samples gathered into a single cluster, while three different geographic areas where distinguished in the Northeastern Atlantic. The fact that geographic areas in the Western Mediterranean were qualitatively indistinct was a consequence of the presence of up to 128 exclusive species (including 10 MFS) found in both sampling areas (the Costa Brava and the Balearic Islands). In contrast, the presence of exclusive species for each one of the three geographic areas of the Northeastern Atlantic (4 in the United Kingdom, 11 in French Brittany, and 92 in Galicia) constituted the basis for distinguishing these areas.

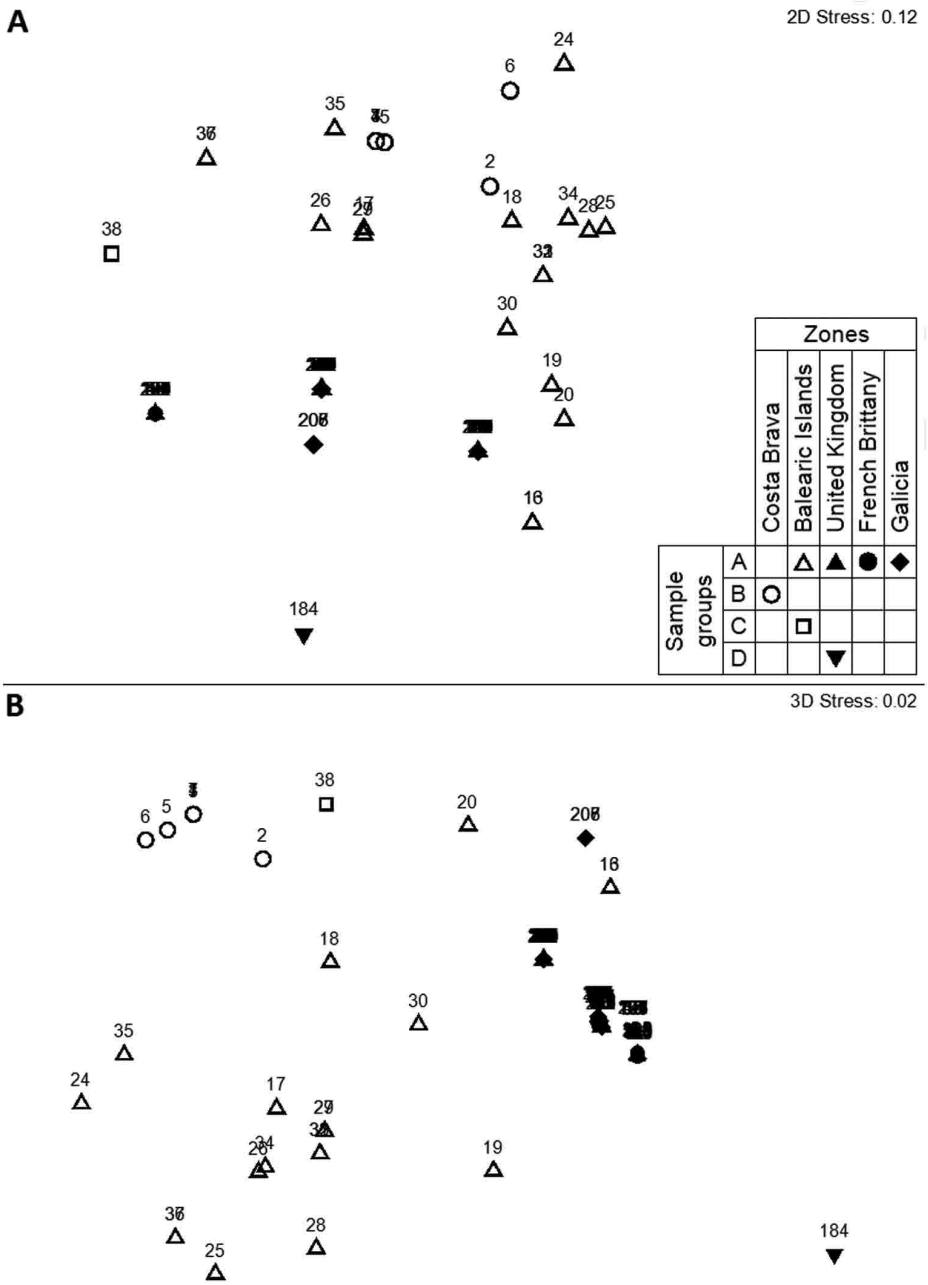

Fig. 4: nMDS ordination (A, 2D nMDS; B, 3D nMDS) based on qualitative data for all the inventories taking into account the maërl-forming species only. The sample groups corresponding to 80% of similarity between samples, and the geographic zones are distinguished by symbols. Sample codes correspond to studies in Table 1.

The macroalgal-dominated coastal detritic samples from the Western Mediterranean and those from the Northeastern Atlantic could not be clearly distinguished according to their MFS composition. In consequence, part of the Western Mediterranean samples gathered with samples from the Northeastern Atlantic, mainly because of the widespread presence of *Lithothamnion corallioides* and *Phymatolithon calcareum* in both regions. Although these two species have been reported to coexist on the same maërl beds (e.g. Jacquotte, 1962; Hily *et al*., 1992; Perrins *et al*., 1995; Peña & Bárbara, 2006), some Northeastern Atlantic locations were characterized by the presence of only one of these species (e.g. Hily *et al*., 1992; Perrins *et al*., 1995; Otero-Schmitt & Pérez-Cirera, 2002). The presence of only *Lithothamnion corallioides* or *Phymatolithon calcareum* at some localities could be a consequence of their misidentification, as these species are known to be morphologically very similar (De Grave & Whitaker, 1999; Peña & Bárbara, 2004). However, it is also possible that specific local environmental conditions influenced the development of only one of these two widespread species.

The distribution of the MFS included in this study generally agrees with the patterns reported by the BI-

Table 4. Sample groups obtained taking into account the non maërl-forming species with 41% similarity: characteristic species (SIMPER test, 70% cumulative similarity), described communities according to literature source, distribution and number of samples. [m], exclusive species from the Western Mediterranean; [a], exclusive species from the Northeastern Atlantic.

