Universitat de Girona

MACROALGAL-DOMINATED COASTAL DETRITIC BOTTOMS OF THE MEDITERRANEAN SEA AND THE NORTHEASTERN ATLANTIC: DESCRIPTION, DISTRIBUTION AND SAMPLING METHODOLOGIES

Sergi Joher Sais

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Tesi dirigida per la

Dra. Conxi Rodríguez-Prieto
Departament de Ciències Ambientals (UdG)

Memòria presentada per a optar al títol de
Doctor per la Universitat de Girona

La Dra. Conxi Rodríguez-Prieto, professora titular del Departament de Ciències Ambientals (UdG),

CERTIFICA:

Que aquest treball, titulat "Macroalgal-dominated coastal detritic bottoms of the Mediterranean Sea and the Northeastern Atlantic: description, distribution and sampling methodologies", que presenta Sergi Joher Sais per a l'obtenció del títol de doctor, ha estat realitzat sota la seva direcció.

Dra. Conxi Rodríguez-Prieto
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Directora de la tesi

Girona, novembre de 2015

Acknowledgements / Agraïments

Crec que a vegades no he sabut expressar massa bé com d'agraït estic a tothom que m'ha ajudat ara i sempre, ni que fos donant-me una petita empenta. Els agraïments de la tesi són un bon espai per intentar solucionar-ho, i espero que així es reflecteixi. Segurament deixaré de mencionar a algú (no serà per no voler fer-ho, si no que per descuit) i a alguns els nombraré més d'una vegada. Als primers només els puc demanar disculpes per endavant.

Primer, donar les gràcies a la meva família que, tot i no estar molt segurs de què estava fent, sempre m'han donat el seu suport per tirar endavant. Als meus pares, la Dolors i en Ramon; germanes, la Marina, l'Esther i la Lidia; cunyats, en Pitu i en Josep; nebots la Inés, l'Aina, en Marc, l'Aleix, la Maria i la Berta; i cosins que també coneixen aquesta aventura que suposa un doctorat, com en Pere, la Mariona, la Carme...

Pel que fa a aquesta tesi, dono les gràcies a Conxi, per creure en mi i donar-me el seu suport durant tot el temps que la tesi ha trigat en veure la llum. Sense la seva paciència, consells i ajut no hauria estat possible. També agrair fortament la ajuda d'en Kike per la seva gran contribució tant en els articles com en altres parts de la tesi. I gràcies també a l'Emma i la Noe, que també són coautores del primer capítol.

Dins l'àmbit universitari, gràcies a tots aquells que m'han ajudat des que un dia vaig començar a col·laborar amb el grup de recerca d'Algues Bentòniques Marines. En especial, una vegada més, a la Conxi que, a més d'aguantar-me tots aquest anys, m'ha ensenyat moltíssimes coses i m'ha encomanat la seva passió per la ciència, en general, i per les algues, en particular. I la resta de membres del grup i de l'àrea de Botànica: en Miquel, la Noemí, l'Emma, en Jordi, en Polo, l'Alba, en Lluís i en Joan. També els companys del departament de Ciències Ambientals que m'ha donat suport i ajut en qualsevol moment que ho he necessitat: la Marta, en Josep L., la Margarida, en Pere, en Pitu, la Silvia A., en David, en Josep R., l'Eulàlia, l'Anna, la Gemma, la Sílvia T., etc. A tots els doctorands del departament i la facultat que he conegut i amb els quals em compartit moltes coses (dinars, sopars, cerveses...): en Miquel, la Kate, la Meri, la Dolors F., en Harold, la Mercè, en Josep R., la Dolors C., l'Alba, l'Arantxa, l'Anna, la Laura D., la Irene, la Laura B., en Roberto, la Núria, en David, etc.

També vull agrair a tots els grans amics que he fet a la UdG, tant durant la llicenciatura com al doctorat, que s'han creuat amb mi a classe o al laboratori: en Miquel, l'Albert, en Xavier, la Judit, l'Amanda, la Núria, en Rubén, la Marta, l'Anna, la Cristina, la Sabina D., la Sabina H., l'Arantxa... Encara que no mantingui contacte amb alguns d'ells, no els oblidaré!

Un cas a part és el Centre Oceanogràfic de Balears (IEO), ja que sense la seva inestimable col·laboració aquesta tesi no s'hauria pogut fer. Un agraïment especial a l'Enric Massutí, que va impulsar la col·laboració entre el grup de recerca d'Algues Bentòniques Marines i el Centre Oceanogràfic de Balears. Agrair molt fortament als grans amics que hi he fet, amb els que no em cansaré de fer campanyes: la Bea, en Xisco, l'Ana M., la Montse, la Maria, l'Aina, la Vanessa, la Carmen, la Marta, la Núria i en Toni. També la resta de companys que he conegut durant les campanyes balears, tant del centre com d'altres institucions, i a les tripulacions dels bucs oceanogràfics Cornide de Saavedra, Miguel Oliver, MarViva Med i Francisco de Paula Navarro.

Finalment, donar les gràcies a altres persones que no tant directament m'ha ajudat en la tesi. A Marc Verlaque, Julio Afonso-Carrillo, Giovanni Furnari i Mario Cormaci per ajudar en la determinació d'espècies. A Daniela Basso, Jacques Grall, Jason M. Hall-Spencer, Viviana Peña i el servei d'obtenció de documents de la biblioteca per ajudar-me en la cerca de dades i bibliografia. A en Kike, l'Anna M., la Carmen i en Diego Kurt Kersting per les fotografies incloses en la introducció de la tesi.

Sincerament, gràcies a tots.

Structure of the thesis

This dissertation is structured as a collection of three scientific papers. In the moment of presentation of this thesis they are published or under revision as detailed below. For all of them, and specially for those that have been published, a copy of the manuscript including figures and tables is given, in agreement with the copyright policy of the corresponding journals.

The scientific articles are preceded by a **General Introduction** (Chapter 1), in which the descriptions of the macroalgal-dominated coastal detritic bottoms and the main sampling methods are presented, as well as the main characteristics of the study area. **Objectives** (Chapter 2) summarizes the main objectives of this dissertation. The **Materials and methods** are included in the corresponding chapter as they differ from one work to another. **Results and Discussion** (Chapter 3) included the scientific papers, named as **Sections I, II and III**. Following, the **General Discussion** (Chapter 4), where the main outcomes of the thesis are discussed, and the main **Conclusions** (Chapter 5) are given, as well as a compendium of the **Bibliography** (Chapter 6) used. Finally, the checklist of the flora identified in the works presented here concerning the Balearic Islands and the first page of the published or in revision works are given in the **Appendix I** and **Appendix II**, respectively.

The publications included in this thesis are:

Chapter III–1

Sergi Joher, Enric Ballesteros, Emma Cebrian, Noemí Sánchez, and Conxi Rodríguez-Prieto. 2012. Deep-water macroalgal-dominated coastal detritic assemblages on the continental shelf off Mallorca and Menorca (Balearic Islands, Western Mediterranean). *Botanica Marina*, 55 (5): 485-497.

Chapter III–2

Sergi Joher, Enric Ballesteros and Conxi Rodríguez-Prieto. 2015. Contribution to the study of deep coastal detritic bottoms: the algal communities of the continental shelf off the Balearic Islands, Western Mediterranean. *Mediterranean Marine Science*, 16(3): 573-590.

Chapter III–3

Sergi Joher, Enric Ballesteros and Conxi Rodríguez-Prieto. Macroalgal-dominated coastal detritic communities from the NE Atlantic and the Mediterranean. *Mediterranean Marine* Science, under revision.

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Summary

The deep-water macroalgal-dominated coastal detritic bottoms develop in soft bottoms, which are characterized by a high amount of carbonated particles mainly originated by floral and faunal organisms. The development of these bottoms need low irradiance levels, moderate currents, low to moderate sedimentation rates and constant water temperatures. The oligotrophic waters off the Balearic Islands, specifically around Mallorca and Menorca, allow their development in deeper waters than those from the nearest continental shelfs.

This Ph.D. dissertation aims to describe the main algal detritic bottoms found in the continental shelf off Mallorca and Menorca, and also to provide effective methods for their sampling. Further, the distribution of the macroalgal-dominated coastal detritic communities throughout the Mediterranean and the NE Atlantic is assessed by a qualitative comparison of our own data and data published in literature.

The description of the main algal-dominated coastal detritic assemblages found in the continental shelf off Mallorca and Menorca was performed in the late spring (May/June) of 2007 and 2008 during the MEDITS_ES05 surveys performed by means of bottom trawling (mesh size: 20 mm), which allowed to cover large areas. A total of 29 samples were collected, sorted and identified to the lowest taxonomic level. The abundance of each taxon was measured as algal surface area (Sa, in cm^2) and, then, standardized (in cm^2 m^{-2}). The statistical analyses allowed to distinguish a total of six assemblages: the *Osmundaria volubilis* and *Phyllophora crispa* meadows, and two different *Peyssonnelia* beds dominated by *Peyssonnelia inamoena* and *Peyssonnelia rubra*, respectively, found in a shallower distribution (52 to 65 m); the maërl beds and *Laminaria rodriguezii* beds were found at deeper waters (77 to 81 m); and the *Phyllophora crispa* with *Halopteris filicina* meadows in both shallow and deep-waters (57 to 93 m). The development of those assemblages with a restricted range of distribution seemed to be influenced by depth, which is closely related to seasonal variability in water temperature. Besides, the eurybathic *Phyllophora crispa* with *Halopteris filicina* meadows could be an artifact caused by the use of bottom trawl in highly heterogeneous bottoms and/or by the mixing two or more different assemblages.

Three of the communities that characterized the assemblages found in the coasts off Mallorca and Menorca were located by ROV immersions in the Menorca channel (maërl of *Spongites fruticulosus* and kelp forests of *L. rodriguezii*) and in the Southern coasts of Menorca (*P. inamoena* beds) during

the CANAL0209 survey (February/March 2009). Then, during the MEDITS_ES05_09 survey (May 2009), the samples were taken by means of beam trawling (for the forests of *L. rodriguezii* and the *P. inamoena* beds) and Box-Corer dredging (for the maërl of *S. fruticulosus*), as these methods presented small sampling surface and reduced (beam trawl; mesh size: 10 mm) or null (Box-Corer dredge) loss of biomass. For each community, the samples were sorted and identified to the minimum taxonomic level, and each taxa was quantified measuring its algal surface (Sa, in cm^2) and biomass (B, dry weigh in g). Quantitative data was also standardized (Sa, cm^2 m^{-2}; B, g m^{-2}). The *L. rodriguezii* forests and the *P. inamoena* beds revealed as the richer communities in terms of species composition and, in the case of the kelp forest, as the most diverse studied community. Contrasting, the maërl beds of *S. fruticulosus*, presented low number of species and diversity indexes as presented a low developed erect stratum.

The qualitative comparison of the macroalgal-dominated coastal detritic communities from the European coasts included our own data from the Balearic Islands and some published works performed in the NE Atlantic and the Mediterranean. The analyses revealed that the NE Atlantic communities differed from those found in the Mediterranean in terms of species composition. The quantitatively described macroalgal detritic communities of the European coasts (mainly maërl beds, *L. rodriguezii* kelp forests, *Peyssonnelia* beds and *Saccharina latissima* kelp forests) could not been distinguished in the qualitative approach. Then, due to the general presence of a basal substratum characterized by *Lithothamnion corallioides* and *Phymatolithon calcareum*, and a more or less developed erect substratum, taking in account only its specific composition, all these communities could be considered as maërl beds. According to differences in the species composition of the erect and the basal stratums, they can be divided in seven different kinds of maërl beds, two of them found in the NE Atlantic and the other five in the Mediterranean. Further, the qualitative comparison of the macroalgal-dominated coastal detritic communities also confirmed the widespread distribution of *L. corallioides* and *P. calcareum*, and that some other important maërl-forming species are restricted to the Mediterranean (e.g. *S. fruticulosus* and *Lithothamnion valens*).

The qualitative analyses also indicated that the three communities described in the Mallorca-Menorca continental shelf presented a restricted distribution in the Mediterranean, more concretely in the Balearic Islands. Further, the *L. rodriguezii* forest and the *P. inamoena* beds were the most similar communities, while the maërl of *S. fruticulosus* was distinguished not only from these two communities, but also from other maërl beds found in coasts near the Balearic Islands, which presented a similar species composition of the basal stratum.

Summary

The methodology used in this study, usually traditionally used in studies dealing on demersal and benthic fauna, let us to take representative samples from the deep-water macroalgal-dominated coastal detritic bottoms of the continental shelf off Mallorca and Menorca. Bottom trawl revealed as a good method in the assemblage approach, mainly thanks to the high to moderate sampling surface and the relatively low biomass loss during the sampling due to it small mesh size (20 mm). Besides, the combination of observational (ROV dives) and sampling methods (Box-Corer dredging and beam trawling) allowed the location and collection of representative samples in the community approach by the founding of homogeneous zones and low (beam trawl; mesh size: 10 mm) to null (Box-Corer dredge) loss of biomass.

Resum

Els fons detrítics costaners d'aigües profundes dominats per macroalgues es desenvolupen en fons tous caracteritzats per grans quantitats de partícules carbonatades, principalment, d'origen vegetal i animal. La formació d'aquests fons requereix nivells baixos d'irradiància, corrents moderats, taxes de sedimentació entre baixes i moderades, i temperatura de l'aigua constant. Les aigües oligotròfiques de les illes Balears, especialment al voltant de Mallorca i Menorca, permeten el seu desenvolupament en aigües més profundes que en les plataformes continentals properes.

Aquesta tesi pretén descriure el principals fons detrítics algals trobats a la plataforma continental de Mallorca i Menorca, i també proporcionar mètodes efectius per al seu mostreig. A més, s'avalua la distribució de les comunitats dominades per macroalgues del detrític costaner del Mediterrani i del NE Atlàntic per mitjà de la comparació qualitativa de les nostres dades i d'aquelles publicades en la bibliografia.

La descripció dels principals paisatges dominats per macroalgues del detrític costaner trobats a la plataforma continental de Mallorca i Menorca es va efectuar a finals de primavera (Maig/Juny) de 2007 i 2008, durant les campanyes MEDITS_ES05 efectuades amb arrossegament de fons (mida de malla: 20 mm), que permet cobrir grans àrees. En total es van recollir 29 mostres, de les quals se'n van classificar i identificar els taxons arribant al nivell taxonòmic més baix possible. La seva abundància es va mesurar com a superfície algal (Sa, en cm^2) i va ser estandarditzada (en cm^2 m^{-2}). Els anàlisis estadístics van permetre la distinció de fins a sis paisatges: les praderies de *Osmundaria volubilis* i *Phyllophora crispa* i dos llits de *Peyssonnelia* dominats per *Peyssonnelia inamoena* i *Peyssonnelia rubra*, respectivament, amb una distribució més superficial (de 52 a 65 m); els llits de maërl i els llits de *Laminaria rodriguezii*, trobats en aigües més profundes (de 77 a 81 m); i les praderies de *Phyllophora crispa* i *Halopteris filicina*, tant en aigües superficials com profundes (de 57 a 93 m). El desenvolupament dels paisatges amb un rang de distribució restringit pot estar influenciat per la fondària, que està estretament relacionada amb la variació estacional de la temperatura de l'aigua. En canvi, les àmpliament distribuïdes praderies de *Phyllophora crispa* i *Halopteris filicina* podrien correspondre a un artefacte causat pel mostreig amb arrossegament de fons en zones altament heterogènies i/o per la barreja de dos o més paisatges.

Tres de les comunitats que caracteritzen els paisatges trobats a les costes de Mallorca i Menorca es van localitzar mitjançant immersions de ROV en el Canal de Menorca (maërl de *Spongites fruticulosus* i boscs de *L. rodriguezii*) i

a les costes meridionals de Menorca (llits de *P. inamoena*) durant la campanya CANAL0209 (Febrer/Març 2009). Més tard, durant la campanya MEDITS_ES05_09 (Maig 2009), les mostres es van obtenir per mitjà del patí epibentònic (per als boscos de *L. rodriguezii* i els llits de *P. inamoena*) i la draga Box-Corer (pel maërl de *S. fruticulosus*), ja que aquests mètodes presenten una àrea de mostreig petita, i reduïda (patí epibentònic; mida de malla: 10 mm) o nul·la (draga Box-Corer) pèrdua de biomassa. Per cada comunitat, les mostres es van triar i identificar al mínim nivell taxonòmic, i cada taxó es va quantificar mesurant-ne la superfície algal (Sa, en cm^2) i la biomassa (B, pes sec en g). Les dades quantitatives també van ser estandarditzades (Sa, cm^2 m^{-2}; B, g m^{-2}). Els boscos de *L. rodriguezii* i els llits de *P. inamoena* es van mostrar com les comunitats més riques en composició específica i, en el cas dels boscos de laminarials, com la comunitat estudiada més diversa. En contrast, el maërl de *S. fruticulosus* van presentar valors baixos de nombre d'espècies i diversitat, degut al baix desenvolupament de l'estrat erecte.

La comparació qualitativa de les comunitats algals dels fons detrítics de les costes europees va incloure les nostres dades de les illes Balears i d'alguns treballs publicats realitzats al NE Atlàntic i al Mediterrani. Els anàlisis van mostrar que les comunitats atlàntiques difereixen de les mediterrànies en la seva composició específica. Les comunitats detrítiques dominades per macroalgues de les costes europees descrites quantitativament (principalment llits de maërl, boscos de *L. rodriguezii*, llits de *Peyssonnelia* i boscos de *Saccharina latissima*) no es van poder distingir qualitativament. Així, degut a la presència generalitzada d'un estrat basal caracteritzat per *Lithothamnion corallioides* i *Phymatolithon calcareum*, i un estrat erecte més o menys desenvolupat, tenint en compte només la seva composició específica, aquestes comunitats es poden considerar com a llits de maërl. A partir de les diferències en la composició específica dels estrats erecte i basal, es poden dividir en set tipus de llits de maërl, dos trobats al NE Atlàntic i els altres cinc, al Mediterrani. A més, la comparació qualitativa de les comunitats del detrític costaner dominades per macroalgues també va confirmar la àmplia distribució de *L. corallioides* i *P. calcareum*, i que altres espècies formadores de maërl importants es troben restringides al Mediterrani (per exemple, *S. fruticulosus* i *Lithothamnion valens*).

Els anàlisis qualitatius també van indicar que les tres comunitats descrites a la plataforma continental de Mallorca i Menorca presenten una distribució restringida al Mediterrani, més concretament a les illes Balears. A més, els boscos de *L. rodriguezii* i els llits de *P. inamoena* són les comunitats més similars, mentre que el maërl de *S. fruticulosus* es va distingir d'aquestes dues comunitats i també d'altres llits de maërl de les costes properes a les illes Balears amb similar composició específica de l'estrat basal.

La metodologia usada en aquest estudi, tradicionalment utilitzada en estudis de la fauna demersal i bentònica, ens va permetre recollir mostres representatives dels fons detrítics costaners dominats per macroalgues en les aigües profundes de la plataforma continental de Mallorca i Menorca. L'ús de l'arrossegament de fons va resultar un bon mètode per a la aproximació paisatgística, sobretot gràcies a la entre moderada i elevada àrea de mostreig i la relativa pèrdua de biomassa durant el mostreig gràcies a la petita mida de malla (20 mm). Per altra banda, la combinació dels mètodes observacional (immersions de ROV) i de mostreig (draga Box-Corer i patí epibentònic) va permetre localitzar i recol·lectar mostres representatives en l'estudi de comunitats gràcies a trobar zones homogènies i perdre poca (patí epibentònic; mida de malla: 10 mm) o gens (draga Box-Corer) biomassa.

Resumen

Los fondos detríticos costeros de aguas profundas dominados por macroalgas se desarrollan en fondos blandos caracterizados por grandes cantidades de partículas carbonatadas, principalmente, de origen vegetal y animal. La formación de estos fondos requiere niveles bajos de irradiación, corrientes moderadas, tasas de sedimentación entre bajas y moderadas, y temperatura del agua constante. Las aguas oligotróficas de las islas Baleares, especialmente alrededor de Mallorca y Menorca, permiten su desarrollo en aguas más profundas que en las plataformas continentales próximas.

Esta tesis pretende describir los principales fondos detríticos algales encontrados en la plataforma continental de Mallorca y Menorca, y también proporcionar métodos efectivos para su muestreo. Además, se evalúa la distribución de las comunidades dominadas por macroalgas del detrítico costero del Mediterráneo y el NE Atlántico mediante la comparación cualitativa de nuestros datos y los publicados en la bibliografía.

La descripción de los principales paisajes dominados por macroalgas del detrítico costero encontradas en la plataforma continental de Mallorca y Menorca se efectuó a finales de primavera (Mayo/Junio) de 2007 y 2008, durante las campañas MEDITS_ES05 efectuadas mediante arrastre de fondo (tamaño de malla: 20 mm), que permite cubrir grandes áreas. En total se recolectaron 29 muestras, de las cuales se clasificaron e identificaron los taxones llegando al nivel taxonómico más bajo posible. Su abundancia se mesuró como superficie algal (Sa, en cm^2) y fue estandarizada (en $cm^2\ m^{-2}$). Los análisis estadísticos permitieron la distinción de hasta seis paisajes: las praderas de *Osmundaria volubilis* y *Phyllophora crispa* y dos lechos de *Peyssonnelia* dominados por *Peyssonnelia inamoena* y *Peyssonnelia rubra*, respectivamente, con una distribución más superficial (de 52 a 65 m); los lechos de maërl y los lechos de *Laminaria rodriguezii*, encontrados en aguas más profundas (de 77 a 81 m); y las praderas de *Phyllophora crispa* y *Halopteris filicina*, tanto en aguas superficiales como profundas (de 57 a 93 m). El desarrollo de los paisajes con un rango de distribución restringido puede estar influenciado por la profundidad, que está estrechamente ligada a los cambios estacionales de la temperatura del agua. En cambio, las ampliamente distribuidas praderas de *Phyllophora crispa* y *Halopteris filicina* podrían corresponder a un artefacto causado por el muestreo con arrastre de fondo en zonas altamente heterogéneas y/o por la mezcla de dos o más paisajes.

Tres de las comunidades que caracterizan los paisajes encontrados en las costas de Mallorca y Menorca se localizaron mediante inmersiones de ROV en el canal de Menorca (maërl de *Spongites fruticulosus* y bosques de *L. rodriguezii*) y en las costas meridionales de Menorca (lechos de *P. inamoena*) durante la campaña CANAL0209 (Febrero/Marzo 2009). Más tarde, durante la campaña MEDITS_ES05_09, las muestras se obtuvieron por medio del patín epibentónico (para los bosques de *L. rodriguezii* y los lechos de *P. inamoena*) y la draga Box-Corer (para el maërl de *S. fruticulosus*), ya que estos métodos presentan un área de muestreo pequeña, y reducida (patín epibentónico, tamaño de malla: 10 mm) o nula (draga Box-Corer) pérdida de biomasa. Para cada comunidad, las muestras fueron clasificadas e identificadas al mínimo nivel taxonómico, y cada taxón fue cuantificado midiendo su superficie algal (Sa, en cm^2) y biomasa (B, peso seco en g). Los datos cuantitativos también fueron estandarizados (Sa, cm^2 m^{-2}; B, g m^{-2}). Los bosques de *L. rodriguezii* y los lechos de *P. inamoena* se mostraron como las comunidades más ricas en composición específica y, en el caso de los bosques de laminariales, como la comunidad estudiada más diversa. Por el contrario, el maërl de *S. fruticulosus* presentó los valores más bajos de número de especies y diversidad, debido al bajo desarrollo del estrato erecto.

La comparación cualitativa de les comunidades algales de los fondos detríticos de las costas europeas incluyó nuestros datos de las islas Baleares y los de algunos trabajos publicados realizados en el NE Atlántico y el Mediterráneo. Los análisis mostraron que las comunidades atlánticas difieren de las mediterráneas en su composición específica. Las comunidades detríticas dominadas por macroalgas de las costas europeas descritas cuantitativamente (principalmente lechos de maërl, bosques de *L. rodriguezii*, lechos de *Peyssonnelia* y bosques de *Saccharina latissima*) no pudieron distinguirse cualitativamente. Así, debido a la presencia generalizada de un estrato basal caracterizado por *Lithothamnion corallioides* y *Phymatolithon calcareum*, y un estrato erecto más o menos desarrollado, teniendo solo en cuenta su composición específica, estas comunidades se pueden considerar como lechos de maërl. A partir de las diferencias en la composición específica de los estratos erecto y basal, se pueden dividir en siete tipos de lechos de maërl, dos en el NE Atlántico y cinco, en el Mediterráneo. Además, la comparación cualitativa de las comunidades del detrítico costero dominadas por macroalgas también confirmó la amplia distribución de *L. corallioides* y *P. calcareum*, y que otras especies formadoras de maërl importantes se encuentran restringidas en el Mediterráneo (por ejemplo, *S. fruticulosus* y *Lithothamnion valens*).

Los análisis cualitativos también indicaron que las tres comunidades descritas en la plataforma continental de Mallorca y Menorca presentan una distribución restringida en el Mediterráneo, más concretamente en las islas Baleares. Además, los bosques de *L. rodriguezii* y los lechos de *P. inamoena* son las comunidades más similares, mientras que el maërl de *S. fruticulosus* se distinguió de estas comunidades y también de otros lechos de maërl de las costas cercanas a las islas Baleares con similar composición específica del estrato basal.

La metodología usada en este estudio, tradicionalmente utilizada en estudios de la fauna demersal y bentónica, nos permitió recolectar muestras representativas de los fondos detríticos costeros dominados por macroalgas de aguas profundas de la plataforma continental de Mallorca y Menorca. El uso del arrastre de fondo resultó un buen método en la aproximación paisajística, sobre todo gracias a la entre moderada y elevada área de muestreo, y la relativa pérdida de biomasa durante el muestreo gracias al pequeño tamaño de malla (20 mm). Por otro lado, la combinación de métodos observacional (inmersiones de ROV) y de muestreo (draga Box-Corer y patín epibentónico) permitió localizar y recolectar muestras representativas en el estudio de comunidades gracias a encontrar zonas homogéneas y perder poca (patín epibentónico, tamaño de malla: 10 mm) o nula (draga Box-Corer) biomasa.

I. General introduction

Introducció general

I. General introduction

Foreword

The coasts of the Balearic Islands have been largely studied since the late 19th century and, specially, since Odón de Buen founded the Laboratorio Biológico-Marino de Baleares in 1906, which became part of the Instituto Español de Oceanografía (IEO) in 1914, together with the laboratories of Santander and Málaga. In the first decades of the 20th century, its research was devoted to the study of the oceanography and plankton communities of Palma bay, and the biology of the main commercially interesting species. In the 1970s, the collaboration with the Balearic fishing fleet begun, leading to a better knowledge of the fish stocks and the bionomy of the bottoms off the Balearic Islands. Later on, more research subjects, such as sedimentology and micropaleontology, flourished. The name of the Laboratorio Biológico-Marino de Baleares was changed in the 1980s to Centre Oceanogràfic de Balears (COB).

Nowadays, the COB performs multi-disciplinary studies of the marine environment, including its ecosystems and living resources. One of the main interests of the COB is the study of the demersal ecosystems and their relationship with environmental factors, which is conducted by the research group of Ecosistemas, Recursos Demersales y Bentos (ERDEB). Since 2007, this group has been involved in the MEDITS survey programme, an international bottom trawl survey promoted by the European Commission in 1993 and performed all across the Mediterranean. The goal of this programme is to produce basic information on benthic and demersal species in terms of population distribution as well as demographic structure, on the continental shelves and along the upper slopes at a regional scale within the Mediterranean Sea (Bertrand *et al*. 2002). In order to accomplish this goal, a number of MEDITS surveys are performed through the Mediterranean Geographical Sub-Areas (GSA); the ERDEB group is in charge of the surveys conducted in the Balearic Islands, more specifically in Mallorca and Menorca (GSA-05).

To complement the information obtained from the faunistic data of the MEDITS_ES05 surveys with data from the vegetal part, the ERDEB group contacted with members of the research group of Algues Bentòniques Marines (ABM) from the Universitat de Girona (UdG). The collaboration between these groups started with the first MEDITS_ES05 survey performed in Mallorca and Menorca, in early summer 2007, and is still currently working. The ABM group has been involved not only in the MEDITS_ES05 surveys, but also in other field missions performed in some other locations of the Balearic continental shelf, such as the Menorca Channel (CANAL0209 and CANAL0811) and the Southern coasts off Mallorca (DRAGONSAL0712 and DRAGONSAL0914). As a result, the ERDEB group has published several works where data on commercially valuable species is related to the algal benthic assemblages (e.g. Ordines and Massutí 2009, Ordines *et al*. 2009, 2011, 2015), and to the distribution of the main detritic bottoms at a local scale (e.g. Barberá *et al*. 2009, 2012, 2014). Besides, the ABM group has focused in the better knowledge of the deep-water macroalgal-dominated coastal detritic seascapes and communities as reflected in this Ph.D. dissertation.

Study area: the Balearic Islands

The sampling area of this study is located in the continental shelf off Mallorca and Menorca (Balearic Islands). The Balearic Islands are located in the center of the Western Mediterranean Sea and include four major islands: Mallorca, Menorca, Eivissa and Formentera (Fig. 1). These islands are the emergent parts of the Balearic Promontory, which is a prolongation of the Betic

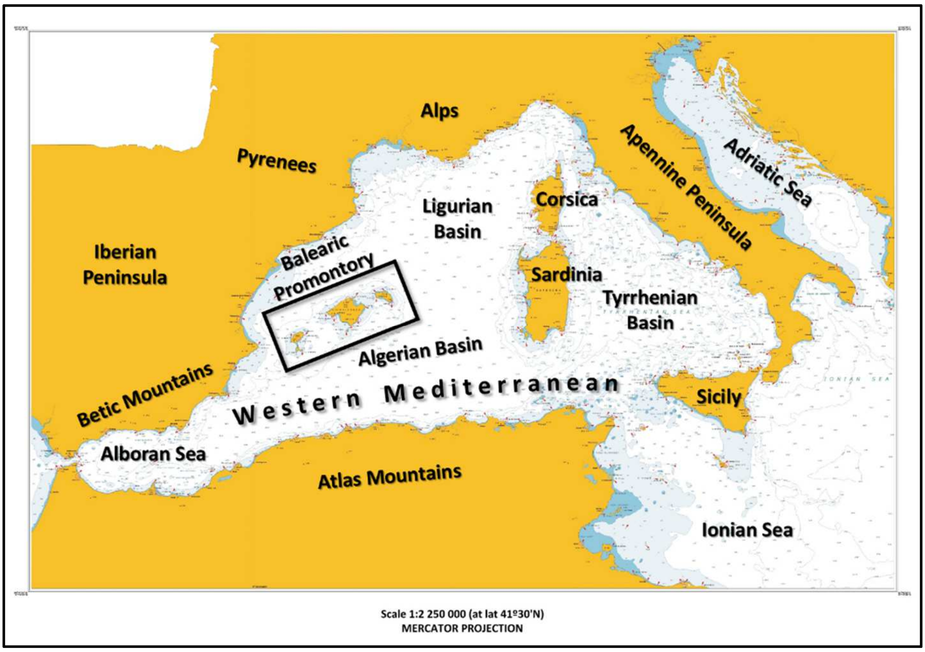


Figure 1 – INT301 nautical chart of the Western Mediterranean showing the location of the Balearic Islands. Source: Instituto Hidrográfico de la Marina (no date), http://highsea.cz/map.htm.

Mountains in the Iberian Peninsula (Canals and Ballesteros 1997, Acosta *et al*. 2002). They are surrounded by the Ligurian Basin in the North and the Northwest, and the Algerian Basin in the Southeast (Acosta *et al*. 2002).

The continental shelf of the Balearic Islands is nearly horizontal and situated at 93 m depth on average. It is separated from the Iberian Peninsula shelf by the Eivissa Channel (up to 800 m depth), while the sector of the Ligurian Basin situated between the Northwestern coast of the Balearic Islands and the Iberian Peninsula (the Valencia Trough) is deeper than the Eivissa Channel and increase gently in depth to the Northeast arriving at depths about 2800 m (Fig. 2) (Acosta *et al*. 2002). Contrastingly, the continental shelf is abruptly limited by the Emile Baudot Scarpment in the Southeastern coasts, which begins at depths of 200-800 m and extends to 2000 m at its base (Acosta *et al*. 2002). From here, the Algerian basin extends Southeastern arriving nearly at 2800 m depth.

The Balearic shelf is divided into two geographic sectors separated by the Mallorca Channel, which is up to 600 m depth, and the Central Depression, with depths always above 1000 m (Fig. 2). The larger unit is constituted by the Mallorca-Menorca shelf, covering 6418 km^2, while the smaller one is the Eivissa-Formentera shelf, which covers a total surface of 2709 km^2 (Canals and Ballesteros 1997, Acosta *et al*. 2002). The continental shelf of Mallorca and Menorca is generally narrow, except at the South of Mallorca and in Menorca and Cabrera channels, where it becomes larger and has a gentle slope. The shelf-break is located at 139 m depth on average (Acosta *et al*. 2002).

The waters of the continental shelf off the Balearic Islands are

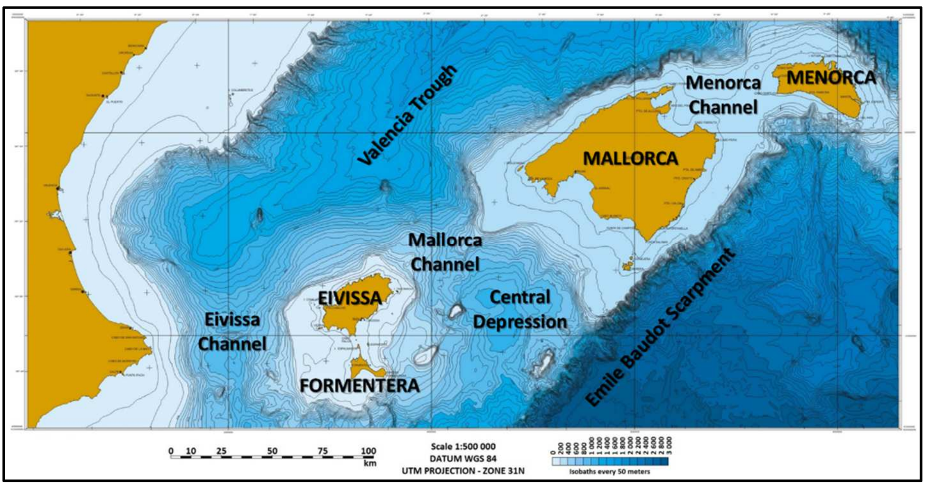


Figure 2 – Bathymetric map of the Balearic Islands and the gulf of Valencia, Western Mediterranean. Source: Grupo de trabajo ZEE (2001), http://www.ieo.es/cartografia.

characterized by a high transparency, which is mainly due to the absence of rivers and the infiltration of rainfall in the karstic soils, reducing the presence of terrestrial sediments (Canals and Ballesteros 1997). Besides, the islands are surrounded by two oligotrophic masses of water situated at different depth ranges (Canals and Ballesteros 1997). The shallow water mass (above 60 m) is influenced by the North Atlantic Surface Waters and the Gulf of Lions Cold Waters, with temperatures higher than 25ºC in summer and salinities lesser than 38 %. The deep water mass, found between 60 and 200 m depth, belongs to the Intermediate Western Mediterranean Water and it is characterized by temperatures around 12-13ºC and salinities from 38.1 % to 38.2 % (Canals and Ballesteros 1997). The oligotrophic waters largely contribute to the high water transparency, and this, in turn, is the main factor determining the depth distribution of the algal benthic communities (Ballesteros and Zabala 1993). Thus, as in the Balearic Islands the 0.05 % of the surface irradiance reaches 110 m depth, the circalittoral zone extends deeper than to any other Western Mediterranean continental coast (Ballesteros and Zabala 1993, Canals and Ballesteros 1997, Fornós and Ahr 1997).

