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Deep-water macroalgal-dominated coastal detritic assemblages on the continental shelf off Mallorca and Menorca (Balearic Islands, Western Mediterranean)

Abstract: We present a quantitative physiognomic characterization of major macroalgal-dominated assemblages on coastal detritic bottoms of the continental shelf off Mallorca and Menorca (Balearic Islands, Western Mediterranean). In late spring of 2007 and 2008, 29 samples were collected by bottom trawling at depths between -52 and -93 m. These samples were then sorted and identified to their lowest taxonomic level. Statistical analyses distinguished six different assemblage types: shallower water environments (-52 to -65 m in depth) were characterized by *Osmundaria volubilis* and *Phyllophora crispa* meadows and two types of *Peyssonnelia* beds; two assemblage types, *Laminaria rodriguezii* beds and maërl beds, were only present in deep-water environments (-77 to -81 m); and an assemblage dominated by *P. crispa* and *Halopteris filicina* was found in both shallow and deep waters (-57 to -93 m). We assess the distribution of these six assemblage types through the studied area.

Keywords: algal assemblages; bottom trawl; detritic bottoms; macroalgae; Mediterranean Sea.

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Introduction

Coastal detritic bottoms are characterized by a large amount of particles of organic origin, a low percentage of silt, and, typically, by the absence of muddy particles (Pérès 1985). They constitute a main habitat within the sedimentary bottoms of continental shelves occurring close to shore, usually at more than -25 m in depth (Pérès 1985). Assemblages developing in these coastal detritic bottoms encompass a large range of species and functional diversities and also harbor a vast number of rare and interesting species that are often restricted to these kinds of assemblages (Cabioch 1969, Ballantine et al. 1994, Bellan-Santini et al. 1994, Grall and Glémarec 1997, Foster 2001, Steller et al. 2003). In addition, coastal detritic assemblages act as nursery grounds for various invertebrates and fishes, including commercial species (Massutí et al. 1996, Colloca et al. 2003, Kamenos et al. 2004, Massutí and Reñones 2005), and they shelter many calcareous algae and calcareous invertebrates, which indicates that these assemblages are major carbonate producers (Ballesteros 1994, Canals and Ballesteros 1997).

The Mediterranean Sea has a long tradition in the study of coastal detritic assemblages. Research on the flora began at the end of the 19th century and the beginning of the 20th century (Rodríguez-Femenías 1889, Mazza 1903, de Buen 1905, 1934, Bellón-Urriarte 1921). Later, diverse authors highlighted the high biodiversity and reported different assemblage types such as *Laminaria rodriguezii* beds, maërl beds, and free-living *Peyssonnelia* beds (Pérès and Picard 1963, 1964, Picard 1965, Giaccone 1973, Augier and Boudouresque 1978, Bourcier 1982, Ballesteros et al. 1993). Besides this major literature, other significant studies have focused on maërl (Dieuzede 1940, Feldmann 1943, Gautier and Picard 1957, Jacquotte 1961, 1962, Ballesteros 1988, Basso 1995a,b, Bordehore et al. 2003, Piazzini et al. 2003, 2004, Agnesi et al. 2011), *L. rodriguezii* beds (Feldmann 1934, Molinier 1956, 1960), and *Peyssonnelia* beds (Huvé 1954, Carpine 1958, Laborel et al. 1961,

Ballesteros 1994). However, all these different assemblage types have been described separately, and although they have several species in common, no attempts have been made to find out whether they are different and can be distinguished by statistical methods.

Direct sampling (e.g., scuba diving) in the deep waters of the continental shelf, where coastal detritic bottoms develop, has severe limitations due to restricted sampling time, long decompression stops, and diver performance decrease (UNEP-MAP-RAC/SPA 2008). Although scuba diving has been occasionally used to describe species composition on coastal detritic bottoms (Giaccone 1972, Ballesteros 1988, 1994, Piazzini et al. 2003, 2004), indirect sampling methods (e.g., dredging, trawling, or video surveys with remotely operated vehicles) are those usually used (Cailliet et al. 1999, Bax and Williams 2001). Thus, dredges are the most common practice used in the description of algal assemblages (Basso 1995a,b, Bordehore et al. 2003), whereas trawls are probably the most frequently used method in the description of fish and invertebrate assemblages (Bertrand et al. 2002, Massutí and Reñones 2005, Fanelli et al. 2007, García-Muñoz et al. 2008, Ordines and Massutí 2009).

The Balearic Islands have a central position in the western Mediterranean Sea and are the emergent parts of a promontory including four major islands. The Balearic shelf can be divided into two geographic sectors: the Mallorca-Menorca shelf, covering 6418 km², and the smaller Eivissa-Formentera shelf, with a total surface of 2709 km² (Acosta et al. 2002). Coastal detritic bottoms have been largely identified on the Mallorca-Menorca shelf (de Buen 1934, Alonso et al. 1988, Fornós et al. 1988, Canals and Ballesteros 1997, Fornós and Ahr 1997, Massutí and Reñones 2005) and have been characterized in terms of Foraminifera (Milker et al. 2009) and megabenthos (Massutí et al. 1996, Massutí and Reñones 2005, Ordines and Massutí 2009). Seaweeds are a major component of these coastal detritic bottoms, but they have been taken into account in a somewhat cursory manner in descriptive studies that try to cover all benthic groups (e.g., de Buen 1934, Canals and Ballesteros 1997); the only literature providing a full list of seaweeds thriving on these bottoms is the description of *Peyssonnelia* and maërl beds by Ballesteros (1994).

Hence, in this study we attempted to identify the main assemblage types that can be distinguished on coastal detritic bottoms of the continental shelf off Mallorca and Menorca, according to the abundance of the different algal species. We used bottom trawling as a sampling technique. In addition, we provide geographical and bathymetric distributions of these assemblages.