	Group A	**Group B**	**Group C**	**Group D**	**Group E**
Characteristic species	*Cryptonemia tuniformis*[m] *Peyssonnelia rosa-marina*[m] *Kallymenia requienii*[m] *Dictyota dichotoma* *Hydrolithon farinosum*[m] *Irvinea boergesenii*[m] *Osmundaria volubilis*[m] *Peyssonnelia harveyana*[m] *Peyssonnelia rubra*[m] *Phyllophora crispa*[m] *Polysiphonia subulifera*[m] *Eupogodon planus*[m] *Hypoglossum hypoglossoides* *Leptofauchea coralligena*[m] *Halopteris filicina* *Gloiocladia furcata*[m] *Flabellia petiolata*[m] *Contarinia peyssonneliaeformis*[m]	*Cladophora* sp.[m] *Dictyota implexa*[m] *Laurencia obtusa*[m] *Peyssonnelia harveyana*[m]	*Chylocladia verticillata* *Saccharina latissima*[a]	*Dictyota dichotoma* *Halarachnion ligulatum*[a] *Polysiphonia flexella*[a] *Stenogramma interruptum*[a] *Cryptopleura ramosa* *Hypoglossum hypoglossoides* *Nitophyllum punctatum* *Brongniartella byssoides* *Rhodophyllis divaricata* *Ulva* sp.[a] *Chondria dasyphylla*[a] *Polysiphonia stricta* *Ceramium echionotum*[a]	*Cruoria cruoriiformis* *Cutleria multifida*[a] *Dasysiphonia japonica*[a] *Gelidiella calcicola*[a] *Plocamium cartilagineum* *Acrosorium ciliolatum* *Pterothamnion plumula* *Ulva rigida*[a] *Cryptopleura ramosa* *Erythroglossum laciniatum*[a] *Dictyota dichotoma* *Stenogramma interruptum*[a] *Kallymenia reniformis*[a] *Halarachnion ligulatum*[a] *Ahnfeltiopsis devoniensis*[a] *Spermothamnion repens*[a] *Callophyllis laciniata* *Compsothamnion thuyoides*[a] *Brongniartella byssoides* *Antithamnionella ternifolia*[a] *Apoglossum ruscifolium* *Halurus flosculosus*[a] *Hypoglossum hypoglossoides* *Myriogramme minuta*[a] *Callithamnion tetragonum*[a] *Trailliella intricata*[a] *Gayliella flaccida*[a] *Chaetomorpha aerea*[a] *Cladophora rupestris*[a]
Described communities	*Laminaria rodriguezii* forests Maërl of *Phymatolithon calcareum* Maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* Maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* and *Lithothamnion valens* *Peyssonnelia* beds	Maërl of *Phymatolithon calcareum*	Maërl of *Lithothamnion corallioides* Maërl of *Phymatolithon calcareum* Maërl of *Lithothamnion corallioides* and *Phymatolithon calcareum* *Saccharina latissima* forests	Maërl of *Lithothamnion corallioides*	Maërl of *Phymatolithon calcareum* Maërl of *Lithothamnion corallioides* and *Phymatolithon calcareum*
Distribution (number of samples)	Balearic Islands (30) Costa Brava (7)	Balearic Islands (1)	United Kingdom (146) Galicia (8)	French Brittany (21)	Galicia (11)

OMAERL team (1999) and Peña & Bárbara (2008). The former authors presented a distribution map of the main MFS along the European coasts; here we propose the addition of *Spongites fruticulosus* as a characteristic species for the Mediterranean (Fig. 5), because this species can be remarkably abundant, at least, in some habitats described in the Costa Brava and the Balearic Islands (Ballesteros, 1988; Joher *et al*., 2012, 2015). Although other MFS have been reported to be present on the detritic bottoms of European coasts (e.g. *Lithophyllum dentatum*, *Neogoniolithon brassica-florida* and *Phymatolithon purpureum*), we did not take them into account here as they were not present in the inventories included in the current study while some of them show restricted distribution or need taxonomic review (Pardo *et al*., 2014). This is also the case for different *Mesophyllum* species, whose identification has to be revisited. In fact, Peña *et al*. (2015) did not find *M. lichenoides* nor *M. alternans* in the Mediterranean but *M. sphaericum* and *M. macroblastum* (Kaleb *et al*., 2011; Peña *et al*., 2011), which creates certain doubts about the correct identification of most specimens corresponding to the genus *Mesophyllum*.

The different algal communities considered in the selected literature (maërl beds, kelp forests and *Peyssonnelia* beds) have usually been described from a quantitative point of view, i.e. on the basis of the most abundant and/or representative species. Our results suggest that despite these communities present some differences in species composition, they cannot be easily distinguished qualitatively, especially those developing in the Western Mediterranean, as pointed out previously for the macroalgal-dominated detritic bottoms of Port-Cros National Park (France) (Augier & Boudouresque, 1978). Consequently, all the macroalgal-dominated coastal detritic bottoms in the Western Mediterranean and the Northeastern Atlantic should be qualitatively considered as maërl beds, due to the presence of a basal stratum composed mainly of *Lithothamnion corallioides*, *Phymatolithon calcareum* and *Spongites fruticulosus*, and a more-or-less developed erect stratum. However, these beds present different morphologies pertaining to their composition and vertical structure, i.e. the species richness of the basal and erect stratums. Moreover, the macroalgal-dominated coastal detritic bottoms in the Western Mediterranean showed similar composition of the well-developed erect stratum, but they differed as regards the MFS found in the basal stratum. In contrast, bottoms developing in the Northeastern Atlantic presented high similarities in the composition of the basal stratum, but they differed greatly as regards the development of the erect stratum. Thus, five

