Botanica Complutensis 28: 27-37. 2004 ISSN: 0214-4565

Floristic study of a maërl and gravel subtidal bed in the 'Ría de Arousa' (Galicia, Spain)

Ignacio Bárbara (*), Javier Cremades (*) & Alfredo J. Veiga (**)

Resumen: Bárbara, I.; Cremades, J. & Veiga, A. J. 2004. Estudio florístico en un banco de maërl y cascajo de la ría de Arousa (Galicia, España). *Bot. Complut. 28: 27-37.*

Se presenta un catálogo de 68 especies de las algas marinas existentes en un banco de maërl y cascajo de la ría de Arousa (Galicia, España). *Colacodictyon reticulatum* y *Gelidiella calcicola* son novedad para la Península Ibérica. Otras especies de interés son *Stylonema cornu-cervi*, *Cruoria rosea*-stadium, *C. cruoriaeformis*, *Trailliella intricata*-stadium, *Hymenoclonium serpens*-stadium, *Dasya punicea*, *Heterosiphonia japonica*, *Symphyocarpus strangulans* y *Desmarestia dudresnayi*. Se describen, por primera vez, los estiquidios de espermatocistes de *Dasya punicea*. Se comentan las variaciones florísticas estacionales de la comunidad. Son abundantes las formas biológicas costrosas o reptantes adaptadas al sustrato inestable, como *Cruoria cruoriaeformis, C. rosea*-stadium*, Peyssonnelia dubyi*, *Symphyocarpus strangulans, Aglaozonia parvula*-stadium y *Gelidiella calcicola*. La flora muestra grandes variaciones estacionales: en invierno la vegetación está latente (como formas costrosas) pero en verano crece rápidamente y son abundantes talos foliosos erectos. La alternancia de estados biológicos favorece las especies con ciclos heteromórficos en los cuales las fases costrosas aseguran el mantenimiento de poblaciones estables para el desarrollo posterior de las fases erguidas.

Palabras clave: algas marinas, maërl, Península Ibérica, España, Galicia, infralitoral, *Colacodictyon reticulatum*, *Gelidiella calcicola*.

Abstract: Bárbara, I.; Cremades, J. & Veiga, A. J. 2004. Floristic study of a maërl and gravel subtidal bed in the 'Ría de Arousa' (Galicia, Spain). *Bot. Complut. 28: 27-37.*

A catalogue of 68 species of seaweeds associated with a subtidal maërl and gravel bed in the «Arousa Ría» (Galicia, Spain) is presented. *Colacodictyon reticulatum* and *Gelidiella calcicola* are new for the Iberian Peninsula. Other interesting species are *Stylonema cornu-cervi*, *Cruoria rosea*-stage, *C. cruoriaeformis*, *Trailliella intricata*-stage, *Hymenoclonium serpens*-stage, *Dasya punicea*, *Heterosiphonia japonica*, *Symphyocarpus strangulans* and *Desmarestia dudresnayi*. In *Dasya punicea* spermatangial stichidia are described for the first time. Seasonal floristic variations in the subtidal maërl and gravel bed are described. Species adapted to this biogenic, unstable substratum with crustose or prostrate forms, like *Cruoria cruoriaeformis, C. rosea*-stage*, Peyssonnelia dubyi*, *Symphyocarpus strangulans, Aglaozonia parvula*-stage and *Gelidiella calcicola*, are abundant. The vegetation exhibits prominent seasonal variations: in winter the vegetation remains dormant (as crustose growth forms) but in summer produces erect foliose thalli. The alternation of these biological stages has heteromorphic cycles in which the crustose stages provide constant populations during the unfavourable season and the later development of the erect phase of species.

Key words: seaweeds, maërl, Iberian Peninsula, Spain, Galicia, subtidal, *Colacodictyon reticulatum*, *Gelidiella calcicola.*

INTRODUCTION

The benthic marine flora of the 'Arousa Ría' (Northwest Iberian Peninsula) has been relatively well studied by Donze (1968), who found 344 species. Most of the algal samples were collected from the intertidal zone and subtidal samples were taken by dredging. Even though Donze collected only a few subtidal species, he noted that large parts of the sandy bottom of the Ría are covered by maërl beds. Similar vegetation has been studied on the Northwest Iberian Peninsula by Miranda (1934) at the 'Ría de Pontevedra', Adey & McKibbin (1970) and Barberá *et al*. (2003) at the 'Ría de Vigo', and at the northern 'Ría de Muros' by Otero-Schmitt & Pérez-Cirera (2002).