Sediments are usually of biogenic origin and contain a high percentage of carbonate, as they are constituted mainly by fragments of red algae (50%), molluscs (15%), foraminifers (6%) and bryozoans (5%) (Alonso *et al*. 1988, Canals and Ballesteros 1997, Fornós and Ahr 1997, Acosta *et al*. 2002).

Macroalgal-dominated coastal detritic bottoms

Macroalgal-dominated coastal detritic bottoms constitute a main habitat within the sedimentary bottoms of the continental shelves occurring close to shore (Pérès 1985, Pérès and Picard 1964, Picard 1965). They develop in soft bottoms composed of low percentages of silt, sand and gravels, mixed with a high amount of calcareous skeletons from benthic organisms such as molluscs, bryozoans, cnidarians, echinoderms and macroalgae. Both alive and dead free-living members of the orders Corallinales and Peyssonneliales (Rhodophyta) are their major constituents (Pérès 1985, Klein and Verlaque 2009). Animal skeletons and calcareous algae create a secondary hard substratum that allows the settlement of organisms usually found in rocky bottoms (Bianchi 2001), contributing to the presence of a high species diversity (with taxa typical both from soft and hard bottoms) and a high functional diversity (Cabioch 1969, Ballantine *et al*. 1994, Birkett *et al*. 1998, Foster 2001, Steller *et al*. 2003). Besides, they also harbor a vast number of rare and interesting species often restricted to this kind of assemblages (Laborel 1987, Birkett *et al*. 1998). The distribution of macroalgal-dominated coastal detritic bottoms is ruled mainly by light, current conditions, sedimentation and temperature (Pérès and Picard 1964, Augier and Boudouresque 1978, Ros *et al*. 1985, Ballesteros 1992a), preferring open waters close to islands, capes or cliffs with high exposure to waves and particles, and a rather constant water temperature (Ballesteros *et al*. 2013).

The depth distribution of the macroalgal-dominated coastal detritic bottoms geographically differs according to the latitude and water transparency. The high light transmittance and the low water turbidity found in Mediterranean waters, specially recognized in the Balearic Islands (Ballesteros and Zabala 1993, Canals and Ballesteros 1997, Fornós and Ahr 1997), allows a wide bathymetric distribution of these bottoms (25 to -130 m) (Pérès 1985, Giaccone *et al*. 1994, Bellan-Santini *et al*. 2002, Hall-Spencer *et al.* 2010). In contrast, those found in the NE Atlantic, usually develop at depths above 30 m (Pérès and Picard 1964, Birkett *et al*. 1998, Grall 2003, Peña 2010, Peña *et al*. 2014).

Macroalgal-dominated detritic bottoms from the NE Atlantic have been studied since the beginning of the 20th century (e.g. Joubin 1909). However, it is not until the second half of the 20th century when accurate descriptions of their structure (e.g. Blunden *et al*. 1977, Hily *et al*. 1992, Perrins *et al*. 1995, Peña and Bárbara 2006), and human impacts (e.g. Birkett *et al*. 1998, Hall-Spencer 1998, De Grave *et al*. 2000, Hall-Spencer and Moore 2000, Grall and Hall-Spencer 2003) are made.

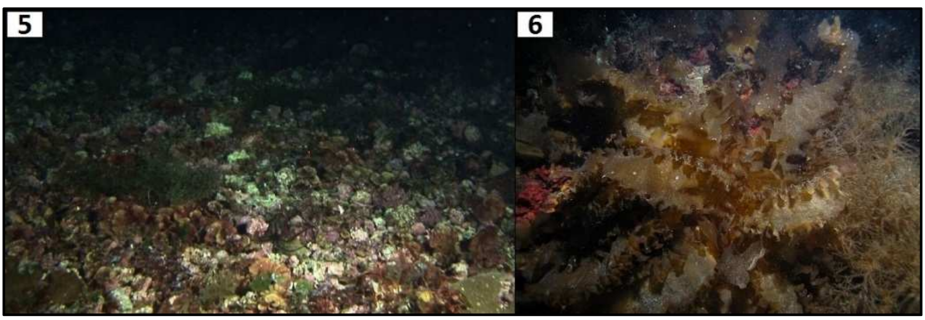
The study of macroalgal-dominated coastal detritic bottoms in the Mediterranean Sea began at the end of the 19th century and the beginning of the 20th century with checklists (e.g. Rodríguez-Femenías 1889, Mazza 1903, Bellón-Uriarte 1921) and the description of some bottoms (e.g. de Buen 1905). Although these kinds of bottoms are widespread in the Mediterranean (Pérès and Picard 1964), the majority of studies have been performed in the Western Mediterranean and, more concretely, in the French coasts (e.g. Huvé 1954, 1956, Jacquotte 1962, Pérès and Picard 1963, 1964, Picard 1965,

Figures 3-4 – Maërl beds. **3.** Tossa de Mar (Girona, Spain). Source: E. Ballesteros. **4.** Columbretes Islands (Castelló de la Plana, Spain). Source: E. Ballesteros.

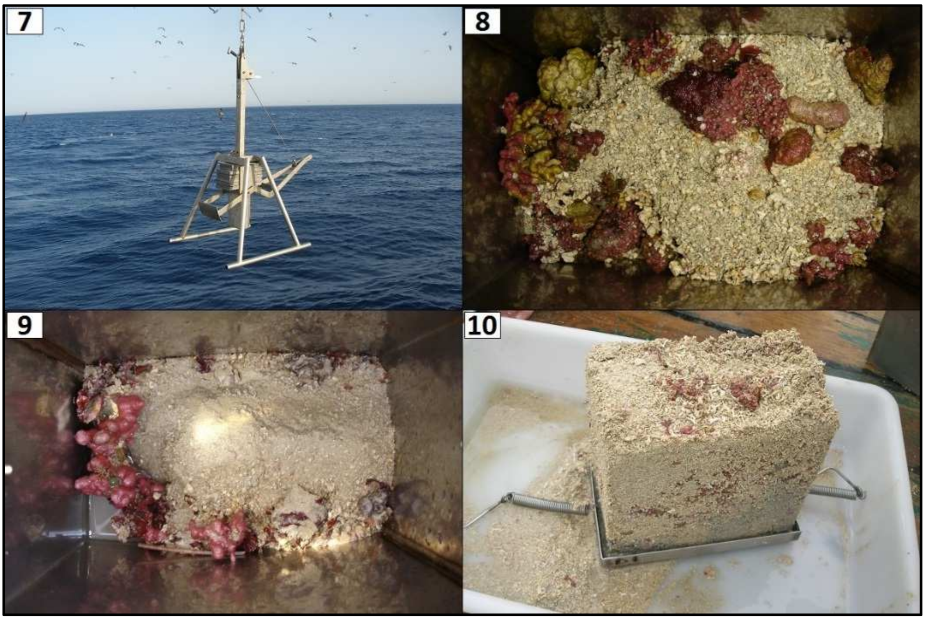
Bourcier 1968, Augier and Boudouresque 1978). Contrastingly, few studies have been performed in the Eastern Mediterranean (e.g. Jacquotte 1962, Atabey 1998).

Many authors have highlighted the high biodiversity of the macroalgal-dominated detritic bottoms and, in the European coasts (NE Atlantic and Mediterranean), a number of categories, habitats, subhabitats or facies, each one characterized by one or a reduced number of more or less exclusive species, have been described (e.g. Dieuzede 1940, Huvé 1954, 1956, Jacquotte 1962, Pérès and Picard 1963, 1964, Picard 1965, Giaccone 1967, Bourcier 1968, Augier and Boudouresque 1978, Augier 1982, Ballesteros 1988, 1994, Giaccone *et al*. 1994). Among these categories, the maërl beds (Fig. 3 and 4) are the most studied, as they show a widespread distribution in European coasts (e.g. Jacquotte 1962, Pérès and Picard 1963, 1964, Cabioch 1969, Augier 1982, Ballesteros 1988, Peña 2010). However, the Mediterranean Sea is home to other categories: the forests of *Laminaria rodriguezii* (Fig. 5) (e.g. Huvé 1955, Molinier 1956, Giaccone 1971, Fredj 1972, Augier 1982), several kinds of *Peyssonnelia* beds (Huvé 1954, Carpine 1958, Pérès and Picard 1963, 1964, Augier and Boudouresque 1978, Augier 1982, Basso 1990, Ballesteros 1994), the meadows of *Osmundaria volubilis* with *Rytiphlaea tinctoria* (e.g. Pérès and Picard 1964, Picard 1965, Augier 1982), the *Halarachnion spatulatum* beds (Costa 1960, Pérès and Picard 1964, Augier 1982), the *Kallymenia spathulata* and *Haliclona simulans* beds (Augier 1982), and the *Gracilaria corallicola* beds (Augier 1982). In fact, Templado *et al*. (2012) distinguish up to 9 different habitats corresponding to these macroalgal-dominated coastal detritic bottoms from the Mediterranean Spanish coasts.

In the Balearic Islands, deep-water coastal detritic bottoms have been largely reported (e.g. de Buen 1934, Alonso *et al*. 1988, Fornós *et al*. 1988,



Figures 5-6 – Forests of *Laminaria rodriguezii*. **5.** Menorca Channel (Balearic Islands, Spain). Source: COB-INDEMARES. **6.** Columbretes Islands (Castelló de la Plana, Spain). Source: Diego Kurt Kersting.



Figures 7-10 – Box-Corer dredging on maërl beds with *Spongites fruticulosus* during the MEDITS_ES05_09 survey. Source: COB-IEO (7, 10) and S. Joher (8, 9).

Figures 11-14 – Beam trawl sampling on forests of *Laminaria rodriguezii* during the MEDITS_ES05_09 survey. Source: COB-IEO (11, 12, 13) and S. Joher (14).

Canals and Ballesteros 1997, Fornós and Ahr 1997, Massutí and Reñones 2005), and they have been characterized in terms of foraminifer composition (Milker *et al*. 2009) and megabenthos (Massutí *et al*. 1996, Massutí and Reñones 2005, Ordines and Massutí 2009). However, despite seaweeds usually are a major component of these coastal detritic bottoms and several habitats (e.g. maërl beds, *Osmundaria volubilis* meadows, *Peyssonnelia* beds and *L. rodriguezii* forests) have been reported (Canals *et al*. 1988, Fornós *et al*. 1988, Ballesteros 1994, Barberá *et al*. 2009, 2012, 2014), they have been roughly taken into account in the descriptive studies dealing with all benthic groups (e.g. de Buen 1934, Canals and Ballesteros 1997). In fact, the study of the *Peyssonnelia* beds by Ballesteros (1994) is the only reference of an exhaustive ecological study of the macroalgal-dominated detritic communities performed in the Balearic Islands until now.

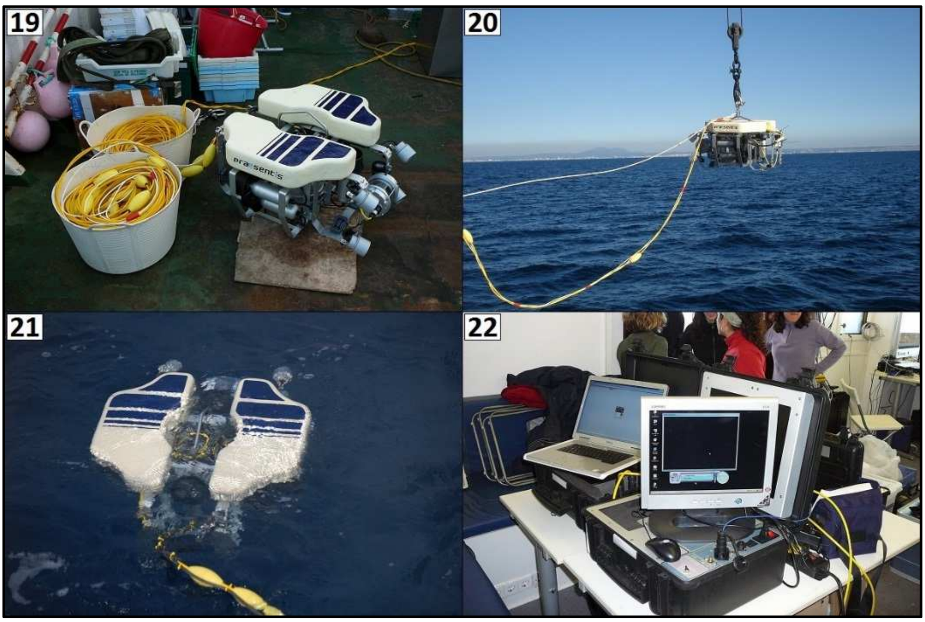
Sampling algae in deep-waters

Direct sampling methods based on Scuba diving have been traditionally used in the study of shallow algal communities (e.g. Ballesteros 1992b, Ballesteros *et al*. 1993), but they have been typically limited to depths above 60 m due to safety concerns (Lang *et al*. 2013). In fact, they have seldom been used to describe species composition in deep-water coastal detritic bottoms (e.g. Giaccone 1972, Ballesteros 1988, 1994, Piazzi *et al*. 2003, 2004) because, despite the improvements in diving technology, they have severe limitations such as restricted sampling times, long decompression stops, and occasionally physiological diseases such as the decompression sickness (UNEP-MAP-RAC/SPA 2008, Lang *et al*. 2013). Therefore, indirect sampling methods are those usually preferred for deep-water sampling (Cailliet *et al*. 1999, Bax and Williams 2001), being dredging (Fig. 6) and beam trawling (Fig. 7) the most used ones (Dieuzede 1940, Huvé 1956, Costa 1960, Bourcier 1968, Blunden *et al*. 1977, Basso, 1995a, 1995b, 1996, Bordehore *et al.* 2000a, 2003, Bárbara *et al*. 2004, Peña 2010, Barberá *et al*. 2012, Ellis *et al.* 2013).

This work

During the sampling surveys organized by the COB, the work of the ABM group has focused on complementing the study of the benthic ecosystems by the characterization of the macroalgal-dominated coastal detritic bottoms. As COB members used bottom trawl (Fig. 8) and beam trawl (Fig. 7) as sampling techniques (e.g. Massutí and Moranta 2003, Guijarro and Massutí 2006,

Figures 15-18 – Bottom trawl sampling on *Peyssonnelia* spp. beds during the MEDITS_ES05_10 survey. Source: COB-IEO.



Figures 19-22 – ROV dive in the Menorca Channel during the CANAL02_09 survey. Source: COB-INDEMARES (19, 20, 22) and COB-IEO (21).

Barberá *et al*. 2012, Ramón *et al*. 2014, Valls *et al*. 2014, Ordines *et al*. 2015), we applied these same methods to the quantitative study of the algae thriving in these bottoms by means of two different levels: seascape and community. When sampling macroalgal-dominated detritic bottoms in terms of seascape we used bottom trawling, which cover large areas. For community characterization, homogenous areas were located with ROV dives (Fig. 9) and, once located, they were sampled using beam trawling, which covers smaller areas than bottom trawling. Moreover, Box-Corer dredging was also used to sample those communities presenting a small scale patchy distribution, which required a smaller sampling surface than that provided by beam trawling.

Pròleg

Les costes de les illes Balears han estat llargament estudiades des de finals del segle XIX i, especialment, des que Odón de Buen va fundar el Laboratorio Biológico-Marino de Baleares el 1906, que esdevindria part del Instituto Español de Oceanografía el 1914, junt els laboratoris de Santander i Málaga. En les primeres dècades del segle XX, la seva recerca es centrava en l'estudi de la oceanografia i les comunitats planctòniques de la badia de Palma, i en la biologia de les principals espècies d'interès comercial. En la dècada de 1970, la col·laboració amb la flota pesquera balear va començar, portant a un millor coneixement dels estocs pesquers i de la bionomia dels fons de les illes Balears. Més tard, noves línies de recerca van aparèixer, com la sedimentologia i la micropaleontologia. El nom del Laboratorio Biológico-Marino de Baleares canviaria durant la dècada de 1980 passant a ser anomenat Centre Oceanogràfic de Balears (COB).

Avui dia, el COB desenvolupa estudis multidisciplinaris en el medi marí, incloent els seus ecosistemes i recursos vius. Un dels principals interessos del COB és l'estudi dels ecosistemes demersals i la seva relació amb els factors ambientals, que és desenvolupat per l'equip de recerca de Ecosistemas, Recursos Demersales y Bentos (ERDEB). Des del 2007, aquest grup s'ha implicat en el programa MEDITS, una campanya internacional basada en l'arrossegament de fons, promoguda per la Comissió Europea el 1993 i que té lloc per tot el Mediterrani. L'objectiu d'aquest programa és la producció d'informació bàsica sobre espècies bentòniques i demersals relacionada amb la distribució de les poblacions i la seva estructura demogràfica, en la plataforma continental i la zona superior del talús a escala regional dins el Mediterrani (Bertrand *et al*. 2002). Per acomplir aquest objectiu, varies campanyes MEDITS es desenvolupen en les Subàrees Geogràfiques del Mediterrani (GSA); el grup ERDEB s'encarrega de les campanyes realitzades a les illes Balears, més concretament a Mallorca i Menorca (GSA-05).

Per complementar la informació obtinguda de les dades faunístiques durant les campanyes MEDITS_ES05 amb dades de la fracció vegetal, el grup ERDEB va contactar amb els membres del grup de recerca d'Algues Bentòniques Marines (ABM) de la Universitat de Girona (UdG). La col·laboració entre aquests dos grups va començar amb la primera campanya MEDITS_ES05 realitzada a Mallorca i Menorca, a principis de l'estiu de 2007, i encara continua actualment. El grup ABM no només ha participat en les campanyes MEDITS_ES05, sinó també en altres campanyes desenvolupades en altres zones de la plataforma continental balear, com el Canal de Menorca (CANAL0209 i CANAL0811) i les costes meridionals de Mallorca (DRAGONSAL0712 i DRAGONSAL 0914). Com a resultat, el grup ERDEB ha publicat diferents treballs on dades sobre espècies d'interès comercial s'han relacionat amb els paisatges bentònics algals (per exemple, Ordines i Massutí 2009, Ordines *et al*. 2009, 2011, 2015), i sobre la distribució dels principals fons detrítics a escala local (per exemple, Barberá *et al*. 2009, 2012, 2014). Per altra banda, el grup ABM s'ha centrat en el millor coneixement dels paisatges i comunitats dominats per macroalgues del detrític costaner, tal i com es reflecteix en aquesta tesi doctoral.

Àrea d'estudi: les illes Balears

L'àrea de mostreig d'aquest estudi es localitza a la plataforma continental de Mallorca i Menorca (illes Balears). Les illes Balears es troben al centre del Mediterrani Occidental i inclouen quatre illes principals: Mallorca, Menorca, Eivissa i Formentera (Fig. 1). Aquestes illes corresponen a les parts emergides del Promontori Balear, que és una prolongació de la Serralada Bètica situada a la Península Ibèrica (Canals i Ballesteros 1997, Acosta *et al*. 2002). Estan envoltades per la Conca de Ligúria al Nord i al Nord-Oest, i per la Conca d'Algèria al Sud-Est (Acosta *et al*. 2002).

La plataforma continental de les illes Balears és pràcticament horitzontal i es troba a uns 93 m de fondària. Està separada de la plataforma de la Península Ibèrica pel Canal d'Eivissa (que arriba als 800 m) i per part de la Conca de Ligúria situada entre les costes Nord-Occidentals de les illes Balears i la Península Ibèrica (la Depressió de València) que és més fonda que el Canal d'Eivissa i augmenta en fondària cap al Nord-Est arribant fins els 2800 m (Fig. 2) (Acosta *et al*. 2002). Per contra, la plataforma continental és limitada abruptament pel cingle Emile Baudot a les costes Sud-Orientals, que comença a fondàries de 200-800 m i s'estén fins els 2000 m a la seva base (Acosta *et al*. 2002). A partir d'aquí, la Conca d'Algèria s'estén cap al Sud-Est arribant als 2800 m de fondària.

La plataforma balear està dividida en dos sectors geogràfics separats pel canal de Mallorca, que arriba als 600 m de fondària, i per la Depressió Central, que es troba per sota els 1000 m (Fig. 2). La unitat més extensa està constituïda per la plataforma de Mallorca-Menorca, cobrint 6418 km^2, mentre que la més petita és la plataforma de Eivissa-Formentera, que ocupa una superfície total de 2709 km^2 (Canals i Ballesteros 1997, Acosta *et al*. 2002). La plataforma continental de Mallorca i Menorca és generalment estreta, excepte al Sud de Mallorca i als canals de Menorca i Cabrera, on es fa més ampla i presenta un talús suau. El principi del talús es localitza a uns 139 m de fondària mitjana (Acosta *et al*. 2002).

Les aigües de la plataforma continental de les illes Balears es caracteritzen per una alta transparència, que és deguda principalment a la absència de rius i a la infiltració de les pluges en el sòl càrstic, reduint la presència de sediments terrestres (Canals i Ballesteros 1997). D'altra banda, les illes estan envoltades de dues masses d'aigua oligotròfica situades a diferents rangs de fondària (Canals i Ballesteros 1997). La massa d'aigua més superficial (per sobre els 60 m) està influenciada per les Aigües Superficials de l'Atlàntic Nord i les Aigües Fredes del Golf de Lleó, amb temperatures superiors als 25ºC a l'estiu i salinitats menors al 38 %. La massa d'aigua profunda, que es troba entre els 60 i 200 m de fondària, pertany a les Aigües Intermèdies del Mediterrani Occidental i es caracteritza per temperatures d'entre 12-13ºC i salinitats del 38.1 % al 38.2 % (Canals i Ballesteros 1997). Les aigües oligotròfiques també contribueixen a l'alta transparència, i aquest és el principal factor en determinar la distribució en fondària de les comunitats d'algues bentòniques (Ballesteros i Zabala 1993). Així, ja que el 0.05 % de la irradiància superficial arriba als 110 m de fondària a les Illes Balears, la zona circalitoral s'estén a major fondària que en cap altra costa continental del Mediterrani Occidental (Ballesteros i Zabala 1993, Canals i Ballesteros 1997, Fornós i Ahr 1997).

Els sediments tenen un origen biogènic i contenen un alt percentatge de carbonats, ja que estan constituïts principalment de fragments d'algues vermelles (50%), mol·luscs (15%), foraminífers (6%) i briozous (5%) (Alonso *et al*. 1988, Canals i Ballesteros 1997, Fornós i Ahr 1997, Acosta *et al*. 2002).

Els fons dominats per macroalgues del detrític costaner

Els fons dominats per macroalgues del detrític costaner són l'hàbitat dels fons sedimentaris de la plataforma continental més propers a la costa (Pérès 1985, Pérès i Picard 1964, Picard 1965). Es desenvolupen en fons tous formats per baixos percentatges de llim, sorra i grava, barrejats amb grans quantitats d'esquelets calcaris provinents d'organismes bentònics com mol·luscs, briozous, cnidaris, equinoderms i macroalgues. Tant els tal·lus morts com els vius dels membres dels ordres Corallinales i Peyssonneliales (Rhodophyta) en són els majors constituents (Pérès 1985, Klein i Verlaque 2009). Els esquelets animals i les algues calcàries creen un substrat dur secundari que permet la colonització d'organismes trobats normalment en substrats durs (Bianchi 2001), contribuint a la presència d'una alta diversitat d'espècies (amb taxons típics tant de substrats durs com tous) i una alta diversitat funcional (Cabioch 1969, Ballantine *et al*. 1994, Birkett *et al*. 1998, Foster 2001, Steller *et al*.

2003). A més, aquests fons allotgen un gran nombre d'espècies rares i interessants sovint restringides a aquest tipus de fons (Laborel 1987, Birkett *et al*. 1998). La distribució dels fons dominats per macroalgues del detrític costaner està influenciada principalment per la llum, els corrents, la sedimentació i la temperatura (Pérès i Picard 1964, Augier i Boudouresque 1978, Ros *et al*. 1985, Ballesteros 1992a), trobant-se especialment a mar obert a prop d'illes o al peu de caps i penya-segats amb altes taxes de corrent i sedimentació, i temperatura més o menys constants (Ballesteros *et al*. 2013).

La distribució en fondària dels fons dominats per macroalgues del detrític costaner difereix geogràficament segons la latitud i la transparència de l'aigua. La major transmitància de la llum i la baixa terbolesa de l'aigua trobades en el Mediterrani, especialment reconegudes a les illes Balears (Ballesteros i Zabala 1993, Canals i Ballesteros 1997, Fornós i Ahr 1997), permeten una àmplia distribució batimètrica d'aquests fons (dels 25 als 130 m) (Pérès 1985, Ballesteros 1993, Giaccone *et al*. 1994, Bellan-Santini *et al*. 2002, Hall-Spencer *et al.* 2010). Per contra, els fons trobats al NE Atlàntic normalment es desenvolupen a fondàries per sobre els 30 m (Pérès i Picard 1964, Birkett *et al*. 1998, Grall 2003, Peña 2010, Peña *et al*. 2014).

Els fons detrítics dominats per macroalgues del NE Atlàntic han estat estudiats des de principis del segle XX (per exemple, Joubin 1909). No obstant, no va ser fins la segona meitat del segle XX quan se'n van produir descripcions acurades de la seva estructura (per exemple, Blunden *et al*. 1977, Hily *et al*. 1992, Perrins *et al*. 1995, Peña i Bárbara 2006) i dels impactes humans (per exemple, Birkett *et al*. 1998, Hall-Spencer 1998, De Grave *et al*. 2000, Hall-Spencer i Moore 2000, Grall i Hall-Spencer 2003).

L'estudi dels fons dominats per macroalgues del detrític costaner en el Mediterrani va començar a finals del segle XIX i a principis del segle XX amb llistats d'espècies (per exemple, Rodríguez-Femenías 1889, Mazza 1903, Bellón-Uriarte 1921) i descripcions d'alguns fons (per exemple, de Buen 1905). Tot i que aquests fons es troben àmpliament distribuïts al Mediterrani (Pérès i Picard 1964), la majoria d'estudis s'han desenvolupat al Mediterrani Occidental i, més concretament, a les costes franceses (per exemple, Huvé 1954, 1956, Jacquotte 1962, Pérès i Picard 1963, 1964, Picard 1965, Bourcier 1968, Augier i Boudouresque 1978). Per contra, pocs estudis s'han efectuat al Mediterrani Oriental (per exemple, Jacquotte 1962, Atabey 1998).

Varis autors han destacat la alta biodiversitat dels fons detrítics dominats per macroalgues i, en les costes europees (NE Atlàntic i Mediterrani), diferents categories, hàbitats, subhàbitats i fàcies s'han descrit, cadascuna d'elles caracteritzada per una o poques espècies més o menys exclusives (per exemple, Dieuzede 1940, Huvé 1954, 1956, Jacquotte 1962, Pérès i Picard 1963, 1964, Picard 1965, Giaccone 1967, Bourcier 1968, Augier i

Boudouresque 1978, Augier 1982, Ballesteros 1988, 1994, Giaccone *et al*. 1994). Entre aquestes categories, els llits de maërl (Figures 3 i 4) són els més estudiats, ja que presenten una àmplia distribució en les costes europees (per exemple, Jacquotte 1962, Pérès i Picard 1963, 1964, Cabioch 1969, Augier 1982, Ballesteros 1988, Peña 2010). No obstant, al Mediterrani s'han identificat altres categories: els boscos de *Laminaria rodriguezii* (Fig. 5) (per exemple, Huvé 1955, Molinier 1956, Giaccone 1971, Fredj 1972, Augier 1982), diferents tipus de llits de *Peyssonnelia* (Huvé 1954, Carpine 1958, Pérès i Picard 1963, 1964, Augier i Boudouresque 1978, Augier 1982, Basso 1990, Ballesteros 1994), les praderies de *Osmundaria volubilis* amb *Rytiphlaea tinctoria* (per exemple, Pérès i Picard 1964, Picard 1965, Augier 1982), els llits de *Halarachnion spatulatum* (Costa 1960, Pérès i Picard 1964, Augier 1982), els llits de *Kallymenia spathulata* i *Haliclona simulans* (Augier 1982), i els llits de *Gracilaria corallicola* (Augier 1982). En aquest sentit, Templado *et al*. (2012) diferencia fins a 9 hàbitats diferents corresponents als fons dominats per macroalgues en el detrític costaner de les costes espanyoles del Mediterrani.

A les illes Balears, els fons del detrític costaner d'aigües profundes han estat llargament identificats (per exemple, de Buen 1934, Alonso *et al*. 1988, Fornós *et al*. 1988, Canals i Ballesteros 1997, Fornós i Ahr 1997, Massutí i Reñones 2005), i han estat caracteritzats a partir de la seva composició en foraminífers (Milker *et al*. 2009) i megabentos (Massutí *et al*. 1996, Massutí i Reñones 2005, Ordines i Massutí 2009). Tanmateix, tot i que les algues acostumen a ser el major component dels fons detrítics costaners i diferents hàbitats han estat identificats (per exemple, llits de maërl, praderies de *Osmundaria volubilis*, llits de *Peyssonnelia* i boscos de *Laminaria rodriguezii*) (Canals *et al*. 1988, Fornós *et al*. 1988, Ballesteros 1994, Barberá *et al*. 2009, 2012, 2014), rarament s'han tingut en compte en els estudis descriptius que han tractat tots els grups bentònics (per exemple, de Buen 1934, Canals i Ballesteros 1997). De fet, l'estudi dels llits de *Peyssonnelia* de Ballesteros (1994) és la única referència d'un estudi ecològic exhaustiu d'una comunitat detrítica dominada per macroalgues realitzat a les illes Balears fins ara.

Mostrejant algues en aigües profundes

Els mètodes directes basats en el submarinisme han estat utilitzats tradicionalment en l'estudi de les comunitats algals de poca profunditat (per exemple, Ballesteros 1992b, Ballesteros *et al*. 1993), però estan restringits a fondàries de menys de 60 m degut qüestions de seguretat (Lang *et al*. 2013). Efectivament, aquests mètodes han estat poc usats per descriure la composició específica dels fons profunds del detrític costaner (per exemple, Giaccone 1972, Ballesteros 1988, 1994, Piazzi *et al*. 2003, 2004) ja que, tot i les millores en la tecnologia del busseig, presenten limitacions importants, com temps de mostreig restringits, llargues parades de descompressió i ocasionals malalties fisiològiques com la síndrome de descompressió (UNEP-MAP-RAC/SPA 2008, Lang *et al*. 2013). Per aquesta raó, els mètodes de mostreig indirectes són utilitzats preferentment pel mostreig en aigües profundes (Cailliet *et al*. 1999, Bax i Williams 2001), dels quals la draga (Fig. 6) i el patí epibentònic (Fig. 7) són els més utilitzats (Dieuzede 1940, Huvé 1056, Costa 1960, Bourcier 1968, Blunden *et al*. 1977, Basso 1995a, 1995b, 1996, Bordehore *et al*. 2000a, 2003, Bárbara *et al*. 2004, Peña 2010, Barberá *et al*. 2012, Ellis *et al*. 2013).

Aquest treball

Durant les campanyes de mostreig organitzades pel COB, la tasca del grup ABM s'ha centrat en complementar l'estudi dels ecosistemes bentònics per mitjà de la caracterització dels fons dominats per macroalgues del detrític costaner. Ja que els membres del COB utilitzen l'arrossegament de fons (Fig. 8) i el patí epibentònic (Fig. 7) com a mètodes de mostreig (per exemple, Massutí i Moranta 2003, Guijarro i Massutí 2006, Barberá *et al*. 2012, Ramón *et al*. 2014, Valls *et al*. 2014, Ordines *et al*. 2015), vam aplicar aquests mètodes a l'estudi quantitatiu de les algues que prosperen en aquests fons per mitjà de dues aproximacions diferents: paisatge i comunitat. Al mostrejar els fons dominats per macroalgues del detrític costaner en termes de paisatge vam usar l'arrossegament de fons, ja que cobreix grans àrees. Per la caracterització de les comunitats, es van localitzar àrees homogènies amb immersions de ROV (Fig. 9) i, una vegada localitzades, van ser mostrejades per mitjà del patí epibentònic, que cobreix àrees més petites que l'arrossegament de fons. A més, la draga Box-Corer també es va usar per mostrejar les comunitats amb baixa distribució irregular, ja que requerien una superfície de mostreig menor a la utilitzada amb el patí epibentònic.

Peus de figura

Figura 1 – Carta nàutica INT301 del Mediterrani Occidental mostrant la localització de les Illes Balears. Font: Instituto Hidrográfico de la Marina (sense data), http://highsea.cz/map.htm.

Figura 2 – Mapa batimètric de les Illes Balears i el golf de València, Mediterrani Occidental. Font: Grupo de trabajo ZEE (2001), http://www.ieo.es/cartografia.

Figures 3-4 – Llits de maërl. **3.** Tossa de Mar (Girona, Espanya). Font: E. Ballesteros. **4.** Illes Columbretes (Castelló de la Plana, Espanya). Font: E. Ballesteros.

Figures 5-6 – Boscos de *Laminaria rodriguezii*. **5.** Canal de Menorca (Illes Balears, Espanya). Font: COB-INDEMARES. **6.** Illes Columbretes (Castelló de la Plana, Espanya). Font: Diego Kurt Kersting.

Figures 7-10 – Mostreig amb draga Box-Corer en llits de maërl amb *Spongites fruticulosus* durant la campanya MEDITS_ES05_09. Font: COB-IEO (7, 10) i S. Joher (8, 9).

Figures 11-14 – Mostreig amb patí epibentònic en boscos de *Laminaria rodriguezii* durant la campanya MEDITS_ES05_09. Font: COB-IEO (11, 12, 13) i S. Joher (14).

Figures 15-18 – Mostreig amb arrossegament de fons en llits de *Peyssonnelia* spp. durant la campanya MEDITS_ES05_10. Font: COB-IEO.

Figures 19-22 – Immersió de ROV al Canal de Menorca durant la campanya CANAL02_09. Font: COB-INDEMARES (19, 20, 22) i COB-IEO (21).

II. Objectives

Objectius

II. Objectives

The main objectives of this memory are (1) the identification of the main macroalgal-dominated deep-water coastal detritic seascapes from the Balearic Islands (**Chapter I**), and (2) the description of the communities present in some of these seascapes (**Chapter II**). Simultaneously, we try to validate the use of indirect sampling methods, providing useful and alternative methodologies for the study of the macroalgal-dominated deep-water coastal detritic bottoms. Thus, the use of the bottom trawl will be endorsed for sampling in the study at the seascape level as it covers mid-large surfaces (**Chapter I**). Besides, a combination of observational (ROV immersions) and sampling methods (Box-Corer dredging and beam trawling) will be used for obtaining representative samples for the study at the community level (**Chapter II**). A third objective is (3) to outline the distribution of the studied communities in their biogeographical context by the comparison of our own data and the data published in the literature coming from European waters (NE Atlantic and Mediterranean included) (**Chapter III**).

Objectius

Els principals objectius d'aquesta memòria són (1) la identificació dels principals paisatges del detrític costaner d'aigües profundes dominats per macroalgues de les illes Balears (**Capítol I**), i (2) la descripció de les comunitats presents en alguns d'aquests paisatges (**Capítol II**). Simultàniament, intentarem validar la utilització de mètodes de mostreig indirecte, suggerint mètodes alternatius i útils per l'estudi dels fons del detrític costaner d'aigües profundes dominats per macroalgues. Així doncs, es validarà l'ús de l'arrossegament de fons com a mètode de mostreig en l'estudi paisatgístic, ja que cobreix àrees moderadament extenses (**Capítol I**). D'altra banda, la combinació de mètodes observacionals (ROV) i de mostreig (draga Box-Corer i patí epibentònic) s'utilitzarà per obtenir mostres representatives per l'estudi de comunitats (**Capítol II**). El tercer objectiu és (3) esbossar la distribució de les comunitats estudiades en el seu context biogeogràfic per mitjà de la comparació de les nostres dades amb les publicades en la literatura referida a les costes d'Europa (incloent en el NE Atlàntic i el Mediterrani) (**Capítol III**).