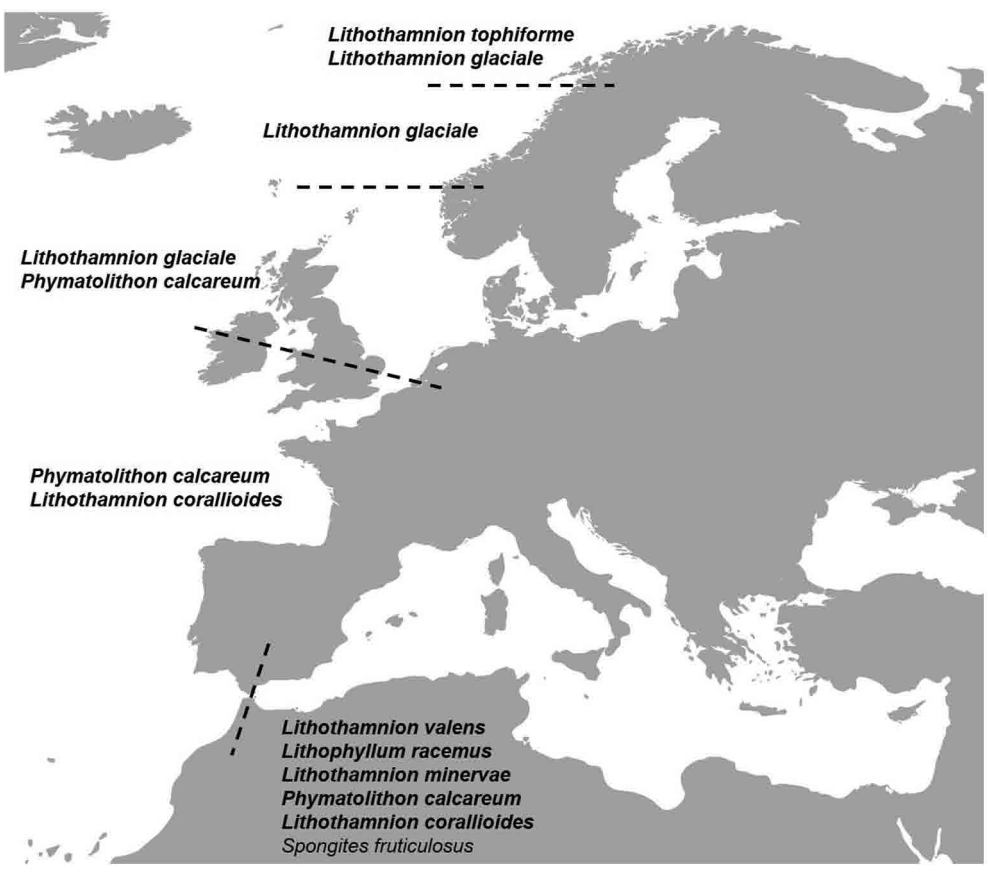

Fig. 5: Distribution map of the maërl-forming species based on the one proposed by the BIOMAERL team (1999). The species in bold correspond to those displayed on the original map. The species that are not in bold are proposed in this study.

Table 5. Sample groups obtained taking into account the maërl-forming species with 80% similarity: characteristic species (SIMPER test, 70% cumulative similarity), described communities according to literature source, distribution and number of samples. [m], exclusive species from the Western Mediterranean.

	Group A	Group B	Group C	Group D
Characteristic species	*Lithothamnion corallioides* *Phymatolithon calcareum*	*Lithophyllum* sp.[m] *Mesophyllum expansum*[m] *Phymatolithon calcareum* *Spongites fruticulosus*[m]	*Lithophyllum* sp.[m] *Lithophyllum stictaeforme*[m]	No MFS
Described communities	*Laminaria rodriguezii* forests Maërl of *Lithothamnion corallioides* Maërl of *Phymatolithon calcareum* Maërl of *Lithothamnion corallioides* and *Phymatolithon calcareum* Maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* Maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* and *Lithothamnion valens* *Peyssonnelia* beds	Maërl of *Spongites fruticulosus* with *Phymatolithon calcareum*	*Peyssonnelia* beds	*Saccharina latissima* forests
Distribution (number of samples)	United Kingdom (145) French Brittany (21) Galicia (19) Balearic Islands (30)	Costa Brava (7)	Balearic Islands (1)	United Kingdom (1)

different morphologies for the macroalgal-dominated detritic bottoms of the European coasts are proposed here (Table 6):

- Western Mediterranean maërl of *Phymatolithon calcareum*, *Spongites fruticulosus*, *Mesophyllum expansum* and *Lithophyllum* sp. with a well-developed erect stratum, found in the Costa Brava.
- Western Mediterranean maërl of *Phymatolithon calcareum, Spongites fruticulosus* and *Lithothamnion valens* with a well-developed erect stratum, in the Balearic Islands.
- Northeastern Atlantic maërl of *Phymatolithon calcareum* and *Lithothamnion corallioides* with a poor erect stratum, distributed in the United Kingdom and some localities of Galicia.
- Northeastern Atlantic maërl of *Lithothamnion corallioides* with a well-developed erect stratum, in French Brittany.
- Northeastern Atlantic maërl of *Lithothamnion corallioides* and *Phymatolithon calcareum* with a well-developed erect stratum, in some localities of Galicia.

The distribution of the proposed five detritic bottom types can be associated with some biogeographic models, such as the one proposed by Spalding *et al*. (2007). Thus, all the European macroalgal detritic bottoms belong to the Temperate Northern Atlantic realm. However, those of the Western Mediterranean are found only in one province, the Mediterranean Sea Province, while those of the Northeastern Atlantic are more diverse. In this area, the maërl beds of *Lithothamnion corallioides* with a well-developed erect stratum are restricted to the Northern European Seas province, the maërl beds of *Lithothamnion corallioides* and *Phymatolithon calcareum* with a well-developed erect stratum are found in the Lusitanian province only, and the maërl bottoms of *Phymatolithon calcareum* and *Lithothamnion corallioides* with a poor erect stratum are found in the Northern European Seas and the Lusitanian provinces. In our opinion, the samples from Galicia that cluster with the ones of the United Kingdom showed in the later morphology, correspond to impoverished Galician maërl beds.

As noted before, the differing bathymetrical distribution of macroalgal-dominated coastal detritic bottoms in the Mediterranean and the Northeastern Atlantic is well-known (e.g. Pérès & Picard, 1964; Picard, 1965; Pérès, 1985; Birkett *et al*., 1998; BIOMAERL team, 1999; Bellan-Santini *et al*., 2002; Hall-Spencer *et al.*, 2010; Peña, 2010; Peña *et al*., 2014), but there is a lack of knowledge concerning their geographic distribution. Future studies could reveal the presence of more algal communities on the detritic bottoms of the Eu-

Table 6. Main morphologies of coastal detritic bottoms found in the Western Mediterranean and the Northeastern Atlantic: characteristic MFS, characteristic non-MFS, and zonal and biogeographic distributions. [m], exclusive species from the Mediterranean; [a], exclusive species from the Northeastern Atlantic.