On the eastern Atlantic coast, the maërl algal beds have been studied by Lemoine (1910), Boillot (1961), Cabioch (1964, 1966, 1968, 1969), Bouxin & Dizerbo (1971), Blunden *et al*. (1977), Potin *et al*. (1990) and Grall & Glémarec (1997) in France; Farnham & Jephson (1977), Blunden *et al*. (1981), Maggs

* Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía. Facultade de Ciencias. Universidade da Coruña. 15071 A Coruña. Spain. barbara@udc.es

** Aquarium Finisterrae, Museos Científicos Coruñeses, Ayuntamiento de A Coruña. Spain.

Recibido: 9 de julio de 2003. Aceptado: 18 de noviembre de 2003

(1983), Foster-Smith & Davies (1993), Hall-Spencer (1995), Connor *et al*. (1997) and Birkett *et al*. (1998) in the British Isles; Cabioch (1974) in Madeira, and Afonso-Carrillo & Gil-Rodríguez (1982) as well as Ballesteros (1993) in the Canary Islands. In the Mediterranean Sea the maërl algal community has been studied by Feldmann (1943), Huvé (1956), Jacquotte (1962) and Basso (1995). It was denominated *Phymatholitho-Lithothamnietum* by Giaccone (1965) and Boudouresque (1985) described the ecological group of sciophilic species of smooth substrata (*Phymatolithikon*), adding a list of characteristic species. In the SE Iberian Peninsula, this algal community has been studied by Soto (1990). In the NE Iberian Peninsula, Ballesteros (1989) described the structure and specific composition of maërl beds from Girona, and Ballesteros (1994) studied the deep-water *Peyssonnelia* beds from the Balearic Islands.

According to Cabioch (1974), the maërl is a 'formation végétale marine constituée par l'accumulation de thalles de Corallinacées arbusculaires libres qui forment, de ce fait, l'essentiel du substrat'. In this habitat, the slow growth of coralline algae, a high vegetative multiplication of the associated flora causing the consolidation of substrata by agglomeration of the coralline algae, a permanent canopy of small seaweeds and a top layer with great annual variations constitute the main features of this biotope. Detached branches of *Phymatolithon calcareum* and *Lithothamnion corallioides*, as well as broken shells, gravels and pebbles shape the morphological adaptations of the epibiontic flora. Maërl substrata are unstable, by abrasion and erosion of materials, and input of new material. Displacements of shells, stones and the coralline algae are frequent but a relative cohesion among materials takes place by means of entangled seaweeds attached to the substrata. Therefore, depth and nature of maërl substrata determine the appearance of the characteristic flora.

MATERIAL AND METHODS

The studied area is located (Fig. 1) at the Piedra Seca lighthouse (42° 32.9' N, 8° 55.2' W) in the 'Arousa Ría' (Northwest Iberian Peninsula), where tidal currents are strong due to its proximity to the Ría central channel. Substratum are made of free branches of *Lithothamnion corallioides* and *Phymatolithon calcareum* mixed with broken shells and pebbles (Fig. 2) which are deposited over gentle slopes.

Field research was carried out from June 1995 to September 1997 by SCUBA diving and dredging. Samples were preserved in 4% formalin seawater at 4 °C in the dark. Algal sections were made by hand with a stainless steel razor blade. Permanent slides were prepared and mounted in 12% and 25% aqueous Karo-syrup. The herbarium sheets have been deposited in the herbarium SANT of the University of Santiago de Compostela.

We studied substrata down to 35 metres depth but only floristic data for the best developed maërl and gravel bed, from 10-16 metres depth, are presented here. Visual subtidal estimates of cover and size for each species were made in squares $1m^2$. To synthesize and emphasize seasonal differences, relative abundance (1=little abundant, 2=abundant, 3=very abundant) is provided for all the species in the table I.