Materials and methods

The present study was located on the continental shelf off Mallorca and Menorca (Balearic Islands, Western Mediterranean; Figure 1). This shelf is generally narrow, except at the south of Mallorca and in the channels between Mallorca and Menorca and Mallorca and Cabrera, where it becomes larger and has a gentle slope (Acosta et al. 2002). The absence of rivers reduces the presence of terrestrial sediments, and therefore, most of the sediments are usually of biogenic origin (Canals and Ballesteros 1997, Fornós and Ahr 1997) and contain a high percentage of carbonates (Acosta et al. 2002). In addition, light transmittance through the water is very high (Ballesteros and Zabala 1993, Canals and Ballesteros 1997), allowing algal-dominated benthic communities to develop deeper than on other Mediterranean continental coasts (Ballesteros and Zabala 1993).

Samples of coastal detritic assemblages were collected at depths ranging from -52 to -93 m (Figure 1) in the late spring (May/June) of 2007 and 2008 during the MEDITS_ES05 bottom trawl surveys. Samples were collected with experimental GOC73 equipment and followed the general specifications for the MEDITS surveys (Dremière et al. 1999, Fiorentini et al. 1999, Bertrand et al. 2002). A total of 29 samples were collected; each sample consisted on a haul obtained during 30 min at a vessel speed of 3 knots. When the hauls arrived on board, algae were sorted and a 6 l sample was obtained from every haul and preserved in 4% formalin in seawater. Once in the laboratory, samples were washed, sorted, and identified to the lowest taxonomic level. For each sample (6 l), the abundance of each taxon was measured as algal surface area (S_{a_i}) in square centimeters (Ballesteros 1992a). Subsequently, these data were standardized as algal surface area per haul ($S_{a_{HH}}$), expressed in square centimeters per square meters, as follows:

$$S_{a_{HH}} = \frac{S_{a_i} \times WW_H}{S_H \times WW_S}$$

where S_{a_i} is the algal surface area of each species (cm²), WW_H is the wet weight of algae for each haul (g), S_H is the total haul surface (m²), and WW_S is the wet weight of the algae sampled (g).

To visualize the affinities between samples, we used a nonmetric multidimensional scaling (nMDS) ordination (Kruskal and Wish 1978) based on a Bray-Curtis similarity matrix calculated from $S_{a_{HH}}$ data. A hierarchical group average agglomerative clustering method accompanied by the SIMPROF test (Clarke et al. 2008) adjusted to 9999

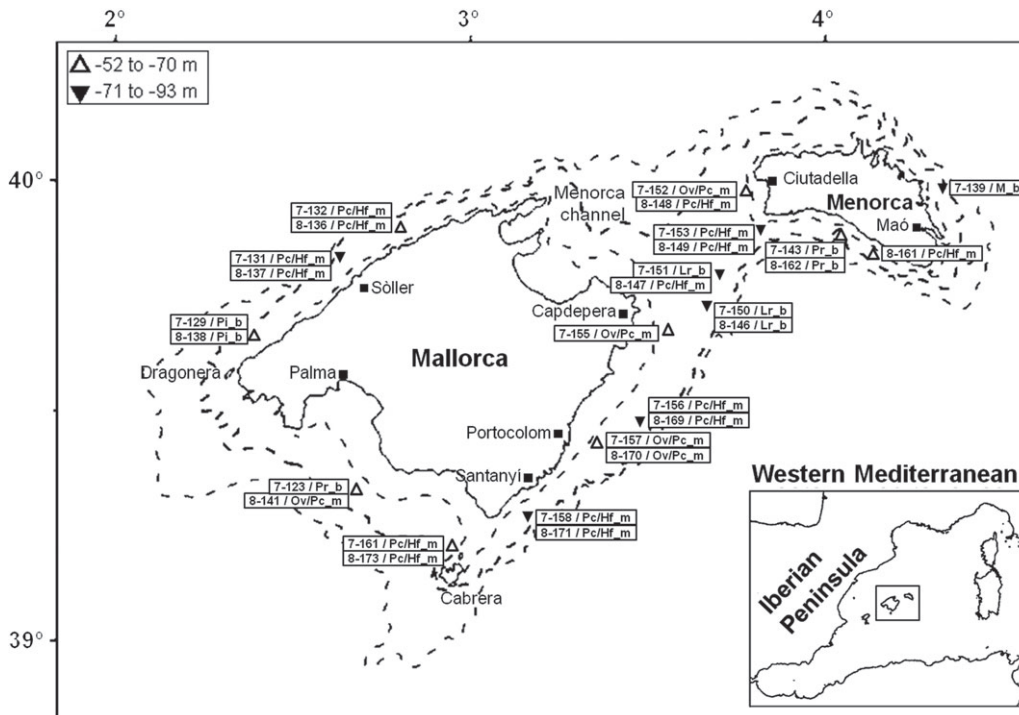


Figure 1 Map of the studied area off Mallorca and Menorca (Balearic Islands, Western Mediterranean) with the -50, -100, and -200 m isobaths.

Samples are displayed indicating their code, depths range, and corresponding assemblage type. The code shows the year of sampling (7, 2007; 8, 2008) followed by the number of the sample. Assemblage types: Lr_b, *Laminaria rodriguezii* beds, M_b, maërl beds; Ov/Pc_m, *Osmundaria volubilis* and *Phyllophora crispera* meadows; Pc/Hf_m, *Phyllophora crispera* and *Halopteris filicina* meadows; Pi_b, *Peyssonnelia inamoena* beds; Pr_b, *Peyssonnelia rubra* beds.

permutations and a 0.1% significance level according to Potter et al. (2001) was used to explore the potential grouping structures among samples. Finally, the percentage similarity routine (SIMPER) was run to quantify the contribution of each species to the similarity/dissimilarity between the varying SIMPROF groups. All the analyses were performed with PRIMER version 6 software (PRIMER-E Ltd., Plymouth, UK; Clarke and Warwick 2001).