Coastal detritic bottom	Western Mediterranean maërl of *Phymatolithon calcareum, Spongites fruticulosus, Mesophyllum expansum* and *Lithophyllum* sp. with a well-developed erect stratum	Western Mediterranean maërl of *Phymatolithon calcareum*, *Spongites fruticulosus* and *Lithothamnion valens* with a well-developed erect stratum	Northeastern Atlantic maërl of *Phymatolithon calcareum* and *Lithothamnion corallioides* with a poor erect stratum	Northeastern Atlantic maërl of *Lithothamnion corallioides* with a well-developed erect stratum	Northeastern Atlantic maërl of *Lithothamnion corallioides* and *Phymatolithon calcareum* with a well-developed erect stratum
CharacteristicMFS	*Phymatolithon calcareum* *Spongites fruticulosus*[m] *Mesophyllum expansum*[m] *Lithophyllum* sp.[m]	*Phymatolithon calcareum* *Spongites fruticulosus*[m] *Lithothamnion valens*[m]	*Phymatolithon calcareum* *Lithothamnion corallioides*	*Lithothamnion corallioides*	*Lithothamnion corallioides* *Phymatolithon calcareum*
Characteristic non MFS	*Contarinia peyssonneliaeformis*[m] *Cryptonemia tuniformis*[m] *Dictyota dichotoma* *Eupogodon planus*[m] *Falkenbergia rufolanosa* *Kallymenia requienii*[m] *Peyssonnelia rosa-marina*[m] *Plocamium cartilagineum* *Rhodymenia delicatula*[m] *Bonnemaisonia asparagoides* *Hydrolithon farinosum*[m] *Ulvella scutata*[m] *Gloiocladia furcata*[m]	*Cryptonemia tuniformis*[m] *Peyssonnelia rosa-marina*[m] *Osmundaria volubilis*[m] *Kallymenia requienii*[m] *Dictyota dichotoma* *Hydrolithon farinosum*[m] *Phyllophora crispa*[m] *Peyssonnelia harveyana*[m] *Peyssonnelia rubra*[m] *Polysiphonia subulifera*[m] *Irvinea boergesenii*[m] *Leptofauchea coralligena*[m] *Hypoglossum hypoglossoides* *Rytiphlaea tinctoria*[m]	*Chylocladia verticillata* *Saccharina latissima*[a]	*Dictyota dichotoma* *Halarachnion ligulatum*[a] *Polysiphonia flexella*[a] *Stenogramma interruptum*[a] *Cryptopleura ramosa* *Hypoglossum hypoglossoides* *Nitophyllum punctatum* *Brongniartella byssoides* *Rhodophyllis divaricata* *Ulva* sp.[a] *Chondria dasyphylla*[a] *Polysiphonia stricta* *Ceramium echionotum*[a]	*Cruoria cruoriiformis* *Cutleria multifida*[a] *Dasysiphonia japonica*[a] *Gelidiella calcicola*[a] *Plocamium cartilagineum* *Acrosorium ciliolatum* *Pterothamnion plumula* *Ulva rigida*[a] *Cryptopleura ramosa* *Erythroglossum laciniatum*[a] *Dictyota dichotoma* *Stenogramma interruptum*[a] *Kallymenia reniformis*[a] *Ahnfeltiopsis devoniensis*[a] *Spermothamnion repens*[a] *Halarachnion ligulatum*[a] *Callophyllis laciniata* *Compsothamnion thuyoides*[a] *Brongniartella byssoides* *Antithamnionella ternifolia*[a] *Apoglossum ruscifolium* *Halurus flosculosus*[a] *Hypoglossum hypoglossoides* *Myriogramme minuta*[a] *Callithamnion tetragonum*[a] *Trailliella intricata*[a]
Zonal distribution	Costa Brava	Balearic Islands	United Kingdom Galicia	French Brittany	Galicia
Biogeographic distribution	Mediterranean Sea province in Temperate Northern Atlantic realm (Spalding *et al*., 2007)	Mediterranean Sea province in Temperate Northern Atlantic realm (Spalding *et al*., 2007)	Northern European Seas and Lusitanian provinces in Temperate Northern Atlantic realm (Spalding *et al*., 2007)	Northern European Seas province in Temperate Northern Atlantic realm (Spalding *et al*., 2007)	Lusitanian province in Temperate Northern Atlantic realm (Spalding *et al*., 2007)

ropean coasts and help to understand the environmental processes involved in their distribution. In this sense, the meadows dominated by the fleshy red algae *Osmundaria volubilis* and *Phyllophora crispa* are widely found on the continental shelf off the Balearic Islands (Ballesteros *et al*., 1993; Joher *et al*., 2012), as well as some other assemblages dominated by fleshy algae such as *Cryptonemia longiarticulata* and *Halopteris filicina*, located in the same zone (C. Rodríguez-Prieto and S. Joher, personal observations), but no exhaustive studies have been performed yet to characterize these communities. These new studies should also include detailed quantitative data in order to improve the identification of the different kinds of macroalgal-dominated coastal detritic bottoms and their characteristic species.

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Appendix 1

Distribution of the taxa found in literature data from the Northeastern Atlantic and the Western Mediterranean according to the studies detailed in table 1. Abbreviations: WM, Western Mediterranean; NEA, Northeastern Atlantic; Cos, Costa Brava; Bal, Balearic Islands; UK, United Kingdom; Bri, French Brittany; Gal, Galicia. *, maërl-forming species; [m], exclusive species from the Western Mediterranean; [a], exclusive species from the Northeastern Atlantic.