RESULTS AND DISCUSSION

FLORISTIC COMMENTS

Table I shows a list of species collected in the maërl and gravel bed of the 'Arousa Ría', at 10-16 metres depth. The relative abundance index of seasonality and substratum for each species are presented. In all, 68 species and life-history stages were identified, highlightling the great number of Rhodophycean algae (56 species, 82%). Most of theses species, like *Colacodyction reticulatum*, *Gelidiella calcicola*, *Drachiella spectabilis*, *Polyneura bonnemaisonii* and *Laurencia pyramidalis*, are restricted to the British Isles and the Atlantic coasts of France and Spain. Other species, like *Desmarestia dudresnayi*, *Scinaia interrupta*, *Halymenia latifolia*, *Ahnfeltiopsis devoniensis*, *Apoglossum ruscifolium*, *Drachiella minuta*, *Erythroglossum laciniatum*, *Cruoria rosea*-stage and *C. cruoriaeformis* are more widely distributed. Therefore, a high number of seaweeds seem to be present only on maërl from the subregion WNE_1 of Hoek & Breeman (1990). A high endemic flora is thus apparent, although alien species such as *Undaria pinnatifida* and *Heterosiphonia japonica* (as *Dasysiphonia* sp. in Bárbara *et al*., 2003) have also been detected with an intermediate abundance in the study area during all seasons of the year.

Several species found in the maërl and gravel bed of the 'Arousa Ría' are biogeographically interesting and most of them had not been previously recorded from the Atlantic coasts of Spain. *Colacodictyon re-*