III. Results and discussion

III-1. 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: **a**lgal assemblages, bottom trawl, detritic bottoms, macroalgae, Mediterranean Sea.

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, de Buen 1934, Bellón-Uriarte 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, 1995b, Bordehore *et al*. 2003, Piazzi *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, Piazzi *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, 1995b, 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 km^2, and the smaller Eivissa-Formentera shelf, with a total surface of 2709 km^2 (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; Fig. 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 (Fig. 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 (Sa_i) in square centimeters (Ballesteros 1992a). Subsequently, these data were standardized as algal surface area per haul (Sa_{iH}), expressed in square centimeters per square meters, as follows:

$$Sa_{iH} = \frac{Sa_i \times WW_H}{S_H \times WW_S}$$

where Sa_i is the algal surface area of each species (cm^2), WW_H is the wet weight of algae for each haul (g), S_H is the total haul surface (m^2), 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 Sa_{iH} data. A hierarchical group average agglomerative clustering method accompanied by the SIMPROF test (Clarke *et al*. 2008) adjusted to 9999 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

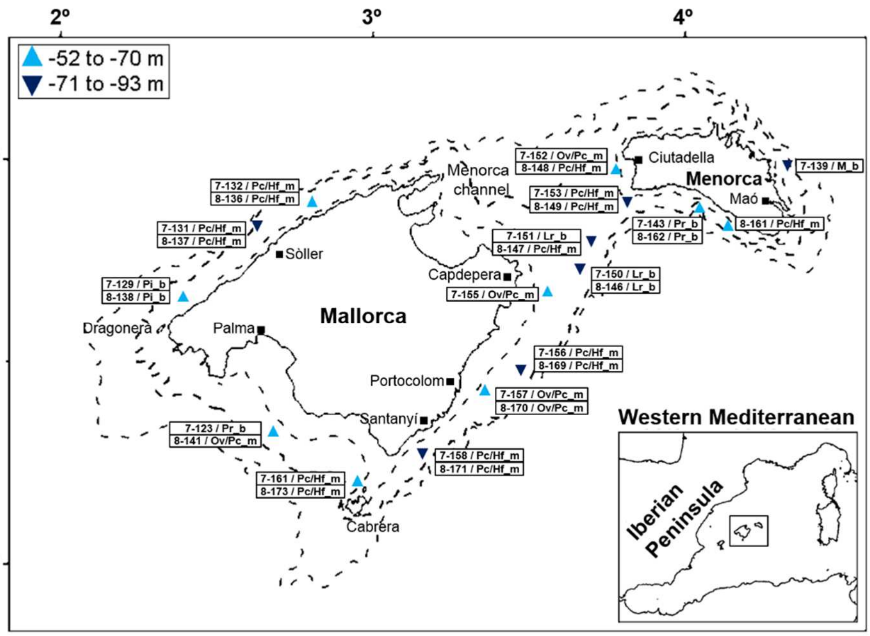


Figure 1 – Map of the studied area off Mallorca and Menorca (Balearic Islands, Western Mediterranean) with the -50, -100, and -200 m isobaths. Samples are displayed indicating their code, depths range, and corresponding assemblage type. The code shows the year of sampling (7, 2007; 8, 2008) followed by the number of the sample. Assemblage types: Lr_b, *Laminaria rodriguezii* beds, M_b, maërl beds; Ov/Pc_m, *Osmundaria volubilis* and *Phyllophora crispa* meadows; Pc/Hf_m, *Phyllophora crispa* and *Halopteris filicina* meadows; Pi_b, *Peyssonnelia inamoena* beds; Pr_b, *Peyssonnelia rubra* beds.

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 specimens or because the specimens were sterile. Some other taxa (Halymeniaceae unidentified 1, *Kallymenia* sp., and *Rhodymenia* sp.) are probably non described 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 cm^2 m^{-2}.

Assemblage type	Depth range (m)	n	n		Sa_{TH} (cm^2 m^{-2})	Sa_{TH} (cm^2 m^{-2})	
			Min	Max		Min	Max
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 ± 495	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 ± 5,005	12,649	22,605
M_b	77	10			306		
Pc/Hf_m	57 to 93	38 ± 9	24	59	3,511 ± 1,963	1,194	6,580

Table 1 – Main characteristics of the different assemblage types: depth range where the assemblages 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 crispa* meadows; Pc/Hf_m, *Phyllophora crispa* and *Halopteris filicina* meadows; Pi_b, *Peyssonnelia inamoena* beds; Pr_b, *Peyssonnelia rubra* beds.

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 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; Fig. 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), maërl beds (M_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 fruticulosus*. This list of common species increased up to 20 when we

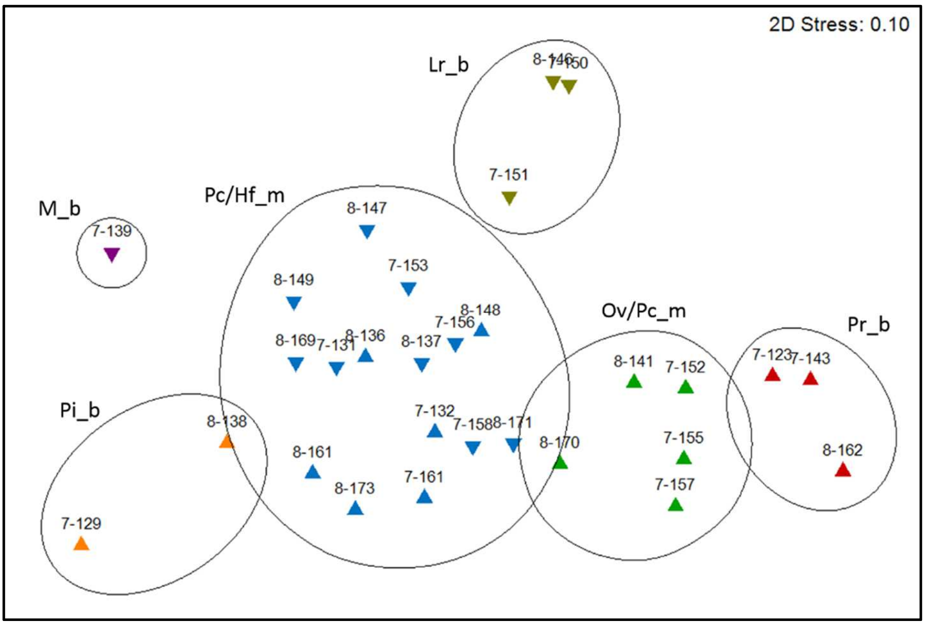


Figure 2 – nMDS ordination with standardized Sa_{iH} (cm^2 m^{-2}). Samples are displayed indicating their code, depths range, and corresponding assemblage type. Code shows the year of sampling (7, 2007; 8, 2008) followed by the number of the sample. Assemblage types: Lr_b, *Laminaria rodriguezii* beds; 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.

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Rhodophyta						
Acrodiscus vidovichii (Meneghini) Zanardini						1.01 ± 3.91
Acrosorium ciliolatum (Harvey) Kylin	3.31 ± 4.74			2.26 ± 3.17		0.32 ± 0.84
Acrothamnion preissii (Sonder) E.M. Wollaston[a]	13.49 ± 19.63	36.11± 0.08	70.45 ± 108.20			57.29 ± 146.10
Alsidium corallinum C. Agardh	3.45 ± 7.71					
Apoglossum ruscifolium (Turner) J. Agardh				1.67 ± 2.89		0.02 ± 0.10
Asparagopsis taxiformis (Delile) Trevisan de Saint-León[a]						0.50 ± 1.35
Balliella cladoderma (Zanardini) Athanasiadis			0.31 ± 0.53			
Bornetia secundiflora (J. Agardh) Thuret						0.02 ± 0.09
Botryocladia chiajeana (Meneghini) Kylin	1.33 ± 2.98		13.50 ± 14.20			0.78 ± 2.65
Botryocladia madagascariensis G. Feldmann[a]	677.94 ± 1,515.92		5,597.08 ± 7,088.13	0.07 ± 0.12		4.64 ± 11.63
Brongniartella byssoides (Goodenough *et* Woodward) F. Schmitz	11.12 ± 23.14					3.00 ± 10.68
Calliblepharis jubata (Goodenough *et* Woodward) Kützing			2.36 ± 4.08			
Callophyllis laciniata (Hudson) Kützing	22.19 ± 49.61		207.66 ± 359.68			1.96 ± 5.45
Champia parvula (C. Agardh) Harvey	0.93 ± 2.08					0.13 ± 0.41
Chrysymenia ventricosa (J.V. Lamouroux) J. Agardh			9.43 ± 16.34			0.01 ± 0.05

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Chrysymenia ventricosa (J.V. Lamouroux) J. Agardh			9.43 ± 16.34			0.01 ± 0.05
Chylocladia verticillata (Lightfoot) Bliding	36.15 ± 56.05		5.04 ± 4.60			3.42 ± 9.97
Chylocladia verticillata (Lightfoot) Bliding						
Corallina elongata J. Ellis *et* Solander						0.01 ± 0.03
Crouania attenuata (C. Agardh) J. Agardh						0.01 ± 0.03
Cryptonemia lomation (Bertoloni) J. Agardh	1.55 ± 2.40	0.29 ± 0.40	2.04 ± 3.53	1.17 ± 2.02		0.19 ± 0.37
Cryptonemia longiarticulata Funk	182.62 ± 224.38	0.32 ± 0.45	44.05 ± 38.19	1.14 ± 1.63		153.30 ± 401.76
Cryptonemia tuniformis (Bertoloni) Zanardini	884.39 ± 1,170.94	24.42 ± 18.30	4,668.64 ± 3,667.67	18.04 ± 31.25		45.98 ± 38.64
Cryptonemia sp.	0.14 ± 0.32		0.36 ± 0.63	0.04 ± 0.08		0.17 ± 0.50
Cryptopleura ramosa (Hudson) L. Newton	1.68 ± 2.58	0.63 ± 0.89	23.66 ± 8.56	3.15 ± 4.82		1.00 ± 2.17
Dasya baillouviana (S.G. Gmelin) Montagne	1.06 ± 2.38					
Dasya rigescens Zanardini						0.03 ± 0.12
Erythroglossum balearicum J. Agardh ex Kylin						0.01 ± 0.03
Ethelia vanbosseae Feldmann						0.03 ± 0.12
Eupogodon planus (C. Agardh) Kützing	23.15 ± 34.14		19.95 ± 2.73			0.18 ± 0.40
Eupogodon spinellus (C. Agardh) Kützing	8.33 ± 13.70					0.89 ± 3.13
Gloiocladia furcata (C. Agardh) J. Agardh	6.16 ± 10.06		86.78 ± 78.32	0.17 ± 0.29		0.60 ± 2.14

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Gloiocladia microspora (Bornet ex Bornet ex Rodríguez y Femenías) N. Sánchez *et* C. Rodríguez- Prieto ex Berecibar, M.J. Wynne, Barbara *et* R. Santos	39.27 ± 50.90		646.67 ± 534.78	10.37 ± 5.29	2.42	14.45 ± 20.34
Gloiocladia repens (C. Agardh) Sánchez *et* Rodríguez-Prieto	25.03 ± 55.96		34.96 ± 60.55	14.20 ± 19.41		0.62 ± 1.31
Gracilaria bursa-pastoris (S.G. Gmelin) P.C. Silva	64.12 ± 90.68	1.93 ± 2.72	2.13 ± 3.70			1.62 ± 5.20
Gracilaria bursa-pastoris (S.G. Gmelin) P.C. Silva						
Gracilaria corallicola Zanardini	5.12 ± 5.12	3.65 ± 0.35	1,936.06 ± 2,633.57	2.62 ± 3.70		49.43 ± 151.74
Gracilaria sp.	17.02 ± 28.06	0.68 ± 0.06	3.16 ± 5.47			1.34 ± 3.45
Griffithsia sp.						0.01 ± 0.02
Haliptilon virgatum (Zanardini) Garbary *et* H.W. Johansen						0.16 ± 0.63
Halopithys incurva (Hudson) Batters	742.69 ± 832.77	14.19 ± 16.55	48.18 ± 65.19			21.16 ± 32.50
Halymenia elongata C. Agardh	2.00 ± 4.46					1.60 ± 5.45
Halymenia latifolia 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					
Haraldia lenormandii (Derbès *et* Solier) Feldmann				0.08 ± 0.14		0.33 ± 1.26
Hypnea spinella (C. Agardh) Kützing	5.42 ± 11.86					0.03 ± 0.11

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Hypoglossum hypoglossoides (Stackhouse) F.S. Collins et Hervey	1.33 ± 1.89		2.99 ± 4.23			0.27 ± 0.68
Irvinea boergesenii (Feldmann) R.J. Wilkes, L.M. McIvor *et* Guiry				0.05 ± 0.08		0.02 ± 0.08
Kallymenia feldmannii Codomier				2.82 ± 4.88		0.05 ± 0.21
Kallymenia patens (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
Kallymenia requienii (J. Agardh) J. Agardh	9.90 ± 8.91		382.12 ± 514.12	80.17 ± 114.02		19.07 ± 36.35
Kallymenia sp.	80.14 ± 95.60		447.25 ± 774.65	0.71 ± 1.23		8.01 ± 21.62
Laurencia chondrioides Børgesen	25.99 ± 34.51					1.08 ± 2.70
Leptofauchea coralligena Rodríguez-Prieto *et* O. De Clerck	40.57 ± 28.39	3.46 ± 4.89	130.80 ± 140.77	3.49 ± 3.32		7.24 ± 9.22
Lithothamnion corallioides (P.L. Crouan et H.M. Crouan) 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
Lithothamnion valens Foslie	197.44 ± 308.70	1.75 ± 1.70	1.086.11 ± 18.30	45.98 ± 40.08	76.55	61.17 ± 83.92
Lomentaria subdichotoma Ercegovic			2.35 ± 4.06			0.08 v 0.22
Lomentaria sp.	0.29 ± 0.66					
Lophocladia lallemandii (Montagne) F. Schmitz[a]		0.04 ± 0.06				0.01 ± 0.03
Meredithia microphylla (J. Agardh) J. Agardh	3.24 ± 7.25		75.84 ± 74.06	0.34 ± 0.58	0.65	0.44 ± 1.01
Mesophyllum expansum (Philippi) Cabioch *et* Mendoza		7.58 v 10.71				

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Myriogramme minuta Kylin						0.01 ± 0.02
Myriogramme tristomatica (J.J. Rodríguez ex Mazza) Boudouresque	23.79 ± 32.59	0.07 ± 0.09	139.48 ± 130.12	10.97 ± 10.55		5.26 ± 7.11
Nemastoma dumontioides J. Agardh						0.01 ± 0.01
Neurocaulon foliosum (Meneghini) Zanardini	14.02 ± 31.35		85.25 ± 144.36	0.42 v 0.72		0.20 ± 0.60
Nitophyllum flabellatum Ercegovic	0.23 ± 0.51					
Nitophyllum punctatum (Stackhouse) Greville			73.21 ± 95.27	1.77 ± 1.54		0.21 ± 0.60
Osmundaria volubilis (Linnaeus) R.E. Norris	10,884.44 ± 6,836.62	5.69 ± 1.49	13,729.07 ± 2,650.39	16.02 ± 9.65		291.04 ± 343.42
Osmundea pelagosae (Schiffner) K.W. Nam	351.88 ± 314.45	1.10 ± 1.56	13.11 ± 12.52	0.15 ± 0.27		11.24 ± 28.76
Peyssonnelia aff. *magna* Ercegovic			347.99 ± 602.74			
Peyssonnelia armorica (P.L. Crouan *et* H.M. Crouan) Weber-van Bosse						0.64 ± 2.47
Peyssonnelia armorica (P.L. Crouan *et* H.M. Crouan) Weber-van Bosse						
Peyssonnelia bornetii Boudouresque *et* Dezinot	0.71 ± 1.59		2,440.80 ± 4,135.88			1.18 ± 3.34
Peyssonnelia dubyi P.L. Crouan *et* H. M. Crouan			79.80 ± 138.22			0.86 ± 3.24
Peyssonnelia harveyana P.L. Crouan *et* H.M. Crouan ex J. Agardh	1.28 ± 2.86		619.88 ± 926.97	4.96 ± 8.59		3.59 ± 11.36
Peyssonnelia inamoena Pilger	317.21 ± 401.10	186.06 ± 82.36	19,001.68 ± 17,403.53	7.69 ± 0.68		23.73 ± 25.08
Peyssonnelia rosa-marina Boudouresque *et* Dezinot	536.12 ± 1,072.35	27.76 ± 12.88	4,021.27 ± 2,975.42			22.39 ± 74.75

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Peyssonnelia rubra (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
Peyssonnelia squamaria (S.G. Gmelin) Decaisne	14.76 ± 16.72	3.51 ± 4.96	2,840.27 ± 4,749.76	1.87 ± 3.03	14.62	2.23 ± 3.98
Peyssonnelia stoechas Boudouresque *et* Dezinot			18.39 ± 16.29	0.94 ± 1.63		0.02 ± 0.07
Peyssonnelia sp.		9.06 ± 12.81	1,191.59 ± 1,878.57			0.18 ± 0.38
Phyllophora crispa (Hudson) P.S. Dixon	7,563.80 ± 4,533.60	28.95 ± 34.08	36,432.34 ± 1,784.54	386.73 ± 110.43	0.72	936.69 ± 938.63
Phyllophora heredia (Clemente) J. Agardh	38.41 ± 28.84	1.02 ± 1.44	2,106.79 ± 1,081.54	100.45 ± 170.53		5.85 ± 12.40
Phymatolithon calcareum (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
Plocamium cartilagineum (Linnaeus) P.S. Dixon		0.06 ± 0.08	7.92 ± 7.87	1.27 ± 1.64		0.45 ± 0.77
Polysiphonia elongata (Hudson) Sprengel	304.56 ± 430.81		45.44 ± 46.42			17.69 ± 57.89
Polysiphonia ornata J. Agardh						0.06 ± 0.18
Polysiphonia perforans Cormaci, G. Furnari, Pizzuto *et* Serio			4.95 ± 7.65			0.01 ± 0.01
Polysiphonia subulifera (C. Agardh) Harvey	841.80 ± 1,523.19	10.21 ± 14.44	0.80 ± 1.38			22.88 ± 60.16
Polysiphonia subulifera (C. Agardh) Harvey						
Polysiphonia sp. 1	538.07 ± 1,067.31	0.07 ± 0.09	130.22 ± 222.25			23.49 ± 81.76
Polysiphonia sp. 2	0.92 ± 2.06					
Pterothamnion crispum (Ducluzeau) Nägeli						0.39 ± 1.29

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Pterothamnion plumula (J. Ellis) Nägeli						0.06 ± 0.16
Radicilingua reptans (Kylin) 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
Rhodymenia sp.	83.25 ± 149.50	5.80 ± 8.20	1,158.36 ± 1,147.10	1.04 ± 1.80		10.77 ± 13.20
Rodriguezella pinnata (Kützing) F. Schmitz ex Falkenberg	21.07 ± 47.11		72.58 ± 117.34			0.07 ± 0.28
Rodriguezella strafforelloi F. Schmitz ex J.J. Rodríguez y Femenías	33.96 ± 70.56		90.62 ± 52.02			0.08 ± 0.31
Rytiphlaea tinctoria (Clemente) C. Agardh	916.19 ± 995.63	0.07 ± 0.10	1,199.27 ± 1,958.53			21.88 ± 45.83
Sebdenia dichotoma Berthold	11.55 ± 19.14					0.29 ± 1.12
Sebdenia monardiana (Montagne) Berthold						0.34 ± 1.30
Sebdenia rodrigueziana (Feldmann) Codomier ex Parkinson			26.84 ± 46.49			
Sphaerococcus coronopifolius Stackhouse	99.05 ± 127.57	0.21 ± 0.30	3,685.12 ± 3,294.16	0.25 ± 0.43		11.69 ± 25.53
Sphaerococcus rhizophylloides J.J. Rodríguez y Femenías	75.58 ± 166.86		579.73 ± 478.23			11.36 ± 31.89
Sphondylothamnion multifidum (Hudson) Nägeli	0.22 ± 0.48					
Spongites fruticulosus Kützing	784.16 ± 1,040.53	34.34 ± 38.71	508.81 ± 385.12	241.69 ± 101.88	190.91	166.72 ± 220.93
Wrangelia penicillata (C. Agardh) C. Agardh						0.11 ± 0.42

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Phaeophyceae (Ochrophyta)						
'Aglaozonia chilosa' Falkenberg stage	5.65 ± 5.37	0.15 ± 0.21				0.17 ± 0.37
Arthrocladia villosa (Hudson) Duby		0.21 ± 0.30				
Asperococcus bullosus J.V. Lamouroux						0.25 ± 0.66
Carpomitra costata (Stackhouse) Batters						0.02 ± 0.07
Cladostephus spongiosus (Hudson) C. Agardh		0.48 ± 0.67				1.80 ± 4.98
Cutleria chilosa (Falkenberg) P.C. Silva			426.70 ± 739.07			
Cystoseira spinosa var. *compressa* (Ercegovic) M. Cormaci, G. Furnari, G. Giaccone, B. Scammacca *et* D. Serio	196.80 ± 352.67	69.15 ± 97.79	119.99 ± 207.83			3.47 ± 5.49
Cystoseira zosteroides C. Agardh			129.75 ± 224.74			30.22 ± 100.62
Cystoseira sp.				4.18 ± 7.23		0.33 ± 1.29
Dictyopteris lucida M. A. Ribera Siguan, A. Gómez Garreta, Pérez Ruzafa, Barceló Martí *et* Rull Lluch	0.23 ± 0.51					5.67 ± 10.76
Dictyopteris polypodioides (A.P. De Candolle) J.V. Lamouroux						12.50 ± 48.39
Dictyota dichotoma (Hudson) J.V. Lamouroux	372.74 ± 573.53	8.56 ± 12.10	31.54 ± 26.77			143.73 ± 303.15
Halopteris filicina (Grateloup) Kützing	1,615.52 ± 3,283.85	66.78 ± 87.13	698.93 ± 946.35	405.91 ± 695.66		611.30 ± 983.66
Hincksia sandriana (Zanardini) P.C. Silva						0.05 ± 0.19

	Ov/Pc_m	Pi_b	Pr_b	Lr_b	M_b	Pc/Hf_m
Laminaria rodriguezii Bornet	800.81 ± 895.50	1.03 ± 1.45	2,346.45 ± 1,793.91	16,285.86 ± 6,008.32		263.80 ± 385.78
Sphacelaria sp.						0.02 ± 0.08
Sporochnus pedunculatus (Hudson) C. Agardh		0.42 ± 0.59				
Zanardinia typus (Nardo) P.C. Silva	181.78 ± 337.31	3.37 ± 4.77				5.24 ± 19.84
Zonaria tournefortii (J.V. Lamouroux) Montagne	79.37 ± 164.91	0.70 ± 0.98	11.97 ± 20.73	3.90 ± 3.45		3.88 ± 6.21
Chlorophyta						
Caulerpa cylindracea Sonder[a]						1.14 ± 3.22
Codium bursa (Olivi) C. Agardh	90.27 ± 168.62	17.91 ± 17.24	4,827.05 ± 7,427.34			27.11 ± 51.43
Flabellia petiolata (Turra) Nizamuddin	101.91 ± 53.58	11.53 ± 11.07	1,000.52 ± 820.63	144.78 ± 168.93	19.03	183.55 ± 325.93
Halimeda tuna (J. Ellis *et* Solander) J.V. Lamouroux	0.54 ± 1.20		94.80 ± 164.19	8.61 ± 14.92		
Microdictyon tenuius J.E. Gray	5.60 ± 10.45		1.78 ± 3.09			0.80 ± 2.23
Palmophyllum crassum (Naccari) Rabenhorst	6.03 ± 12.00		79.18 ± 68.97			0.97 ± 2.42
Umbraulva olivascens (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
Valonia macrophysa Kützing	1.68 ± 2.43	4.63 ± 4.91	135.84 ± 87.38			0.67 ± 1.66

Table 2 – Algal surface area per haul (Sa_{iH}, 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. a Invasive 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.

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 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 ± 15,358 cm^2 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 ± 495,000 cm^2 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 ± 31,210 cm^2 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 fruticulosus* and *Lit. valens* and had a very low number of species (10) and Sa_{TH} (306 cm^2 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 ± 5005 cm^2 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 fruticulosus* were the most abundant species in this group, with 38 ± 9 species and an Sa_{TH} of 3511 ± 1963 cm^2 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 fruticulosus* 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, de Buen 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, Piazzi *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 fruticulosus* 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 cylindracea*, *Asparagopsis taxifomis*, and *Lophocladia lallemandii* were found only occasionally and they were never abundant. Only *Caulerpa 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.

Acknowledgements

We acknowledge the Spanish Institute of Oceanography (IEO) for the organization and provision of all facilities needed for the sampling surveys. We also thank the crew of the R/V *Cornide de Saavedra* and the participants who took part in the MEDITS_ES05 surveys for their help and support during the sampling missions. We would like to thank Marc Verlaque, Giovanni Furnari, and Julio Afonso Carrillo for taxonomic help and Natàlia Comalada and Núria Orra for helping in laboratory tasks. Sampling surveys were supported by the EVADEMED and INDEMARES projects financed by the IEO and the European Union. Emma Cebrian's research was funded by the Juan de la Cierva program (MICINN-JDC).

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Errata

Table 1. The Sa_{TH} ($cm^2\ m^{-2}$) data from the *Peyssonnelia inamoena* beds (Pi_b) is 620±495, not 620,000±495,000.

III-2. Contribution to the study of deep coastal detritic bottoms: the algal communities of the continental shelf off the Balearic Islands, Western Mediterranean

Abstract

Three main algal-dominated coastal detritic communities from the continental shelf off Mallorca and Menorca (Balearic Islands, Western Mediterranean) are described herein: maërl beds dominated by *Spongites fruticulosus* and forests of *Laminaria rodriguezii* located in the Menorca channel, and *Peyssonnelia inamoena* beds found along the Southern coast of Menorca. There seems to be a gradient of disturbance from the highly disturbed *Peyssonnelia* beds to the almost undisturbed *L. rodriguezii* forests. Whether this gradient is the result of current and past anthropogenic pressure (e.g. trawling intensity) or is driven by natural environmental factors needs further assessment. Finally, the location of the target communities by means of ROV dives combined with the use of a Box-Corer dredge and beam trawl proved to be a good methodology in the study of the composition and structure of these deep-water detritic communities.

Keywords: detritic bottoms, *Laminaria rodriguezii*, macroalgae, sampling methods, Mediterranean Sea, *Peyssonnelia inamoena*, *Spongites fruticulosus*.

Introduction

Mediterranean algal-dominated coastal detritic bottoms usually develop at depths between 25 and 130 m (Pérès 1985, Giaccone *et al*. 1994). They are composed of silt, sand, gravels, and calcareous skeletons of benthic organisms such as molluscs, bryozoans, cnidarians, echinoderms and macroalgae. Free-living members of the orders Corallinales and Peyssonneliales (Pérès 1985, Klein and Verlaque 2009) are usually the major components of these bottoms. Both the skeletons and the calcareous algae allow the settlement and growth of organisms usually found on rocky bottoms (Bianchi 2001), creating a special habitat harbouring animals and plants of both soft and hard bottoms (Laborel 1987).

Different assemblages have been recognized in Mediterranean algal-dominated coastal detritic bottoms, each one characterized by either one or a reduced number of more or less exclusive species (e.g. see Dieuzede 1940, Huvé 1954, 1956, Jacquotte 1962, Pérès and Picard 1964, Picard 1965, Giaccone, 1967, Bourcier 1968, Augier and Boudouresque 1978, Ballesteros 1988, 1994, Giaccone *et al*. 1994). The Balearic Islands harbour extensive areas of these kinds of bottoms and different seascapes have been described between 52 and 93 m, using bottom trawls (Joher *et al*. 2012): maërl beds dominated by *Spongites fruticulosus*, deep-water forests of *Laminaria rodriguezii*, two types of *Peyssonnelia* beds (one dominated by *P. inamoena* and the other one by *P. rubra,* both species presenting hypobasal calcification, and the last one presenting some cystolists too), and red algae meadows dominated by *Osmundaria volubilis* and *Phyllophora crispa*.

However, although bottom trawling was effective for the characterization of underwater landscapes, descriptions at community level require the use of smaller sampling areas. Several ROV dives were performed in 2009 in the Menorca channel and along the Southern coast of Menorca (Barberá *et al*. 2009, 2012) in order to locate certain homogeneous areas harbouring the communities that characterized the seascapes found by Joher *et al*. (2012). Three of these areas were located: one with maërl beds of *S. fruticulosus*, another with forests of *L. rodriguezii*, and a last one with *P. inamoena* beds. In contrast, extensive areas covered by the assemblage dominated by *Osmundaria volubilis* and *Phyllophora crispa* were found*,* with a patchy distribution.

Maërl beds dominated by *S. fruticulosus* have seldom been reported from the Balearic Islands (Barberá *et al*. 2012), and their composition and structure have only been studied from Tossa de Mar (Northwestern Mediterranean, Spain) (Ballesteros 1988), where the maërl bed grows in reduced light levels (around 0.3 % of surface PAR irradiance) and moderate temperature range conditions (12.5 to 21.5ºC). Forests of *L. rodriguezii* develop under low light intensities (usually at depths between 50 and 120 m, being more abundant below 70 m), low temperature (less than 14ºC), and unidirectional current conditions (Feldmann 1934, Huvé 1955, Molinier 1960, Pérès and Picard 1964, Giaccone 1967, 1971, Lüning 1990, Giaccone and Di Martino 1997). Most information available about these rarefied kelp forests focuses on species composition although there are no quantified lists of species (Huvé 1955, Molinier 1956, Gautier and Picard 1957). Finally, several authors have reported *Peyssonnelia* beds developing on circalittoral bottoms, mainly along the coasts of Marseille, the Tyrrhenian Sea and the Balearic Islands (e.g. Huvé 1954, Carpine 1958, Parenzan 1960, Augier and Boudouresque 1978, Basso 1990, Ballesteros 1994, Joher *et al*. 2012), highlighting the variety of the dominant *Peyssonnelia* species. These beds also develop under low light conditions but they seem to need pulsing current conditions, which prevent the burial of living *Peyssonnelia* spp. (Bourcier 1968, Basso 1990). Two kinds of *Peyssonnelia* beds, one dominated by *P. rosa-marina* and the other by an unidentified *Peyssonnelia* have been reported previously from the Balearic Islands (Ballesteros 1994), but there is no published information on the beds dominated by *P. inamoena*.

The purpose of this paper is to describe the species composition and abundance of three specific communities from the detritic bottoms off the Balearic Islands (*S. fruticulosus, L. rodriguezii* and *P. inamoena*), which characterized three of the landscapes described previously in Joher *et al.* (2012). Another objective was to check whether Box-Corer dredging and beam trawling, combined with ROV images, are suitable methodologies to characterize deep-water coastal detritic communities.

Materials and methods

The sampling area was located in the Menorca channel and along the Southern coast of Menorca (the Balearic Islands, Western Mediterranean; Fig. 1). The continental shelf bottoms of this area are characterized by sediments of biogenic origin (Canals and Ballesteros 1997, Fornós and Ahr 1997) with a high percentage of carbonates (Acosta *et al*. 2002), and the

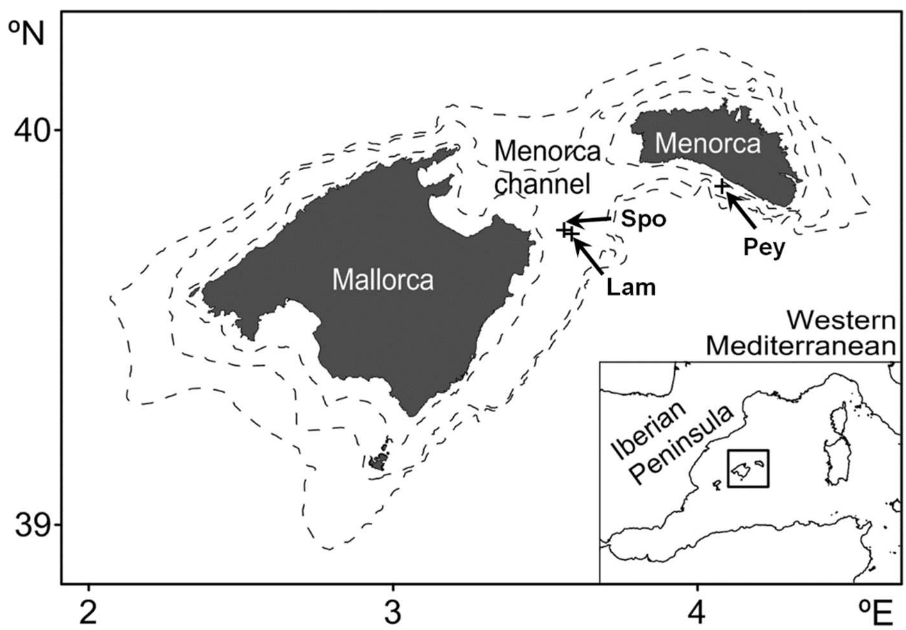

Figure 1 – Sampling locations of the three communities studied in the Menorca Channel and the Southern coast of Menorca. Isobaths of -50, -100 and -200 m are shown. Abbreviations: Spo, *Spongites fruticulosus* beds; Lam, forests of *Laminaria rodriguezii*; Pey, *Peyssonnelia inamoena* beds.

water column presents a high light transmittance (Ballesteros and Zabala 1993, Canals and Ballesteros 1997).

Sampling was performed in May 2009, during the MEDITS_ES05_09 campaign organized by the Centre Oceanogràfic de Balears (Instituto Español de Oceanografía). Target communities had been located previously by ROV during the CANAL0209 research survey (February-March 2009): large areas were occupied by the communities with *Spongites fruticulosus* and *Laminaria rodriguezii* in the Menorca channel at depths between 50 and 62 m, while the community dominated by *Peyssonnelia inamoena* was found on the Southern coast of Menorca, at depths of around 65 m.

Because of the deep-water distribution of these communities, we did not sample them by Scuba diving but used other sampling methods: dredges (e.g. see Dieuzede 1940, Huvé 1956, Costa 1960, Bourcier 1968, Blunden *et al.* 1977, Bordehore *et al.* 2003, Peña 2010) and beam trawls (Barberá *et al*. 2012, Ellis *et al*. 2013). Images obtained by ROV, together with previous results (Joher *et al*. 2012), showed that the community dominated by *S. fruticulosus* was very homogeneous, and composed mainly of small maërl-forming species (*S. fruticulosus* and *Phymatolithon calcareum*). Then, samples were collected using a Box-Corer dredge (sampling area: 200 cm^2). In contrast, communities with *L. rodriguezii* and *P. inamoena* were more heterogeneous because of the size of the algae and the aggregation in clusters of the thalli of the characteristic species. There, the use of a Box-Corer was disregarded, and samples were collected using a beam trawl (horizontal and vertical openings: 1.30 and 0.88 m, respectively; mesh size: 10 mm), at speeds of 2.5-3.0 knots. Trawling time ranged from 5 to 12 seconds and was controlled by a SCANMAR system (Scanmar Maritime Services Inc., Makati City, Philippines) in order to calculate the trawled area, which ranged from 6 to 16 m^2.

We collected seven samples of the *S. fruticulosus* community, which were integrally quantified, and two from the *L. rodriguezii* and *P. inamoena* communities. All samples were preserved on board in 4% formalin:seawater. Samples of *L. rodriguezii* and *P. inamoena* were homogeneously extended occupying the corresponding sampled surface, and we took two replicates of 1.2x1.2 m^2 per sample. Samples and replicates were named *C s-r*, where *C* corresponds to each community, *s* to each sample, and *r* to each replicate. Then, they were sorted and identified to the minimum taxonomic level, and each taxon was quantified measuring its algal surface (Sa_i, in cm^2) and biomass (B_i, as dry weight in g) (Ballesteros 1992). Skeletons of dead Corallinales were rejected because we only wanted to quantify live specimens.