Region	WM	WM	NEA	NEA	NEA
Zone	**Cos**	**Bal**	**UK**	**Bri**	**Gal**
Rhodophyta					
Acrochaetium sp.[m]		x			
Acrosorium ciliolatum (Harvey) Kylin	x	x			x
'*Acrosymphytonema breemaniae*' Boudouresque, Perret-Boudouresque & Knoepffler-Peguy[m]		x			
Acrothamnion preissii (Sonder) E.M. Wollaston[m]		x			
Aglaothamnion bipinnatum (P.L. Crouan & H.M. Crouan) Feldamnn & G. Feldmann[a]					x
Aglaothamnion hookeri (Dillwyn) Maggs & Hommersand[a]					x
Aglaothamnion pseudobyssoides (P.L. Crouan & H.M. Crouan) Halos[a]					x
Aglaothamnion sp.[m]		x			
Aglaothamnion tenuissimum (Bonnemaison) Feldmann-Mazoyer	x	x			x
Aglaothamnion tripinnatum (C. Agardh) Feldmann-Mazoyer	x	x			x
Ahnfeltia plicata (Hudson) E.M. Fries[a]					x
Ahnfeltiopsis devoniensis (Greville) P.C. Silva & DeCew[a]					x
Anotrichium furcellatum (J. Agardh) Baldock[a]					x
Antithamnion cruciatum (C. Agardh) Nägeli	x				x
Antithamnion densum (Suhr) M.A. Howe[a]					x
Antithamnion heterocladum Funk[m]		x			
Antithamnion sp.[m]		x			
Antithamnion tenuissimum (Hauck) Schiffner[m]	x	x			
Antithamnion villosum (Kützing) Athanasiadis[a]					x
Antithamnionella spirographidis (Schiffner) E.M. Wollaston[a]					x
Antithamnionella ternifolia (J.D. Hooker & Harvey) Lyle[a]					x
Aphanocladia stichidiosa (Funk) Ardré[m]	x				
Apoglossum ruscifolium (Turner) J. Agardh	x	x		x	x
Asparagopsis armata Harvey[a]					x
Boergeseniella fruticulosa (Wulfen) Kylin[a]					x
Bonnemaisonia asparagoides (Woodward) C. Agardh	x	x			x
Bonnemaisonia sp.[m]		x			
Botryocladia botryoides (Wulfen) Feldmann[m]		x			
Botryocladia chiajeana (Meneghini) Kylin[m]		x			
Brongniartella byssoides (Goodenough & Woodward) F. Schmitz		x		x	x
Calliblepharis ciliata (Hudson) Kützing[a]				x	x
Calliblepharis jubata (Goodenogh & Woodward) Kützing[a]				x	x
Callithamnion sp.	x		x		
Callithamnion tetragonum (Withering) S.F. Gray[a]					x
Callophyllis laciniata (Hudson) Kützing		x		x	x
Ceramium bertholdii Funk[m]		x			
Ceramium callipterum Mazoyer[a]					x
Ceramium ciliatum (J. Ellis) Ducluzeau[a]					x
Ceramium codii (H. Richards) Mazoyer[m]	x	x			
Ceramium comptum Børgesen[m]		x			
Ceramium echionotum J. Agardh[a]				x	x
Ceramium secundatum Lyngbye[a]					x
Ceramium siliquosum var. *lophophorum* (Feldman-Mazoyer) Serio[m]	x				
Ceramium virgatum Roth[a]			x	x	x
Champia parvula (C. Agardh) Harvey		x		x	x
Chondracanthus acicularis (Roth) Fredericq	x	x			x
Chondracanthus teedei (Mertens ex Roth) Kützing[a]					x
Chondria coerulescens (J. Agardh) Falkenberg[a]					x

(continued)

Appendix 1 *(continued)*

Region	WM	WM	NEA	NEA	NEA
Zone	**Cos**	**Bal**	**UK**	**Bri**	**Gal**
Chondria dasyphylla (Woodward) C. Agardh[a]				x	
Chondria scintillans G. Feldmann[a]					x
Chrysymenia ventricosa (J.V. Lamouroux) J. Agardh[m]		x			
Chylocladia verticillata (Lightfoot) Bliding		x	x	x	x
Claviclonium ovatum (J.V. Lamouroux) Kraft & Min-Thein[a]					x
Colacodictyon reticulatum (Batters) Feldmann[a]					x
Colaconema daviesii (Dillwyn) Stegenga[a]					x
Compsothamnion gracillimum De Toni[m]	x				
Compsothamnion thuyoides (Smith) Nägeli[a]					x
Contarinia peyssonneliaeformis Zanardini[m]	x	x			
Contarinia squamariae (Meneghini) Denizot[m]	x	x			
Cordylecladia erecta (Greville) J. Agardh		x		x	
Crouania attenuata (C. Agardh) J. Agardh[a]					x
Cruoria cruoriiformis (P.L. Crouan & H.M: Crouan) Denizot		x			x
Cryptonemia lomation (Bertoloni) J. Agardh[m]	x	x			
Cryptonemia longiarticulata Funk[m]		x			
Cryptonemia tuniformis (Bertoloni) Zanardini[m]	x	x			
Cryptopleura ramosa (Hudson) L. Newton	x	x		x	x
Dasya baillouviana (S.G. Gmelin) Montagne[m]		x			
Dasya corymbifera J. Agardh[m]		x			
Dasya hutchinsiae Harvey		x			x
Dasya ocellata (Grateloup) Harvey[a]					x
Dasya punicea (Zanardini) Meneghini ex Zanardini[a]					x
Dasya sp.[m]	x	x			
Dasysiphonia japonica (Yendo) H.S. Kim[a]					x
Dermatolithon sp.[m]		x			
Dipterosiphonia rigens (Shousboe ex C. Agardh) Falkenberg[m]		x			
Drachiella spectabilis J. Ernst & Feldmann[a]					x
Dudresnaya sp.[a]			x		
Dudresnaya verticillata (Withering) Le Jolis		x		x	x
Ellisolandia elongata (J. Ellis & Solander) K.R. Hind & G.W. Saunders	x				x
Erythroglossum balearicum J. Agardh[m]		x			
Erythroglossum laciniatum (Lightfoot) Maggs & Hommersand[a]					x
Erythroglossum lusitanicum Ardré[a]					x
Erythroglossum sandrianum (Zanardini) Kylin[m]	x	x			
Erythrotrichia carnea (Dillwyn) J. Agardh		x			x
Eupogodon planus (C. Agardh) Kützing[m]	x	x			
Falkenbergia rufolanosa (Harvey) F. Schimitz	x				x
Felicinia marginata (Roussel) Manghisi, Le Gall, Ribera, Gargiulo & M. Morabito[m]		x			
Gastroclonium reflexum (Chauvin) Kützing[a]					x
Gayliella flaccida (Harvey ex Kützing) T.O. Cho & L.J. McIvor[a]					x
Gelidiella calcicola Maggs & Guiry[a]					x
Gelidiella sp.[m]		x			
Gelidiocolax margaritoides (M.T. Martin & M.A. Pocock) K.-C. Fan & Papenfuss[a]					x
Gelidium maggsiae Rico & Guiry[a]					x
Gelidium pusillum (Stackhouse) Le Jolis	x	x			x
Gelidium spinosum (S.G. Gmelin) P.C. Silva[a]					x
Gigartina pistillata (S.G. Gmelin) Stackhouse[a]					x
Gloiocladia furcata (C. Agardh) J. Agardh[m]	x	x			
Gloiocladia microspora (Bornet ex J.J. Rodríguez y Femenías) Sánchez & Rodríguez-Prieto[m]		x			
Gloiocladia repens (C. Agardh) Sánchez & Rodríguez-Prieto[m]	x	x			
Gracilaria bursa-pastoris (S.G. Gmelin) P.C. Silva[a]				x	
Gracilaria corallicola Zanardini[m]		x			
Gracilaria foliifera (Forsskål) Børgesen[a]				x	
Gracilaria gracilis (Stackhouse) M. Steentoft, L.M. Irvine & W.F. Farnham[a]					x
Gracilaria multipartita (Clemente) Harvey[a]					x