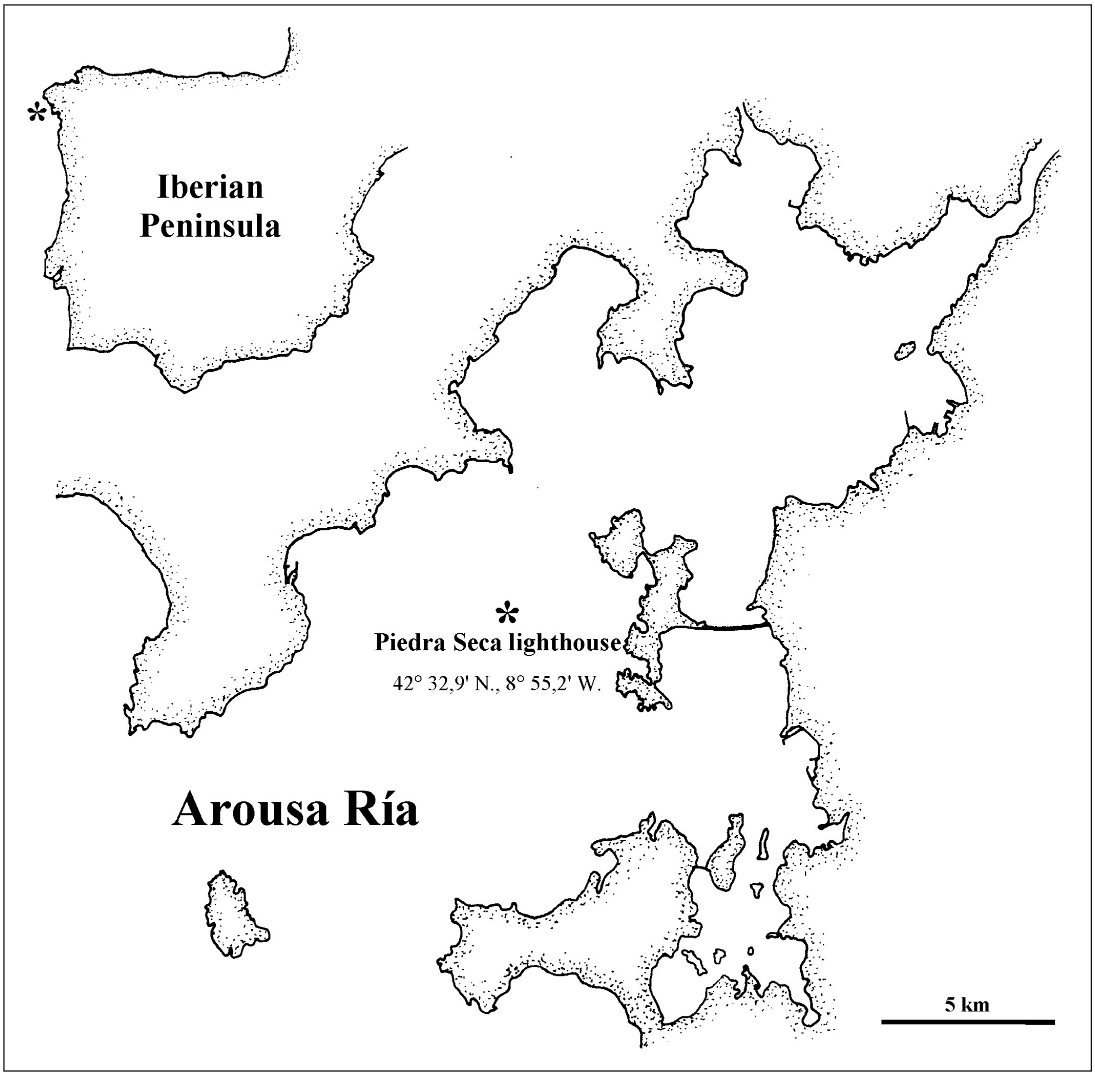


Figure 1.—Geographical location of the Piedra Seca lighthouse in the 'Arousa Ría', northwest Iberian Peninsula.

ticulatum and *Gelidiella calcicola* are new records from Iberian Peninsula. Other interesting records of species rare on the Atlantic coast of Spain are *Stylonema cornu-cervi*, *Cruoria rosea*-stage, *C. cruoriaeformis*, *Trailliella intricata*-stage, *Dasya punicea*, *Symphyocarpus strangulans* and *Desmarestia dudresnayi*.

Colacodyction reticulatum (Fig. 3) is formed by cells (5-10µm) which develop a thick cellular framework among the cortical cells of *Desmarestia dudresnayi*. This is a new record from the Iberian Peninsula and increases the distribution area of the species in the NE Atlantic.

Gelidiella calcicola is composed of a filiform branching axis (Figs. 5 and 9) with several points of growth and regenerating tips. In transverse section (Fig. 8), there is a central row of 8-11 cells. In all our samples, plants were sterile, even in winter. However, tetrasporangial stichidia occur in winter in the British Isles and northern France, which are related to short days and low temperatures (Maggs & Guiry, 1987). Information about the geographical distribution of *G. calcicola* is scarce due to its small size and confusion with other species. *G. calcicola* is a new record for the Iberian Peninsula and it is probably present in other areas like the Azores Islands, as sug-

Table I
Floristic composition and seasonality of the subtidal maërl and gravel bed of the Piedra Seca lighthouse in the 'Arousa Ría', northwest Iberian Peninsula. Relative abundance (1=little abundant, 2=abundant, 3=very abundant). Substratum (m=maërl, g=gravel and pebbles, e=epiphytic).