Results

A total of 6 different assemblages (Table 1) and 132 algal taxa were identified (Table 2). Some of the taxa (*Cystoseira* sp., *Gracilaria* sp., *Griffithsia* sp., *Peyssonnelia* sp., *Polysiphonia* sp. 1 and 2, Rhodophyta unidentified 1 and 2, and *Sphacelaria* sp.) could not be identified to species level because we either had only small pieces of the

Assemblage type	Depth range (m)	n	n		Sa _{TH} (cm ² m ⁻²)	Sa _{TH} (cm ² m ⁻²)	
			Minimum	Maximum		Minimum	Maximum
Ov/Pc_m	-52 to -60	47±6	41	56	30,945±15,358	11,138	51,608
Pi_b	-62	34±11	26	42	620,000±495,000	270	970
Pr_b	-60 to -65	55±7	49	63	138,451±31,210	110,162	171,937
Lr_b	-77 to -81	29±10	20	40	17,926±5005	12,649	22,605
M_b	-77	10			306		
Pc/Hf_m	-57 to -93	38±9	24	59	3511±1963	1194	6580

Table 1 Main characteristics of the different assemblage types: depth range where the assemblage were found, number of species (n), total algal surface per haul (Sa_{TH}), and minimum and maximum values of n and Sa_{TH}. Standard errors are also indicated. Note that M_b is only represented by 1 sample. Assemblage types: Lr_b, *Laminaria rodriguezii* beds; M_b, maërl beds; Ov/Pc_m, *Osmundaria volubilis* and *Phyllophora crispera* meadows; Pc/Hf_m, *Phyllophora crispera* and *Halopteris filicina* meadows; Pi_b, *Peyssonnelia inamoena* beds; Pr_b, *Peyssonnelia rubra* beds.

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Rhodophyta						
<i>Acrodiscus vidovichii</i> (Meneghini) Zanardini	3.31±4.74					1.01±3.91
<i>Acrosorium ciliolatum</i> (Harvey) Kylin	13.49±19.63	36.11±0.08	70.45±108.20	2.26±3.17		0.32±0.84
<i>Acrothamion preissii</i> (Sonder) E.M. Wollaston ^a	3.45±7.71					57.29±146.10
<i>Alsidium corallinum</i> C. Agardh			0.31±0.53			0.02±0.10
<i>Apoglossum ruscifolium</i> (Turner) J. Agardh				1.67±2.89		0.50±1.35
<i>Asparagopsis taxiformis</i> (Delile) Trevisan de Saint-León ^a						0.02±0.09
<i>Baliella cladoderma</i> (Zanardini) Athanasiadis			13.50±14.20			0.78±2.65
<i>Bornetia secundiflora</i> (J. Agardh) Thuret			5597.08±7088.13	0.07±0.12		4.64±11.63
<i>Botryocladia chiajeana</i> (Meneghini) Kylin	1.33±2.98					3.00±10.68
<i>Botryocladia madagascariensis</i> G. Feldmann ^a	677.94±1515.92					1.96±5.45
<i>Brongniartella byssoides</i> (Goodenough et Woodward) F. Schmitz	11.12±23.14					0.13±0.41
<i>Caliblepharis jubata</i> (Goodenough et Woodward) Kützing			2.36±4.08			0.01±0.05
<i>Callophyllis laciniata</i> (Hudson) Kützing	22.19±49.61		207.66±359.68			3.42±9.97
<i>Champia parvula</i> (C. Agardh) Harvey	0.93±2.08		9.43±16.34			0.01±0.03
<i>Chrysymenia ventricosa</i> (J.V. Lamouroux) J. Agardh	36.15±56.05		5.04±4.60			0.01±0.03
<i>Chylocladia verticillata</i> (Lightfoot) Bliding						0.19±0.37
<i>Corallina elongata</i> J. Ellis et Solander	1.55±2.40	0.29±0.40	2.04±3.53	1.17±2.02		0.19±0.37
<i>Crouania attenuata</i> (C. Agardh) J. Agardh	182.62±224.38	0.32±0.45	44.05±38.19	1.14±1.63		153.30±401.76
<i>Cryptonemia lomation</i> (Bertoloni) J. Agardh	884.39±1170.94	24.42±18.30	4668.64±3667.67	18.04±31.25		45.98±38.64
<i>Cryptonemia longiarticulata</i> Funk						0.17±0.50
<i>Cryptonemia tuniformis</i> (Bertoloni) Zanardini	0.14±0.32		0.36±0.63	0.04±0.08		1.00±2.17
<i>Cryptonemia</i> sp.	1.68±2.58	0.63±0.89	23.66±8.56	3.15±4.82		
<i>Cryptopleura ramosa</i> (Hudson) L. Newton	1.06±2.38					0.03±0.12
<i>Dasya baillouviana</i> (S.G. Gmelin) Montagne						0.01±0.03
<i>Dasya rigescens</i> Zanardini						0.03±0.12
<i>ErythroGLOSSUM balearicum</i> J. Agardh ex Kylin						0.18±0.40
<i>Ethelia vanbosseae</i> Feldmann	23.15±34.14		19.95±2.73			0.89±3.13
<i>Eupogodon planus</i> (C. Agardh) Kützing	8.33±13.70					0.60±2.14
<i>Eupogodon spinellus</i> (C. Agardh) Kützing	6.16±10.06		86.78±78.32	0.17±0.29		14.45±20.34
<i>Gloiocladia furcata</i> (C. Agardh) J. Agardh	39.27±50.90		646.67±534.78	10.37±5.29	2.42	
<i>Gloiocladia microspora</i> (Bornet ex Bornet ex Rodríguez y Femenías) N. Sánchez et C. Rodríguez-Prieto ex Berecibar, M.J. Wynne, Barbara et R. Santos						
<i>Gloiocladia repens</i> (C. Agardh) Sánchez et Rodríguez-Prieto	25.03±55.96		34.96±60.55	14.20±19.41		0.62±1.31
<i>Gracilaria bursa-pastoris</i> (S.G. Gmelin) P.C. Silva	64.12±90.68	1.93±2.72	2.13±3.70			1.62±5.20
<i>Gracilaria corallicola</i> Zanardini	5.12±5.12	3.65±0.35	1936.06±2633.57	2.62±3.70		49.43±151.74
<i>Gracilaria</i> sp.	17.02±28.06	0.68±0.06	3.16±5.47			1.34±3.45
<i>Griffithsia</i> sp.						0.01±0.02
<i>Haloptilon virgatum</i> (Zanardini) Garbary et H.W. Johansen	742.69±832.77	14.19±16.55	48.18±65.19			0.16±0.63
<i>Halophyllum incurva</i> (Hudson) Batters	2.00±4.46					21.16±32.50
<i>Halymenia elongata</i> C. Agardh						1.60±5.45