(continued)

Appendix 1 *(continued)*

Region	WM	WM	NEA	NEA	NEA
Zone	Cos	Bal	UK	Bri	Gal
Gracilaria sp.[m]		x			
Gracilariopsis longissima (S.G. Gmelin) M. Steentoft, L. M Irvine & W.F. Farnham[a]				x	
Griffithsia schousboei Montagne[a]					x
Gymnogongrus crenulatus (Turner) J. Agardh[a]				x	x
Gymnogongrus griffithsiae (Turner) Martius[a]				x	
Halarachnion ligulatum (Woodward) Kützing[a]				x	x
Halopithys incurva (Hudson) Batters[m]		x			
Halurus flosculosus (J. Ellis) Maggs & Hommersand[a]					x
Halymenia latifolia P.L. Crouan & H.M. Crouan ex Kützing[a]				x	x
Halymenia sp.[m]		x			
Haraldia lenormandii (Derbès & Solier) Feldmann[m]	x	x			
Herposiphonia secunda (C. Agardh) Ambronn[a]					x
Heterosiphonia plumosa (J. Ellis) Batters[a]				x	x
Hydrolithon farinosum (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain[m]	x	x			
Hydrolithon farinosum var. *chalicodictyum* (W.R. Taylor) Serio[m]	x				
Hydrolithon sp.[m]	x				
'*Hymenoclonium serpens*' (P.L. Crouan & H.M. Crouan) Batters[a]					x
Hypnea musciformis (Wulfen) J.V. Lamouroux[a]					x
Hypoglossum hypoglossoides (Stackhouse) F.S. Collins & Hervey	x	x		x	x
Hypoglossum sp.[a]			x		
Irvinea boergesenii (Feldmann) R.J. Wilkes, L.M. McIvor & Guiry[m]	x	x			
Jania adhaerens J.V. Lamouroux[m]		x			
Jania longifurca Zanardini[a]					x
Jania rubens (Linnaeus) J.V. Lamouroux	x				x
Jania rubens var. *corniculata* cf. (Linnaeus) Yendo[m]		x			
Kallymenia feldmannii Codomier[m]		x			
Kallymenia lacerata Feldmann[m]	x				
Kallymenia patens (J. Agardh) Codomier [m]		x			
Kallymenia reniformis (Turner) J. Agardh[a]				x	x
Kallymenia requienii (J. Agardh) J. Agardh[m]	x	x			
Kallymenia sp.[m]	x	x			
Laurencia obtusa (Hudson) J.V. Lamouroux[m]	x	x			
Laurencia pyramidalis Bory de Saint-Vincent ex Kützing[a]					x
Lejolisia mediterranea Bornet[m]		x			
Leptofauchea coralligena Rodríguez-Prieto & De Clerk[m]		x			
Lithophyllum incrustans Philippi*[a]					x
Lithophyllum racemus (Lamarck) Foslie*[m]	x	x			
Lithophyllum sp.*[m]	x	x			
Lithophyllum stictaeforme (Areschoug) Hauck*[m]		x			
Lithothamnion corallioides (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan*	x	x	x	x	x
Lithothamnion valens Foslie*[m]		x			
Lomentaria articulata var. *linearis* Zanardini[m]		x			
Lomentaria clavellosa (Lightfoot ex Turner) Gaillon		x			x
Lomentaria ercegovicii Verlaque, Boudouresque, Meinesz, Giraud & Marcot-Coqueugniot[m]		x			
Lomentaria subdichotoma Ercegovic[m]		x			
Lophosiphonia obscura (C. Agardh) Falkenberg[m]		x			
Melobesia membranacea (Esper) J.V. Lamouroux		x			x
Meredithia microphylla (J. Agardh) J. Agardh[m]		x			
Mesophyllum alternans (Foslie) Cabioch & M.L. Mendoza*[m]		x			
Mesophyllum expansum (Philippi) Cabioch & M.L. Mendoza*[m]	x	x			
Mesophyllum lichenoides (J. Ellis) Me. Lemoine*[m]	x	x			
Mesophyllum philippii (Foslie) W.H. Adey*[m]		x			
Microcladia glandulosa (Solander ex Turner) Greville[a]				x	x
Monosporus pedicellatus (Smith) Solier		x			x
Myriogramme carnea (J.J. Rodríguez y Femenías) Kylin[m]	x	x			

(continued)