Species	January	March	May	June	September
Rhodophyta					
Acrosorium ciliolatum (Harrey) Kylin	1m	·	2m,g,e	2m,g	1m
Aglaothamnion bipinnatum (P. Crouan & H. Crouan) Mazoyer	1m,e	·	·	·	·
Aglaothamnion tripinnatum (C. Agardh) Mazoyer	·	·	·	·	1e
Ahnfeltiopsis devoniensis (Greville) Silva & DeCew	·	1m,g	·	·	1m,g
Anotrichium furcellatum (J. Agardh) Baldock	·	1g	1m	2m,g	·
Antithamnion densum (Suhr) Howe	·	1m,g	·	·	1m
Antithamnionella spirographidis (Schiffner) Wollaston	1m,e	1e	1e	·	·
Antithamnionella ternifolia (Hooker & Harvey) Lyle	1m,g,e	1e	·	·	·
Apoglossum ruscifolium (Turner) J. Agardh	·	1m,g	1g	·	1e
Bonnemaisonia asparagoides (Woodward) C. Agardh	·	·	2g	·	·
Hymenoclonium serpens Batters stage	·	1m	·	·	·
Brongniartella byssoides (Goodenough & Woodward) Schmitz	1m	·	3m,g	3m,g	2m,g
Callithamnion tetragonum (Withering) Gray	1m	·	·	·	1e
Callophyllis laciniata (Hudson) Kützing	1g	1g	2g	2g	2m,g
Ceramium flaccidum (Kützing) Ardissone	·	·	·	·	1e
Ceramium virgatum Roth	·	·	1g	·	·
Chylocladia verticillata (Lightfoot) Bliding	·	·	2g	·	·
Colacodictyon reticulatum J. Feldmann	·	·	·	1e	1e
Compsothamnion thuyoides (Smith) Nägeli	1m,g	1g	2g	·	1g
Cruoria cruoriaeformis (P. Crouan & H. Crouan) Denizot	1m	2m	1m,g	1m	2m,g
Cryptopleura ramosa (Hudson) Kylin ex Newton	1m,g	1m,g	·	·	1g
Dasya punicea Meneghini ex Zanardini	2m,g	·	·	2m,g	2m,g
Drachiella minuta (Kylin) Maggs & Hommersand	·	1m,g	·	·	1g,e
Drachiella spectabilis Ernst & Feldmann	1g	·	2m,g	2m,g	1m
Erythroglossum laciniatum (Lightfoot) Maggs & Hommersand	1g	1m,g	1g	2m,g	2m
Gelidiella calcicola Maggs & Guiry	3m,g	1m	2m,g	1m	2m
Halarachnion ligulatum (Woodward) Kützing	·	·	3m,g	3m,g	·
Cruoria rosea (P. Crouan & H. Crouan) P. Crouan & H. Crouan stage	1m	1m,g	1m	1m	1m,g
Halurus flosculosus (Ellis) Maggs & Hommersand	1m,g	·	1m,g	·	·
Halymenia latifolia P. Crouan & H. Crouan ex Kützing	·	·	3m,g	2m,g	1m
Heterosiphonia japonica Yendo	1g	2m,g	3m,g	3m,g	3m,g
Hypnea musciformis (Wulfen) Lamouroux	·	·	·	·	1m,g
Hypoglossum hypoglossoides (Stackhouse) Collins & Hervey	·	1m,g	·	·	·
Kallymenia reniformis (Turner) J. Agardh	1m,g	1g	3g	3m,g	3m,g
Lithothamnion corallioides (P. Crouan & H. Crouan) P. Crouan & H. Crouan	2	2	2	2	2
Nitophyllum punctatum (Stackhouse) Greville	·	1m,g	·	1g	·
Peyssonnelia atropurpurea P. Crouan & H. Crouan	·	1m,g	·	·	·
Peyssonnelia dubyi P. Crouan & H. Crouan	2m	·	1g	·	1m,g
Phymatolithon calcareum (Pallas) Adey & McKibbin	2	2	2	2	2
Pleonosporium borreri (Smith) Nägeli ex Hauck	·	·	1m	·	·
Plocamium cartilagineum (Linnaeus) Dixon	2m,g	1m,g	1g	·	2m,g
Polyneura bonnemaisonii (C. Agardh) Maggs & Hommersand	·	1g	3m,g	3m,g	·
Polysiphonia elongata (Hudson) Sprengel	1m	·	·	·	·
Pterosiphonia parasitica (Hudson) Falkenberg	·	·	·	1g	·
Pterothamnion crispum (Ducluzeau) Nägeli	·	1m,g	1m,g,e	·	1m
Pterothamnion plumula (Ellis) Nägeli	1e	1e	1m,g	·	·
Rhodophyllis divaricata (Stackhouse) Papenfuss	·	·	·	·	1e
Rhodymenia pseudopalmata (Lamouroux) Silva	·	1g	·	1m,g	·
Scinaia interrupta (A. DC.) Wynne	·	·	·	2m,g	2m,g
Spermothamnion repens (Dillwyn) Rosenvinge	1m,g	·	·	·	1m
Sphondylothamnion multifidum (Hudson) Nägeli	·	·	1g	·	·
Stenogramme interrupta (C. Agardh) Montagne ex Harvey	·	·	2g	2g	2m,g
Stylonema alsidii (Zanardini) Drew	·	·	·	·	1e
Stylonema cornu-cervi (Reinsch) Hauck	·	·	1e	·	·
Trailliella intricata Batters stage	·	·	·	·	1e
Tiffaniella capitata (Schousboe ex Bornet) Doty & Meñez	·	·	·	·	1g

Table I (continuation)
Floristic composition and seasonality of the subtidal maërl and gravel bed of the Piedra Seca lighthouse in the 'Arousa Ría', northwest Iberian Peninsula. Relative abundance (1=little abundant, 2=abundant, 3=very abundant). Substratum (m=maërl, g=gravel and pebbles, e=epiphytic).