Several synthetic parameters were calculated for each sample/replicate: a) the number of species, total algal surface (Sa_T) and total biomass (B_T); b) the Index of Floral Originality (IFO = $(\sum 1/M_i)/n$), where M_i is the number of samples in which the species i occurred and n the number of species in the sample; c) the total algal surface and biomass of the maërl-forming species (MFS_{Sa}, MFS_B); d) Shannon's diversity index ($H' = -\sum p_i \log_2 p_i$), where p_i corresponds to the proportion of the measured parameter (Sa_i/Sa_T or B_i/B_T) for each species; and e) Pielou's evenness index ($J' = H'/\log_2 S$), where H' was based both on algal surface and biomass.

In order to verify the grouping of the samples, cluster analysis accompanied by the SIMPROF test (Clarke *et al*. 2008) adjusted to 9999 permutations and a 0.1% significance level according to Potter *et al*. (2001), based on Sørensen and Bray-Curtis similarity matrices, were performed for each community. Finally, SIMPER tests were used to calculate species contribution to the similarities within each of the three studied communities and their characteristic species. These analyses were performed with PRIMER version 6 software (Clarke and Warwick 2001).

Results

We identified up to 143 algal taxa at specific and infraspecific level (below named species for convenience) (Table 1), although some of them could not be identified to species level because either we had only small fragments of the specimens, they were sterile (e.g. *Aglaothamnion* sp., *Peyssonnelia* sp., *Polysiphonia* sp., unidentified Rhodophyta), or they are probably undescribed species (e.g. *Halymenia* sp., *Rhodymenia* sp.).

A total of 57 algal species were identified on the *Spongites fruticulosus* beds (Table 2), with a dominance (84.6 %) of Rhodophyta (Fig. 2). The number of species per sample was 16±5; the Sa_T per sample 3965±2838 $cm^2\ m^{-2}$; and the B_T per sample 351±270 g dw m^{-2}. Maërl-forming species represented 76.8±21.5 % of total Sa_T per sample, and 94.5±3.7 % of B_T (Fig. 3). The characteristic species of these maërl beds were *S. fruticulosus* and *Phymatolithon calcareum* (SIMPER test, Fig. 4), which accounted for 80 % of Sa_T and 82.6 % of B_T. It should be noted that despite statistical analyses (cluster + SIMPROF), based both on qualitative and algal surface data, indicated that the samples belonged to a single significant group; sample Spo III grouped separately from the other samples in the analysis based on biomass because it presented an extremely low biomass compared to the rest of the samples.

A total of 104 species were identified in samples collected from *Laminaria rodriguezii* forests (Table 2), with Rhodophyta accounting for 85.6 % of the species (Fig. 2). This community presented a mean of 64±8 species per replicate, a Sa_T of 3653±817 cm^2 m^{-2} and a B_T of 106±42 g dw m^{-2} (Fig. 3). The species *Phyllophora crispa*, *Spongites fruticulosus*, *Peyssonnelia coriacea*, *Laminaria rodriguezii*, *Flabellia petiolata* and *Peyssonnelia rubra*, in this order, were found to be the main characterizing species in terms of algal surface, according to the SIMPER test (Fig. 4). Maërl-forming species represented 21.8±5.7 % of Sa_T but 76.3±5.0 % of B_T, and consequently, as regards biomass, the SIMPER test indicated that the main species were the Corallinales *Spongites fruticulosus*, *Phymatolithon calcareum* and *Lithothamnion valens* (Fig. 4). Statistical analyses based on both qualitative and quantitative data showed no significative differences between replicates of both samples.

A total of 106 species were identified in the community with *Peyssonnelia inamoena* (Table 2), with Rhodophyta accounting for 85.8 % of the species (Fig. 2). The number of species per replicate was 62±14; Sa_T was 1661±1118 cm^2 m^{-2}; and B_T 34±29 g dw m^{-2} (Fig. 3). While the SIMPER test for algal surface indicated that *P. inamoena* and *P. rubra* were the most characteristic species, the analysis performed with the biomass data revealed four *Peyssonnelia* species: *P. inamoena*, *P. rosa-marina*, *P. harveyana* and *P. rubra* (Fig. 4). In this community, maërl-forming species accounted for

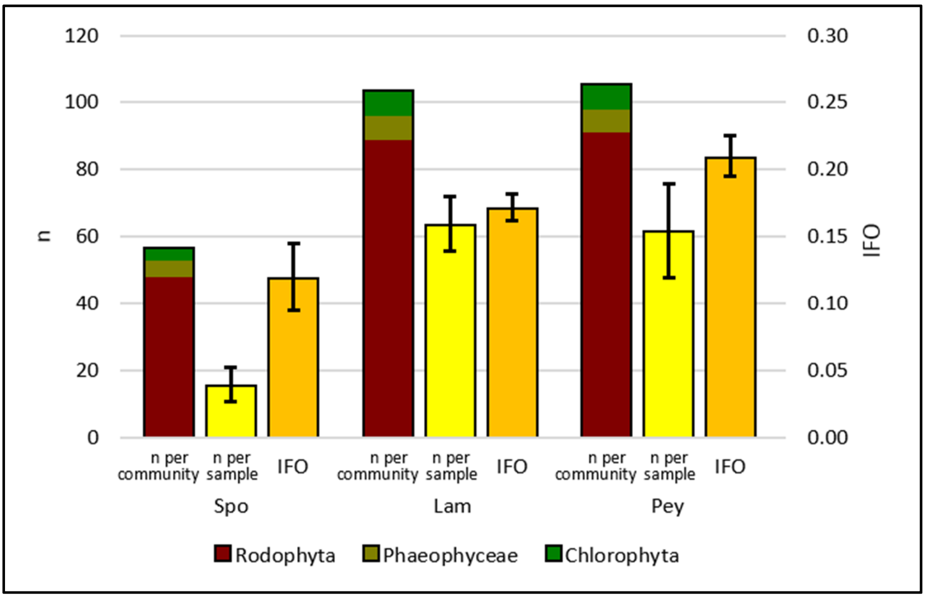

Figure 2 – Number of species (n) per community showing Rhodophyta, Phaeophyceae and Chlorophyta, and number of species and Index of Floral Originality (IFO) per sample (mean and standard deviation). Abbreviations: Spo, *Spongites fruticulosus* beds; Lam, *Laminaria rodriguezii* forests; Pey, *Peyssonnelia inamoena* beds.

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Location	MC	MC	MC	MC	MC	MC	MC	MC	MC	MC	MC	SM	SM	SM	SM
Depth (m)	-110	-110	-110	-110	-110	-110	-110	-61	-61	-62	-62	-64	-64	-65	-65
Date of collection	13/05 /2009	13/05 /2009	13/05 /2009	13/05 /2009	13/05 /2009	13/05 /2009	13/05 /2009	15/05 /2009	15/05 /2009	15/05 /2009	15/05 /2009	19/05 /2009	19/05 /2009	19/05 /2009	19/05 /2009
Rhodophyta															
Acrochaetium sp.					10.0			0.4	0.1	0.1	0.1	0.1	0.1		0.1
					0.100			0.004	0.001	0.001	0.001	0.001	0.001		0.001
Acrosorium ciliolatum (Harvey) Kylin												0.1			
												0.001			
'Acrosymphytonema breemaniae' (stadium) Boudouresque, Perret-Boudouresque & Knoepffler-Peguy *nom. inval.*												0.1			
												0.001			
Acrothamnion preissii (Sonder) E.M. Wollaston*								2.8	5.2	2.8	3.3	7.2	5.4	1.7	2.0
								0.028	0.031	0.028	0.022	0.036	0.021	0.007	0.016
Aglaothamnion tenuissimum (Bonnemaison) Feldmann-Mazoyer					5.0			0.2	9.8			0.1	0.1		
					0.050			0.002	0.099			0.001	0.001		
Aglaothamnion tripinnatum (C. Agardh) Feldmann-Mazoyer								29.1		0.1					
								0.292		0.001					

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Aglaothamnion sp.										0.1		0.1			
										0.001		0.001			
Antithamnion sp.					5.0								0.1		
					0.050								0.001		
Apoglossum ruscifolium (Turner) J. Agardh				5.0				2.2	0.8	3.1	0.1		0.1		0.1
				0.050				0.001	0.028	0.016	0.001		0.001		0.001
Bonnemaisonia asparagoides (Woodward) C. Agardh												0.4			1.3
												0.073			0.013
Bonnemaisonia sp.				5.0									0.1		
				0.050									0.001		
Botryocladia botryoides (Wufen) Feldmann									0.1						
									0.001						
Botryocladia chiajeana (Meneghini) Kylin								0.4	0.6	0.3		0.3	0.5		
								0.014	0.007	0.007		0.001	0.005		
Brongniartella byssoides (Goodenough & Woodward) F. Schmitz												0.1		0.1	
												0.001		0.001	
Callophyllis laciniata (Hudson) Kützing												0.2	0.8	5.3	
												0.002	0.004	0.023	

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Ceramium bertholdii Funk					5.0			0.1							0.1
					0.050			0.001							0.001
Ceramium codii (H. Richards) Mazoyer												0.1	0.1	0.1	0.1
												0.001	0.001	0.001	0.001
Champia parvula (C. Agardh) Harvey									0.2						
									0.007						
Chrysymenia ventricosa (J.V. Lamouroux) J. Agardh											0.1				
											0.001				
Chylocladia verticillata (Lightfoot) Bliding								0.6	0.1				0.1		
								0.014	0.001				0.001		
Contarinia peyssonneliaeformis Zanardini	207.5							0.3	0.3			4.3			
	1.038							0.002	0.001			0.021			
Cordylecladia erecta (Greville) J. Agardh cf			5.0												
			0.050												
Cryptonemia lomation (Bertoloni) J. Agardh									7.8	3.0			0.1		0.1
									0.049	0.015			0.001		0.001
Cryptonemia longiarticulata Funk species inquirendum										0.9		1.9			
										0.005		0.007			

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Cryptonemia tuniformis (A. Bertoloni) Zanardini	9.0		40.0	120.0	48.0	5.0	15.0	8.4	0.5	0.6	1.6	26.1	25.0	2.5	0.5
	0.050		0.245	1.075	0.410	0.050	0.065	0.043	0.007	0.028	0.007	0.127	0.136	0.015	0.003
Cryptopleura ramosa (Hudson) L. Newton			5.0					2.4	0.1			4.7	6.6	6.7	4.1
			0.050					0.014	0.001			0.023	0.027	0.021	0.020
Dasya corymbifera J. Agardh			10.0												
			0.100												
Dasya penicillata Zanardini							5.0						0.1	0.1	0.1
							0.050						0.001	0.001	0.001
Dermatolithon sp.										0.1					
										0.001					
Erythroglossum balearicum J. Agardh *ex* Kylin	13.0	5.0	5.0					1.3	0.9		0.5		0.1		0.1
	0.100	0.050	0.050					0.001	0.007		0.007		0.001		0.001
Erythroglossum sandrianum (Kützing) Kylin									0.1						
									0.001						
Erythrotrichia carnea (Dillwyn) J. Agardh								0.1	0.1						
								0.001	0.001						
Eupogodon planus (C. Agardh) Kützing				5.0								1.5	0.9	0.4	0.1
				0.050								0.006	0.005	0.003	0.001

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Felicinia marginata (Roussel) Manghisi, Le Gall, Ribera, Gargiulo et M. Morabito								6.9	78.1			2.4	1.6		
								0.069	0.781			0.014	0.008		
Gloiocladia furcata (C. Agardh) J. Agardh						5.0		0.3			0.1	0.5	0.8	0.7	0.9
						0.050		0.001			0.001	0.003	0.005	0.005	0.004
Gloiocladia microspora (Bornet ex J.J. Rodríguez y Femenías) Berecibar, M.J.Wynne, Barbara & R.Santos								0.3	50.0	58.3	59.9	1.9		0.6	0.2
								0.001	0.340	0.292	0.285	0.017		0.002	0.002
Gloiocladia repens (C. Agardh) Sánchez & Rodríguez-Prieto								2.2	52.4	63.7	11.5				
								0.035	0.594	0.465	0.076				
Gracilaria corallicola Zanardini					12.0			1.5	1.8	10.8	0.2	11,1	23,3		0,7
					0.105			0.014	0.018	0.039	0.002	0.066	0.085		0.006
Halymenia sp.										0.6				0.3	
										0.003				0.001	
Haraldia lenormandii (Derbès & Solier) Feldmann									0.1						
									0.001						
Hydrolithon farinosum (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain								7.4	0.3	0.1	0.1	0.1			
								0.699	0.003	0.001	0.006	0.001			

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Hypoglossum hypoglossoides (Stackhouse) F.S. Collins & Hervey		9.0	5.0	56.0	154.0		5.0	1.8	0.8	0.1	0.5	0.0		0.2	0.1
		0.070	0.050	0.125	0.250		0.050	0.015	0.008	0.001	0.007	0.000		0.001	0.001
Irvinea boergesenii (Feldmann) R.J. Wilkes, L.M. McIvor & Guiry		5.0	5.0	6.0	5.0		5.0	0.4	0.6	0.1	0.1	0.2	0.1	0.2	0.3
		0.050	0.050	0.050	0.050		0.050	0.014	0.007	0.001	0.007	0.002	0.002	0.002	0.001
Jania virgata (Zanardini) Montagne								0.1							
								0.007							
Kallymenia feldmannii Codomier								0.7	5.9	0.7		0.1			
								0.014	0.015	0.003		0.001			
Kallymenia patens (J. Agardh) Codomier *ex* P.G. Parkinson								588.3	31.5	67.4	46.7	2.4	3.3	0.1	0.6
								3.266	0.190	0.674	0.203	0.015	0.016	0.001	0.004
Kallymenia requienii (J. Agardh) J. Agardh	20.0	130.0	14.0	19.5	14.0	30.0	5.0	18.0	8.4	9.9	27.3	4.0	2.2	4.4	0.3
	0.200	0.710	0.050	0.095	0.050	0.135	0.050	0.067	0.035	0.057	0.090	0.023	0.014	0.018	0.002
Kallymenia sp.								5.6	1.2	8.1		1.7			
								0.028	0.007	0.042		0.009			
Lejolisia mediterranea Bornet					5.0							0.3	0.1	0.1	
					0.050							0.003	0.001	0.001	
Leptofauchea coralligena Rodríguez-Prieto & De Clerk			2.0		5.0		18.0	2.2	1.0	0.7	0.4	2.0	3.5	1.9	0.4
			0.050		0.050		0.125	0.001	0.007	0.005	0.007	0.013	0.014	0.009	0.002

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Lithophyllum racemus (Lamarck) Foslie[#]								27.8							
								2.778							
Lithophyllum stictaeforme (Areschoug) Hauck[#]								11.8	0.4	16.0		0.5	0.8	1.4	3.0
								1.181	0.042	1.604		0.049	0.083	0.139	0.257
Lithophyllum sp. [#]															0.7
															0.069
Lithothamnion corallioides (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan[#]		100.0								25.1	27.8	29.3	18.6	6.9	4.5
		10.000								2.449	2.778	2.931	1.861	0.694	0.451
Lithothamnion valens Foslie[#]	375.0	900.0		1300.0	250.0	250.0	200.0	196.4	190.3	24.8	31.3	2.1	5.2	2.8	
	37.500	90.000		130.000	25.000	25.000	20.000	19.462	19.028	2.483	3.125	0.208	0.521	0.278	
Lomentaria clavellosa (Lightfoot ex Turner) Gaillon											0.8				
											0.008				
Lomentaria ercegovicii Verlaque, Boudouresque, Meinesz, Giraud & Marcot-Coqueugniot														0.1	
														0.001	
Lomentaria subdichotoma Ercegovic			20.0									0.1	0.1		0.1
			0.120									0.001	0.002		0.001
Lophosiphonia obscura (C. Agardh) Falkenberg												0.1			
												0.001			

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Melobesia membranacea (Esper) J.V. Lamouroux[#]									0.1			0.2	0.1		0.1
									0.001			0.002	0.001		0.001
Meredithia microphylla (J. Agardh) J. Agardh									42.1	17.2	3.5				
									0.272	0.118	0.014				
Mesophyllum alternans (Foslie) Cabioch & M.L. Mendoza[#]	25.0								2.4						
	2.500								0.243						
Mesophyllum expansum (Philippi) Cabioch & M.L. Mendoza[#]								0.2				5.9			
								0.021				1.381			
Monosporus pedicellatus (Smith) Solier									0.1						
									0.001						
Myriogramme carnea (J.J. Rodríguez y Femenías) Kylin								1.6				0.8		1.1	0.3
								0.001				0.006		0.008	0.002
Myriogramme tristromatica (J.J. Rodríguez y Femenías) Boudouresque								0.3	0.7	1.3	0.3	19.7	20.8	9.9	4.3
								0.014	0.014	0.001	0.007	0.072	0.079	0.042	0.015
Neogoniolithon mamillosum (Hauck) Setchell & L.R. Mason[#]							300.0	32.2				2.8			
							30.000	3.215				0.278			
Neurocaulon foliosum (Meneghini) Zanardini												0.3	3.5	0.2	
												0.004	0.031	0.004	

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Nitophyllum micropunctatum Funk								0.1							
								0.001							
Nitophyllum punctatum (Stackhouse) Greville											0.1				
											0.007				
Osmundaria volubilis (Linnaeus) R.E. Norris				720.0				137.8	166.7	40.1	30.6	0.6	0.8		0.7
				5.245				1.107	1.385	0.333	0.194	0.005	0.009		0.004
Osmundea pelagosae (Schiffner) K.W. Nam						5.0						0.3			
						0.050						0.003			
Peyssonnelia armorica (P.L. Crouan & H.M. Crouan) Weber-van Bosse								9.7	24.0	6.3	8.3		2.0		
								0.049	0.120	0.031	0.042		0.010		
Peyssonnelia bornetii Boudouresque & Denizot								81.8	111.6		2.6				83.3
								0.486	1.166		0.007				0.903
Peyssonnelia coriacea Feldmann								427.4	477.5	62.0	346.4	1.2	0.1		
								2.801	3.108	0.285	2.215	0.044	0.002		
Peyssonnelia dubyi P.L. Crouan & H.M. Crouan		5.0	5.0									0.1		6.1	0.1
		0.050	0.050									0.001		0.007	0.001
Peyssonnelia harveyana P.L. Crouan & H.M. Crouan ex J. Agardh			3.0					6.6	8.5	2.8	0.7	177.4	760.4	60.5	6.9
			0.050					0.165	0.213	0.070	0.018	4.435	19.010	1.513	0.173

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Peyssonnelia inamoena Pilger	94.0		17.5				0.150	1.444	0.177	1.485	3.535	14.653	8.392	3.366	2.339
	0.725		0.113				0.105	1.270	0.205	1.454	1.944	27.226	11.222	2.207	3.676
Peyssonnelia rosa-marina Boudouresque & Denizot[#]								21.9	12.5	15.0	18.4	161.8	116.0	15.3	1.4
								1.874	1.486	1.276	1.424	15.142	9.123	0.965	0.198
Peyssonnelia rubra (Greville) J. Agardh								400.6	542.2	208.3	23.5	760.4	322.9		505.8
								3.745	3.518	1.938	0.240	5.826	2.201		4.535
Peyssonnelia squamaria (S.G. Gmelin) Decaisne										458.2					5.6
										3.431					0.042
Peyssonnelia stoechas Boudouresque & Denizot										2.3					
										0.012					
Peyssonnelia sp.					5.0				0.4	9.6		0.2			
					0.050				0.001	0.048		0.001			
Phyllophora crispa (Hudson) P.S. Dixon		337.5						486.1	569.3	758.3	433.9	24.8	42.3	34.7	20.2
		2.400						4.321	4.867	6.507	3.354	0.149	0.285	0.232	0.150
Phyllophora herediae (Clemente) J. Agardh												0.3	0.6	1.1	
												0.004	0.006	0.010	
Phymatolithon calcareum (Pallas) W.H. Adey & D.L. McKibbin[#]	2100.0	2475.0	50.0	550.0	155.0	2075.0	700.0	35.9	219.2	55.4	99.3	4.5			
	210.000	247.500	5.000	55.000	15.500	207.500	70.000	3.594	21.877	5.366	9.931	0.451			

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Plocamium cartilagineum (Linnaeus) P.S. Dixon								1.4	0.3			1.4	0.8	0.9	0.4
								0.021	0.014			0.009	0.007	0.004	0.002
Polysiphonia ornata J. Agardh						5.0		0.1							
						0.050		0.001							
Polysiphonia perforans Cormaci, G. Furnari, Pizzuto & Serio								2.9							
								0.191							
Polysiphonia subulifera (C. Agardh) Harvey					46.0			0.1	2.4	3.2	0.2	0.7	0.1		0.1
					0.220			0.001	0.024	0.032	0.001	0.006	0.001		0.001
Polysiphonia sp.					5.0			262.0	7.1	0.1	8.5			1.6	
					0.050			2.618	0.072	0.001	0.085			0.016	
Pterothamnion crispum (Ducluzeau) Nägeli					5.0							0.1	0.1		0.1
					0.050							0.001	0.001		0.001
Pterothamnion plumula (J. Ellis) Nägeli				5.0											
				0.050											
Ptilocladiopsis horrida Berthold								0.1	0.1			0.1			
								0.001	0.001			0.001			
Ptilothamnion pluma (Dillwyn) Thuret				5.0	5.0				13.8		8.5	0.1			
				0.050	0.050				0.138		0.085	0.001			

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Ptilothamnion sp.													0.1		
													0.001		
Radicilingua thysanorhizans (Holmes) Papenfuss								0.1	2.1	1.7	0.1				
								0.014	0.007	0.007	0.007				
Radicilingua sp.											0.7				
											0.007				
Rhodophyllis divaricata (Stackhouse) Papenfuss										0.5					
										0.005					
Rhodophyllis strafforelloi Ardissone					4.5					1.6	1.4	9.9	0.1	0.9	0.7
					0.050					0.008	0.011	0.047	0.001	0.007	0.007
Rhodymenia sp.								0.5	0.4	10.8	0.2	30.7	1.2		2.0
								0.001	0.004	0.108	0.002	0.104	0.007		0.010
Rodriguezella bornetii (J.J. Rodríguez y Femenías) F. Schmitz ex J.J. Rodríguez y Femenías															2.3
															0.014
Rodriguezella pinnata (Kützing) F. Schmitz ex Falkenberg												0.1			
												0.001			
Rodriguezella strafforelloi F. Schmitz ex J.J. Rodríguez y Femenías													6.9		
													0.026		

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Rytiphlaea tinctoria (Clemente) C. Agardh														0.2	
														0.003	
Sahlingia subintegra (Rosenvinge) Kornmann											0.6	0.4	0.3		0.1
											0.015	0.004	0.003		0.001
Sebdenia rodrigueziana (Feldmann) Athanasiadis												0.1	0.1		
												0.000	0.001		
Sphaerococcus coronopifolius Stackhouse								4.7				14.2	8.9	4.0	2.6
								0.022				0.064	0.048	0.017	0.014
Sphaerococcus rhizophylloides J.J. Rodríguez y Femenías	21.0							36.8	64.9	109.4	58.4	1.5	0.1		0.3
	0.095							0.257	0.315	0.528	0.272	0.014	0.001		0.001
Spongites fruticulosus Kützing[#]	3475.0	3825.0	50.0	1500.0	585.0	850.0	1285.0	899.0	620.8	444.8	271.2	58.7	41.7	11.5	
	347.500	382.500	5.000	150.000	58.500	85.000	128.500	89.896	62.083	44.479	27.118	5.868	4.167	1.146	
Stylonema alsidii (Zanardini) K.M. Drew													0.1		0.1
													0.001		0.001
Titanoderma pustulatum (J.V. Lamouroux) Nägeli								0.2	0.1						
								0.017	0.001						
Titanoderma sp.		5.0						0.3				0.2	0.1	0.1	
		0.050						0.022				0.002	0.001	0.001	

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Titanoderma sp.		5.0						0.3				0.2	0.1	0.1	
		0.050						0.022				0.002	0.001	0.001	
Womersleyella setacea (Hollenberg) R.E. Norris*					5.0							0.1			
					0.050							0.001			
Unidentified Ceramiaceae				0.5					4.7						
				0.050					0.047						
Unidentified Corallinaceae	400.0	250.0		205.0	5.0		150.0	29.1	86.3	64.8	18.4	9.6	10.2	5.3	3.0
	40.000	25.000		20.500	0.050		15.000	0.991	7.010	1.106	1.840	0.924	1.006	0.522	0.299
Unidentified Delesseriaceae										0.3	0.1				
										0.002	0.001				
Unidentified Halymeniaceae								0.2							
								0.001							
Unidentified Rhodomelaceae				5.0					0.1						
				0.050					0.001						
Unidentified Rhodophyta 1												2.8	3.5	1.0	
												0.014	0.017	0.005	
Unidentified Rhodophyta 2								0.2		0.2					
								0.002		0.006					

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Phaeophyceae (Ochrophyta)															
Asperococcus bullosus J.V. Lamouroux												0.3			
												0.015			
Carpomitra costata (Stackhouse) Batters											93.9				
											0.939				
Cutleria chilosa (Falkenberg) P.C. Silva									1.4	0.3	0.1			0.4	
									0.001	0.003	0.007			0.004	
Dictyopteris lucida M.A. Ribera Siguán, A. Gómez Garreta, Pérez Ruzafa, Barceló Martí & Rull Lluch			10.0							0.2		3.5	0.1		0.6
			0.050							0.001		0.011	0.001		0.002
Dictyota dichotoma (Hudson) J.V. Lamouroux		3.5	14.0		98.0	12.5	5.0	47.2	15.8	21.5	8.7	0.1	2.7	0.5	0.6
		0.050	0.120		0.350	0.070	0.050	0.146	0.069	0.076	0.028	0.002	0.010	0.003	0.004
Halopteris filicina (Grateloup) Kützing		5.0	8.0		4.0		4.0	2.8	3.0	9.3	3.1	11.0	5.6	4.5	3.0
		0.050	0.050		0.050		0.050	0.014	0.014	0.028	0.007	0.033	0.021	0.010	0.019
Laminaria rodriguezii Bornet								121.5	88.0	593.2	359.0				
								0.826	0.472	3.285	2.368				
Sphacelaria plumula Zanardini					5.0	10.0									
					0.050	0.100									

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Zanardinia typus (Nardo) P.C. Silva								7.8	16.7	12.2	20.4				
								0.097	0.153	0.138	0.215				
Zonaria tournefortii (J.V. Lamouroux) Montagne	36.0											0.6	0.6		0.5
	0.125											0.008	0.004		0.005
Unidentified encrusting Phaeophyceae													2.1		
													0.021		
Chlorophyta															
Cladophora sp.									0.1						0.1
									0.001						0.001
Derbesia tenuissima (Moris & De Notaris) P.L. Crouan & H.M. Crouan															0.1
															0.001
Flabellia petiolata (Turra) Nizamuddin				725.0				264.0	342.7	145.8	95.8	4.1	7.6	7.2	3.5
				3.650				1.473	2.319	1.090	0.646	0.028	0.048	0.036	0.030
Halimeda tuna (J. Ellis & Solander) J.V. Lamouroux								0.6							
								0.021							
Microdictyon umbilicatum (Velley) Zanardini												0.2	0.5	0.1	
												0.002	0.008	0.001	
Palmophyllum crassum (Naccari) Rabenhorst								25.7	31.1	66.0	51.0				
								0.340	0.396	0.896	0.646				

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Pseudochlorodesmis furcellata (Zanardini) Børgesen				5.5					33.0	0.1	0.1		7.6		1.2
				0.195					0.330	0.001	0.001		0.076		0.012
Ulvella scutata (Reinke) R. Nielsen, C.J. O'Kelly & B. Wysor									0.1						
									0.001						
Umbraulva dangeardii M.J. Wynne et G. Furnari												0.1		0.2	
												0.001		0.001	
Uronema marinum Womersley					5.0				65.9			0.2	0.1		1.2
					0.050				0.659			0.002	0.001		0.012
Valonia macrophysa Kützing				4.0			6.0	12.2	19.8	7.8	11.1	2.4	1.0		0.2
				0.065			0.050	0.222	0.377	0.146	0.125	0.034	0.014		0.006

Table 1 – Species composition of the collected samples/replicates. For each taxon, the upper value corresponds to the algal surface (Sa, in $cm^2\ m^{-2}$) in the sample or replicate, and the lower value, the biomass as dry weight (B, in $g\ dw\ m^{-2}$). The introduced species are marked with an asterisk (*), and the maërl-forming species, with a hashtag ($^{\#}$). Abbreviations: Spo, *Spongites fruticulosus* beds; Lam, *Laminaria rodriguezii* forests; Pey, *Peyssonnelia inamoena* beds; MC, Menorca Channel; SM, Southern Menorca.

6.3±3.6 % of Sa_T and 30.6±15.0 % of B_T (Fig. 3). According to the statistical analyses, replicates of both samples did not present significant differences in quantitative and qualitative species composition.

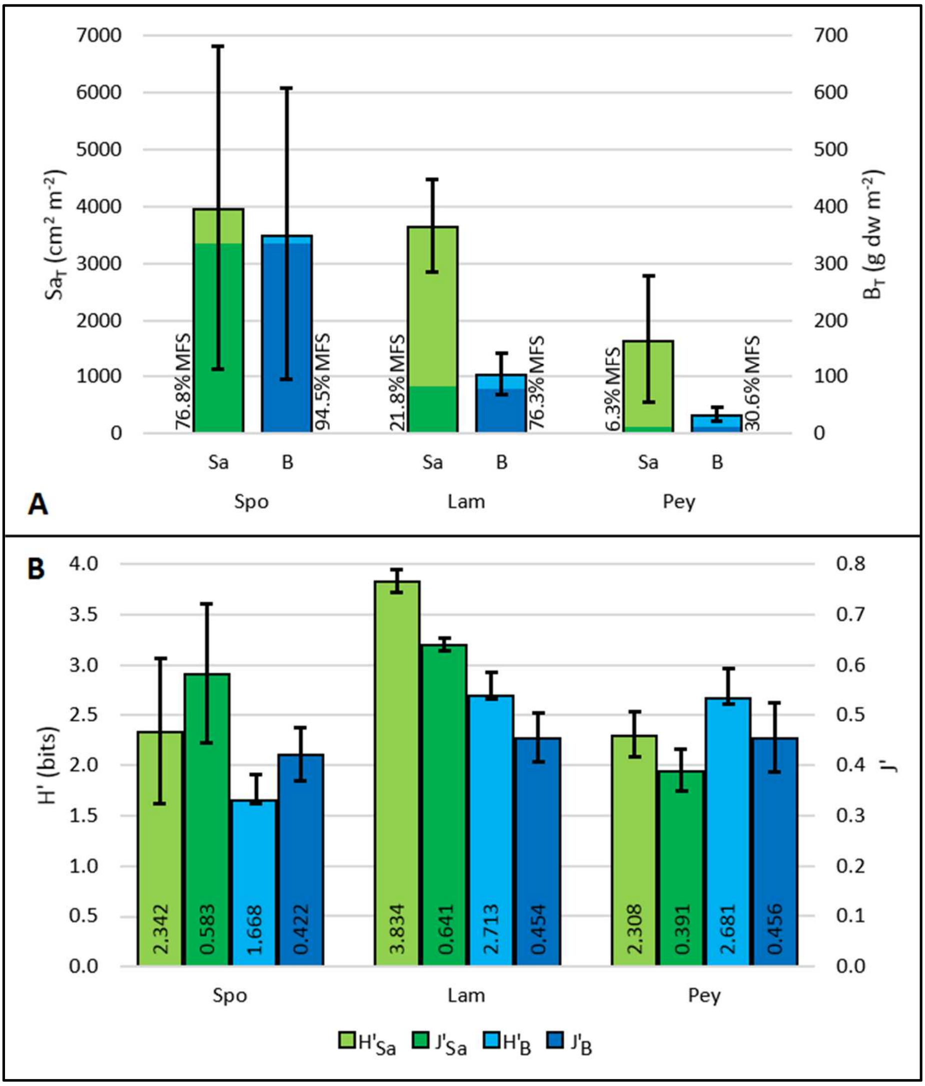

Figure 3 – Characteristics of the three studied communities (mean and standard deviation). A) Total algal surface (Sa_T) and total biomass (B_T). The percentage of the maërl-forming species is given for both parameters. B) Shannon's diversity (H') and Pielou's evenness (J') both based on algal surface

Discussion

Spongites fruticulosus beds presented a very low number of species, H'_B and J'_B, which could also be a sampling artifact due to the small sampling areas. Besides, our results show that they were mostly characterized by the calcareous species of the basal stratum (mainly *Spongites fruticulosus* and *Phymatolithon calcareum*), which accounted for 76.8±21.5 % of Sa_T and 94.5±3.3 % of B_T, erect algae being irrelevant. This relatively low development of fleshy species was also been observed previously in Tossa de Mar (Spain, Northwestern Mediterranean) and although it might be caused by low irradiance levels (Ballesteros 1988), we still do not have the clues to explain this situation as the other communities studied here thrive at the same irradiance levels.

A contrasting case is displayed by the kelp forest of *Laminaria rodriguezii,* which showed a well-developed erect stratum, composed of dispersed clusters of thalli of *L. rodriguezii*, interspersed with free-living corallines and sand patches. Free-living corallines *S. fruticulosus* and *P. calcareum* were far less abundant (21.8±5.7 % of Sa_T and 76.3±4.9 % of B_T) than on *Spongites fruticulosus* beds. As expected, the forest presented higher values of H' and J' when compared to *Spongites fruticulosus* beds (Table 2), due to higher complexity. Diversity values based on algal surface are amongst the highest in Mediterranean algal communities, and similar to those found on free-living

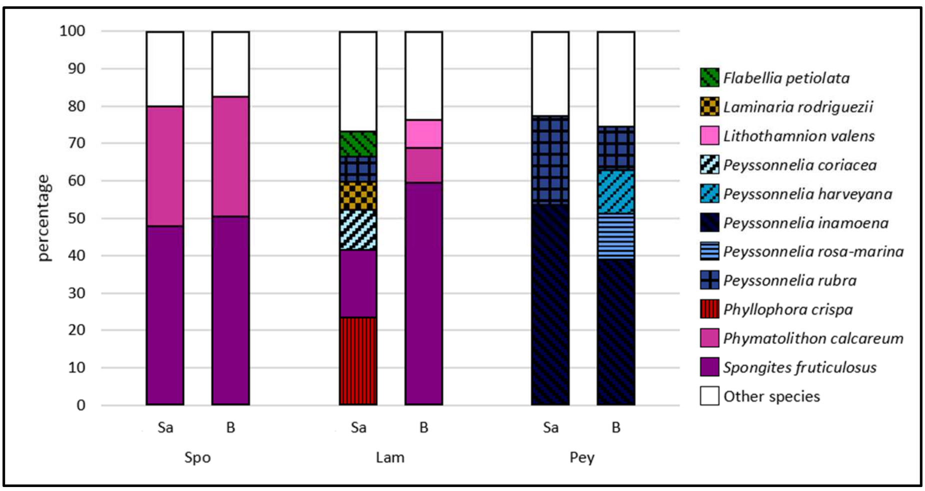

Figure 4 – Results of the SIMPER test based on algal surface (Sa) and biomass (B) for the three communities. The species summarizing 70 % of total contribution to the similarity of the samples are given. Abbreviations: Spo, *Spongites fruticulosus* beds; Lam, *Laminaria rodriguezii* forests; Pey, *Peyssonnelia inamoena* beds.

Peyssonnelia beds (Ballesteros 1994) or other deep-water communities along the Northeastern coast of Spain (*Cystoseira zosteroides, Halimeda tuna, Lithophyllum stictaeforme* and *Phymatolithon calcareum*) (Ballesteros 1988, 1992). The kelp forest of *L. rodriguezii* studied here was very similar in species composition to that found in Hyères Islands (France, Northwestern Mediterranean) (Gautier and Picard 1957), and even to that found growing over coralligenous concretions at Ustica (Tyrrhenian Sea, Italy) (Giaccone 1967), suggesting a high homogeneity of these forests in the Western Mediterranean Sea.