Appendix 1 *(continued)*

Region	WM	WM	NEA	NEA	NEA
Zone	**Cos**	**Bal**	**UK**	**Bri**	**Gal**
Myriogramme minuta Kylin[a]					x
Myriogramme tristromatica (J.J. Rodríguez y Femenías ex Mazza) Boudouresque[m]	x	x			
Neogoniolithon mamillosum (Hauck) Setchell & L.R. Mason*[m]		x			
Neurocaulon foliosum (Meneghini) Zanardini[m]		x			
Nitophyllum micropunctatum Funk[m]		x			
Nitophyllum punctatum (Stackhouse) Greville		x		x	x
Ophidocladus simpliciusculus (P.L. Crouan & H.M. Crouan) Falkenberg[a]					x
Osmundaria volubilis (Linnaeus) R.E. Norris[m]		x			
Osmundea pelagosae (Schiffner) K.W. Nam[m]		x			
Osmundea pinnatifida (Hudson) Stackhouse[a]					x
Peyssonnelia armorica (P.L. Crouan & H.M. Crouan) Weber-van Bosse[m]		x			
Peyssonnelia atropurpurea P.L. Crouan & H.M. Crouan[a]					x
Peyssonnelia bornetii Boudouresque & Denizot[m]		x			
Peyssonnelia coriacea Feldmann[m]		x			
Peyssonnelia crispata Boudouresque & Denizot[m]		x			
Peyssonnelia dubyi P.L. Crouan & H.M. Crouan		x			x
Peyssonnelia harveyana P.L. Crouan & H.M. Crouan[m]	x	x			
Peyssonnelia inamoena Pilger[m]		x			
Peyssonnelia rosa-marina Boudouresque & Denizot[m]	x	x			
Peyssonnelia rubra (Greville) J. Agardh[m]	x	x			
Peyssonnelia sp.[m]	x	x			
Peyssonnelia squamaria (S.G. Gmelin) Decaisne[m]		x			
Peyssonnelia stoechas Boudouresque & Denizot[m]		x			
Phyllophora crispa (Hudson) P.S. Dixon[m]	x	x			
Phyllophora herediae (Clemente) J. Agardh[m]		x			
Phyllophora pseudoceranoides (S.G. Gmelin) Newroth & A.R.A. Taylor[a]				x	
Phymatolithon calcareum (Pallas) W.H. Adey & D.L. McKibbin*	x	x	x		x
Pleonosporium borreri (Smith) Nägeli[a]					x
Pleonosporium flexuosum (C. Agardh) Bornet ex De Toni[a]					x
Plocamium cartilagineum (Linnaeus) P.S. Dixon	x	x		x	x
Pneophyllum fragile Kützing[m]		x			
Polyneura bonnemaisonii (C. Agardh) Maggs & Hommersand[a]					x
Polysiphonia atlantica Kapraun & J.N. Norris		x		x	
Polysiphonia banyulensis Coppejans[m]	x	x			
Polysiphonia elongata (Hudson) Sprengel		x			x
Polysiphonia fibrillosa (Dillwyn) Sprengel		x		x	
Polysiphonia flexella (C. Agardh) J. Agardh[a]				x	
Polysiphonia flocculosa cf. (C. Agardh) Endlichter[m]		x			
Polysiphonia furcellata (C. Agardh) Harvey[m]	x	x			
Polysiphonia nigra (Hudson) Batters[a]				x	
Polysiphonia ornata J. Agardh[m]		x			
Polysiphonia perforans Cormaci, G. Furnari, Pizzuto & Serio[m]		x			
Polysiphonia sp.[m]		x			
Polysiphonia stricta (Dillwyn) Greville		x		x	x
Polysiphonia subulifera (C. Agardh) Harvey[m]	x	x			
Porphyrostromium ciliare (Carmichael) M.J. Wynne[a]					x
Pterocladiella capillacea (S.G. Gmelin) Santelices & Hommersand[a]					x
Pterosiphonia ardreana Maggs & Hommersand[a]					x
Pterosiphonia complanata (Clemente) Falkenberg[a]					x
Pterosiphonia parasitica (Hudson) Falkenberg		x		x	x
Pterosiphonia pennata (C. Agardh) Sauvageau[a]				x	x
Pterothamnion crispum (Ducluzeau) Nägeli	x	x			x
Pterothamnion plumula (J. Ellis) Nägeli	x	x			x
Ptilocladiopsis horrida Berthold[m]		x			
Ptilothamnion pluma (Dillwyn) Thuret[m]		x			
Ptilothamnion sp.[m]		x			

(continued)