Species	January	March	May	June	September
Phaeophyta					
Cutleria multifida (Smith) Greville		·	·	2m,g	·
Aglaozonia parvula (Greville) Zanardini stage	2g	3g	3g	2g	2g
Desmarestia dudresnayi Lamouroux ex Leman	·	·	1g	3g	2g
Dictyopteris ambigua (Clemente) Cremades	·	·	1g	·	·
Dictyota dichotoma (Hudson) Lamouroux	·	·	2m,g	1g	1g
Sphacelaria cirrosa (Roth) C. Agardh	·	·	1e	·	·
Symphyocarpus strangulans Rosenvinge	1m,g	·	·	·	1m
Undaria pinnatifida (Harvey) Suringar	·	·	2g	2m,g	1m,g
Chlorophyta					
Cladophora laetevirens (Dillwyn) Kützing	1m,g	1m,g	·	·	·
Codium vermilara (Olivi) Delle Chiaje	·	·	·	·	1m,g
Ulva olivascens Dangeard	·	·	2g	2m,g	1g
Ulva rigida C. Agardh	1g	1m,g	2m,g	·	·

gested by the record of *Gelidiella* sp. on maërl beds from this archipelago (Cabioch 1974). It is worth mentioning that Maggs & Guiry (1987) assigned to *Gelidiella calcicola*, a *Gelidiella* sp. described from Roscoff by Cabioch (1964) ecologically similar to *Gelidiella* sp. described from the Azores.

In *Dasya punicea*, male thalli were unknow (Maggs & Hommersand, 1993), but we have observed, in September, spermatangial stichidia (Fig. 4) developing from pseudolaterals of male plants. The spermatangial stichidia, (200) 280-480 (500) µm long and (60) 80-120 (150) µm diameter are cylindrical and they bear ellipsoidal spermatangia, 2-3µm diameter.

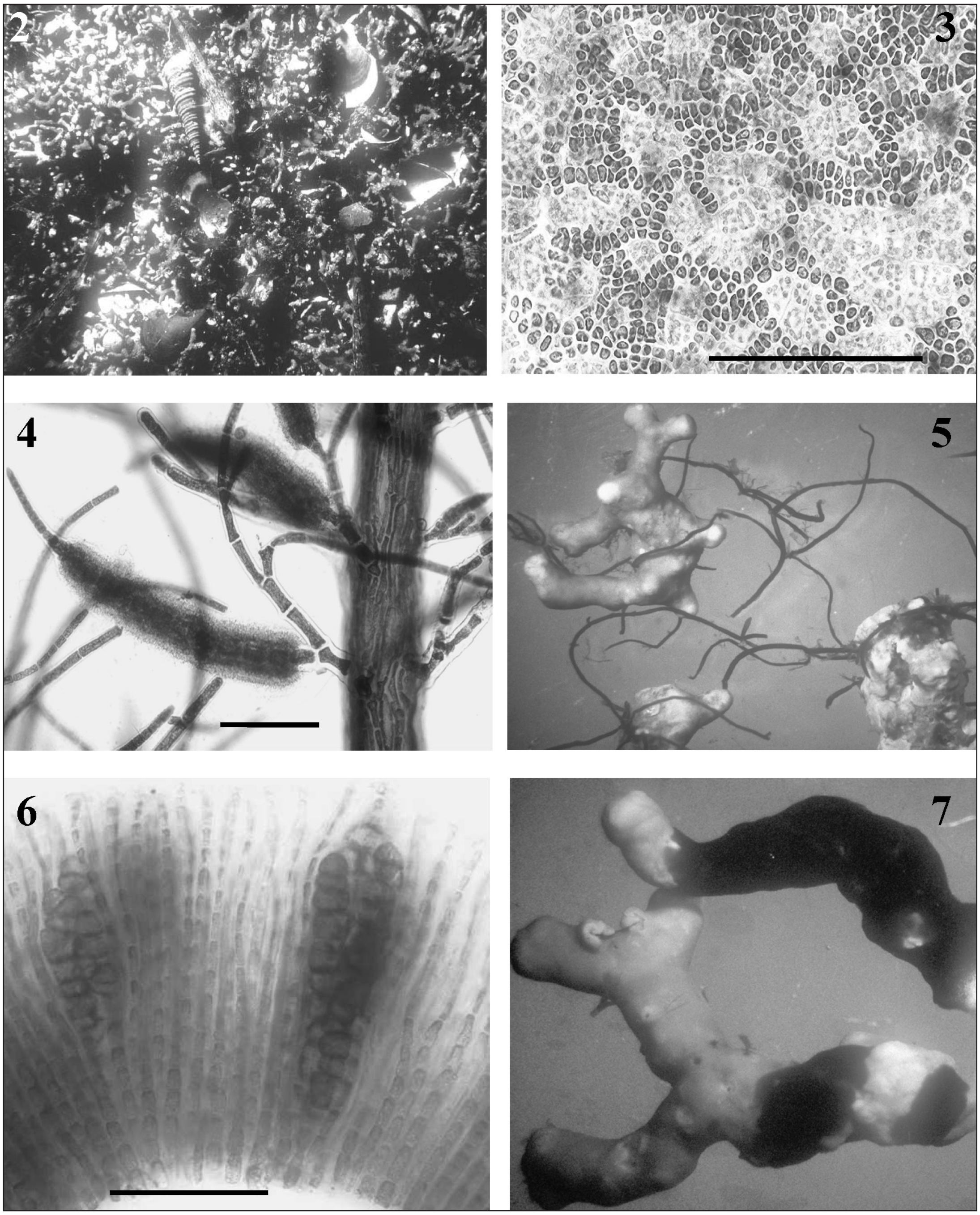
Cruoria cruoriaeformis growes over calcareum substrum of maërl (Fig. 7) forming crusts up to 300 µm thickness and 20 cells. Gonimoblasts (Fig. 6) and tetrasporangial (75 µm long) were observed in this study. In the northeastern Atlantic Ocean, *C. cruoriaeformis* is presented in the British Isles (Hardy & Guiry, 2003) and France (Dixon & Irvine, 1977). In the atlantic coast of Iberian Peninsula was former reported to the Pontevedra Ría —as *Cruoria purpurea*— by Miranda (1934) and it was latterly reported to the Muros Ría by Otero-Schmitt & Pérez-Cirera (2002). The present record in the 'Arousa Ría' and the harvest of this species all over the year confirm that *C. cruoriaeformis* forms attached populations over maërl in Galicia.