(Table 2 continued)

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
<i>Halymenia latifolia</i> P.L. Crouan et H.M. Crouan ex Kützing	0.75±1.68		4.90±8.48	2.70±4.68		2.65±5.13
Halymeniaceae unidentified 1	176.33±167.76	7.87±2.26	720.53±903.28	61.65±42.33	0.35	103.11±168.52
Halymeniaceae unidentified 2	0.13±0.29					
<i>Haraldia lenormandii</i> (Derbès et Solier) Feldmann				0.08±0.14		0.33±1.26
<i>Hypnea spinella</i> (C. Agardh) Kützing	5.42±11.86					0.03±0.11
<i>Hypoglossum hypoglossoides</i> (Stackhouse) F.S. Collins et Hervey	1.33±1.89		2.99±4.23			0.27±0.68
<i>Irvinia boergerenii</i> (Feldmann) R.J. Wilkes, L.M. McIvor et Guiry				0.05±0.08		0.02±0.08
<i>Kallymenia feldmannii</i> Codomier				2.82±4.88		0.05±0.21
<i>Kallymenia patens</i> (J. Agardh) Codomier ex P.G. Parkinson	3.04±3.59		122.06±211.41	2.24±3.89	0.34	0.15±0.59
<i>Kallymenia requierii</i> (J. Agardh) J. Agardh	9.90±8.91		382.12±514.12	80.17±114.02		19.07±36.35
<i>Kallymenia</i> sp.	80.14±95.60		447.25±774.65	0.71±1.23		8.01±21.62
<i>Laurencia chondrioides</i> Børgesen	25.99±34.51			3.49±3.32		1.08±2.70
<i>Leptofaucha coralligena</i> Rodríguez-Prieto et O. De Clerck	40.57±28.39	3.46±4.89	130.80±140.77			7.24±9.22
<i>Lithothamnion corallioides</i> (P.L. Crouan et H.M. Crouan)	317.31±328.64	10.26±13.92	255.55±325.14	25.35±29.33		19.93±23.86
P.L. Crouan et H.M. Crouan						
<i>Lithothamnion valens</i> Foslie	197.44±308.70	1.75±1.70	1.086.11±18.30	45.98±40.08	76.55	61.17±83.92
<i>Lomentaria subdichotoma</i> Ercegovic			2.35±4.06			0.08 v 0.22
<i>Lomentaria</i> sp.	0.29±0.66					
<i>Lophocladia lallemantii</i> (Montagne) F. Schmitz ^a		0.04±0.06				0.01±0.03
<i>Mereditia microphylla</i> (J. Agardh) J. Agardh	3.24±7.25		75.84±74.06	0.34±0.58	0.65	0.44±1.01
<i>Mesophyllum expansum</i> (Philippi) Cabioch et Mendoza		7.58 v 10.71				
<i>Myriogramme minuta</i> Kytlin						0.01±0.02
<i>Myriogramme tristomatica</i> (J.J. Rodríguez ex Mazza)	23.79±32.59	0.07±0.09	139.48±130.12	10.97±10.55		5.26±7.11
Boudouresque						
<i>Nemastoma dumontioides</i> J. Agardh			85.25±144.36	0.42 v 0.72		0.01±0.01
<i>Neurocaulon foliosum</i> (Meneghini) Zanardini	14.02±31.35					0.20±0.60
<i>Nitophyllum flabellatum</i> Ercegovic	0.23±0.51					
<i>Nitophyllum punctatum</i> (Stackhouse) Greville			73.21±95.27	1.77±1.54		0.21±0.60
<i>Osmundaria volubilis</i> (Linnaeus) R.E. Norris	10,884.44±6836.62	5.69±1.49	13,729.07±2650.39	16.02±9.65		291.04±343.42
<i>Osmundea pelagosae</i> (Schiffner) K.W. Nam	351.88±314.45	1.10±1.56	13.11±12.52	0.15±0.27		11.24±28.76
<i>Peyssonnelia</i> aff. <i>magna</i> Ercegovic			347.99±602.74			
<i>Peyssonnelia armorica</i> (P.L. Crouan et H.M. Crouan)						0.64±2.47
Weber-van Bosse						
<i>Peyssonnelia bornetii</i> Boudouresque et Dezinot	0.71±1.59		2440.80±4135.88			1.18±3.34
<i>Peyssonnelia dubyi</i> P.L. Crouan et H.M. Crouan			79.80±138.22			0.86±3.24
<i>Peyssonnelia harveyana</i> P.L. Crouan et H.M. Crouan ex J. Agardh			619.88±926.97	4.96±8.59		3.59±11.36
<i>Peyssonnelia inamoena</i> Pilger	317.21±401.10	186.06±82.36	19,001.68±17,403.53	7.69±0.68		23.73±25.08
<i>Peyssonnelia rosa-marina</i> Boudouresque et Dezinot	536.12±1072.35	27.76±12.88	4021.27±2975.42			22.39±74.75
<i>Peyssonnelia rubra</i> (Greville) J. Agardh	109.49±171.72	2.21±3.13	20,924.58±14,744.64	0.47±0.81	0.50	5.23±13.54
<i>Peyssonnelia squamaria</i> (S.G. Gmelin) Decaisne	14.76±16.72	3.51±4.96	2840.27±4749.76	1.87±3.03	14.62	2.23±3.98
<i>Peyssonnelia stoechas</i> Boudouresque et Dezinot			18.39±16.29	0.94±1.63		0.02±0.07