Appendix 1 *(continued)*

Region	WM	WM	NEA	NEA	NEA
Zone	**Cos**	**Bal**	**UK**	**Bri**	**Gal**
Ptilothamnion sphaericum (P.L. Crouan & H.M. Crouan ex J. Agardh) Maggs & Hommersand[a]					x
Radicilingua sp.[m]		x			
Radicilingua thysanorhizans (Holmes) Papenfuss[m]		x			
Rhodophyllis divaricata (Stackhouse) Papenfuss	x	x		x	x
Rhodophyllis strafforelloi Ardissone[m]		x			
Rhodothamniella floridula (Dillwyn) Feldmann[a]					x
Rhodymenia delicatula P.J.L. Dangeard[m]	x	x			
Rhodymenia pseudopalmata (J.V. Lamouroux) P.C. Silva[a]					x
Rhodymenia sp.[m]	x	x			
Rodriguezella bornetii (J.J. Rodríguez y Femenías) F. Schmitz[m]		x			
Rodriguezella pinnata (Kützing) F. Schmitz ex Falkenberg[m]		x			
Rodriguezella strafforelloi F. Schmitz[m]	x	x			
Rytiphlaea tinctoria (Clemente) C. Agardh[m]		x			
Sahlingia subintegra (Rosenvinge) Kornmann		x			x
Schizymenia dubyi (Chauvin ex Duby) J. Agardh[m]		x			
Scinaia furcellata (Turner) J. Agardh[a]					x
Scinaia interrupta (A.P. De Candolle) M.J. Wynne[a]					x
Sebdenia rodrigueziana (Feldmann) Codomier[m]	x	x			
Seirospora interrupta (Smith) F. Schmitz[m]		x			
Solieria chordalis (C. Agardh) J. Agardh[a]				x	
Spermothamnion repens (Dillwyn) Rosenvinge[a]					x
Sphaerococcus coronopifolius Stackhouse[m]	x	x			
Sphaerococcus rhizophylloides J.J. Rodríguez y Femenías[m]		x			
Sphondylothamnion multifidum (Hudson) Nägeli[a]					x
Spongites fruticulosus Kützing*[m]	x	x			
Spyridia filamentosa (Wulfen) Harvey[a]				x	
Spyridia griffithsiana (J.E. Smith) G.C. Zuccarello, Prud'homme van Reine & H. Stegenga[a]					x
Stenogramma interruptum (C. Agardh) Montagne[a]				x	x
Stylonema alsidii (Zanardini) K.M. Drew		x			x
Stylonema cornu-cervi Reinsch[a]					x
Thuretella schousboei cf. (Thuret) F. Schmitz[m]		x			
Tiffaniella capitata (Schousboe ex Bornet) Doty & Meñez[a]					x
Titanoderma pustulatum (J.V. Lamouroux) Nägeli		x			x
Titanoderma sp.[m]		x			
Trailliella intricata Batters[a]					x
Womersleyella setacea (Hollenberg) R.E. Norris[m]		x			
Wrangelia penicillata (C. Agardh) C. Agardh[m]	x				
Phaeophyceae					
Acinetospora crinita (Carmicheal) Sauvageau[a]					x
Aglaozonia sp.[m]		x			
Arthrocladia villosa (Hudson) Duby[m]	x				
Asperococcus bullosus J.V. Lamouroux[m]		x			
Asperococcus ensiformis (Delle Chiaje) M.J. Wynne[a]					x
Carpomitra costata (Stackhouse) Batters	x	x			x
Castagnea sp.[m]		x			
Colpomenia peregrina Sauvageau[a]				x	x
Cutleria chilosa (Falkenberg) P.C. Silva[m]	x	x			
Cutleria multifida (Turner) Greville[a]				x	x
Cystoseira baccata (S.G. Gmelin) P.C. Silva[a]					x
Cystoseira nodicaulis (Withering) M. Roberts[a]					x
Cystoseira usneoides (Linnaeus) M. Roberts[a]					x
Desmarestia dudresnayi J.V: Lamouroux ex Léman[a]					x
Desmarestia viridis (O.F. Müller) J.V. Lamouroux[a]			x		
Dictyopteris lucida M.A. Ribera Siguán, A. Gómez Garreta, Pérez Ruzafa, Barceló Martí & Rull Lluch[m]		x			

(continued)

Appendix 1 *(continued)*

Region	WM	WM	NEA	NEA	NEA
Zone	**Cos**	**Bal**	**UK**	**Bri**	**Gal**
Dictyopteris polypodioides (A.P. De Candolle) J.V. Lamouroux[a]					x
Dictyota dichotoma (Hudson) J.V. Lamouroux	x	x	x	x	x
Dictyota implexa (Desfontaines) J.V. Lamouroux[m]		x			
Elachista sp.[m]		x			
Halopteris filicina (Grateloup) Kützing	x	x			x
Laminaria ochroleuca Bachelot de la Pylaie[a]					x
Laminaria rodriguezii Bornet[m]		x			
Leathesia mucosa Feldmann[m]		x			
Lobophora variegata (J.V. Lamouroux) Womerley ex E.C. Oliveira[m]		x			
Myriactula sp.[m]		x			
Saccharina latissima (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders[a]			x	x	
Saccorhiza polyschides (Lightfoot) Batters[a]					x
Sargassum muticum (Yendo) Fensholt[a]					x
Scytosiphon lomentaria (Lyngbye) Link[a]					x
Sphacelaria cirrosa (Roth) C. Agardh		x			x
Sphacelaria plumula Zanardini	x	x			x
Sphacelaria rigidula Kützing[a]					x
Sporochnus pedunculatus (Hudson) C. Agardh[m]		x			
Stictyosiphon adriaticus Kützing[m]		x			
Stilophora tenella (Esper) P.C. Silva[m]		x			
Stypocaulon scoparium (Linnaeus) Kützing[a]					x
Symphyocarpus strangulans Rosenvinge[a]					x
Undaria pinnatifida (Harvey) Suringar[a]					x
Zanardinia typus (Nardo) P.C. Silva[m]		x			
Zonaria tournefortii (J.V. Lamouroux) Montagne[m]		x			
Zosterocarpus oedogonium (Meneghini) Bornet[m]	x				
Chlorophyta					
Bryopsis hypnoides J.V. Lamouroux[m]	x	x			
Bryopsis plumosa (Hudson) C. Agardh	x				x
Chaetomorpha aerea (Dillwyn) Kützing[a]					x
Cladophora albida (Nees) Kützing[m]		x			
Cladophora hutchinsiae (Dillwyn) Kützing[a]					x
Cladophora laetevirens (Dillwyn) Kützing[a]					x
Cladophora prolifera (Roth) Kützing[m]	x				
Cladophora rupestris (Linnaeus) Kützing[a]					x
Cladophora sp.[m]		x			
Codium tomentosum Stackhouse[a]					x
Codium vermilara (Olivi) Delle Chiaje	x				x
Derbesia tenuissima (Moris & De Notaris) P.L. Crouan & H.M. Crouan	x	x			x
Flabellia petiolata (Turra) Nizamuddin[m]	x	x			
Halimeda tuna (J. Ellis & Solander) J.V. Lamouroux[m]		x			
Microdictyon tenuius J.E. Gray[m]		x			
Palmophyllum crassum (Naccari) Rabenhorst[m]	x	x			
Pseudochlorodesmis furcellata (Zanardini) Børgesen[m]	x	x			
Ulothrix subflaccida Wille[a]					x
Ulva rigida C. Agardh[a]					x
Ulva sp.[a]				x	
Ulvella lens P.L. Crouan & H.M. Crouan[a]					x
Ulvella scutata (Reinke) R. Nielsen, C.J. O'Kelly & B. Wysor[m]	x	x			
Umbraulva dangeardii M.J. Wynne & G. Furnari		x			x
Uronema marinum Womersley[m]		x			
Valonia macrophysa Kützing[m]	x	x			
Valonia utricularis (Roth) C. Agardh[m]		x			
Thacheophyta					
Posidonia oceanica (Linnaeus) Delile[m]		x			
Zostera sp.[a]			x		