Peyssonnelia inamoena beds were quite diverse because soft erect algae and prostrate species were relatively abundant. These beds were as rich in species as the *L. rodriguezii* forests but showed lower values of H' and J' (Table 2). They displayed the lowest percentage of free living corallines of the three communities (6.3±3.6 % of Sa_T and 30.6±15.0 % of B_T) and, in addition, 45 % of MFS_{Sa} and 41 % of MFS_B belonged to the calcified species *Peyssonnelia rosa-marina*. Similar low abundances of members of the order Corallinales (<2 %) have been found on other *Peyssonnelia* beds dominated by *P. rosa-marina* or *Peyssonnelia* sp. in the Balearic Islands (Ballesteros 1994), which has been explained by the burial of corallines in bottoms with a high sedimentation rate, while *Peyssonnelia* and other fleshy species accumulate

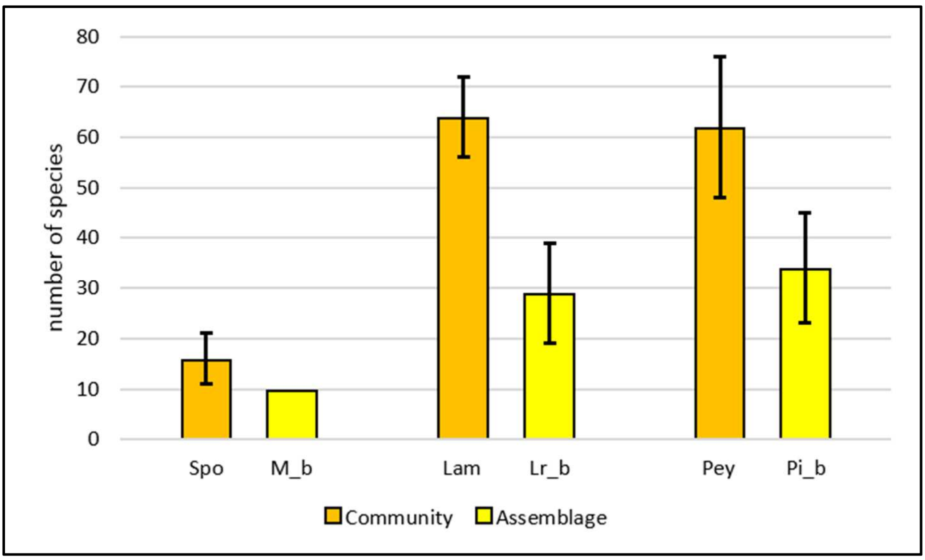

Figure 5 – Comparison of the number of species (mean and standard deviation) of the communities studied here and the corresponding assemblages described in Joher *et al.* (2012). Abbreviations: Spo, *Spongites fruticulosus* beds; M_b, maërl beds in Joher *et al*. (2012); Lam, *Laminaria rodriguezii* forests; Lr_b, *Laminaria rodriguezii* beds in Joher *et al*. (2012); Pey, *Peyssonnelia inamoena* beds; Pi_b, *P. inamoena* beds in Joher *et al*. (2012).

	Spo I	Spo II	Spo III	Spo IV	Spo V	Spo VI	Spo VII	Lam I-1	Lam I-2	Lam II-1	Lam II-2	Pey I-1	Pey I-2	Pey II-1	Pey II-2
Location	MC	MC	MC	MC	MC	MC	MC	MC	MC	MC	MC	SM	SM	SM	SM
Depth (m)	-110	-110	-110	-110	-110	-110	-110	-61	-61	-62	-62	-64	-64	-65	-65
Date of collection	13/05/ 2009	13/05 /2009	13/05 /2009	13/05 /2009	13/05 /2009	13/05 /2009	13/05 /2009	15/05 /2009	15/05 /2009	15/05 /2009	15/05 /2009	19/05 /2009	19/05 /2009	19/05 /2009	19/05 /2009
n	12	14	18	19	26	10	15	70	71	60	54	77	67	45	57
IFO	0.107	0.087	0.139	0.142	0.134	0.142	0.088	0.182	0.178	0.168	0.159	0.230	0.203	0.214	0.194
Sa_T (cm^2 m^{-2})	6776	8055	269	5242	1451	3248	2718	4426	4065	3577	2545	2886	2311	541	906
MFS_{Sa} (cm^2 m^{-2})	5975	7300	100	3350	990	3175	2485	1225	1046	581	448	266	182	38	10
H'_{Sa} (bits)	1.880	1.957	3.564	2.641	2.853	1.380	2.121	3.832	3.989	3.755	3.760	2.326	2.534	2.370	2.004
J'_{Sa}	0.524	0.514	0.855	0.622	0.607	0.416	0.543	0.625	0.649	0.636	0.653	0.371	0.418	0.431	0.344
B_T (g dw m^{-2})	640	758	11	366	101	318	264	148	134	81	60	68	48	8	11
MFS_B (g dw m^{-2})	598	730	10	335	99	318	249	122	105	58	44	26	16	3	1
H'_B (bits)	1.564	1.677	1.809	1.909	1.583	1.218	1.916	2.425	2.718	2.766	2.944	2.635	2.594	3.074	2.419
J'_B	0.436	0.441	0.434	0.449	0.337	0.367	0.490	0.396	0.442	0.468	0.512	0.421	0.428	0.560	0.415

Table 2 – Main characteristics of the collected samples/replicates. Abbreviations: Spo, *Spongites fruticulosus* beds; Lam, *Laminaria rodriguezii* forests; Pey, *Peyssonnelia inamoena* beds; MC, Menorca Channel; SM, Southern Menorca; n, Number of species; IFO, Index of Floral Originality; Sa_T, total algal surface; B_T, total biomass; MSF_{Sa} and MSF_B, maërl-forming species according to total algal surface and biomass; H'_{Sa} and H'_B, Shannon's diversity based on algal surface and biomass; J'_{Sa} and J'_B, Pielou's evenness based on algal surface and biomass.

in ripple mark depressions (Ballesteros 1994, Bordehore *et al*. 2003). Values of H' and J' in relation to algal surface were similar to values found on *S. fruticulosus* beds, but in relation to biomass, the *P. inamoena* community presented higher values of H'_B and J'_B (Fig. 3). *Peyssonnelia* beds seem to be abundant and diverse on the continental shelf of the Balearic Islands. In this regard, besides the *P. inamoena* and *P. rubra* identified here and in a previous work (Joher *et al.* 2012), some bottoms dominated by different *Peyssonnelia* species have been identified previously in the Balearic Islands (Ballesteros 1994) as well as in other areas of the Western Mediterranean Sea (Huvé 1954, Carpine 1958, Parenzan 1960, Bourcier 1968, Augier and Boudouresque 1978, Basso 1990). In addition, the *P. inamoena* beds studied here also show a great abundance of other congeneric species (*P. rosa-marina*, *P. harveyana*, *P. rubra*), suggesting that all *Peyssonnelia* beds could constitute a single habitat, where the different species could become dominant as a response to slightly different environmental conditions. However, further studies are required on this issue.

Although the spatial structure of the communities studied here was different, differences in species composition were small, as reflected in the low values of IFO calculated for each of the studied communities (Fig. 1). In this sense, previous reports of bottoms dominated by the kelp *L. rodriguezii* as 'fonds à prâlines et *Laminaria rodriguezii*' (Molinier 1956, Gautier and Picard 1957, Pérès and Picard 1964), together with the high similarities between *S. fruticulosus* beds and *L. rodriguezii* forests highlighted in this study, suggest the existence of a gradient moving from the *S. fruticulosus* beds to the *L. rodriguezii* forests. Whether this is driven by natural environmental factors or by anthropogenic pressures would require further work. However, in this sense, recent studies pointed out that the abundances of this endemic kelp on detritic bottoms geographically differ depending on commercial trawling pressure, since well-developed *L. rodriguezii* kelps are only found in specific areas of the Menorca channel with low trawling pressure (Joher *et al*. 2012). Finally, the development of *Peyssonnelia* spp. communities could also be favoured by adverse local environmental conditions for the development of maërl beds. Thus, the natural presence of high sedimentation rates and/or changes induced by trawling, such as turbidity, could enhance the abundance of Peyssonneliaceae over Corallinales, as previously observed in Alicante (Spain) and Malta (Bordehore *et al*. 2000).

ROV dives have been extremely useful for finding extensive beds of the three targeted communities and, in fact, this is the most advisable method to localize specific communities in deep-water, highly patchy detritic landscapes, rather than using destructive dredges or Scuba-diving. Regarding the sampling method, the number of species reported for each community in this work is significantly higher than the values found in corresponding assemblages sampled by bottom trawling (Fig. 5) (Joher *et al*. 2012). This was unexpected since the sampled surface was much larger in the collections made by bottom trawling. Bottom trawls have a larger mesh size than beam trawls (20 mm *vs* 10 mm), which could explain this increase in the *L. rodriguezii* and *P. inamoena* communities, even when sampling much smaller surfaces. In the case of the *S. fruticulosus* community, Box-Corer dredges completely prevented any loss of sample and probably this is the reason explaining the increase. Thus, Box-Corer dredges or beam trawls seem to be good sampling methods for studying the composition and structure of deep-water detritic communities, although bottom trawls are equally effective if the main assemblages have to be identified in large areas.

Acknowledgements

We thank Marc Verlaque, Giovanni Furnari and Julio Afonso Carrillo for taxonomic help, and Emma Cebrian for helping with statistical analyses. We acknowledge the Centre Oceanogràfic de Balears – Instituto Español de Oceanografía for the organization and provision of all the facilities needed for the sampling surveys, and thank Enric Massutí and his team, in particular, who coordinated the surveys. We thank the crews of R/V MarViva Med and R/V Cornide de Saavedra, and the sampling survey participants for their help and support during sampling. The CANAL0209 survey was financed by the MarViva Foundation, the Govern de les Illes Balears and the IEO. The MEDITS_ES05_09 survey was supported by the BADEMECO project, financed by the IEO and the European Union.

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III-3. Macroalgal-dominated coastal detritic communities from the NE Atlantic and the Mediterranean

Abstract

This is a qualitative comparison of the distribution of macroalgal-dominated coastal detritic communities from the European coasts (the NE Atlantic and the Mediterranean included) based on our own data from the Balearic Islands (Western Mediterranean) and available data from literature. The algal detritic communities from the NE Atlantic and the Mediterranean differ mainly because of the presence of regional exclusive non-carbonated species, and the presence of a high number of maërl-forming species in the Mediterranean. The similarities in community structure suggest that the European macroalgal-dominated coastal detritic communities correspond to maërl beds, characterized by a basal substratum usually dominated by *Lithothamnion corallioides* and *Phymatolithon calcareum*, and a differing erect stratum. According to the differences in the species composition, seven different types of macroalgal-dominated detritic communities can be distinguished. Their main characteristic species and their biogeographical distribution are detailed.

Keywords: coastal detritic bottoms, distribution, *Laminaria rodriguezii*, *Lithothamnion corallioides*, macroalgae, maërl, Mediterranean Sea, NE Atlantic Ocean, *Peyssonnelia* spp., *Phymatolithon calcareum*, *Spongites fruticulosus*.

Introduction

Macroalgal-dominated coastal detritic bottoms constitute main habitats of continental shelves occurring close to shore (Pérès 1985, Pérès and Picard 1964, Picard 1965). The soft bottoms where these coastal detritic bottoms develop are composed of low percentages of silt, sand and gravels, mixed with a high amount of calcareous skeletons from benthic organisms such as molluscs, bryozoans, corals, echinoderms and macroalgae, being the free-living members of the orders Corallinales and Peyssonneliales the major constituents of these bottoms (Pérès 1985, Klein and Verlaque 2009). Animal skeletons and calcareous algae create a secondary hard substratum that allows the settlement of organisms usually found in rocky bottoms (Bianchi 2001), contributing to the presence of a high species diversity (with taxa typical both from soft and hard bottoms), and a 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 and Picard 1964, Ros *et al*. 1985, Ballesteros 1992, Sciberras *et al*. 2009). Thus, the high light transmittance and the low water turbulence of Mediterranean waters (especially in the Balearic Islands; Ballesteros and Zabala 1993, Basso 1996, Canals and Ballesteros 1997, Fornós and Ahr 1997, Birkett *et al.* 1998, BIOMAERL 1999), allow the development of macroalgal-dominated detritic bottoms down to 90-130 m (Picard 1965, Augier 1982, Pérès 1985, BIOMAERL team 1999, Bellan-Santini *et al*. 2002, Hall-Spencer *et al.* 2010), while in the NE Atlantic they are only present at depths above 30 m (Pérès and 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 NE Atlantic and the Mediterranean), have been considered as analogous habitats (Pérès and Picard 1964).

European macroalgal-dominated detritic assemblages have been largely studied. Maërl and rhodolith beds have been widely reported in the NE Atlantic (e.g. Jacquotte 1962, Hily *et al*. 1992, Perrins *et al*. 1995, Otero-Schmitt and Pérez-Cirera 2002, Bárbara *et al*. 2004, Peña and Bárbara 2006), suggesting that they are the predominant kind of detritic bottoms in these regions. Besides, various categories or facies have been described in the Mediterranean (Pérès and 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*. in press), kelp forests of *Laminaria rodriguezii* (Joher *et al*. in press), and *Peyssonnelia* beds (e.g. Huvé 1954, Ballesteros 1994, Joher *et al*. in press) have been studied at the community level.

Despite the amount of descriptive literature focused on the algal detritic communities in the European coasts, a quantitative comparison of the composition and distribution of macroalgal-dominated coastal detritic bottoms of the European coasts is not easy to perform because most of the available data is presented whether as a checklist of a wide geographical zone (e.g. Peña and Bárbara 2008), or as semi-quantitative data in a phytosociological scale (e.g. Otero-Schmitt and Pérez-Cirera 2002). Even if maërl beds and their associated flora have been qualitatively compared at the European level (BIOMAERL team 1999, Peña and Bárbara 2008; Peña *et al*. 2014) we do not know of any attempt that have tried to compare the species composition and distribution of all algal-dominated coastal detritic assemblages at a European scale. Thus, our aim here is the comparison of the species composition and distribution of macroalgal-dominated coastal detritic communities described so far from the NE Atlantic and the Mediterranean Sea.

Material and methods

Samples were collected in the Menorca Channel and Southern Menorca during the MEDITS_ES05_09 sampling survey by means of Box-Corer dredging and beam trawling, as detailed in Joher *et al*. (in press). However, most data used in this paper comes from other studies performed in the NE Atlantic [United Kingdom, French Brittany, and Galicia (Spain)] and the Mediterranean Sea [Costa Brava and Balearic Islands (Spain), Provence and Corsica (France), Tunisia and Greece]. Checklists concerning wide areas were disregarded since they could include species coming from several different assemblages. Only qualitative data was used for the analysis.

A total of 13 studies and 265 inventories of macroalgal communities were selected from the references (see details in Table 1): 190 inventories from the NE Atlantic and 75 from the Mediterranean.

A similarity matrix was constructed based on the Sørensen similarity index with all the inventories. An nMDS ordination was used to visualize patterns of similarities between samples (Kruskal and Wish 1978), and a cluster analysis using single linkage was performed to obtain the groups of samples according to the percentage of similarity that presented the better fit with the pattern shown in the nMDS. The main characteristic species for each group of samples was obtained with the SIMPER test, which used the percentage of appearance of the species in the samples of each group to analyze the contribution of the species to the similarity within each group. These analyses (nMDS, cluster analysis and SIMPER test) were performed taking into account all the species, and also for those species considered as non maërl-forming (non-MFS) and those considered as maërl-forming species (MFS), to elucidate the importance of the different kind of species in the groups differences. Statistical analyses were performed with PRIMER version 6 software (Clarke and Warwick 2001).

Results

A total of 381 taxa found in the inventories were taken into account (Fig. 1). The Mediterranean Sea was the richest zone with 266 species, 199 of those exclusive from this region, while the NE Atlantic Ocean harbored 182 species,

Area	Locality	Depth (m)	Type of detritic bottom	Code	References
NE Atlantic Ocean					
United Kingdom	Fal Estuary	Unknown	Maërl beds	1-74	Perrins *et al.* 1995
	Fal Estuary	2.4-7.5	Maërl beds	75-145	Perrins *et al.* 1995
	Fal Estuary	2.4-7.5	Saccharina latissima forests	146	Perrins *et al.* 1995
Brittany, France	Morlaix	Unknown	Maërl beds	147-149	Jacquotte 1962
	Brest	Unknown	Maërl beds	150	Jacquotte 1962
	Brest	0-2	Maërl beds	151-171	Hily *et al.* 1992
Galicia, Spain	Several locations	4-26	Maërl beds	172-177	Peña and Bárbara 2006
	Muros	10-20	Maërl beds	178-185	Otero-Schmitt and Pérez-Cirera 2002
	Arousa	10-16	Maërl beds	186-190	Bárbara *et al.* 2004
Mediterranean Sea					
Costa Brava, Spain	Cap de Creus	Unknown	Maërl beds	191-192	Jacquotte 1962
	Tossa de Mar	40-51	Maërl beds	193-199	Ballesteros 1988
Provence, France	Marseille	30-42	*Peyssonnelia* beds	200-202	Huvé 1954
	Marseille	40-45	Maërl beds	203-207	Huvé 1956
	Marseille	-50-60	Maërl beds	208	Costa 1960
	Riou Is.	Unknown	Maërl beds	209-222	Jacquotte 1962
	Riou Is.	Unknown	Maërl beds	223	Jacquotte 1962
	Embiez	Unknown	Maërl beds	224	Jacquotte 1962

Area	Locality	Depth (m)	Type of detritic bottom	Code	References
Balearic Is., Spain	Palma Bay	40-50	Maërl beds	225-233	Gómez *et al*. 1986
	Cabrera Channel	40-54	Maërl beds	234	Ballesteros 1994
	Several locations	40-79	*Peyssonnelia* beds	235-240	Ballesteros 1994
	Menorca Channel	61-62	*Laminaria rodriguezii* forests	241-244	Joher *et al*. 2015 (in press)
	Menorca Channel	50-60	Maërl beds	245-251	Joher *et al*. 2015 (in press)
	South Menorca	64-65	*Peyssonnelia* beds	252-255	Joher *et al*. 2015 (in press)
Corsica, France	Cap Corse	Unknown	Maërl beds	256	Jacquotte 1962
	Strait of Bonifacio	Unknown	Maërl beds	257	Jacquotte 1962
Tunisia	Gabès Gulf	Unknown	Maërl beds	258	Jacquotte 1962
Greece	Aegean Sea	Unknown	Maërl beds	259-262	Jacquotte 1962
	Samothrace	Unknown	Maërl beds	263	Jacquotte 1962
	Mytilene	Unknown	Maërl beds	264	Jacquotte 1962
	Kalamata Gulf	Unknown	Maërl beds	265	Jacquotte 1962

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

from which 115 exclusive. Furthermore, 67 species (17.6 %) were present in the two regions (see Appendix 1 for a complete list of the taxa). All regions and zones presented maërl-forming species (MFS) (up to 18 different species), being the Mediterranean the region with higher number of MFS (Fig. 1).

Four different macroalgal detritic communities were represented in the inventories included in this study: maërl beds in the two regions, kelp forests of *Laminaria rodriguezii* and *Peyssonnelia* beds only in the Mediterranean, and kelp forests of *Saccharina latissima* in the NE Atlantic (Table 1).

Analyses involving all the species

Ten main groups were distinguished at 51 % similarity, which included 258 samples, and 7 other groups including the remaining 7 samples (Fig 2). Samples from the NE Atlantic were grouped in five clusters (A, B, C, D and E) including mainly samples from the United Kingdom (group E), the French Brittany (groups C and D), and Galicia (groups A, B and E). The Mediterranean samples grouped in five main groups (F, G, H, I and J), which presented samples mainly from the Costa Brava (group F), Balearic Islands (groups G, H, I and J), and Provence, Greece and Corsica (group J). The sample from Tunisia

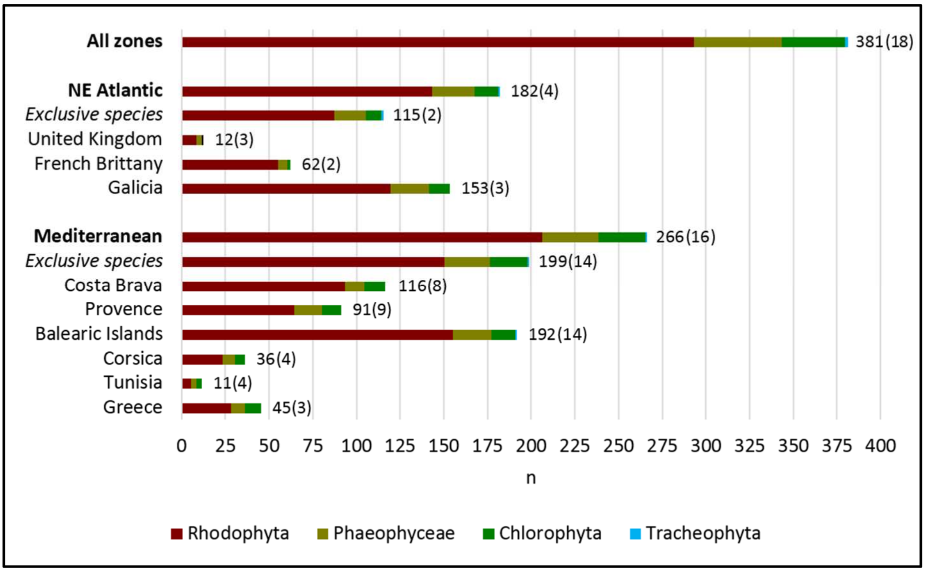

Figure 1 – Number of taxa (n) found in the studies used for the comparison of the algal detritic bottoms from the NE Atlantic and the Mediterranean. Data is given for all the zones and the two main regions (in bold), and separetely for each zone. The number of exclusive species for the corresponding regions and the number of maërl-forming species for all geographical areas (in brackets) are also given.

was situated in one cluster (group P), close to Mediterranean samples from Provence and Corsica.

Almost all samples from the NE Atlantic were identified as maërl beds, with the exception of one sample from the United Kingdom, which corresponded to a *Saccharina latissima* kelp forest (Table 1). The majority of those from the French Brittany (group C) and part of the samples from the United Kingdom (group E) were characterized by *L. corallioides*, and some samples from the United Kingdom, by *P. calcareum* (Table 2). The rest of samples from the United Kingdom (group E) and the French Brittany (group D), and those from Galicia (groups A and B) were characterized by *Lithothamnion corallioides* and *Phymatolithon calcareum*. Moreover, the sample corresponding to a *Saccharina latissima* forest, and also two samples from Provence (*Peyssonnelia* beds) and one from Costa Brava (maërl of *L. corallioides* and *P. calcareum*) were grouped between the maërl beds from the United Kingdom (group E). The number of species decreased with latitude, being higher in Galicia and very low in the United Kingdom (Fig. 1). The five main clusters were characterized by some Atlantic soft algae (e.g. *Cutleria multifida, Polysiphonia flexella* or *Stenogramma interruptum*) and

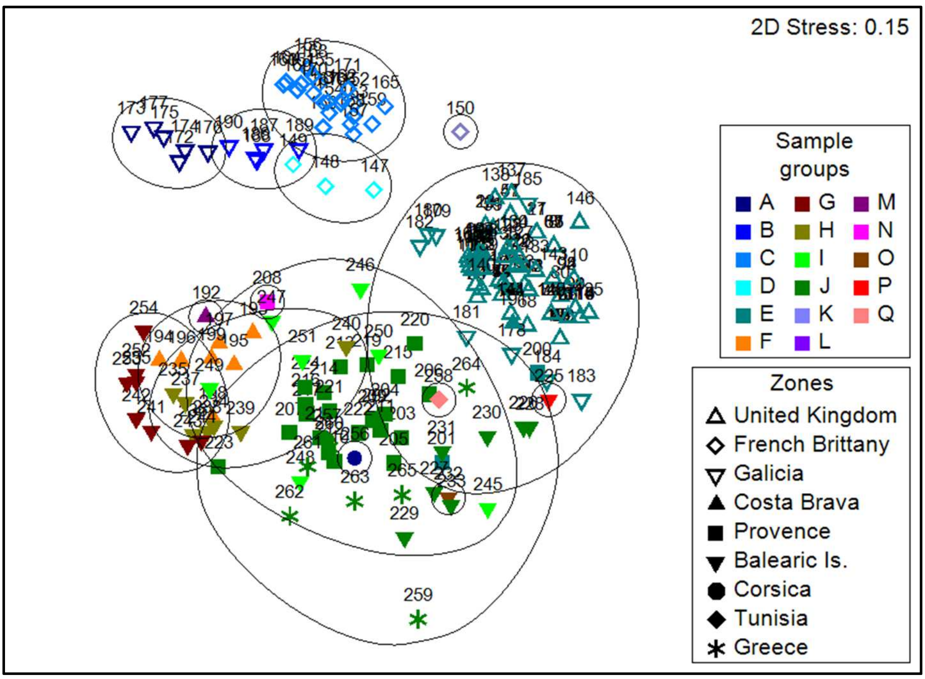

Figure 2 – nMDS ordination including all the species. The overlay clusters corresponding to 51 % of similarity between samples and geographical zones are displayed. Sample codes correspond to studies in Table 1.

	Group A	Group B	Group C	Group D	Group E
Characteristic species	*Ahnfeltiopsis devoniensis*[a] *Chaetomorpha aerea*[a] *Cladophora rupestris* *Cruoria cruoriiformis* *Cryptopleura ramosa* *Cutleria multifida*[a] *Dasysiphonia japonica*[a] *Corallina elongata* *Gelidiella calcicola*[a] *Gelidium maggsiae*[a] *Gracilaria gracilis*[a] *Gracilaria multipartita*[a] *Hypoglossum hypoglossoides* *Lithothamnion corallioides* *Melobesia membranacea* *Phymatolithon calcareum* *Plocamium cartilagineum* *Pterocladiella capillacea*[a] *Pterothamnion plumula* *Ptilothamnion sphaericum*[a] *Spermothamnion repens*[a] *Ulva rigida*[a] *Ceramium echionotum*[a] *Pterosiphonia complanata*[a] *Antithamnionella ternifolia*[a]	*Callophyllis laciniata* *Cruoria cruoriiformis* *Cutleria multifida*[a] *Dasysiphonia japonica*[a] *Erythroglossum laciniatum*[a] *Gelidiella calcicola*[a] *Halarachnion ligulatum* *Kallymenia reniformis*[a] *Lithothamnion corallioides* *Myriogramme minuta*[a] *Phymatolithon calcareum* *Acrosorium ciliolatum* *Brongniartella byssoides* *Drachiella spectabilis*[a] *Compsothamnion thuyoides*[a] *Plocamium cartilagineum* *Gelidiella calcicola*[a]	*Dictyota dichotoma* *Halarachnion ligulatum* *Lithothamnion corallioides* *Polysiphonia flexella*[a] *Stenogramma interruptum*[a] *Cryptopleura ramosa* *Hypoglossum hypoglossoides* *Nitophyllum punctatum* *Brongniartella byssoides* *Rhodophyllis divaricata* *Ulva* sp.[a] *Chondria dasyphylla* *Polysiphonia stricta* *Ceramium echionotum*[a]	*Gracilaria foliifera*[a] *Lithothamnion corallioides* *Peyssonnelia dubyi* *Phymatolithon calcareum* *Plocamium cartilagineum* *Pterothamnion plumula* *Rhodymenia pseudopalmata*[a] *Spyridia filamentosa*[a]	*Phymatolithon calcareum* *Lithothamnion corallioides*

	Group A	Group B	Group C	Group D	Group E
Characteristic species	*Erythroglossum lusitanicum*[a] *Acrosorium ciliolatum* *Chondracanthus acicularis* *Cladophora hutchinsiae*[a] *Dictyota dichotoma* *Falkenbergia rufolanosa* *Stenogramma interuptum*[a] *Trailliella intricata*[a]				
Number of samples	6	5	21	3	157
Described communities	Maërl of *L. corallioides* and *P. calcareum*	Maërl of *L. corallioides* and *P. calcareum*	Maërl of *L. corallioides*	Maërl of *L. corallioides* and *P. calcareum*	Maërl of *L. corallioides* Maërl of *P. calcareum* Maërl of *L. corallioides* and *P. calcareum* *Peyssonnelia* beds *S. latissima* forests
Distribution (number of samples)	Galicia (6)	Galicia (5)	French Brittany (21)	French Brittany (3)	United Kingdom (146) Galicia (8) Provence (2) Costa Brava (1)

Table 2 – Characteristics of the main NE Atlantic groups obtained by the comparison of all species at 51% of similarity: characteristic species (SIMPER test, 70% of cumulative similarity), number of samples, described communities according to literature source, and distribution. [a], exclusive species from the NE Atlantic.

	Group F	Group G	Group H	Group I	Group J
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} Unidentified Melobesiae A^{m} *Bonnemaisonia asparagoides* *Hydrolithon farinosum*^{m} *Ulvella scutata*^{m}	*Acrothamnion preissii*^{m} *Cryptonemia tuniformis*^{m} *Dictyota dichotoma* *Flabellia petiolata*^{m} *Halopteris filicina* *Irvinea boergesenii*^{m} *Kallymenia patens*^{m} *Kallymenia requienii*^{m} *Leptofauchea coralligena*^{m} *Myriogramme tristromatica*^{m} *Peyssonnelia harveyana*^{m} *Peyssonnelia inamoena*^{m} *Peyssonnelia rosa-marina*^{m} *Phyllophora crispa*^{m} Unidentified Corallinaceae B^{m} *Gloiocladia microspora*^{m} *Hypoglossum hypoglossoides* *Lithothamnion valens*^{m} *Spongites fruticulosus*^{m} *Lithophyllum stictaeforme*^{m} *Acrochaetium* sp.^{m} *Gracilaria corallicola*^{m} *Osmundaria volubilis*^{m} *Peyssonnelia rubra*^{m} *Polysiphonia subulifera* *Rhodymenia* sp.^{m}	*Cryptonemia tuniformis*^{m} *Derbesia tenuissima* *Hydrolithon farinosum*^{m} *Laurencia obtusa* *Peyssonnelia crispata*^{m} *Peyssonnelia rosa-marina*^{m} *Peyssonnelia* sp.^{m} *Phymatolithon calcareum* *Polysiphonia subulifera* *Rytiphlaea tinctoria*^{m} *Dictyota dichotoma* *Halopithys incurva* *Leptofauchea coralligena*^{m} *Osmundaria volubilis*^{m} *Osmundea pelagosae*^{m} *Peyssonnelia harveyana*^{m} *Phyllophora crispa*^{m} *Brongniartella byssoides* *Ceramium codii*^{m} *Peyssonnelia rubra*^{m} *Stictyosiphon adriaticus*^{m}	*Kallymenia requienii*^{m} *Phymatolithon calcareum* *Spongites fruticulosus*^{m} *Lithothamnion valens*^{m} *Cryptonemia tuniformis*^{m} *Dictyota dichotoma* Unidentified Corallinaceae B^{m}	*Phymatolithon calcareum* *Lithothamnion corallioides* *Cryptonemia tuniformis*^{m} *Peyssonnelia rubra*^{m} *Peyssonnelia polymorpha*^{m} *Eupogodon planus*^{m} *Polysiphonia subulifera* *Osmundaria volubilis*^{m} *Valonia macrophysa*^{m} *Jania rubens* *Cruoria cruoriiformis* *Gelidium* sp.^{m} *Contarinia squamariae*^{m}

	Group F	Group G	Group H	Group I	Group J
Characteristic species		*Sphaerococcus rhizophylloides*[m] *Valonia macrophysa*[m] *Lithothamnioin corallioides* *Rhodophyllis straforelloi*[m] *Gloiocladia furcata*[m] *Apoglossum ruscifolium*			
Number of samples	**7**	**8**	**7**	**7**	**37**
Described communities	Maërl of *S. fruticulosus* with *P. calcareum*	*L. rodriguezii* forests *Peyssonnelia* beds	*Peyssonnelia* beds	Maërl of *S. fruticulosus* with *P. calcareum* and *L. valens*	Maërl of *L. corallioides* Maërl of *P. calcareum* Maërl of *L. corallioides* and *P. calcareum* *Peyssonnelia* beds
Distribution (number of samples)	Costa Brava (7)	Balearic Islands (8)	Balearic Islands (7)	Balearic Islands (7)	Provence (22) Balearic Islands (7) Greece (7) Corsica (1)

Table 3 – Characteristics of the main Mediterranean groups obtained by the comparison of all species at 51% of similarity: characteristic species (SIMPER test, 70% of cumulative similarity), number of samples, described communities according to literature source, and distribution. [m], exclusive species from the Mediterranean.

other species with a wider distribution (Table 2).

In the Mediterranean, samples corresponded to maërl beds, kelp forests of *Laminaria rodriguezii* and *Peyssonnelia* beds (Table 1). Samples from the Costa Brava (group F) were maërl beds of *S. fruticulosus* with *P. calcareum* (Table 3). Three groups presented samples only from the Balearic Islands, corresponding to three communities: maërl of *S. fruticulosus* with *P. calcareum* and *L. valens* (group I), *Laminaria rodriguezii* forests (group G), *Peyssonnelia* beds (groups G, H and J). Finally, samples from Provence, Balearic Islands, Greece and Corsica grouped in a unique group (J), corresponding to maërl beds of *L. corallioides* and/or *P. calcareum* and, some samples, to *Peyssonnelia* beds. All Mediterranean groups were characterized by some Mediterranean exclusive species (e.g. *Cryptonemia tuniformis, Flabellia petiolata* or *Peyssonnelia harveyana*), which were more abundant in groups F, G and H (Table 3).

Groups composed by only one sample (K to Q) differed from the others by a reduced number of species with a contrasting appearance frequency and included samples mainly from the Mediterranean (Fig. 2).

Analyses involving only the non-MFS

In the nMDS performed only with the non-MFS, 12 main groups of samples were identified (including 250 of the 265 samples) at a 51 % of similarity, and the remaining 15 samples were included in 15 small groups (Fig. 3). The majority of groups found in these analyses generally corresponded with those from the analyses performed with all the species. In consequence, the location of the samples and the identified communities of the main groups are almost the same (Tables 4 and 5).

Thus, the samples from the NE Atlantic were included in 5 groups (A, B, C, D and E). Some samples from the United Kingdom and some from Galicia (group E) were distinct from the samples of the French Brittany (groups C and D) and the rest of Galician samples (group A and B). Main differences can be attributed to a clear gradient of increasing number of non-MFS from South to North (Table 4). The identified communities corresponding to the samples of each group were the same described for the analyses performed with all species (see Tables 2 and 4).

Moreover, the majority of the Mediterranean samples were found grouped into 7 main groups (F to L), characterized by a high number of species, including a high number of exclusive Mediterranean species (Table 5). The grouping generally agreed with the results of the analyses performed with all the species, with the exception of the samples from Provence, Balearic Islands, Greece and Provence, which were included in three different groups (J, K and L) instead of one single group. Similarly to the NE Atlantic, the communities associated to each group were almost coincident with those found in the analyses with all the species (see Tables 3 and 5).

The other 15 groups (M to AA) were constituted by a single sample each, and included one sample from the NE Atlantic and some samples from the Mediterranean. Similarly to the minor groups found in the analyses performed with all the species, the ones found here also differed from the major groups by a reduced number of species with a contrasting appearance frequency.