(Table 2 continued)

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
<i>Peyssonnelia</i> sp.		9.06±12.81	1191.59±1878.57			0.18±0.38
<i>Phyllophora crispa</i> (Hudson) P.S. Dixon	7563.80±4533.60	28.95±34.08	36,432.34±1784.54	386.73±110.43	0.72	936.69±938.63
<i>Phyllophora heredia</i> (Clemente) J. Agardh	38.41±28.84	1.02±1.44	2106.79±1081.54	100.45±170.53		5.85±12.40
<i>Phymatolithon calcareum</i> (Pallas) W.H. Adey et D.L. McKibbin	260.59±311.72	3.28±1.32	29.98±19.31	6.82±7.45		6.56±9.44
<i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon		0.06±0.08	7.92±7.87	1.27±1.64		0.45±0.77
<i>Polysiphonia elongata</i> (Hudson) Sprengel	304.56±430.81		45.44±46.42			17.69±57.89
<i>Polysiphonia ornata</i> J. Agardh						0.06±0.18
<i>Polysiphonia perforans</i> Cormaci, G. Furnari, Pizzuto et Serio	841.80±1523.19	10.21±14.44	4.95±7.65			0.01±0.01
<i>Polysiphonia subulifera</i> (C. Agardh) Harvey	538.07±1067.31	0.07±0.09	0.80±1.38			22.88±60.16
<i>Polysiphonia</i> sp. 1			130.22±222.25			23.49±81.76
<i>Polysiphonia</i> sp. 2	0.92±2.06					
<i>Pterothamnion crispum</i> (Ducluzeau) Nägeli						0.39±1.29
<i>Pterothamnion plumula</i> (J. Ellis) Nägeli						0.06±0.16
<i>Radiclingua reptans</i> (Kyllin) Papenfuss				0.39±0.68		0.01±0.02
Rhodophyta unidentified 1	0.09±0.21		15.45±13.39	0.43±0.75		1.43±4.20
Rhodophyta unidentified 2	14.97±22.63	1.53±1.65	176.78±253.94	7.69±13.33		9.78±15.80
<i>Rhodomyenia</i> sp.	83.25±149.50	5.80±8.20	1158.36±1147.10	1.04±1.80		10.77±13.20
<i>Rodriguezella pinnata</i> (Kützling) F. Schmitz ex Falkenberg	21.07±47.11		72.58±117.34			0.07±0.28
<i>Rodriguezella strafforelloi</i> F. Schmitz ex J.J. Rodriguez y Femenías	33.96±70.56		90.62±52.02			0.08±0.31
<i>Ryphiacea tinctoria</i> (Clemente) C. Agardh	916.19±995.63	0.07±0.10	1199.27±1958.53			21.88±45.83
<i>Sebenia dichotoma</i> Berthold	11.55±19.14					0.29±1.12
<i>Sebenia monardiana</i> (Montagne) Berthold						0.34±1.30
<i>Sebenia rodrigueziana</i> (Feldmann) Codomier ex Parkinson			26.84±46.49			
<i>Sphaerococcus coronopifolius</i> Stackhouse	99.05±127.57	0.21±0.30	3685.12±3294.16	0.25±0.43		11.69±25.53
<i>Sphaerococcus rhizophylloides</i> J.J. Rodriguez y Femenías	75.58±166.86		579.73±478.23			11.36±31.89
<i>Sphondylthamnion multifidum</i> (Hudson) Nägeli	0.22±0.48					
<i>Spongites fruticulosa</i> Kützling	784.16±1040.53	34.34±38.71	508.81±385.12	241.69±101.88	190.91	166.72±220.93
<i>Wrangelia penicillata</i> (C. Agardh) C. Agardh						0.11±0.42
Chlorophyta						
<i>Caulerpa racemosa</i> var. <i>cylindracea</i> (Sonder) Verlaque,						1.14±3.22
Huisman et Boudouresque ^a						
<i>Codium bursa</i> (Olivier) C. Agardh	90.27±168.62	17.91±17.24	4827.05±7427.34			27.11±51.43
<i>Flabellia petiolata</i> (Turra) Nizamuddin	101.91±53.58	11.53±11.07	1000.52±820.63	144.78±168.93	19.03	183.55±325.93
<i>Halimeda tuna</i> (J. Ellis et Solander) J.V. Lamouroux	0.54±1.20		94.80±164.19	8.61±14.92		
<i>Microdictyon tenuius</i> J.E. Gray	5.60±10.45		1.78±3.09			0.80±2.23
<i>Palmophyllum crassum</i> (Naccari) Rabenhorst	6.03±12.00		79.18±68.97			0.97±2.42
<i>Umbraulva olivascens</i> (P.J.L. Dangeard) G. Furnari	7.76±17.36	1.27±1.79	95.36±88.24	0.54±0.94		8.22±21.71
<i>Valonia macrophysa</i> Kützling	1.68±2.43	4.63±4.91	135.84±87.38			0.67±1.66
Ochrophyta-Phaeophyceae						
<i>Aglaozonia chilosa</i> Falkenberg stage	5.65±5.37	0.15±0.21				0.17±0.37
<i>Arthrocladia villosa</i> (Hudson) Duby		0.21±0.30				

(Table 2 continued)

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
<i>Asperococcus bullosus</i> J.V. Lamouroux						0.25±0.66
<i>Carpomitra costata</i> (Stackhouse) Batters		0.48±0.67				0.02±0.07
<i>Cladostephus spongiosus</i> (Hudson) C. Agardh			426.70±739.07			1.80±4.98
<i>Cutleria chilosa</i> (Falkenberg) P.C. Silva		69.15±97.79	119.99±207.83			3.47±5.49
<i>Cystoseira spinosa</i> var. <i>compressa</i> (Ercegovic) M. Cormaci, G. Furnari, G. Giaccone, B. Scammacca et D. Serio	196.80±352.67		129.75±224.74			30.22±100.62
<i>Cystoseira zosteroides</i> C. Agardh				4.18±7.23		0.33±1.29
<i>Cystoseira</i> sp.						5.67±10.76
<i>Dictyopteris lucida</i> M.A. Ribera Siguan, A. Gómez Garreta, Pérez Ruzafa, Barceló Martí et Rull Lluch	0.23±0.51					
<i>Dictyopteris polypodioides</i> (A.P. De Candolle) J.V. Lamouroux		8.56±12.10	31.54±26.77			12.50±48.39
<i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux	372.74±573.53					143.73±303.15
<i>Halopteris filicina</i> (Grateloup) Kützing	1615.52±3283.85	66.78±87.13	698.93±946.35	405.91±695.66		611.30±983.66
<i>Hinckesia sandriana</i> (Zanardini) P.C. Silva						0.05±0.19
<i>Laminaria rodriguezii</i> Bornet	800.81±895.50	1.03±1.45	2346.45±1793.91	16,285.86±6008.32		263.80±385.78
<i>Sphacelaria</i> sp.						0.02±0.08
<i>Sporochinus pedunculatus</i> (Hudson) C. Agardh		0.42±0.59				
<i>Zanardinia typus</i> (Nardo) P.C. Silva	181.78±337.31	3.37±4.77				5.24±19.84
<i>Zonaria tournefortii</i> (J.V. Lamouroux) Montagne	79.37±164.91	0.70±0.98	11.97±20.73	3.90±3.45		3.88±6.21

Table 2 Algal surface area per haul ($S_{a,HP}$ in $cm^2 m^{-2}$) for species in each assemblage type.

Means and standard errors are given except for M_b (single value) because there was only 1 sample. ^aInvasive species. Assemblage types: Lr_b, *Laminaria rodriguezii* beds; M_b, maërl beds; Ov/Pc_m, *Osmundaria volubilis* and *Phyllophora crispa* meadows; Pc/Hf_m, *Phyllophora crispa* and *Halopteris filicina* meadows; Pi_b, *Peyssonnelia inamoena* beds; Pr_b, *Peyssonnelia rubra* beds.

specimens or because the specimens were sterile. Some other taxa (Halymeniaceae unidentified 1, *Kallymenia* sp., and *Rhodymenia* sp.) are probably undescribed species. Red algae (Rhodophyta) were the best represented group, with 105 taxa (79.5% of the total taxa), followed by brown algae (Phaeophyceae; 19 taxa, 14.4%), and then green algae (Chlorophyta; 8 taxa, 6.1%). The most abundant species, accounting for 70% of the total algal surface area, were *Phyllophora crispa* (24.0%), *Osmundaria volubilis* (14.8%), *Laminaria rodriguezii* (9.4%), *Peyssonnelia rubra* (9.3%), *Peyssonnelia inamoena* (8.7%), *Halopteris filicina* (3.0%), and the introduced invasive species *Botryocladia madagascariensis* (3.0%). The number of species per haul ranged from 10 to 63, and the total algal surface per haul (Sa_{TH}) ranged from 270 to 171,931 cm² m⁻².

Five introduced species, the red algae *Acrothamnion preissii* (found at 10 localities), *Asparagopsis taxiformis* (2 localities), *B. madagascariensis* (11 localities), and *Lophocladia lallemandii* (2 localities), and the green alga *Caulerpa racemosa* var. *cylindracea* (2 localities), were collected (Table 2).

The nMDS plot based on species abundances shows patterns of resemblance among the species composition of different trawls (nMDS stress 0.1; Figure 2). According to the SIMPROF test, the samples may be classified into

six different groups assigned to six different assemblages. They are *O. volubilis* and *P. crispa* meadows (Ov/Pc_m), two different kinds of *Peyssonnelia* beds, one dominated by *Peyssonnelia inamoena* (Pi_b) and another by *Peyssonnelia rubra* (Pr_b), *L. rodriguezii* beds (Lr_b), and *P. crispa* and *H. filicina* meadows (Pc/Hf_m) (Table 1). Looking at the species composition in the six assemblages, some of them had exclusive species, whereas some other species were found throughout the continental shelf off Mallorca and Menorca: *Flabellia petiolata*, Halymeniaceae unidentified 1, *Lithothamnion valens*, *Peyssonnelia rubra*, *Peyssonnelia squamaria*, *P. crispa*, and *Spongites fruticulosa*. This list of common species increased up to 20 when we considered those present in all the assemblages other than maërl beds where erect species were scarce. The assemblage with the maximum number of exclusive species was Pc/Hf_m, with 24 exclusive species, followed by Ov/Pc_m with 7 exclusive species, Pr_b with 5 exclusive species, and Pi_b with 3 exclusive species. The remaining assemblages did not have any exclusive species (Table 2).

The assemblages Ov/Pc_m, Pi_b, and Pr_b were located in shallow waters (-52 to -65 m) and characterized by a great abundance of *O. volubilis*, *P. crispa*, and *Peyssonnelia* spp., whereas they differed from each other not only in the relative abundance of these species but also in the abundances