Analyses involving only the MFS

Five main groups, including 256 of the 265 total samples, and 6 minor groups with 9 samples were distinguished by the nMDS at an 85 % of similarity, (Fig. 4). These analyses did not show groups with a clear geographical pattern because the widespread distribution of some MFS. Three main groups (A, B and C) included samples from diverse zones of the European coasts and were characterized by *L. corallioides* and/or *P. calcareum* (Table 6). Part of the Mediterranean samples included in group C

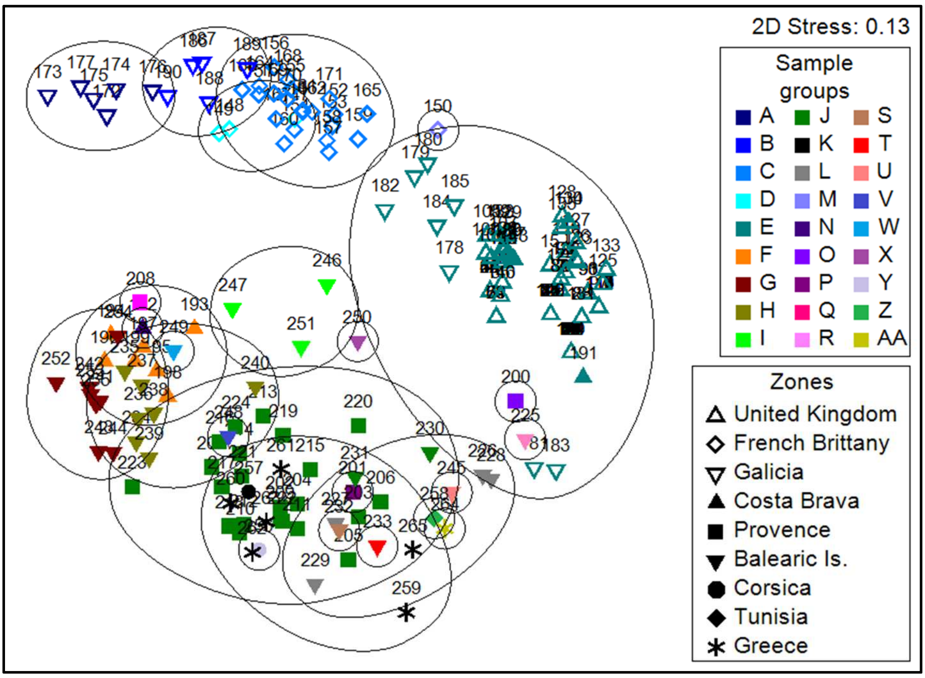

Figure 3 – nMDS ordination based on qualitative data for all the inventories taking into account only non maërl-forming species. The overlay clusters corresponding to 51 % of similarity between samples and geographical zones are displayed. Sample codes correspond to studies in Table 1.

	Group A	Group B	Group C	Group D	Group E
Characteristic species	*Ahnfeltiopsis devoniensis*[a] *Chaetomorpha aerea*[a] *Cladophora rupestris* *Cruoria cruoriiformis* *Cryptopleura ramosa* *Cutleria multifida*[a] *Dasysiphonia japonica*[a] *Corallina elongata* *Gelidiella calcicola*[a] *Gelidium maggsiae*[a] *Gracilaria gracilis*[a] *Gracilaria multipartita*[a] *Hypoglossum hypoglossoides* *Melobesia membranacea* *Plocamium cartilagineum* *Pterocladiella capillacea*[a] *Pterothamnion plúmula* *Ptilothamnion sphaericum*[a] *Spermothamnion repens*[a] *Ulva rigida*[a] *Ceramium echionotum*[a] *Pterosiphonia complanata*[a] *Antithamnionella ternifolia*[a] *Erythroglossum lusitanicum*[a] *Acrosorium ciliolatum*	*Callophyllis laciniata* *Cruoria cruoriiformis* *Cutleria multifida*[a] *Dasysiphonia japonica*[a] *Erythroglossum laciniatum*[a] *Gelidiella calcicola*[a] *Halarachnion ligulatum* *Kallymenia reniformis*[a] *Myriogramme minuta*[a] *Acrosorium ciliolatum* *Brongniartella byssoides* *Drachiella spectabilis*[a] *Compsothamnion thuyoides*[a] *Plocamium cartilagineum* *Anotrichium furcellatum*[a] *Polyneura bonnemaisonii*[a]	*Dictyota dichotoma* *Halarachnion ligulatum* *Polysiphonia flexella*[a] *Stenogramma interruptum*[a] *Cryptopleura ramosa* *Hypoglossum hypoglossoides* *Nitophyllum punctatum* *Brongniartella byssoides* *Rhodophyllis divaricata* *Ulva* sp.[a] *Chondria dasyphylla* *Polysiphonia stricta* *Ceramium echionotum*[a]	*Gracilaria foliifera*[a] *Peyssonnelia dubyi* *Plocamium cartilagineum* *Pterothamnion plúmula* *Rhodymenia pseudopalmata*[a] *Spyridia filamentosa*[a] *Cruoria cruoriiformis*	*Chylocladia verticillata* *Saccharina latissima*[a]

	Group A	Group B	Group C	Group D	Group E
Characteristic species	*Chondracanthus acicularis* *Cladophora hutchinsiae*[a] *Dictyota dichotoma* *Falkenbergia rufolanosa* *Stenogramma interruptum*[a] *Trailliella intricata*[a] *Gayliella flaccida*[a]				
Number of samples	6	5	21	3	155
Described communities	Maërl of *L. corallioides* and *P. calcareum*	Maërl of *L. corallioides* and *P. calcareum*	Maërl of *L. corallioides*	Maërl of *L. corallioides* and *P. calcareum*	Maërl of *L. corallioides* Maërl of *P. calcareum* Maërl of *L. corallioides* and *P. calcareum* *Peyssonnelia* beds *S. latissima* forests
Distribution (number of samples)	Galicia (6)	Galicia (5)	French Brittany (21)	French Brittany (3)	United Kingdom (146) Galicia (8) Costa Brava (1)

Table 4 – Characteristics of the main NE Atlantic groups obtained taking into account the non maërl-forming species at 51% of similarity: characteristic species (SIMPER test, 70% of cumulative similarity), number of samples, described communities according to literature source, and distribution. [a], exclusive species from the NE Atlantic.

	Group F	Group G	Group H	Group I	Group J	Group K	Group L
Characteristic species	*Contarinia peyssonneliae_formis*[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]	*Acrothamnion preissii*[m] *Cryptonemia tuniformis*[m] *Dictyota dichotoma* *Flabellia petiolata*[m] *Halopteris filicina* *Irvinea boergesenii*[m] *Kallymenia patens*[m] *Kallymenia requienii*[m] *Leptofauchea coralligena*[m] *Myriogramme tristromatica*[m] *Peyssonnelia harveyana*[m] *Peyssonnelia inamoena*[m] *Peyssonnelia rosa-marina*[m] *Phyllophora crispa*[m] *Gloiocladia microspora*[m] *Hypoglossum hypoglossoides* *Acrochaetium* sp.[m]	*Cryptonemia tuniformis*[m] *Derbesia tenuissima* *Hydrolithon farinosum*[m] *Laurencia obtusa* *Peyssonnelia crispata*[m] *Peyssonnelia rosa-marina*[m] *Peyssonnelia* sp.[m] *Polysiphonia subulifera* *Rytiphlaea tinctoria*[m] *Dictyota dichotoma* *Halopithys incurva* *Leptofauchea coralligena*[m] *Osmundaria volubilis*[m] *Osmundea pelagosae*[m] *Peyssonnelia harveyana*[m] *Phyllophora crispa*[m] *Brongniartella byssoides*	*Dictyota dichotoma* *Halopteris filicina* *Hypoglossum hypoglossoides* *Irvinea boergesenii*[m] *Kallymenia requienii*[m]	*Cryptonemia tuniformis*[m] *Peyssonnelia rubra*[m] *Jania rubens* *Eupogodon planus*[m] *Polysiphonia subulifera* *Gelidium* sp.[m] *Contarinia squamariae*[m] *Peyssonnelia polymorpha*[m] *Valonia macrophysa*[m] *Peyssonnelia harveyana*[m]	*Osmundaria volubilis*[m] *Peyssonnelia polymorpha*[m] *Rytiphlaea tinctoria*[m] *Palmophyllum crassum*[m] *Cryptonemia tuniformis*[m] *Valonia macrophysa*[m] *Jania* sp.[m] *Flabellia petiolata*[m] *Zanardinia typus*[m] *Dictyota dichotoma*	*Hydrolithon farinosum*[m] *Osmundaria volubilis*[m] *Peyssonnelia rosa-marina*[m] *Rytiphlaea tinctoria*[m]

	Group F	Group G	Group H	Group I	Group J	Group K	Group L
Characteristic species		*Gracilaria corallicola*[m] *Osmundaria volubilis*[m] *Peyssonnelia rubra*[m] *Polysiphonia subulifera* *Rhodymenia* sp.[m] *Sphaerococcus rhizophylloides*[m] *Valonia macrophysa*[m] *Rhodophyllis strafforelloi*[m] *Gloiocladia furcata*[m] *Apoglossum ruscifolium* *Cryptopleura ramosa*	*Ceramium codii*[m] *Peyssonnelia rubra*[m] *Stictyosiphon adriaticus*[m]				
Number of samples	7	8	7	3	24	7	4
Described communities	Maërl of *S. fruticulosus* with *P. calcareum*	*L. rodriguezii* forests *Peyssonnelia* beds	*Peyssonnelia* beds	Maërl of *S. fruticulosus* with *P. calcareum* and *L. valens*	Maërl of *L. corallioides* Maërl of *P. calcareum* Maërl of *L. corallioides* and *P. calcareum* *Peyssonnelia* beds	Maërl of *L. corallioides* and *P. calcareum*	Maërl of *P. calcareum*

	Group F	Group G	Group H	Group I	Group J	Group K	Group L
Distribution (number of samples)	Costa Brava (7)	Balearic Islands (8)	Balearic Islands (7)	Balearic Islands (3)	Provence (22) Balearic Islands (2)	Greece (7) Corsica (1)	Balearic Islands (4)

Table 5 – Characteristics of the main Mediterranean groups obtained taking into account the non maërl-forming species at 51% of similarity: characteristic species (SIMPER test, 70% of cumulative similarity), number of samples, described communities according to literature source, and distribution. ^{m}, exclusive species from the Mediterranean.

were characterized not only by *L. corallioides* and *P. calcareum* but also by other MFS. Moreover, the other two main groups also presented other MFS than *L. corallioides* and *P. calcareum*: group D included only samples from the Balearic Islands and was characterized by *S. fruticulosus*, *L. valens* and *P. calcareum*, while group E included samples from Costa Brava and were characterized by *S. fruticulosus, P. calcareum, Mesophyllum expansum* and *Lithophyllum* sp.

The other groups (E to G) were composed by *P. calcareum* and/or other MFS with a Mediterranean distribution: *Lithophyllum racemus, Lithothamnion valens, Mesophyllum expansum, M. lichenoides*, *M. philippii* and *S. fruticulosus*.

Finally, no MFS were found in the sample from the United Kingdom found in group H, as it corresponded to a forest of *Saccharina latissima*, composed only by *Dictyota dichotoma* and *Saccharina latissima*.

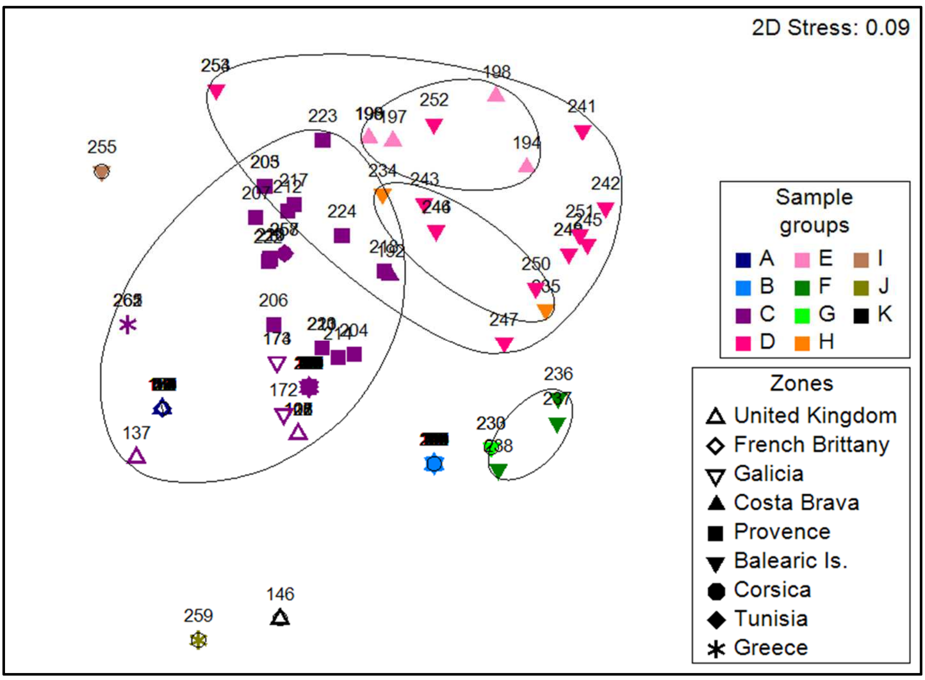

Figure 4 – nMDS ordination based on qualitative data for all the inventories taking into account only the maërl-forming species. The overlay clusters corresponding to 85 % of similarity between samples and geographical zones are displayed. Sample codes correspond to studies in Table 1.

	Group A	Group B	Group C	Group D	Group E
Characteristic species	*Lithothamnion corallioides*	*Phymatolithon calcareum*	*Lithothamnion corallioides* *Phymatolithon calcareum*	*Spongites fruticulosus*^{m} *Lithothamnion valens* *Phymatolithon calcareum*	*Lithophyllum* sp.^{m} *Mesophyllum expansum*^{m} *Phymatolithon calcareum* *Spongites fruticulosus*^{m} Unidentified Melobesiae A^{m}
Number of samples	36	56	142	14	7
Described communities	Maërl of *L. corallioides*	Maërl of *P. calcareum* Maërl of *L. corallioides* and *P. calcareum* *Peyssonnelia* beds	Maërl of *L. corallioides* Maërl of *P. calcareum* Maërl of *L. corallioides* and *P. calcareum* *Peyssonnelia* beds *S. latissima* forests	Maërl of *S. fruticulosus* with *P. calcareum* and *L. valens* *L. rodriguezii* forests *Peyssonnelia* beds	Maërl of *S. fruticulosus* with *P. calcareum*
Distribution (number of samples)	French Brittany (22) United Kingdom (14)	United Kingdom (42) Balearic Islands (7) Galicia (4) Provence (2) Greece (1)	United Kingdom (89) Provence (23) Galicia (15) Greece (5) French Brittany (3)	Balearic Islands (14)	Costa Brava (7)

Table 6 – Characteristics of the main groups obtained taking into account the maërl-forming species at 85% of similarity: characteristic species (SIMPER test, 70% of cumulative similarity), number of samples, described communities according to literature source, and distribution. ^{m}, exclusive species from the Mediterranean.

Discussion

There are significant qualitative biogeographical differences between the algal detritic communities of the two studied regions, reflected in their bathymetrical distribution and species composition.

Algal-dominated detritic bottoms present in the NE Atlantic are usually found above 30 m depth and those from the Mediterranean down to 90-130 m (e.g. Picard 1965, Pérès 1985, Guiry and Blunden 1991, Birkett *et al*. 1998, BIOMAERL team 1999, Bellan-Santini *et al*. 2002, Grall 2003, Ordines and Massutí 2009, Hall-Spencer *et al*. 2010, Peña *et al*. 2014).

The number of species increased from North to South (Fig. 1), including both non-MFS and MFS, although this gradient could also be attributed to differences in sampling effort (Peña *et al*. 2014). The differences in the number of species found within the Mediterranean could correspond mainly to a highest sampling effort in the Western Mediterranean than in the Eastern Mediterranean, as reflected by the number of studies performed in the two subregions. The differences in the species composition were also reflected in the number of exclusive species, which was higher in the Mediterranean than in the NE Atlantic, representing 52.4 % and 30.3 % of the total species, respectively. Thus, the NE Atlantic and the Mediterranean differed in species composition, as both endemic and subtropical species would be found in the Mediterranean while in the NE Atlantic, boreal and North-Atlantic temperate species were common.

Most exclusive species were non-carbonated and thus macroalgal-dominated detritic communities from the NE Atlantic and the Mediterranean cannot be distinguished by the MSF, mainly because of the widespread presence of *L. corallioides* and *P. calcareum* in all the studied regions (e.g. Birkett *et al*. 1998, Grall 2003, Peña and Bárbara 2008). The distribution of the MFS generally agreed with the patterns reported by BIOMAERL team (1999) and Peña and Bárbara (2008). Although *L. corallioides* and *P. calcareum* have been reported to coexist in the same maërl beds (e.g. Jacquotte 1962, Hily *et al*. 1992, Perrins *et al*. 1995, Peña and Bárbara 2006), we found some beds dominated by only one of these species in the three zones of the NE Atlantic and in Provence (Mediterranean) (e.g. Huvé 1956, Hily *et al*. 1992, Perrins *et al*. 1995, Otero-Schmitt and Pérez-Cirera 2002). However, it is possible that the presence of only one of these species in some localities could be a consequence of their misidentification, as these species are known to be morphologically very similar (De Grave and Whitaker 1999, Peña and Bárbara 2004). The other MFS seemed to be restricted to the Mediterranean, as already pointed out for some of these species (Birkett *et al*. 1998, BIOMAERL team 1999, Peña and Bárbara 2008), with the exceptions of *Lithophyllum* *incrustans* also found in Galicia, and the unidentified Corallinaceae A, found also in the United Kingdom.

The geographical distribution of the MFS confirms that the diversity of MFS in the detritic bottoms increases from North to South as pointed by the BIOMAERL team (1999), who presented a distribution map of the main maërl-forming species in the European coasts. We propose the addition to this document of *S. fruticulosus* as characteristic species in the Mediterranean (Fig. 5). Different *Mesophyllum* species were also found as characteristic of the Mediterranean communities, but we disregarded to include them in the distribution map, as their identification has to be revisited. In fact, Peña *et al*. (2015) did not found *M. lichenoides* and *M. alternans* in the Mediterranean but *M. sphaericum* and *M. macroblastum* (Kaleb *et al*. 2011, Peña *et al*. 2011), which arises some doubts on the correct identification of most individuals.

Different communities have been considered in the selected literature

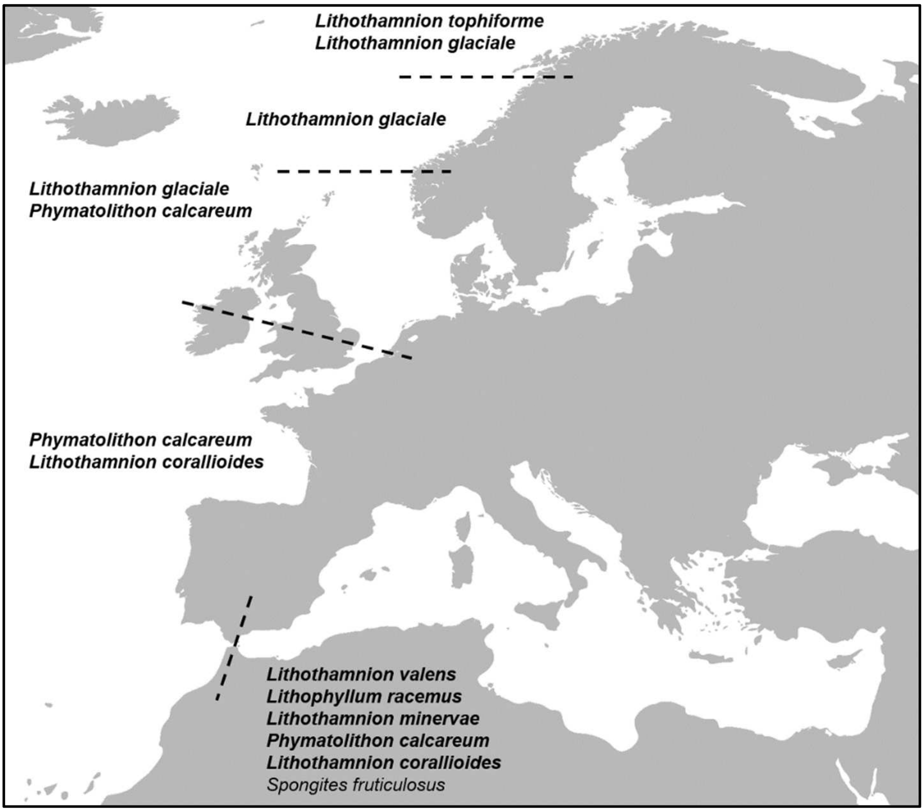

Figure 5 – Distribution map of the maërl-forming species based on the one proposed by BIOMAERL team (1999). The species in bold correspond to those displayed in the original map. The species not in bold is proposed in this study.

(maërl beds, kelp forests and *Peyssonnelia* beds), which have been usually described on the basis of the most abundant and/or representative species (e.g. *Laminaria rodriguezii*, *Lithothamnion corallioides*, *Phymatolithon calcareum*, *Peyssonnelia inamoena, Peyssonnelia rosa-marina*, *Peyssonnelia rubra, Peyssonnelia polymorpha* or *Saccharina latissima*). Our results suggest that despite some differences in the species composition, these communities cannot be easily distinguished qualitatively, in concordance with the conclusions of Augier and Boudouresque (1978) in the comparison of the detritic bottoms of Port-Cros National Park (France). While different maërl beds were distinguished according to their associated flora, like those described in the NE Atlantic (Table 2), some samples corresponding to different communities were grouped together due to high similarities in their species composition, such as the kelp forest of *L. rodriguezii* and some *Peyssonnelia* beds from the Balearic Islands (Table 5). Consequently, from a qualitative point of view, the macroalgal-dominated detritic bottoms of the European coasts should be considered as maërl beds, as they presented a basal stratum composed mainly by *L. corallioides* and *P. calcareum*, and a more-or-less developed erect stratum. However, these beds present different morphologies attending to their composition and vertical structure (see details in Table 7):

- the NE Atlantic maërl of *L. corallioides* and *P. calcareum* with a poor erect stratum, distributed in the United Kingdom and some localities of Galicia;
- the NE Atlantic maërl of *L. corallioides* and/or *P. calcareum* with a well-developed erect stratum, in the French Brittany and some localities of Galicia;
- the Mediterranean maërl of *P. calcareum* and/or *L. corallioides* with a well-developed erect stratum, in Costa Brava, Provence, Balearic Islands, Corsica, Tunisia and Greece;
- the Mediterranean maërl of *P. calcareum* and different *Peyssonnelia* species and a well-developed erect stratum, in the Balearic Islands;
- the Mediterranean maërl of *S. fruticulosus* with *P. calcareum* with a well-developed erect stratum, only found in Costa Brava;
- the Mediterranean maërl of *S. fruticulosus* with *P. calcareum* and *L. valens* with a poor erect stratum, in the Balearic Islands; and
- the Mediterranean maërl of *S. fruticulosus* with *L. corallioides* and *L. valens* with different *Peyssonnelia* species and a well-developed erect stratum, also in the Balearic Islands.

These seven proposed types seem to match with the biogeographical models proposed by Spalding *et al*. (2007) (Fig. 6). Thus, the macroalgal detritic bottoms of the NE Atlantic would belong to different biogeographical

	NE Atlantic maërl of *L. corallioides* and *P. calcareum* with a poor erect stratum	NE Atlantic maërl of *L. corallioides* and/or *P. calcareum* with a well-developed erect stratum	Mediterranean maërl of *P. calcareum* and/or *L. corallioides* with a well-developed erect stratum	Mediterranean maërl of *P. calcareum* and different *Peyssonnelia* species and a well-developed erect stratum	Mediterranean maërl of *S. fruticulosus* with *P. calcareum* with a well-developed erect stratum	Mediterranean maërl of *S. fruticulosus* with *P. calcareum* and *L. valens* with a poor erect stratum	Mediterranean maërl of *S. fruticulosus* with *L. corallioides* and *L. valens* with different *Peyssonnelia* species and a well-developed erect stratum
Characteristic MFS	*Lithothamnion corallioides* *Phymatolithon calcareum*	*Lithothamnion corallioides* *Phymatolithon calcareum*	*Phymatolithon calcareum* *Lithothamnion corallioides*	*Phymatolithon calcareum*	*Spongites fruticulosus*[m] *Phymatolithon calcareum* *Mesophyllum expansum*[m] *Lithophyllum* sp.[m] Unidentified Melobesiae A[m]	*Spongites fruticulosus*[m] *Phymatolithon calcareum* *Lithothamnion valens*[m] Unidentified Corallinaceae B[m]	*Spongites fruticulosus*[m] *Lithothamnion corallioides* *Lithothamnion valens*[m] *Lithophyllum stictaeforme*[m] Unidentified Corallinaceae B[m]
Characteristic non MFS	*Chylocladia verticillata* *Saccharina latissima*[a]	*Halarachnion ligulatum* *Dictyota dichotoma* *Stenogramma interruptum*[a] *Cryptopleura ramosa* *Hypoglossum hypoglossoides* *Plocamium cartilagineum*	*Cryptonemia tuniformis*[m] *Peyssonnelia rubra*[m] *Peyssonnelia polymorpha*[m] *Eupogodon planus*[m] *Polysiphonia subulifera* *Osmundaria volubilis*[m]	*Cryptonemia tuniformis*[m] *Derbesia tenuissima* *Hydrolithon farinosum*[m] *Laurencia obtusa* *Peyssonnelia crispata*[m] *Peyssonnelia rosa-marina*[m] *Peyssonnelia* sp.[m]	*Contarinia peyssonneliae_formis*[m] *Cryptonemia tuniformis*[m] *Dictyota dichotoma* *Eupogodon planus*[m] *Falkenbergia rufolanosa* *Kallymenia requienii*[m]	*Kallymenia requienii*[m] *Cryptonemia tuniformis*[m] *Dictyota dichotoma*	*Acrothamnion preissii*[m] *Cryptonemia tuniformis*[m] *Dictyota dichotoma* *Flabellia petiolata*[m] *Halopteris filicina* *Irvinea boergesenii*[m] *Kallymenia patens*[m]

	NE Atlantic maërl of *L. corallioides* and *P. calcareum* with a poor erect stratum	NE Atlantic maërl of *L. corallioides* and/or *P. calcareum* with a well-developed erect stratum	Mediterranean maërl of *P. calcareum* and/or *L. corallioides* with a well-developed erect stratum	Mediterranean maërl of *P. calcareum* and different *Peyssonnelia* species and a well-developed erect stratum	Mediterranean maërl of *S. fruticulosus* with *P. calcareum* with a well-developed erect stratum	Mediterranean maërl of *S. fruticulosus* with *P. calcareum* and *L. valens* with a poor erect stratum	Mediterranean maërl of *S. fruticulosus* with *L. corallioides* and *L. valens* with different *Peyssonnelia* species and a well-developed erect stratum
Characteristic non MFS		*Rhodophyllis divaricata* *Brongniartella byssoides* *Polysiphonia flexella*[a] *Nitophyllum punctatum* *Ceramium echionotum*[a] *Spyridia filamentosa*[a] *Polysiphonia stricta* *Gracilaria foliifera*[a] *Callophyllis laciniata*	*Valonia macrophysa*[m] *Jania rubens* *Cruoria cruoriiformis* *Gelidium* sp. [m] *Contarinia squamariae*[m]	*Polysiphonia subulifera* *Rytiphlaea tinctoria*[m] *Dictyota dichotoma* *Halopithys incurva* *Osmundaria volubilis*[m] *Osmundea pelagosae*[m] *Peyssonnelia harveyana*[m] *Phyllophora crispa*[m] *Leptofauchea coralligena*[m] *Brongniartella byssoides* *Ceramium codii*[m] *Peyssonnelia rubra*[m] *Stictyosiphon adriaticus*[m]	*Peyssonnelia rosa-marina*[m] *Plocamium cartilagineum* *Rhodymenia delicatula*[m] *Bonnemaisonia asparagoides* *Hydrolithon farinosum*[m] *Ulvella scutata*[m]		*Kallymenia requienii*[m] *Leptofauchea coralligena*[m] *Myriogramme tristromatica*[m] *Peyssonnelia harveyana*[m] *Peyssonnelia inamoena*[m] *Peyssonnelia rosa-marina*[m] *Phyllophora crispa*[m] *Gloiocladia microspora*[m] *Hypoglossum hypoglossoides* *Acrochaetium* sp.[m] *Gracilaria corallicola*[m] *Osmundaria volubilis*[m] *Peyssonnelia rubra*[m]

	NE Atlantic maërl of ***L. corallioides*** and ***P. calcareum*** with a poor erect stratum	NE Atlantic maërl of ***L. corallioides*** and/or ***P. calcareum*** with a well-developed erect stratum	Mediterranean maërl of ***P. calcareum*** and/or ***L. corallioides*** with a well-developed erect stratum	Mediterranean maërl of ***P. calcareum*** and different ***Peyssonnelia*** species and a well-developed erect stratum	Mediterranean maërl of ***S. fruticulosus*** with ***P. calcareum*** with a well-developed erect stratum	Mediterranean maërl of ***S. fruticulosus*** with ***P. calcareum*** and ***L. valens*** with a poor erect stratum	Mediterranean maërl of ***S. fruticulosus*** with ***L. corallioides*** and ***L. valens*** with different ***Peyssonnelia*** species and a well-developed erect stratum
Characteristic non MFS							*Polysiphonia subulifera* *Rhodymenia* sp.[m] *Sphaerococcus rhizophylloides*[m] *Valonia macrophysa*[m] *Rhodophyllis strafforelloi*[m] *Gloiocladia furcata*[m] *Apoglossum ruscifolium*
Zonal distribution	United Kingdom Galicia	French Brittany Galicia	Provence Balearic Islands Corsica Tunisia Greece	Balearic Islands	Costa Brava	Balearic Islands	Balearic Islands
Biogeographic distribution	Northern European Seas province in Temperate Northern Atlantic realm (Spalding *et al*. 2007)	Lusitanian province in Temperate Northern Atlantic realm (Spalding *et al*. 2007)	Mediterranean Sea province in Temperate Northern Atlantic realm (Spalding *et al*. 2007)	Mediterranean Sea province in Temperate Northern Atlantic realm (Spalding *et al*. 2007)	Mediterranean Sea province in Temperate Northern Atlantic realm (Spalding *et al*. 2007)	Mediterranean Sea province in Temperate Northern Atlantic realm (Spalding *et al*. 2007)	Mediterranean Sea province in Temperate Northern Atlantic realm (Spalding *et al*. 2007)

Table 7 – Characteristics of the main kind of coastal detritic bottoms found in the NE Atlantic and the Mediterranean: characteristic MFS, characteristic non-MFS, and zonal and biogeographic distributions. [a], exclusive species from the NE Atlantic; [m], exclusive species from the Mediterranean.

provinces than those from the Mediterranean, although they would all belong to the Temperate Northern Atlantic realm. Thus, the NE Atlantic maërl of *L. corallioides* and *P. calcareum* with a poor erect stratum would be in the Northern European Seas province although it can also appear in the Lusitanian province; the NE Atlantic maërl of *L. corallioides* and *P. calcareum* with a well-developed erect stratum, in the Lusitanian province; and the five Mediterranean bottoms, in the Mediterranean Sea province.

Future studies could reveal the presence of more types of detritic bottoms in these zones and help to understand the environmental processes

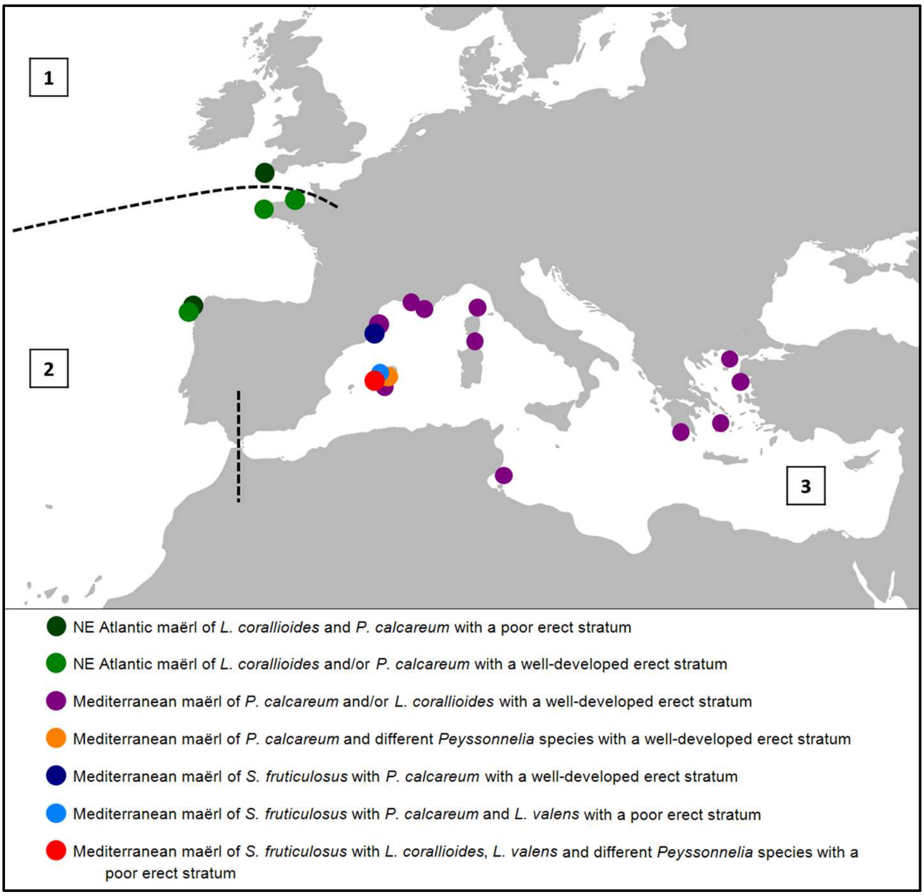

Figure 6 – Distribution of the main macroalgal-dominated detritic communities found in the European coasts. The localities according to Table 1 and the biogeographical divisions of Spalding et al. (2007) are given. Spalding et al. (2007) biogeographical limits in dotted line: 1, Northern European Seas province (Temperate Northern Atlantic realm); 2, Lusitanian province (Temperate Northern Atlantic realm); 3, Mediterranean Sea province (Temperate Northern Atlantic realm).

involved in their distribution. In this sense, the meadows dominated by the fleshy red algae *Phyllophora crispa* and *Osmundaria volubilis* are widely found in 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 too (C. Rodríguez-Prieto and S. Joher, personal observations), but no exhaustive studies have been performed yet to characterize these communities.

Acknowledges

We thank Emma Cebrian for her support and advice on statistical analyses. We acknowledge the Centre Oceanogràfic de Balears – Instituto Español de Oceanografía for the organization and provision of all the facilities needed for the sampling surveys, and thank Enric Massutí and his team, in particular, who coordinated the surveys. We thank the crews of R/V MarViva Med and R/V Cornide de Saavedra, and the sampling survey participants for their help and support during sampling. The CANAL0209 survey was financed by the MarViva Foundation, the Govern de les Illes Balears and the IEO. The MEDITS_ES05_09 survey was supported by the BADEMECO project, financed by the IEO and the European Union.

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Appendix 1 – Distribution of the taxa found in the literature data from the NE Atlantic and the Mediterranean according to the studies detailed in Table 1. Abbreviations: NEA, NE Atlantic; Med, Mediterranean; Uni, United Kingdom; Bri, French Brittany; Gal, Galicia; Cos, Costa Brava; Pro, Provence; Bal, Balearic Islands; Cor, Corsica; Tun, Tunisia, Gre, Greece. *, maërl-forming species (MFS); [a], exclusive species from the NE Atlantic; [m], exclusive species from the Mediterranean.