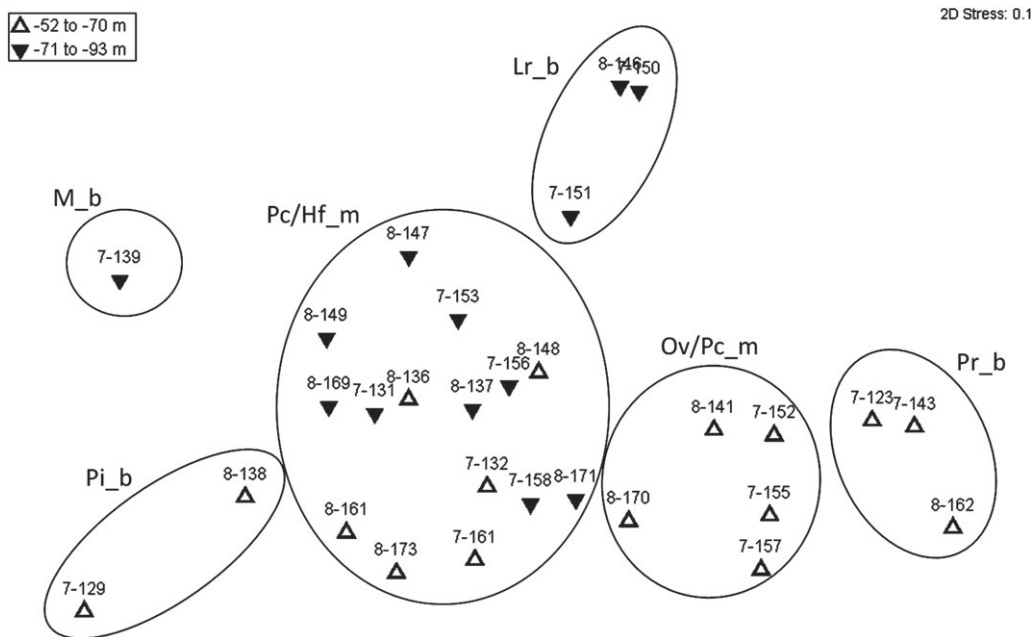


Figure 2 nMDS ordination with standardized Sa_{TH} (cm² m⁻²).

Samples are displayed indicating their code, depths range, and corresponding assemblage type. Code shows the year of sampling (7, 2007; 8, 2008) followed by the number of the sample. Assemblage types: Lr_b, *Laminaria rodriguezii* beds; M_b, maërl beds; Ov/Pc_m, *Osmundaria volubilis* and *Phyllophora crispa* meadows; Pc/Hf_m, *Phyllophora crispa* and *Halopteris filicina* meadows; Pi_b, *Peyssonnelia inamoena* beds; Pr_b, *Peyssonnelia rubra* beds.

of accompanying species. Hence, Ov/Pc_m was formed by 5 samples located at depths between -52 and -60 m, in which both *O. volubilis* and *P. crispa* were identified as the main species according to the SIMPER test. These meadows were characterized by a high number of species (47 ± 6 per haul) and an Sa_{TH} of $30,945 \pm 15,358 \text{ cm}^2 \text{ m}^{-2}$ per haul. Pi_b and Pr_b were both *Peyssonnelia* beds, but they had very different species composition and Sa_{TH} values. Thus, Pi_b, formed by only 2 samples located at -62 m depth, was characterized by the species *Peyssonnelia inamoena*, *A. preissii*, and *Peyssonnelia rosa-marina*, and had a low number of species (34 ± 11) but a high Sa_{TH} ($620,000 \pm 495,000 \text{ cm}^2 \text{ m}^{-2}$). In contrast, the 3 samples of Pr_b, located between -60 and -65 m, were characterized by *P. crispa*, *O. volubilis*, and *Peyssonnelia rubra* and had a greater number of species (mean = 55 ± 7) and lower Sa_{TH} ($138,451 \pm 31,210 \text{ cm}^2 \text{ m}^{-2}$) than Pi_b.

In deeper waters (from -77 to -81 m), two groups were identified, M_b and Lr_b. The M_b included only 1 sample dominated by the corallines *Spongites fruticulosa* and *Lit. valens* and had a very low number of species (10) and Sa_{TH} ($306 \text{ cm}^2 \text{ m}^{-2}$) in comparison with the rest of the samples. In contrast, Lr_b, comprising 3 samples, was dominated by *L. rodriguezii* and had a higher number of species (29 ± 10) and Sa_{TH} ($17,926 \pm 5005 \text{ cm}^2 \text{ m}^{-2}$).

Finally, Pc/Hf_m included 15 samples collected in a large range of depths (from -57 to -93 m). *Phyllophora crispa*, *H. filicina*, *O. volubilis*, and *Spongites fruticulosa* were the most abundant species in this group, with 38 ± 9 species and an Sa_{TH} of $3511 \pm 1963 \text{ cm}^2 \text{ m}^{-2}$.

Discussion and conclusions

Six different coastal detritic bottom assemblages were distinguished on the continental shelf off Mallorca and Menorca based on haul sampling. In general, depth was an important correlate of the distribution of the different assemblages, with the exception of Pc/Hf_m, which occurred in a wide range of depths. Moreover, the limit that separated the relatively shallow from the deep assemblages was situated at around -70 m in depth. Although the decrease in light availability may certainly play an important role in the segregation of these assemblages (Ballesteros and Zabala 1993), we argue here that hydrographic characteristics at the different depths might also contribute to this segregation. The deep waters (from -70 to -200 m) on the Balearic shelf have characteristics of the Intermediate Western Mediterranean Waters whose temperatures are always between 12.5°C and 13°C and have salinities at around 38.15. This is in contrast with

shallower waters, which are influenced by both the North Atlantic Surface Waters and the Gulf of Lion Cold Waters and have salinities usually <38 and seasonal temperatures ranging from 14°C to 27°C (Salat and Font 1985, Vives and López-Jurado 1988). The minimal oscillation of temperature in the deeper waters may allow the development of stenothermal species whose growth would be limited in the shallow waters.

The *Osmundaria volubilis* and *Phyllophora crispa* meadows (Ov/Pc_m) were found off southeastern Mallorca and western Menorca and were closely related to the assemblage of *O. volubilis* from the coastal detritic bottoms described previously by Pérès and Picard (1963) at Port-Cros (France). However, these authors reported that *O. volubilis* is usually associated with *Rytiphlaea tinctoria* rather than *P. crispa*. Even though *O. volubilis* is very common in these and other coastal detritic assemblages, it is not a species that can be considered as exclusively associated to these kinds of assemblages, as it is also very abundant on some types of coralligenous outcrops (Ballesteros 1992b) and on infralittoral rocky bottoms (Boudouresque 1973, Augier and Boudouresque 1975, 1978, Serio and Pizzuto 1990, 1992, Ballesteros et al. 1993).