Region	**NEA**	**NEA**	**NEA**	**Med**	**Med**	**Med**	**Med**	**Med**	**Med**
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Rhodophyta									
Acrochaetium sp.[m]						x			
Acrodiscus vidovichii (Meneghini) Zanardini[m]					x				x
Acrosorium ciliolatum (Harvey) Kylin			x	x		x			
Acrosymphyton purpuriferum (J. Agardh) Sjöstedt[m]				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 tenuissimum (Bonnemaison) Feldmann-Mazoyer			x	x		x			
Aglaothamnion tripinnatum (C. Agardh) Feldmann-Mazoyer			x	x		x			
Aglaothamnion sp.[m]						x			
Ahnfeltia plicata (Hudson) E.M. Fries[a]			x						

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Ahnfeltiopsis devoniensis (Greville) P.C. Silva & DeCew[a]			x						
Amphiroa sp.[m]					x				
Anotrichium furcellatum (J. Agardh) Baldock[a]			x						
Antithamnion cruciatum (C. Agardh) Nägeli			x	x	x				
Antithamnion cruciatum var. *typicum* Feldmann-Mazoyer[m]					x				
Antithamnion densum (Suhr) M.A. Howe[a]			x						
Antithamnion heterocladum Funk[m]						x			
Antithamnion tenuissimum (Hauck) Schiffner[m]				x		x			
Antithamnion villosum (Kützing) Athanasiadis[a]			x						
Antithamnion sp.[m]						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			x		x				
Boergeseniella fruticulosa (Wulfen) Kylin[a]			x						
Bonnemaisonia asparagoides (Woodward) C. Agardh			x	x		x			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	Uni	Bri	Gal	Cos	Pro	Bal	Cor	Tun	Gre
Bonnemaisonia sp.[m]						x			
Botryocladia botryoides (Wufen) Feldmann[m]						x			x
Botryocladia chiajeana (Meneghini) Kylin[m]						x	x		
Brongniartella byssoides (Goodenough & Woodward) F. Schmitz		x	x	x	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	x			
Ceramium callipterum Mazoyer[a]			x						
Ceramium ciliatum (J. Ellis) Ducluzeau			x		x				
Ceramium codii (H. Richards) Mazoyer[m]				x		x			
Ceramium comptum Børgesen[m]					x	x			
Ceramium echionotum J. Agardh[a]		x	x						
Ceramium secundatum Lyngbye[a]			x						
Ceramium siliquosum var. *lophophorum* (Feldman-Mazoyer) Serio[m]				x					

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Ceramium virgatum Roth[a]	x	x	x						
Ceramium sp. [a]		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 capillaris (Hudson) M.J. Wynne[m]				x					
Chondria coerulescens (J. Agardh) Falkenberg[a]			x						
Chondria dasyphylla (Woodward) C. Agardh		x		x					x
Chondria scintillans G. Feldmann[a]			x						
Chrysymenia ventricosa (J.V. Lamouroux) J. Agardh[m]				x		x			
Chylocladia verticillata (Lightfoot) Bliding	x	x	x	x		x			
Claviclonium ovatum (J.V. Lamouroux) Kraft & Min-Thein[a]		x	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			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Contarinia squamariae (Meneghini) Denizot[m]				x	x	x			
Corallina elongata J. Ellis & Solander			x	x					
Corallina sp.[m]					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	x	x	x			x
Cryptonemia lomation (Bertoloni) J. Agardh[m]				x	x	x			
Cryptonemia longiarticulata Funk[m]						x			
Cryptonemia tuniformis (Bertoloni) Zanardini[m]				x	x	x	x		x
Cryptopleura ramosa (Hudson) L. Newton		x	x	x		x			
Dasya baillouviana (S.G. Gmelin) Montagne[m]				x	x	x			
Dasya corymbifera J. Agardh[m]						x			
Dasya hutchinsiae Harvey			x			x			
Dasya ocellata (Grateloup) Harvey			x	x					
Dasya punicea (Zanardini) Meneghini ex Zanardini[a]			x						
Dasya sp.[m]				x		x			
Dasysiphonia japonica (Yendo) H.S. Kim[a]			x						

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Dermatolithon sp.[m]						x			
Dipterosiphonia rigens (Shousboe ex C. Agardh) Falkenberg[m]						x			
Drachiella spectabilis J. Ernst & Feldmann[a]			x						
Dudresnaya verticillata (Withering) Le Jolis		x	x			x			
Dudresnaya sp.[a]	x								
Erythroglossum balearicum J. Agardh[m]						x			
Erythroglossum laciniatum (Lightfoot) Maggs & Hommersand[a]			x						
Erythroglossum lusitanicum Ardré[a]			x						
Erythroglossum sandrianum (Zanardini) Kylin		x		x		x			
Erythrotrichia carnea (Dillwyn) J. Agardh			x			x			
Eupogodon planus (C. Agardh) Kützing[m]				x	x	x			x
Falkenbergia rufolanosa (Harvey) F. Schimitz			x	x					
Felicinia marginata (Roussel) Manghisi, Le Gall, Ribera, Gargiulo & M. Morabito[m]						x			
Galaxaura sp.[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						

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Gelidiella sp.[m]						x			
Gelidiocolax margaritoides (M.T. Martin & M.A. Pocock) K.-C. Fan & Papenfuss[a]			x						
Gelidium bipectinatum G. Furnari[m]									x
Gelidium maggsiae Rico & Guiry[a]			x						
Gelidium pulchellum (Turner) Kützing[a]		x							
Gelidium pusillum (Stackhouse) Le Jolis		x	x	x		x			
Gelidium spinosum (S.G. Gmelin) P.C. Silva[a]		x	x						
Gelidium sp.[m]					x				
Gigartina pistillata (S.G. Gmelin) Stackhouse[a]			x						
Gloiocladia furcata (C. Agardh) J. Agardh[m]				x	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	x			x
Gracilaria bursa-pastoris (S.G. Gmelin) P.C. Silva		x			x				
Gracilaria corallicola Zanardini[m]					x	x	x		x
Gracilaria dura (C. Agardh) J. Agardh[m]					x				
Gracilaria foliifera (Forsskål) Børgesen[a]		x							
Gracilaria gracilis (Stackhouse) M. Steentoft, L.M. Irvine & W.F. Farnham[a]			x						

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Gracilaria multipartita (Clemente) Harvey[a]			x						
Gracilaria sp.[m]					x	x	x		x
Gracilariopsis longissima (S.G. Gmelin) M. Steentoft, L. M Irvine & W.F. Farnham		x			x				
Griffithsia schousboei Montagne[a]			x						
Griffthsia sp.[m]					x				
Gulsonia nodulosa (Ercegovic) Feldmann & G. Feldmann[m]				x					
Gymnogongrus crenulatus (Turner) J. Agardh[a]		x	x						
Gymnogongrus griffithsiae (Turner) Martius[a]		x							
Halarachnion ligulatum (Woodward) Kützing		x	x	x					
Halopithys incurva (Hudson) Batters		x			x	x			
Halurus flosculosus (J. Ellis) Maggs & Hommersand[a]			x						
Halymenia elongata C. Agardh[m]					x				
Halymenia floresii (Clemente) C. Agardh[m]				x	x				
Halymenia latifolia P.L. Crouan & H.M. Crouan ex Kützing		x	x	x					
Halymenia sp. [m]					x	x	x		
Haraldia lenormandii (Derbès & Solier) Feldmann[m]				x		x			
Herposiphonia secunda (C. Agardh) Ambronn[a]			x						

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
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	x			x
Jania adhaerens J.V. Lamouroux[m]						x			
Jania longifurca Zanardini[a]			x						
Jania rubens (Linnaeus) J.V. Lamouroux			x	x	x				x
Jania rubens var. *corniculata* cf. (Linnaeus) Yendo[m]						x			
Jania sp.[m]									x
Kallymenia feldmannii Codomier[m]						x			
Kallymenia lacerata Feldmann[m]				x					
Kallymenia patens (J. Agardh) Codomier [m]						x			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Kallymenia reniformis (Turner) J. Agardh[a]		x	x						
Kallymenia requienii (J. Agardh) J. Agardh[m]				x	x	x			
Kallymenia tenuifolia Feldmann[m]					x				
Kallymenia sp.[m]				x	x	x			
Laurencia obtusa (Hudson) J.V. Lamouroux		x		x	x	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	x			
Lithophyllum incrustans Philippi*[a]			x						
Lithophyllum racemus (Lamarck) Foslie*[m]				x	x	x			
Lithophyllum stictaeforme (Areschoug) Hauck*[m]						x			
Lithophyllum sp.*[m]				x		x			
Lithothamnion corallioides (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan*	x	x	x	x	x	x	x	x	x
Lithothamnion crispatum Hauck*[m]					x				
Lithothamnion valens Foslie*[m]						x			
Lomentaria articulata var. *linearis* Zanardini[m]					x	x	x		
Lomentaria clavellosa (Lightfoot ex Turner) Gaillon			x			x			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
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	x			x
Meredithia sp.[m]									x
Mesophyllum alternans (Foslie) Cabioch & M.L. Mendoza*[m]						x			
Mesophyllum expansum (Philippi) Cabioch & M.L. Mendoza*[m]				x	x	x	x	x	
Mesophyllum lichenoides (J. Ellis) Me. Lemoine*[m]				x	x	x	x	x	x
Mesophyllum philippii (Foslie) W.H. Adey*[m]					x	x			
Microcladia glandulosa (Solander ex Turner) Greville[a]		x	x						
Monosporus pedicellatus (Smith) Solier			x		x	x			
Myriogramme carnea (J.J. Rodríguez y Femenías) Kylin[m]				x		x			
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	x			
Neosiphonia collabens (C. Agardh) Diaz-Tapia & Bárbara[m]				x					

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Neurocaulon foliosum (Meneghini) Zanardini[m]				x	x	x			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	x	x	x	x
Osmundea pelagosae (Schiffner) K.W. Nam[m]				x	x	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			x	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			x			
Peyssonnelia harveyana P.L. Crouan & H.M. Crouan[m]				x	x	x	x		
Peyssonnelia inamoena Pilger[m]						x			
Peyssonnelia polymorpha (Zanardini) F. Schmitz[m]				x	x		x		x
Peyssonnelia rosa-marina Boudouresque & Denizot[m]				x		x			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Peyssonnelia rubra (Greville) J. Agardh[m]				x	x	x	x		x
Peyssonnelia squamaria (S.G. Gmelin) Decaisne[m]				x	x	x	x		x
Peyssonnelia stoechas Boudouresque & Denizot[m]						x			
Peyssonnelia sp.[m]				x		x			
Phyllophora crispa (Hudson) P.S. Dixon[m]				x		x	x		x
Phyllophora epiphylla (O.F. Müller) Batters[a]		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	x	x	x	x	x
Platoma cyclocolpum (Montagne) F. Schmitz[m]				x					
Pleonosporium borreri (Smith) Nägeli		x	x		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			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Polysiphonia elongata (Hudson) Sprengel			x			x			
Polysiphonia fibrillosa (Dillwyn) Sprengel		x		x	x	x	x		
Polysiphonia flexella (C. Agardh) J. Agardh[a]		x							
Polysiphonia flocculosa cf. (C. Agardh) Endlichter[m]				x	x	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 sanguinea (C. Agardh) Zanardini[m]					x				
Polysiphonia stricta (Dillwyn) Greville		x	x			x			
Polysiphonia subulifera (C. Agardh) Harvey		x		x	x	x			
Polysiphonia sp.[m]						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			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Pterosiphonia pennata (C. Agardh) Sauvageau[a]		x	x						
Pterothamnion crispum (Ducluzeau) Nägeli			x	x		x			
Pterothamnion plumula (J. Ellis) Nägeli		x	x	x		x			
Ptilocladiopsis horrida Berthold[m]						x			
Ptilothamnion pluma (Dillwyn) Thuret[m]						x			
Ptilothamnion sphaericum (P.L. Crouan & H.M. Crouan ex J. Agardh) Maggs & Hommersand[a]			x						
Ptilothamnion sp.[m]						x			
Radicilingua thysanorhizans (Holmes) Papenfuss[m]						x			
Radicilingua sp.[m]						x			
Rhodophyllis divaricata (Stackhouse) Papenfuss		x	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	x						
Rhodymenia sp.[m]				x	x	x			x
Rodriguezella bornetii (J.J. Rodríguez y Femenías) F. Schmitz[m]						x			
Rodriguezella pinnata (Kützing) F. Schmitz ex Falkenberg[m]						x			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Rodriguezella strafforelloi F. Schmitz[m]				x	x	x	x		
Rytiphlaea tinctoria (Clemente) C. Agardh[m]				x		x	x		x
Sahlingia subintegra (Rosenvinge) Kornmann			x			x			
Schizymenia dubyi (Chauvin ex Duby) J. Agardh[m]						x			
Scinaia complanata (F.S. Collins) A.D. Cotton[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 apiculata (Meneghini) G. Feldmann-Mazoyer[m]							x		
Seirospora interrupta (Smith) F. Schmitz[m]						x			
Seirospora sphaerospora Feldmann[m]				x					
Solieria chordalis (C. Agardh) J. Agardh[a]		x							
Spermothamnion repens (Dillwyn) Rosenvinge[a]			x						
Sphaerococcus coronopifolius Stackhouse[m]				x	x	x	x		x
Sphaerococcus rhizophylloides J.J. Rodríguez y Femenías[m]						x			
Sphondylothamnion multifidum (Hudson) Nägeli[a]			x						
Spongites fruticulosus Kützing*[m]				x	x	x			

Region	**NEA**	**NEA**	**NEA**	**Med**	**Med**	**Med**	**Med**	**Med**	**Med**
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
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						
Unidentified Ceramiaceae[m]						x			
Unidentified Corallinaceae A*[a]	x								
Unidentified Corallinaceae B*[m]						x			
Unidentified Dasyaceae[m]				x					
Unidentified Delesseriaceae[m]						x			
Unidentified encrusting Florideae[m]				x					
Unidentified Gigartinales[m]				x					

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Unidentified Halymeniaceae[m]						x			
Unidentified Melobesiae A*[m]				x					
Unidentified Melobesiae B*[m]						x			
Unidentified Rhodomelaceae[m]						x			
Unidentified Rhodophyta A[m]						x			
Unidentified Rhodophyta B[m]						x			
Womersleyella setacea (Hollenberg) R.E. Norris[m]						x			
Wrangelia penicillata (C. Agardh) C. Agardh[m]				x					
Phaeophyceae (Ochrophyta)									
Acinetospora crinita (Carmicheal) Sauvageau[a]			x						
Aglaozonia sp.[m]						x			x
Arthrocladia villosa (Hudson) Duby[m]				x	x		x		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						

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Cutleria chilosa (Falkenberg) P.C. Silva[m]				x	x	x			
Cutleria multifida (Turner) Greville[a]		x	x						
Cystoseira baccata (S.G. Gmelin) P.C. Silva[a]			x						
Cystoseira foeniculacea (Linnaeus) Greville[m]								x	x
Cystoseira nodicaulis (Withering) M. Roberts[a]			x						
Cystoseira spinosa Sauvageau[m]					x				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			
Dictyopteris polypodioides (A.P. De Candolle) J.V. Lamouroux			x	x	x		x		
Dictyota dichotoma (Hudson) J.V. Lamouroux	x	x	x	x	x	x	x		x
Dictyota implexa (Desfontaines) J.V. Lamouroux[m]					x	x			
Elachista sp.[m]						x			
Halopteris filicina (Grateloup) Kützing			x	x	x	x	x	x	x
Laminaria ochroleuca Bachelot de la Pylaie[a]			x						
Laminaria rodriguezii Bornet[m]						x			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Leathesia mucosa Feldmann[m]						x			
Lobophora variegata (J.V. Lamouroux) Womerley ex E.C. Oliveira[m]						x			
Myriactula sp.[m]						x			
Nereia filiformis (J. Agardh) Zanardini[m]				x	x				
Padina pavonica (Linnaeus) Thivy[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						
Sargassum sp.									x
Scytosiphon lomentaria (Lyngbye) Link[a]			x						
Spermatochnus paradoxus (Roth) Kützing[m]					x				
Sphacelaria cirrosa (Roth) C. Agardh			x		x	x			
Sphacelaria plumula Zanardini		x	x	x	x	x			
Sphacelaria rigidula Kützing[a]			x						
Sphacelaria sp.[m]					x				
Sporochnus pedunculatus (Hudson) C. Agardh[m]				x	x	x	x		
Stictyosiphon adriaticus Kützing[m]					x	x			

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Stilophora tenella (Esper) P.C. Silva[m]					x	x	x		
Stypocaulon scoparium (Linnaeus) Kützing[a]			x						
Symphyocarpus strangulans Rosenvinge[a]			x						
Undaria pinnatifida (Harvey) Suringar[a]			x						
Unidentified encrusting Phaeophyceae[m]						x			
Zanardinia typus (Nardo) P.C. Silva[m]					x	x	x		x
Zonaria tournefortii (J.V. Lamouroux) Montagne[m]						x		x	
Zosterocarpus oedogonium (Meneghini) Bornet[m]				x					
Chlorophyta									
Acetabularia acetabulum (Linnaeus) P.C. Silva[m]				x	x				
Bryopsis hypnoides J.V. Lamouroux[m]				x		x			
Bryopsis plumosa (Hudson) C. Agardh			x	x					
Caulerpa prolifera (Forsskål) J.V. Lamouroux[m]									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						

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
Cladophora prolifera (Roth) Kützing[m]				x					
Cladophora rupestris (Linnaeus) Kützing			x		x				
Cladophora sp.[m]						x	x		x
Codium bursa (Olivi) C. Agardh[m]					x				
Codium coralloides (Kützing) P.C. Silva[m]					x				
Codium dichotomum S.F. Gray[m]					x				
Codium effusum (Rafinesque) Delle Chiaje[m]					x				
Codium tomentosum Stackhouse[a]			x						
Codium vermilara (Olivi) Delle Chiaje			x	x	x			x	x
Dasycladus vermicularis (Scopoli) Krasser[m]									x
Derbesia tenuissima (Moris & De Notaris) P.L. Crouan & H.M. Crouan			x	x		x			
Enteromorpha sp.[a]		x							
Flabellia petiolata (Turra) Nizamuddin[m]				x	x	x	x	x	x
Halicystis sp.[m]							x		
Halimeda tuna (J. Ellis & Solander) J.V. Lamouroux[m]					x	x	x		x
Microdictyon tenuius J.E. Gray[m]						x			x
Palmophyllum crassum (Naccari) Rabenhorst[m]				x	x	x	x		x

Region	NEA	NEA	NEA	Med	Med	Med	Med	Med	Med
Zone	**Uni**	**Bri**	**Gal**	**Cos**	**Pro**	**Bal**	**Cor**	**Tun**	**Gre**
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				x		x			
Umbraulva dangeardii M.J. Wynne & G. Furnari			x			x			
Unidentified Cladophoraceae[m]				x					
Uronema marinum Womersley[m]						x			
Valonia macrophysa Kützing[m]				x	x	x	x	x	x
Valonia utricularis (Roth) C. Agardh[m]						x			
Tracheophyta									
Posidonia oceanica (Linnaeus) Delile[m]						x			
Zostera sp.[a]	x								

IV. General discussion

Discussió general

IV. General discussion

The European macroalgal-dominated coastal detritic bottoms have been studied since the end of the 19th century in certain zones of the Mediterranean Sea (e.g. the French coasts and the Tyrrhenian Sea), leading to the publication of general descriptions that tried to synthetize the knowledge concerning these habitats (e.g. Pérès and Picard 1963, 1964, Bourcier 1968, 1982, Augier 1982). However, the distribution of the variability of these bottoms throughout the Mediterranean and even the European coasts remains mostly unknown. Furthermore, although the presence of macroalgal-dominated coastal detritic bottoms from the Balearic Islands is known since two centuries ago (e.g. Rodríguez-Femenías 1889, Bellón-Uriarte 1921, Ballesteros *et al*. 1993), no descriptive studies have been performed, with the only exception of the description of the *Peyssonnelia* beds by Ballesteros (1994). Problems related with deep-water sampling probably are the main reason for the lack of studies concerning these bottoms. This dissertation tries both to increase the knowledge of the macroalgal-dominated coastal detritic bottoms by describing those found in the continental shelf off Mallorca and Menorca (Balearic Islands), and to provide effective methods for their sampling.

Macroalgal-dominated coastal detritic bottoms from the Balearic Islands

The macroalgal-dominated benthic communities from the Balearic Islands have a lower limit of distribution that is much deeper than in the closer continental coasts. Macroalgal growth is favored by the high water transparency, as the 0.05% of surface irradiance reaches 110 m depth (Ballesteros and Zabala 1993).

The continental shelf off Mallorca and Menorca harbors a rich macroalgal-dominated coastal detritic landscape. Here we have identified up to six different assemblages, being five of them included in the Spanish List of Marine Habitats (Templado *et al*. 2012), with the exception of the meadow of *Phyllophora crispa* with *Halopteris filicina*. Their distribution is related to depth, which is closely related to seasonal variability in water temperature (Ballesteros and Zabala 1993). Both meadows of *Osmundaria volubilis* and *Phyllophora crispa* and beds of *Peyssonnelia inamoena* and *Peyssonnelia rubra* dominate above 65 meters depth, and are present mainly in the Southern coasts of the studied area. In contrast, *Laminaria rodriguezii* kelp beds and maërl beds develop in the Menorca Channel and the Northern coast of Menorca, respectively, between 77 and 81 meters depth. Finally, the meadow of *Phyllophora crispa* with *Halopteris filicina* has a wider bathymetric distribution throughout the studied area (57 to 93 m).

We investigated further the kelp forests of *L. rodriguezii*, the *P. inamoena* beds and the maërl of *Spongites fruticulosus*. They had been widely reported in the Western Mediterranean (e.g. Huvé 1954, 1955, 1956, Costa 1960, Jacquotte 1962, Gómez *et al*. 1986), but only the *Peyssonnelia* beds (Ballesteros 1994) and the maërl of *S. fruticulosus* (Ballesteros 1988) had been exhaustively studied. Forests of *L. rodriguezii* and beds of *P. inamoena* present a complex community structure, which is reflected in a high number of species and, in the case of the kelp forests, also in a high diversity. These high diversity values are comparable with the values already reported for the *Peyssonnelia* beds and the maërl of *S. fruticulosus* (Ballesteros 1988, 1994). Moreover, the diversity indexes found here are also similar to those found in communities developing at deep-water rocky bottoms, such as the communities of *Cystoseira zosteroides, Halimeda tuna, Lithophyllum stictaeforme* and *Phymatolithon calcareum* from Tossa de Mar (Spain) (Ballesteros 1992a), and the *O. volubilis* meadows from the Balearic Islands (Ballesteros 1992b). In contrast, maërl beds of *S. fruticulosus* are the simplest studied community as erect algae were scarcely developed, matching the same community studied in Tossa de Mar (Spain) (Ballesteros 1988).

The three studied communities present moderate to high number of shared species, as previously reported by Pérès and Picard (1964) for the Mediterranean algal detritic bottoms. This probably stems from a common pool of species adapted to these detritic bottoms and to a possible shift from one to another community in relation to anthropogenic disturbances. For example, the high algal similarity between the basal stratums of the forests of *L. rodriguezii* and the maërl of *S. fruticulosus*, suggests the existence of a gradient in the abundance of *L. rodriguezii*, which thrives in areas devoid of bottom trawling but is completely absent in heavily trawled bottoms (C. Rodríguez-Prieto and S. Joher, personal observations). In a similar way, changes in the sedimentation rates would prompt the increase in abundance of Peyssonneliales over Corallinales, as reported in Alicante (Spain) and Malta (Bordehore *et al*. 2000a).

As regards to the qualitative comparison of the macroalgal-dominated coastal detritic communities from the European coasts, those described in the Balearic Islands can be distinguished not only from those found in the NE Atlantic, but also from those in other Mediterranean areas, mainly because of its high species richness. However, the forests of *L. rodriguezii* and the *Peyssonnelia* beds are difficult to be distinguished, as they present a high number of erect and prostrate species in common. Besides, the maërl of *S.*

fruticulosus studied in the Balearic Islands differed not only from these studied communities but also from other maërl beds found in closer areas.

Sampling methods

The sampling methods used in this dissertation have been traditionally used in studies dealing on demersal and benthic fauna (e.g. Bertrand *et al*. 2002, Massutí and Reñones 2005, Fanelli *et al*. 2007, García-Muñoz *et al*. 2008, Ordines and Massutí 2009, Ramón *et al*. 2014), and they also have been useful to study the macroalgal component of coastal detritic bottoms.

The bottom trawl with a small mesh size (20 mm) has allowed the characterization of the main macroalgal coastal detritic assemblages, as it captured the majority of the species developing in these habitats. However, this method presented some limitations, as trawling can be performed above assemblages with a patchy distribution, which results in a mixing sample and, thus, not convenient for assemblage characterization. However, the identification of macroalgae present in scientific bottom trawling can be used to complement the information obtained by faunal studies, similarly to those of the MEDITS programme performed in Mallorca and Menorca.

On the other hand, Box-corer dredging and beam trawling were effective on providing representative samples. However, they required the previous location of homogenous areas by means of ROV dives. The combination of visual and sampling techniques are suitable for the surveys performed with the purpose of characterizing the main algal-dominated communities, as it has been conducted in the INDEMARES (Barberá *et al*. 2009, 2012) and DRAGONSAL projects.

Future perspectives

The deep-water macroalgal-dominated coastal detritic bottoms of the Mediterranean Sea still remain mostly unknown, as the majority of studies only covered the Western Mediterranean, especially some locations of the Spanish, French and Italian coasts (Huvé 1954, 1956, Jacquotte 1962, Pérès and Picard 1964, Picard 1965, Bourcier 1968, Fredj 1972, Augier and Boudouresque 1978, Augier 1982, Ballesteros 1998, 1994, this dissertation). Furthermore, few studies have also been performed in the NE Atlantic, although there are exhaustive studies of the maërl bottoms from Galicia and the diversity assessment of the epiflora on the maërl beds from this region (Peña 2010, Peña *et al*. 2014). Future studies are needed to increase the knowledge of the macroalgal coastal detritic bottoms in the Balearic Islands and other zones of the Mediterranean and the NE Atlantic.

This dissertation is a contribution to the better understanding of the macroalgal-dominated coastal detritic bottoms found in the continental shelf off Mallorca and Menorca, starting for the characterization of the main assemblages and the description of three of the communities that constitute them. Simultaneously to the work presented in this dissertation, the members of the group of Algues Bentòniques Marines from the Universitat de Girona also contributed to the characterization of the macroalgal coastal detritic bottoms of the Menorca Channel (CANAL0209 and CANAL0811 surveys) (Fig. 23) and the Southern coasts of Mallorca (DRAGONSAL0712 and DRAGONSAL0914 surveys), as reflected in some published works (Barberá *et al*. 2009, 2012, 2014). In future projects, the identification and location of the macroalgal-dominated coastal detritic bottoms could be extended to other zones of the Balearic continental shelf.

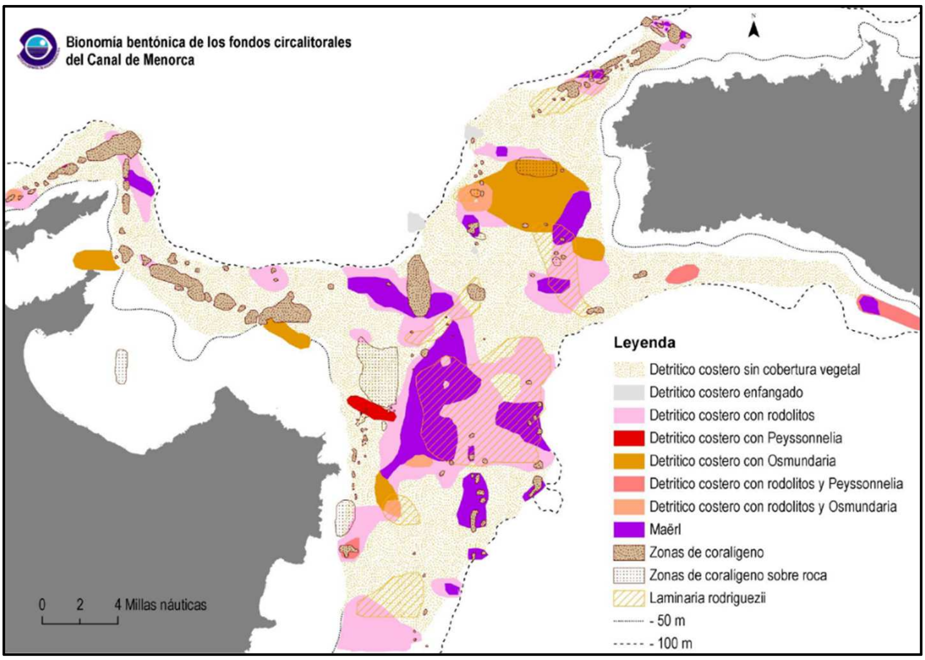

Figure 23 – Distribution map of the deep-water algal-dominated coastal detritic habitats in the Menorca Channel. Source: Barberá *et al*. (2009).

Els fons detrítics costaners dominats per macroalgues europeus han estat estudiats des de finals del segle XIX en algunes zones del mar Mediterrani (per exemple, les costes franceses i el mar Tirrè), portant a la publicació de descripcions generals que han intentat sintetitzar el coneixement sobre aquests hàbitats (per exemple, Pérès i Picard 1963, 1964, Bourcier 1968, 1982, Augier 1982). No obstant, la distribució de la variabilitat d'aquests fons en el Mediterrani i, fins i tot, en les costes europees segueix majoritàriament desconegut. A més, tot i que la presència dels fons detrítics costaners dominats per macroalgues a les illes Balears es coneixen des de fa dos segles (per exemple, Rodríguez-Femenías 1889, Bellón-Uriarte 1921, Ballesteros *et al*. 1993), no s'hi han dut a terme estudis quantitatius, amb l'excepció de la descripció dels llits de *Peyssonnelia* de Ballesteros (1994). Els problemes relacionats amb el mostreig en aigües profundes són la principal raó per la falta d'estudis relacionats amb aquests fons. Aquesta tesi pretén contribuir al coneixement dels fons detrítics costaners dominats per macroalgues descrivint els que es troben a la plataforma continental de Mallorca i Menorca (illes Balears), i proveir mètodes efectius per al seu mostreig.

Fons detrítics costaners dominats per macroalgues de les illes Balears

Les comunitats bentòniques dominades per macroalgues de les illes Balears presenten un límit de distribució inferior més profund que el trobat en les costes continentals properes. El creixement de les macroalgues es veu afavorit per la elevada transparència de l'aigua, ja que el 0.05 % de la irradiància superficial arriba als 110 m de fondària (Ballesteros i Zabala 1993).

La plataforma continental de Mallorca i Menorca presenta un ric paisatge detrític costaner dominat per macroalgues. Hem identificat un total de sis paisatges diferents, cinc dels quals estan inclosos a la Llista Espanyola d'Hàbitats Marins (Templado *et al*. 2012), amb l'excepció de les praderies de *Phyllophora crispa* amb *Halopteris filicina*. La seva distribució està relacionada amb la fondària i aquesta amb la variació estacional de la temperatura de l'aigua (Ballesteros i Zabala 1993). Tant les praderies de *Osmundaria volubilis* i *Phyllophora crispa* com els llits de *Peyssonnelia inamoena* i *Peyssonnelia rubra* dominen les profunditats per sobre els 65 m, i es troben principalment en les costes meridionals de l'àrea estudiada. En contrast, els llits de *Laminaria rodriguezii* i els llits de maërl es desenvolupen en el canal de Menorca i la costa Nord Oriental de Menorca, respectivament, entre els 77 i

81 m de fondària. Finalment, les praderies de *Phyllophora crispa* amb *Halopteris filicina* tenen una àmplia distribució batimètrica en tota l'àrea estudiada (de 57 a 93 m).

A més, hem estudiat els boscos de *L. rodriguezii*, els llits de *P. inamoena* i el maërl de *Spongites fruticulosus*, que han estat àmpliament citats al Mediterrani Occidental (per exemple, Huvé 1954, 1955, 1956, Costa 1960, Jacquotte 1962, Gómez *et al*. 1986), però només els llits de *Peyssonnelia* (Ballesteros 1994) i el maërl de *S. fruticulosus* (Ballesteros 1988) han estat estudiats exhaustivament. Els boscos de *L. rodriguezii* i els llits de *P. inamoena* presenten una estructura de la comunitat complexa, que es reflecteix en l'elevat nombre d'espècies i, en el cas del bosc de laminarials, també en l'alta diversitat. Aquests valors de diversitat són comparables amb els trobats en els llits de *Peyssonnelia* i el maërl de *S. fruticulosus* (Ballesteros 1988, 1994). A més, els valors de diversitat trobats aquí també són similars als trobats en comunitats que es desenvolupen en fons rocosos d'aigües profundes, com les comunitats de *Cystoseira zosteroides, Halimeda tuna, Lithophyllum stictaeforme* i *Phymatolithon calcareum* de Tossa de Mar (Espanya) (Ballesteros 1992a), i les praderies de *O. volubilis* de les illes Balears (Ballesteros 1992b). En contrast, el maërl de *S. fruticulosus* és la comunitat més simple de les estudiades degut al pobre desenvolupament de les algues erectes, coincidint amb la mateixa comunitat estudiada a Tossa de Mar (Espanya) (Ballesteros 1988).

Les tres comunitats estudiades presenten un nombre d'espècies en comú entre moderat i alt, tal com ja indicaven Pérès i Picard (1964) pels fons detrítics costaners mediterranis. Aquest fet probablement es deu a un grup d'espècies adaptades a aquests fons detrítics i a possibles canvis d'una comunitat a una altra relacionats amb pertorbacions antropogèniques. Per exemple, la elevada similitud algal entre els estrats basals dels boscos de *L. rodriguezii* i del maërl de *S. fruticulosus*, suggereix la existència d'un gradient en l'abundància de *L. rodriguezii*, que prospera en zones amb absència d'arrossegament de fons però que és completament absent en fons molt arrossegats (C. Rodríguez-Prieto i S. Joher, observacions personals). Tanmateix, canvis en les taxes de sedimentació poden incitar l'increment de l'abundància de Peyssonneliales sobre Corallinales, tal com s'ha descrit a Alacant (Espanya) i Malta (Bordehore *et al*. 2000a).

En relació a la comparació qualitativa de les comunitats detrítiques costaneres dominades per macroalgues de les costes europees, les comunitats descrites a les illes Balears es poden distingir tant de les comunitats trobades al NE Atlàntic com de les trobades al Mediterrani, degut principalment a l'elevada riquesa d'espècies. No obstant, els boscos de *L. rodriguezii* i els llits de *Peyssonnelia* no es poden distingir, ja que presenten un elevat nombre d'espècies erectes i prostrades en comú. Per contra, el maërl de *S. fruticulosus* estudiat a les illes Balears difereix tant d'aquestes dues comunitats estudiades com d'altres llits de maërl trobats en zones properes.

Mètodes de mostreig

Els mètodes de mostreig utilitzats en aquesta tesi han estat usats tradicionalment en estudis de la fauna demersal i bentònica (per exemple, Bertrand *et al*. 2002, Massutí i Reñones 2005, Fanelli *et al*. 2007, García-Muñoz *et al*. 2008, Ordines i Massutí 2009, Ramón *et al*. 2014), i han resultat útils per a l'estudi del component vegetal dels fons detrítics costaners.

L'arrossegament de fons, amb mida de malla petita (20 mm) ha permès la caracterització dels principals paisatges dominats per macroalgues del detrític costaner, ja que capturava la majoria de les espècies desenvolupades en aquests hàbitats. No obstant, aquest mètode presenta algunes limitacions, ja que es pot arrossegar sobre paisatges amb una distribució heterogènia, que resulta en mostres barrejades i, en conseqüència, no apropiades per la caracterització de paisatges. Tot i això, la identificació de macroalgues presents en arrossegaments científics es pot utilitzar per complementar la informació obtinguda en els estudis de fauna, similars al programa MEDITS desenvolupat a Mallorca i Menorca.

Per altra banda, la draga Box-Corer i el patí epibentònic van ser efectius en proveir mostres representatives. No obstant, van requerir la prèvia localització de zones homogènies mitjançant immersions de ROV. La combinació de tècniques visuals i de mostreig és recomanable per campanyes desenvolupades amb la finalitat de caracteritzar les principals comunitats dominades per algues, com s'ha fet als projectes INDEMARES (Barberá *et al*. 2009, 2012) i DRAGONSAL.

Perspectives de futur

Els fons detrítics costaners dominats per macroalgues del Mediterrani encara resten majoritàriament desconeguts, ja que la majoria d'estudis s'han realitzat al Mediterrani Occidental, especialment en localitzacions de les costes d'Espanya, França i Itàlia (Huvé 1954, 1956, Jacquotte 1962, Pérès i Picard 1964, Picard 1965, Bourcier 1968, Fredj 1972, Augier i Boudouresque 1978, Augier 1982, Ballesteros 1988, 1994, aquesta tesi). A més, pocs estudis s'han realitzat al NE Atlàntic, tot i que hi ha estudis exhaustius dels fons de maërl de Galicia i avaluacions de la diversitat de l'epiflora dels fons de maërl (Peña 2010, Peña *et al*. 2014). Futurs estudis són necessaris per incrementar el coneixement dels fons detrítics costaners dominats per macroalgues a les illes Balears i en altres zones del Mediterrani i el NE Atlàntic.

Aquesta tesi és una contribució al millor coneixement dels fons detrítics costaners dominats per macroalgues que es troben a la plataforma continental de Mallorca i Menorca, començant per la caracterització de les principals agrupacions i la descripció de tres de les comunitats que les caracteritzen. Simultàniament als objectius presentats en aquesta tesi, els membres del grup d'Algues Bentòniques Marines de la Universitat de Girona també han contribuït a la caracterització dels fons detrítics costaners dominats per macroalgues de canal de Menorca (campanyes CANAL0209 i CANAL0811) (Fig. 23) i a les costes meridionals de Mallorca (campanyes DRAGONSAL0712 i DRAGONSAL 0914), tal i com es reflecteix en alguns treballs publicats (Barberá *et al*. 2009, 2012, 2014). En futurs projectes, la identificació i la localització dels fons detrítics costaners dominats per macroalgues es podran estendre a altres zones de la plataforma continental balear.

Peus de figura

Figura 23 – Mapa de distribució dels hàbitats detrítics costaners dominats per macroalgues d'aigües profundes al canal de Menorca. Font: Barberá *et al*. (2009).

V. Conclusions

Conclusions

V. Conclusions

The main conclusions of this dissertation are synthetized as follow:

Regarding the deep-water algal-dominated coastal detritic bottoms:

- The deep-water algal-dominated coastal detritic bottoms of Mallorca and Menorca presented a high variability, since up to six different algal detritic assemblages were distinguished:
    - The *Osmundaria volubilis* and *Phyllophora crispa* meadows, found at the West coast of Menorca and the Northeast and Southern coasts of Mallorca, and the *Peyssonnelia inamoena* and *Peyssonnelia rubra* beds, at the West coast of Mallorca and the South coasts of Mallorca and Menorca, respectively. They presented a shallow distribution (52 to 65 m depth).
    - The *Laminaria rodriguezii* beds and the maërl beds, were found in the Menorca Channel and at the East coast of Menorca, respectively, and developed at deeper waters (77 to 81 m).
    - The *Phyllophora crispa* and *Halopteris filicina* meadows, which was the most widespread assemblage, distributed thorough the continental shelf of Mallorca and Menorca, and presented a eurybathic distribution (57 to 93 m).
- The three studied communities that characterized some of the macroalgal coastal detritic assemblages presented clear differences in their community structure and diversity values.
    - The maërl of *Spongites fruticulosus* was characterized by maërl-forming species, presented poor development of the erect stratum, and, consequently, hold low diversity values.
    - In contrast, the forests of *Laminaria rodriguezii* presented high number of species and diversity values due to a well-structured erect stratum.
    - Finally, a high number of erect and prostrate species and low presence of carbonated species were found in the *Peyssonnelia inamoena* beds, which presented moderate diversity levels due to the dominance of the *Peyssonnelia* species.
- Despite the changes in community structure, the forests of *Laminaria rodriguezii* and the maërl of *Spongites fruticulosus* presented low differences in the species composition of the basal stratum, which suggests a gradient from the former to the latter leaded by the loss of canopy of the kelp species. Moreover, changes in some environmental

conditions can favor the development of the *Peyssonnelia inamoena* beds, enhancing the abundance of Peyssonneliaceae over Corallinales.

- There are significant qualitative biogeographical differences between the macroalgal coastal detritic communities of the NE Atlantic and the Mediterranean, reflected in their bathymetrical distribution and species composition.
  - While those found in the NE Atlantic develop above 30 m depth, the Mediterranean macroalgal costal detritic communities extend down to 90-130 m.
  - As regards to the species composition, the presence of exclusive species with a restricted distribution distinguished those communities from the NE Atlantic and the Mediterranean. The richest species composition in Southern latitudes would correspond to most favorable environmental conditions, which in the case of the Mediterranean, favors the development of different kind of algal detritic communities. Besides, the high number of species found in the Western Mediterranean in comparison with the Eastern Mediterranean would correspond to a better knowledge of the former area.
- From a qualitative point of view, all European macroalgal-dominated coastal detritic communities studied so far can be considered as maërl beds, with a more or less developed erect stratum. According to differences in the species composition of the basal and erect strata, seven different kinds of algal detritic communities were qualitatively found in the European coasts:
  - The NE Atlantic maërl of *Lithothamnion corallioides* and *Phymatolithon calcareum* with a poor erect stratum, found in the United Kingdom and Galicia.
  - The NE Atlantic maërl of *Lithothamnion corallioides* and/or *Phymatolithon calcareum* with a well-developed erect stratum, in the French Brittany and Galicia.
  - The Mediterranean maërl of *Phymatolithon calcareum* and/or *Lithothamnion corallioides* with a well-developed erect stratum, in Costa Brava, Provence, Balearic Islands, Corsica, Tunisia and Greece.
  - The Mediterranean maërl of *Phymatolithon calcareum* and different *Peyssonnelia* species and a well-developed erect stratum, in the Balearic Islands.
  - The Mediterranean maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* and a well-developed erect stratum, in Costa Brava.

- The Mediterranean maërl of *Spongites fruticulosus* with *Phymatolithon calcareum* and *Lithothamnion valens* with a poor erect stratum, in the Balearic Islands.
- The Mediterranean maërl of *Spongites fruticulosus* with *Lithothamnion corallioides* and *Lithothamnion valens* with different *Peyssonnelia* species and a well-developed erect stratum, in the Balearic Islands.

Concerning the methodology used in this dissertation:

- Bottom trawl proved to be a useful sampling method for the characterization of the macroalgal-dominated coastal detritic assemblages, and is useful to relate benthic assemblages with fish and invertebrate fauna.
- Box-Corer dredging and beam trawling are appropriate methods to study macroalgal-dominated detritic communities when complemented with ROV dives to locate homogenous areas where sampling can be performed.

Conclusions

Les principals conclusions d'aquesta tesi estan sintetitzades a continuació:

Respecte els fons detrítics costaners dominats per macroalgues en aigües profundes:

- Els fons detrítics costaners dominats per macroalgues en aigües profundes de Mallorca i Menorca presenten una alta variabilitat, ja que sis paisatges diferents han estat identificats:
  - Les praderies de *Osmundaria volubilis* i *Phyllophora crispa*, trobades a la costa occidental de Menorca i a les costes Nord-est i meridional de Mallorca, i els llits de *Peyssonnelia inamoena* i *Peyssonnelia rubra*, a la costa occidental de Mallorca i a les costes meridionals de Mallorca i Menorca, respectivament. Aquestes agrupacions van presentar una distribució més superficial (de 52 a 65 m).
  - Els llits de *Laminaria rodriguezii* i els llits de maërl, trobats al canal de Menorca i a la costa Oriental de Menorca, respectivament, i en aigües profundes (de 77 a 81 m).
  - Les praderies de *Phyllophora crispa* amb *Halopteris filicina*, la agrupació més àmpliament distribuïda per tota la plataforma continental de Mallorca i Menorca, amb un rang de distribució ampli (de 57 a 93 m).
- Les tres comunitats estudiades que caracteritzaven alguns dels paisatges detrítics dominats per macroalgues presentaven clares diferències en la seva estructura i valors de diversitat.
  - El maërl de *Spongites fruticulosus* estava caracteritzat per espècies formadores de maërl, presentant un pobre desenvolupament de l'estrat erecte, i, en conseqüència, baixos valors de diversitat.
  - En canvi, els boscos de *Laminaria rodriguezii* presentaven valors alts de nombre d'espècies i diversitat degut a l'estrat erecte ben desenvolupat.
  - Finalment, un alt nombre d'espècies erectes i prostrades junt un baix nombre d'espècies carbonatades es van trobar als llits de *Peyssonnelia inamoena*, que presentaven valors moderats de diversitat degut a la dominància d'espècies del gènere *Peyssonnelia*.
- Tot i els canvis en la estructura de la comunitat, els boscos de *Laminaria rodriguezii* i el maërl de *Spongites fruticulosus* presentaven poques diferències en la composició específica de l'estrat basal, suggerint un gradient des de la primera a la segona degut a la pèrdua de cobertura de *Laminaria rodriguezii*. A més, canvis en les condicions ambientals poden

afavorir el desenvolupament dels llits de *Peyssonnelia* per l'increment de la abundància de Peyssonneliales sobre les Corallinales.

- Existeixen diferencies biogeogràfiques i qualitatives significatives entre les comunitats del detritic costaner dominat per macroalgues del NE Atlàntic i del Mediterrani, reflectides en la seva distribució batimètrica i composició específica.
  - Mentre que les comunitats atlàntiques es desenvolupen per sobre els 30 m de fondària, les comunitats detrítiques costaneres dominades per macroalgues del Mediterrani s'estenen fins als 90-130 m.
  - Pel que fa a la composició específica, la presència d'espècies exclusives amb una distribució restringida va distingir les comunitats del NE Atlàntic i les del Mediterrani. La major riquesa específica de les latituds meridionals correspondria a condicions ambientals més favorables, que en el cas del Mediterrani afavoririen el desenvolupament de diferents tipus de comunitats detrítiques algals. A més, l'elevat nombre d'espècies trobat al Mediterrani Occidental en comparació amb el Mediterrani Oriental correspondria a un millor coneixement de la primera zona.
- Des d'un punt de vista qualitatiu, les comunitats detrítiques costaneres dominades per macroalgues de les costes europees que han estat estudiades poden ser considerades com a llits de maërl, amb un estrat erecte més o menys desenvolupat. D'acord amb les diferències en la composició específica dels estrats basal i erecte, set tipus diferents de comunitats detrítiques algals es van trobar en les costes europees:
  - Maërl NE Atlàntic de *Lithothamnion corallioides* i *Phymatolithon calcareum* amb un pobre estrat erecte, trobat al Regne Unit i Galicia.
  - Maërl NE Atlàntic de *Lithothamnion corallioides* i/o *Phymatolithon calcareum* amb un estrat erecte ben desenvolupat, a la Bretanya francesa i Galicia.
  - Maërl Mediterrani de *Phymatolithon calcareum* i/o *Lithothamnion corallioides* amb un estrat erecte ben desenvolupat, a la Costa Brava, Provença, illes Balears, Còrsega, Tunísia i Grècia.
  - Maërl Mediterrani de *Phymatolithon calcareum* amb diferents espècies de *Peyssonnelia* i un estrat erecte ben desenvolupat, a les illes Balears.
  - Maërl Mediterrani de *Spongites fruticulosus* amb *Phymatolithon calcareum* i un estrat erecte ben desenvolupat, a la Costa Brava.
  - Maërl Mediterrani de *Spongites fruticulosus* amb *Phymatolithon calcareum* i *Lithothamnion valens* amb un estrat erecte ben desenvolupat, a les illes Balears.

- Maërl Mediterrani de *Spongites fruticulosus* amb *Lithothamnion corallioides* i *Lithothamnion valens* amb diferents espècies de *Peyssonnelia* i un estrat erecte ben desenvolupat, a les illes Balears.

Pel que fa a la metodologia utilitzada en aquesta tesi:

- ➢ L’arrossegament de fons és un mètode de mostreig útil per la caracterització dels paisatges detrítics costaners dominats per macroalgues, i és útil per a relacionar-los amb els peixos i la fauna invertebrada.
- ➢ La draga Box-Corer i el patí epibentònic són mètodes apropiats per l’estudi de les comunitats detrítiques dominades per macroalgues si es complementen amb immersions de ROV per a localitzar zones homogènies on poder mostrejar-les.

VI. Bibliography

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Appendix I
Checklist of the flora identified in the continental shelf off Mallorca and Menorca

Checklist of the flora identified in the continental shelf off Mallorca and Menorca

The introduced species are marked with an asterisk (*), and the maërl-forming species with a hashtag (#).

Rhodophyta

Acrochaetium sp.
Acrodiscus vidovichii (Meneghini) Zanardini
Acrosorium ciliolatum (Harvey) *Kylin*
'Acrosymphytonema breemaniae' (stadium) C.F. Boudouresque, M. Perret-Boudouresque & M. Knoepffler-Peguy
Acrothamnion preissii (Sonder) E.M. Wollaston*
Aglaothamnion tenuissimum (Bonnemaison) Feldmann-Mazoyer
Aglaothamnion tripinnatum (C. Agardh) Feldmann-Mazoyer
Aglaothamnion sp.
Alsidium corallinum C. Agardh
Antithamnion sp.
Apoglossum ruscifolium (Turner) J. Agardh
Asparagopsis taxiformis (Delile) Trevisan de Saint-León*
Balliella cladoderma (Zanardini) Athanasiadis
Bonnemaisonia asparagoides (Woodward) C. Agardh
Bonnemaisonia sp.
Bornetia secundiflora (J. Agardh) Thuret
Botryocladia botryoides (Wufen) Feldmann
Botryocladia chiajeana (Meneghini) Kylin
Botryocladia madagascariensis G. Feldmann*
Brongniartella byssoides (Goodenough & Woodward) F. Schmitz
Calliblepharis jubata (Goodenough & Woodward) Kützing
Callophyllis laciniata (Hudson) Kützing
Ceramium bertholdii Funk
Ceramium codii (H. Richards) Mazoyer
Champia parvula (C. Agardh) Harvey
Chrysymenia ventricosa (J.V. Lamouroux) J. Agardh
Chylocladia verticillata (Lightfoot) Bliding
Contarinia peyssonneliaeformis Zanardini
Corallina elongata J. Ellis & Solander
Cordylecladia erecta (Greville) J. Agardh cf
Crouania attenuata (C. Agardh) J. Agardh
Cryptonemia lomation (Bertoloni) J. Agardh

Cryptonemia longiarticulata Funk species inquirendum
Cryptonemia tuniformis (A. Bertoloni) Zanardini
Cryptonemia sp.
Cryptopleura ramosa (Hudson) L. Newton
Dasya baillouviana (S.G. Gmelin) Montagne
Dasya corymbifera J. Agardh
Dasya penicillata Zanardini
Dasya rigescens Zanardini
Dermatolithon sp.
Erythroglossum balearicum J. Agardh ex Kylin
Erythroglossum sandrianum (Kützing) Kylin
Erythrotrichia carnea (Dillwyn) J. Agardh
Ethelia vanbosseae Feldmann
Eupogodon planus (C. Agardh) Kützing
Felicinia marginata (Roussel) Manghisi, Le Gall, Ribera, Gargiulo et M. Morabito
Gloiocladia furcata (C. Agardh) J. Agardh
Gloiocladia microspora (Bornet ex J.J. Rodríguez y Femenías) Berecibar, M.J. Wynne, Barbara & R. Santos
Gloiocladia repens (C. Agardh) Sánchez & Rodríguez-Prieto
Gracilaria bursa-pastoris (S.G. Gmelin) P.C. Silva
Gracilaria corallicola Zanardini
Gracilaria sp.
Griffithsia sp.
Halopithys incurva (Hudson) Batters
Halymenia elongata C. Agardh
Halymenia latifolia P.L. Crouan & H.M. Crouan ex Kützing
Halymenia sp.
Haraldia lenormandii (Derbès & Solier) Feldmann
Hydrolithon farinosum (J.V. Lamouroux) Penrose & Y.M. Chamberlain
Hypnea spinella (C. Agardh) Kützing
Hypoglossum hypoglossoides (Stackhouse) F.S. Collins & Hervey
Irvinea boergesenii (Feldmann) R.J. Wilkes, L.M. McIvor & Guiry
Jania virgata (Zanardini) Montagne
Kallymenia feldmannii Codomier
Kallymenia patens (J. Agardh) Codomier ex P.G. Parkinson
Kallymenia requienii (J. Agardh) J. Agardh
Kallymenia sp.
Laurencia chondrioides Børgesen
Lejolisia mediterranea Bornet
Leptofauchea coralligena Rodríguez-Prieto & De Clerk
Lithophyllum racemus (Lamarck) Foslie[#]

Lithophyllum stictaeforme (Areschoug) Hauck[#]
Lithophyllum sp. [#]
Lithothamnion corallioides (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan[#]
Lithothamnion valens Foslie[#]
Lomentaria clavellosa (Lightfoot ex Turner) Gaillon
Lomentaria ercegovicii Verlaque, Boudouresque, Meinesz, Giraud & Marcot-Coqueugniot
Lomentaria subdichotoma Ercegovic
Lomentaria sp.
Lophocladia lallemandii (Montagne) F. Schmitz*
Lophosiphonia obscura (C. Agardh) Falkenberg
Melobesia membranacea (Esper) J.V. Lamouroux
Meredithia microphylla (J. Agardh) J. Agardh
Mesophyllum alternans (Foslie) Cabioch & M.L. Mendoza[#]
Mesophyllum expansum (Philippi) Cabioch & M.L. Mendoza[#]
Monosporus pedicellatus (Smith) Solier
Myriogramme carnea (J.J. Rodríguez y Femenías) Kylin
Myriogramme minuta Kylin
Myriogramme tristromatica (J.J. Rodríguez ex Mazza) Boudouresque
Nemastoma dumontioides J. Agardh
Neogoniolithon mamillosum (Hauck) Setchell & L.R. Mason[#]
Neurocaulon foliosum (Meneghini) Zanardini
Nitophyllum flabellatum Ercegovic
Nitophyllum micropunctatum Funk
Nitophyllum punctatum (Stackhouse) Greville
Osmundaria volubilis (Linnaeus) R.E. Norris
Osmundea pelagosae (Schiffner) K.W. Nam
Peyssonnelia aff. magna Ercegovic
Peyssonnelia armorica (P.L. Crouan & H.M. Crouan) Weber-van Bosse
Peyssonnelia bornetii Boudouresque & Denizot
Peyssonnelia coriacea Feldmann
Peyssonnelia dubyi P.L. Crouan & H.M. Crouan
Peyssonnelia harveyana P.L. Crouan & H.M. Crouan ex J. Agardh
Peyssonnelia inamoena Pilger
Peyssonnelia rosa-marina Boudouresque & Denizot
Peyssonnelia rubra (Greville) J. Agardh
Peyssonnelia squamaria (S.G. Gmelin) Decaisne
Peyssonnelia stoechas Boudouresque & Denizot
Peyssonnelia sp.
Phyllophora crispa (Hudson) P.S. Dixon
Phyllophora herediae (Clemente) J. Agardh

Phymatolithon calcareum (Pallas) W.H. Adey & D.L. McKibbin#
Plocamium cartilagineum (Linnaeus) P.S. Dixon
Polysiphonia elongata (Hudson) Sprengel
Polysiphonia ornata J. Agardh
Polysiphonia perforans Cormaci, G. Furnari, Pizzuto & Serio
Polysiphonia subulifera (C. Agardh) Harvey
Polysiphonia sp.
Pterothamnion crispum (Ducluzeau) Nägeli
Pterothamnion plumula (J. Ellis) Nägeli
Ptilocladiopsis horrida Berthold
Ptilothamnion pluma (Dillwyn) Thuret
Ptilothamnion sp.
Radicilingua reptans (Kylin) Papenfuss
Radicilingua thysanorhizans (Holmes) Papenfuss
Radicilingua sp.
Rhodophyllis divaricata (Stackhouse) Papenfuss
Rhodophyllis strafforelloi Ardissone
Rhodymenia sp.
Rodriguezella bornetii (J.J. Rodríguez y Femenías) F. Schmitz ex J.J. Rodríguez y Femenías
Rodriguezella pinnata (Kützing) F. Schmitz ex Falkenberg
Rodriguezella strafforelloi F. Schmitz ex J.J. Rodríguez y Femenías
Rytiphlaea tinctoria (Clemente) C. Agardh
Sahlingia subintegra (Rosenvinge) Kornmann
Sebdenia dichotoma Berthold
Sebdenia monnardiana (Montagne) Berthold
Sebdenia rodrigueziana (Feldmann) Athanasiadis
Sphaerococcus coronopifolius Stackhouse
Sphaerococcus rhizophylloides J.J. Rodríguez y Femenías
Sphondylothamnion multifidum (Hudson) Nägeli
Spongites fruticulosus Kützing#
Stylonema alsidii (Zanardini) K.M. Drew
Titanoderma pustulatum (J.V. Lamouroux) Nägeli
Titanoderma sp.
Womersleyella setacea (Hollenberg) R.E. Norris*
Wrangelia penicillata (C. Agardh) C. Agardh
Unidentified *Ceramiaceae*
Unidentified *Corallinaceae*
Unidentified *Delesseriaceae*
Unidentified *Halymeniaceae*
Unidentified *Rhodomelaceae*
Unidentified Rhodophyta 1

Unidentified Rhodophyta 2

Phaeophyceae (Ochrophyta)

'Aglaozonia chilosa' stadium Falkenberg
Arthrocladia villosa (Hudson) Duby
Asperococcus bullosus J.V. Lamouroux
Carpomitra costata (Stackhouse) Batters
Cladostephus spongiosus (Hudson) C. Agardh
Cutleria chilosa (Falkenberg) P.C. Silva
Cystoseira spinosa var. *compressa* (Ercegovic) Cormaci, G. Furnari, Giaccone, Scammacca & D. Serio
Cystoseira zosteroides C. Agardh
Cystoseira sp.
Dictyopteris lucida M.A. Ribera Siguan, A. Gómez Garreta, Pérez Ruzafa, Barceló Martí & Rull Lluch
Dictyopteris polypodioides (A.P. De Candolle) J.V. Lamouroux
Dictyota dichotoma (Hudson) J.V. Lamouroux
Halopteris filicina (Grateloup) Kützing
Hincksia sandriana (Zanardini) P.C. Silva
Laminaria rodriguezii Bornet
Sphacelaria plumula Zanardini
Sphacelaria sp.
Sporochnus pedunculatus (Hudson) C. Agardh
Zanardinia typus (Nardo) P.C. Silva
Zonaria tournefortii (J.V. Lamouroux) Montagne
Unidentified encrusting *Phaeophyceae*

Chlorophyta

Caulerpa cylindracea Sonder*
Cladophora sp.
Codium bursa (Olivi) C. Agardh
Derbesia tenuissima (Moris & De Notaris) P.L. Crouan & H.M. Crouan
Flabellia petiolata (Turra) Nizamuddin
Halimeda tuna (J. Ellis & Solander) J.V. Lamouroux
Microdictyon umbilicatum (Velley) Zanardini
Palmophyllum crassum (Naccari) Rabenhorst
Pseudochlorodesmis furcellata (Zanardini) Børgesen
Ulvella scutata (Reinke) R. Nielsen, C.J. O'Kelly & B. Wysor
Umbraulva dangeardii M.J. Wynne et G. Furnari
Uronema marinum Womersley
Valonia macrophysa Kützing

Appendix II
Front page of the works included in this thesis

Front page of the works included in this thesis

Sergi Joher, Enric Ballesteros, Emma Cebrian, Noemí Sánchez, and Conxi Rodríguez-Prieto. 2012. Deep-water macroalgal-dominated coastal detritic assemblages on the continental shelf off Mallorca and Menorca (Balearic Islands, Western Mediterranean). *Botanica Marina*, 55 (5): 485-497.

DE GRUYTER DOI 10.1515/bot-2012-0113 — Botanica Marina 2012; 55(5): 485–497

Sergi Joher*, Enric Ballesteros, Emma Cebrian, Noemí Sánchez and Conxi Rodríguez-Prieto

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-Uriarte 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, Piazzi 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, Sergi Joher, Enric Ballesteros and Conxi Rodríguez-Prieto. 2015. Contribution to the study of deep coastal detritic bottoms: the algal communities of the continental shelf off the Balearic Islands, Western Mediterranean. *Mediterranean Marine Science*, 16(3): 573-590.

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.1249

Research Article

Contribution to the study of deep coastal detritic bottoms: the algal communities of the continental shelf off the Balearic Islands, Western Mediterranean

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Handling Editor: Konstantinos Tsiamis

Received: 9 February 2015; Accepted: 8 May 2015; Published on line: 14 September 2015

Abstract

Three main algal-dominated coastal detritic communities from the continental shelf off Mallorca and Menorca (Balearic Islands, Western Mediterranean) are described herein: maërl beds dominated by *Spongites fruticulosus* and forests of *Laminaria rodriguezii* located in the Menorca channel, and *Peyssonnelia inamoena* beds found along the Southern coast of Menorca. There seems to be a gradient of disturbance from the highly disturbed *Peyssonnelia* beds to the almost undisturbed *L. rodriguezii* forests. Whether this gradient is the result of current and past anthropogenic pressure (e.g. trawling intensity) or is driven by natural environmental factors needs further assessment. Finally, the location of the target communities by means of ROV dives combined with the use of a Box-Corer dredge and beam trawl proved to be a good methodology in the study of the composition and structure of these deep water detritic communities.

Keywords: detritic bottoms, *Laminaria rodriguezii*, macroalgae, sampling methods, Mediterranean Sea, *Peyssonnelia inamoena*, *Spongites fruticulosus*.

Introduction

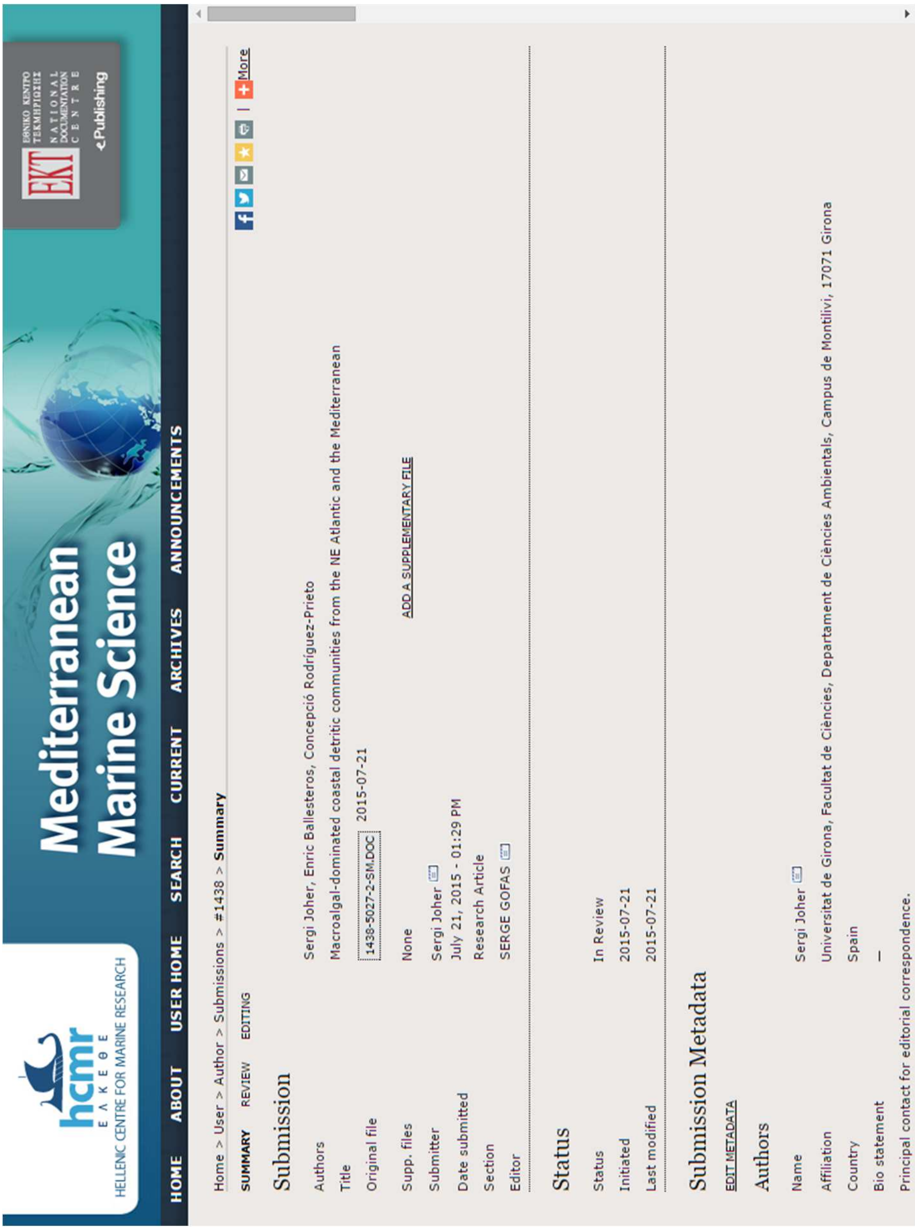
Mediterranean algal-dominated coastal detritic bottoms usually develop at depths between 25 and 130 m (Pérès, 1985; Giaccone *et al*., 1994). They are composed of silt, sand, gravels, and calcareous skeletons of benthic organisms such as molluscs, bryozoans, cnidarians, echinoderms and macroalgae. Free-living members of the orders Corallinales and Peyssonneliales (Pérès, 1985; Klein & Verlaque, 2009) are usually the major components of these bottoms. Both the skeletons and the calcareous algae allow the settlement and growth of organisms usually found on rocky bottoms (Bianchi, 2001), creating a special habitat harbouring animals and plants of both soft and hard bottoms (Laborel, 1987).

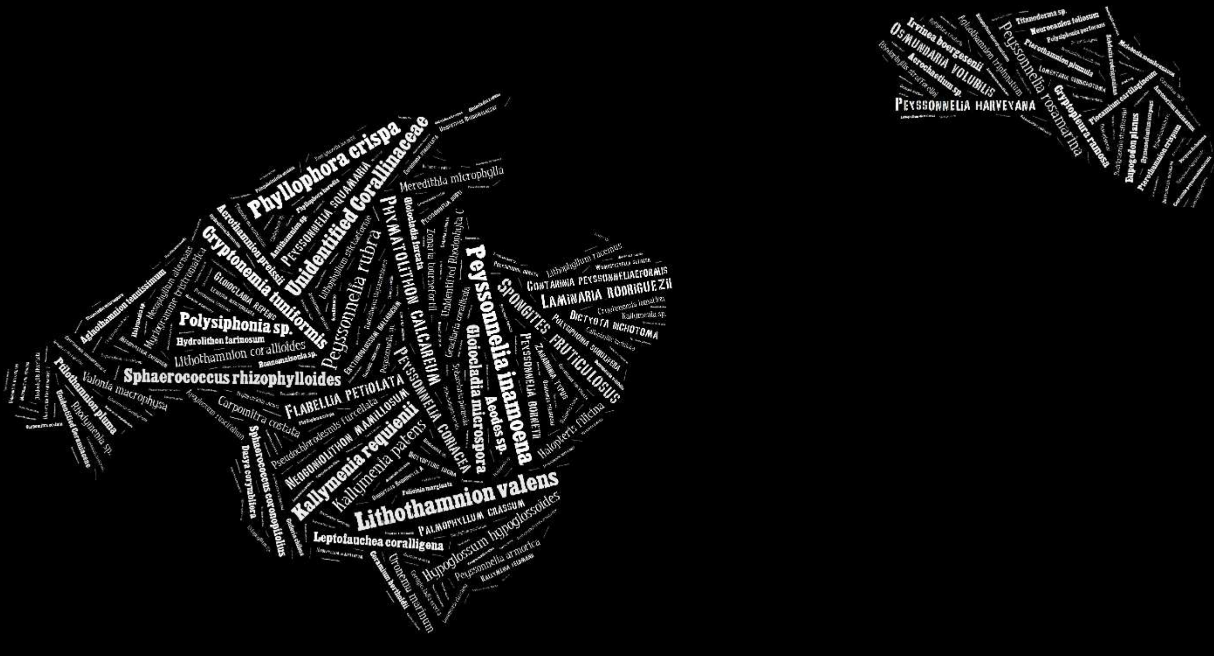
Different assemblages have been recognized in Mediterranean algal-dominated coastal detritic bottoms, each one characterized by either one or a reduced number of more or less exclusive species (e.g. see Dieuzede, 1940; Huvé, 1954, 1956; Jacquotte, 1962; Pérès & Picard, 1964; Picard, 1965; Giaccone, 1967; Bourcier, 1968; Augier & Boudouresque, 1978; Ballesteros, 1988, 1994; Giaccone *et al*., 1994). The Balearic Islands harbour extensive areas of these kinds of bottoms and different seascapes have been described between 52 and 93 m, using bottom trawls (Joher *et al*., 2012): maërl beds dominated by *Spongites fruticulosus*, deep water forests of *Laminaria rodriguezii*, two types of *Peyssonnelia* beds (one dominated by *P. inamoena* and the other one by *P. rubra*, both species presenting hypobasal calcification, and the last one presenting some cystolists too), and red algae meadows dominated by *Osmundaria volubilis* and *Phyllophora crispa*.

However, although bottom trawling was effective for the characterization of underwater landscapes, descriptions at community level require the use of smaller sampling areas. Several ROV dives were performed in 2009 in the Menorca channel and along the Southern coast of Menorca (Barberá *et al*., 2009, 2012) in order to locate certain homogeneous areas harbouring the communities that characterized the seascapes found by Joher *et al*. (2012). Three of these areas were located: one with maërl beds of *S. fruticulosus*, another with forests of *L. rodriguezii*, and a last one with *P. inamoena* beds. In contrast, extensive areas covered by the assemblage dominated by *Osmundaria volubilis* and *Phyllophora crispa* were found, with a patchy distribution.

Maërl beds dominated by *S. fruticulosus* have seldom been reported from the Balearic Islands (Barberá *et al*., 2012), and their composition and structure have only been studied from Tossa de Mar (Northwestern Mediterranean, Spain) (Ballesteros, 1988), where the maërl bed

Sergi Joher, Enric Ballesteros and Conxi Rodríguez-Prieto. Macroalgal-dominated coastal detritic communities from the NE Atlantic and the Mediterranean. *Mediterranean Marine Science*, under revision.




Phyllophora crispa
Unidentified Corallinaceae
Cryptonemia tuniformis
Polysiphonia sp.
Hydrolithon farinosum
Lithothamnion corallioides
Sphaerococcus rhizophylloides
Peyssonnelia rubra
Peyssonnelia squamaria
Aglaothamnion tenuissimum
Valonia macrophysa
Ptilothamnion pluma
Meredithia microphylla
Phymatolithon calcareum
Peyssonnelia inamoena
Gloiocladia microspora
Aeodes sp.
Peyssonnelia coriacea
Flabellia petiolata
Carpomitra costata
Kallymenia requienii
Kallymenia patens
Mesophyllum mamillosum
Sphaerococcus coronopifolius
Dasya corymbifera
Lithothamnion valens
Palmophyllum crassum
Leptofauchea coralligena
Hypoglossum hypoglossoides
Peyssonnelia armorica
Spongites fruticulosus
Contarinia peyssonneliaeformis
Laminaria rodriguezii
Dictyota dichotoma
Lithophyllum racemus
Peyssonnelia dubyi
Halopteris filicina
Irvinea boergesenii
Osmundaria volubilis
Acrochaetium sp.
Peyssonnelia harveyana
Peyssonnelia rosa-marina
Cryptopleura ramosa
Titanoderma sp.
Neurocaulon foliosum