Detritic coastal bottoms dominated by different species of *Peyssonnelia* have been previously reported on several Mediterranean coasts (see Ballesteros 1994 for a review). Pérès and Picard (1963, 1964) reported *Peyssonnelia* beds in Port-Cros (France) that were dominated by *Peyssonnelia rosa-marina* f. *saxicola* together with a smaller quantity of *Peyssonnelia harveyana*. Later, Augier and Boudouresque (1978) reported coastal detritic assemblages dominated by *Peyssonnelia rosa-marina* f. *rosa-marina* and *Peyssonnelia rubra*. Off the Balearic Islands, *Peyssonnelia* beds have been reported by de Buen (1905) off the northeastern coast of Menorca, Cape Formentor (Mallorca), and Cabrera at depths between -60 and -160 m and by Ballesteros (1994) off southern Menorca and in the Cabrera Channel at depths between -40 and -90 m. Additionally, this author (loc. cit.) distinguished two types of *Peyssonnelia* beds, one dominated by *Peyssonnelia rosa-marina* at depths between -48 and -54 m and another by an unidentified *Peyssonnelia* located at depths between -40 and -79 m. In the present work, we found a *Peyssonnelia* bed (Pi_b) situated at -62 m deep near Dragonera (southwestern Mallorca), where *Peyssonnelia inamoena* and *Peyssonnelia rosa-marina* were the most abundant species of *Peyssonnelia*, and other beds (Pr_b) situated at depths between -60 and -65 m (southern coasts of Mallorca and Menorca) where *Peyssonnelia rubra* was the most abundant species of the genus.

Kelp beds dominated by the endemic brown alga *Laminaria rodriguezii* had a low number of species per sample probably because the dense canopy of this kelp prevents the growth of other algae. In fact, Picard (1965) already highlighted that these kelp beds are an impoverished facies on coastal detritic bottoms. Other species that can occasionally be found in these kelp beds are *Cystoseira spinosa* var. *compressa* and *Cystoseira zosteroides*. These two species and *Phyllariopsis brevipes* are usually considered to be common in *L. rodriguezii* beds (Giaccone 1967, UNEP/UICN/GIS Posidonie 1990). The low abundance of these accompanying species in our samples may be related to the frequent trawling in the area sampled. In fact, recent collections (2011) from better preserved detritic bottoms in Mallorca and Menorca showed that *C. spinosa* var. *compressa* and *C. zosteroides* can be also extremely abundant in the *L. rodriguezii* beds off the Balearic Islands (C. Rodríguez-Prieto and S. Joher personal observations). The development of Lr_b seems to be restricted to particular places, such as the Menorca Channel. Hence, its growth is probably determined by the presence of a detritic bottom composed of rhodoliths, dim light conditions, low and constant water temperature (about 14°C), and unidirectional and constant currents (Molinier 1960, Pérès and Picard 1964, Giaccone 1967, 1971). In fact, the lower limit of *L. rodriguezii* distribution seems to depend on light availability, whereas the upper limit probably depends on temperature (UNEP/UICN/GIS Posidonie 1990).

The maërl bed (M_b) sampled in this study on the eastern coast of Menorca was mainly characterized by a great abundance of *Spongites fruticulosa* and *Lithothamnion valens*. However, this assemblage did not have the usual diversity found on these kinds of detritic bottoms off the Balearic Islands, which may be also dominated by other species such as *Lit. corallioides* and *Phymatolithon calcareum* or even *Lithophyllum racemus* (de Buen 1905, 1934, Ballesteros et al. 1993, Ballesteros 1994, E. Ballesteros personal observations). In contrast to other maërl beds from the southwestern Mediterranean (Bordehore et al. 2003, Piazzini et al. 2003, 2004), the M_b found in our study was very poor in erect algae. The development of maërl beds in the Mediterranean seems to depend on the existence of high to moderate unidirectional water currents (Picard 1965), and most of them correspond to the facies of *Spongites fruticulosa* described by Pérès and Picard (1964).

The eurybathic meadow (Pc/Hf_m) mainly differed from the other assemblages by a lower abundance of *O. volubilis*. Due to the fact that this meadow does not seem to correspond to any other known assemblage, we

cannot rule out the possibility that it corresponds to a methodological artifact due to a mixed sampling in relatively small and patchy heterogeneous areas. Moreover, this bottom may correspond to an algal drift accumulation zone.

Among the five introduced species found in the area, *Botryocladia madagascariensis* and *Acrothamnion preissii* were the most widely distributed, whereas *Caulerpa racemosa* var. *cylindracea*, *Asparagopsis taxiformis*, and *Lophocladia lallemandii* were found only occasionally and they were never abundant. Only *Caulerpa racemosa* var. *cylindracea* has been reported to behave as an invasive alien in coastal detritic assemblages of the northwestern Mediterranean (Klein and Verlaque 2009).

In summary, using algal composition and abundances in the samples collected, bottom trawling proved to be a useful method to characterize and describe assemblages of the continental shelf off Mallorca and Menorca. However, doubts arose for some trawls (e.g., those identified as the eurybathic Pc/Hf_m) because we did not know whether sampling had been performed on highly heterogeneous bottoms or if the unique trawl content may represent a mixture of two or more different assemblages. These doubts could also arise when identifying the assemblages according to faunal composition. Dredging, a more frequently used method in the characterization of these algal assemblages, is probably not as useful in describing species groupings, as it does not take into account high spatial heterogeneity. In fact, most of the assemblages found in this study had already been described by other authors using different methodologies (e.g., Pérès and Picard 1964, Ballesteros et al. 1993, Ballesteros 1994), thus confirming that characterization based on algal composition and abundance determined by bottom trawls is a feasible approach for studying deep-water assemblages.

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