Crusts of *Symphyocarpus strangulans* comprising a adhesive monostromatic base and erect filaments up to 100 µm in with ascocysts and plurilocular sporangia are interspersed (Fig. 10). *S. strangulans* is found in cold waters, like Norway, Scandinavia, Greenland, Canada, Baltic Sea, Ireland and Britain. In the north of Spain it is only known in Hendaya (Hoek & Donze, 1966) and 'Arousa Ría' (Donze, 1968), so this record confirm that *S. strangulans* is presented in the Iberian Peninsula. Another record from the southern of Iberian Peninsula (Soto & Conde 1989) requires confirmation (Flores-Moya *et al.,* 1995).

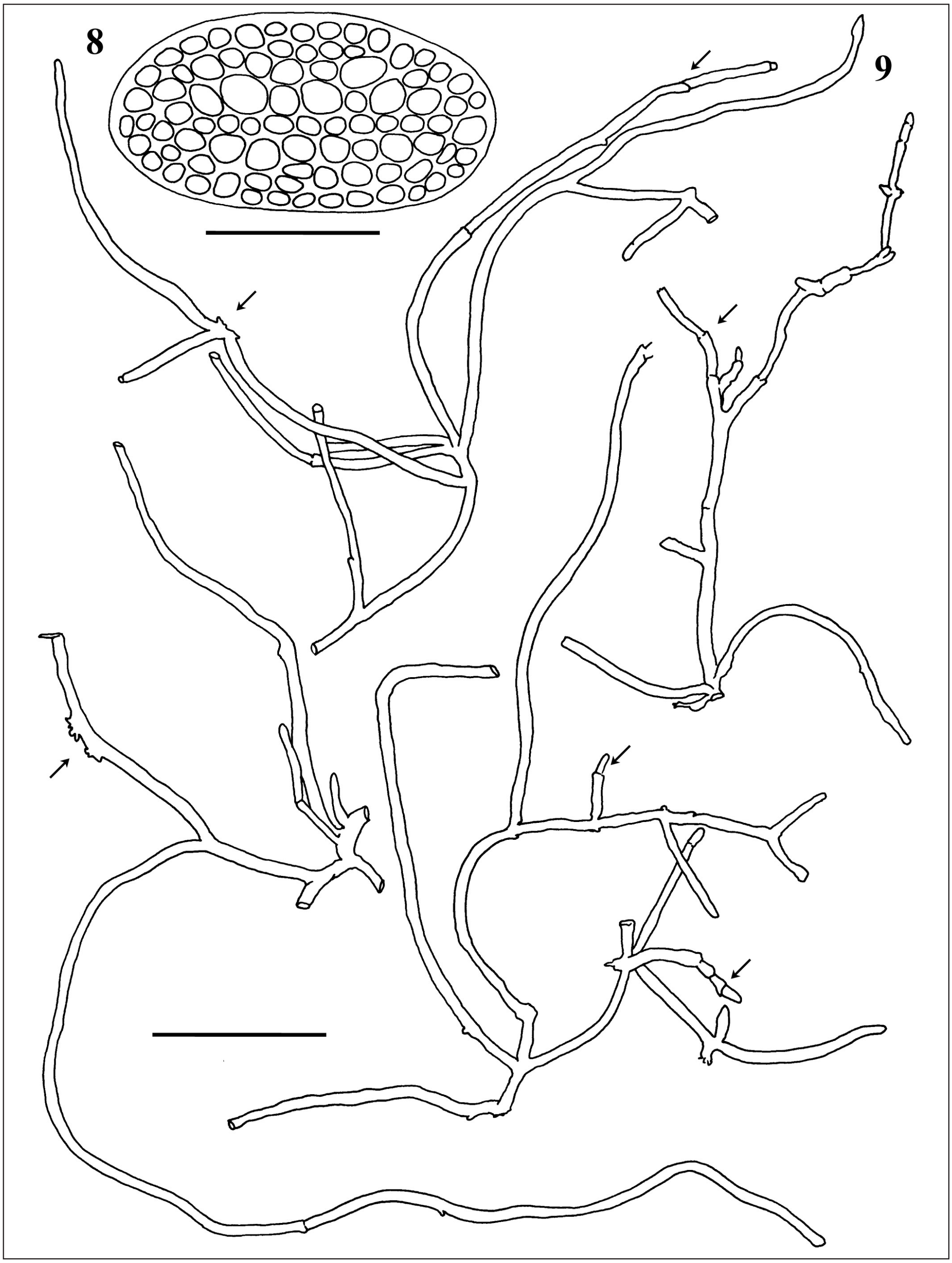
Desmarestia dudresnayi (Fig. 11) was already known from the south of the British Isles, Ireland, France and the north of Iberian Peninsula (Fletcher, 1987). In the Mediterranean it has been located in cold waters (UNEP/IUCN/GIS Posidonie 1990) and associated with strong currents, like the Messina Strait (Drew & Robertson, 1974), and Alborán Island (Rindi & Cinelli, 1995). In the Iberian Peninsula two old collections from the Gulf of Biscay (Hamel, 1931-39 and Sauvageau, 1925) and two new ones from Galicia (Bárbara & Cremades, 1996; Bárbara *et al*., 2002), are known. In the present study, it is confirmed that *D. dudresnayi* forms attached populations in the northwest of the Iberian Peninsula.

Ecological observations

The maërl and gravel substratum in the 'Arousa Ría' supports a subtidal sciaphilic community with its upper limit at 10 metres depth. From 0-10 metres depth, a subtidal photophilic vegetation covers the stones, with *Laminaria ochroleuca* Pylaie, *L. hyperborea* (Gunnerus) Foslie, *Phyllariopsis purpurascens* (C. Agardh)



Figures 2-7.—2. Substratum of maërl and broken shells. 3. *Colacodictyon reticulatum* forming cellular framework among cortical cells of *Desmarestia dudresnayi*; scale bar = 100 µm. 4. Spermatangial stichidia on pseudolaterals of *Dasya punicea*; scale bar = 200 µm. 5. *Gelidiella calcicola* entangled filiform branching axis binding corallinacean algae. 6 and 7. *Cruoria cruoriaeformis*. 6. Transverse section with gonimoblasts; scale bar = 100 µm. 7. Crusts growing over *Lithothamnion corallioides*.



Figures 8 and 9.—*Gelidiella calcicola*. 8. Transverse view showing a central row of 11 cells; scale bar = 100 µm. 9. Filiform branching axis with several points of growth and regenerated tips (arrows); scale bar = 5 mm.

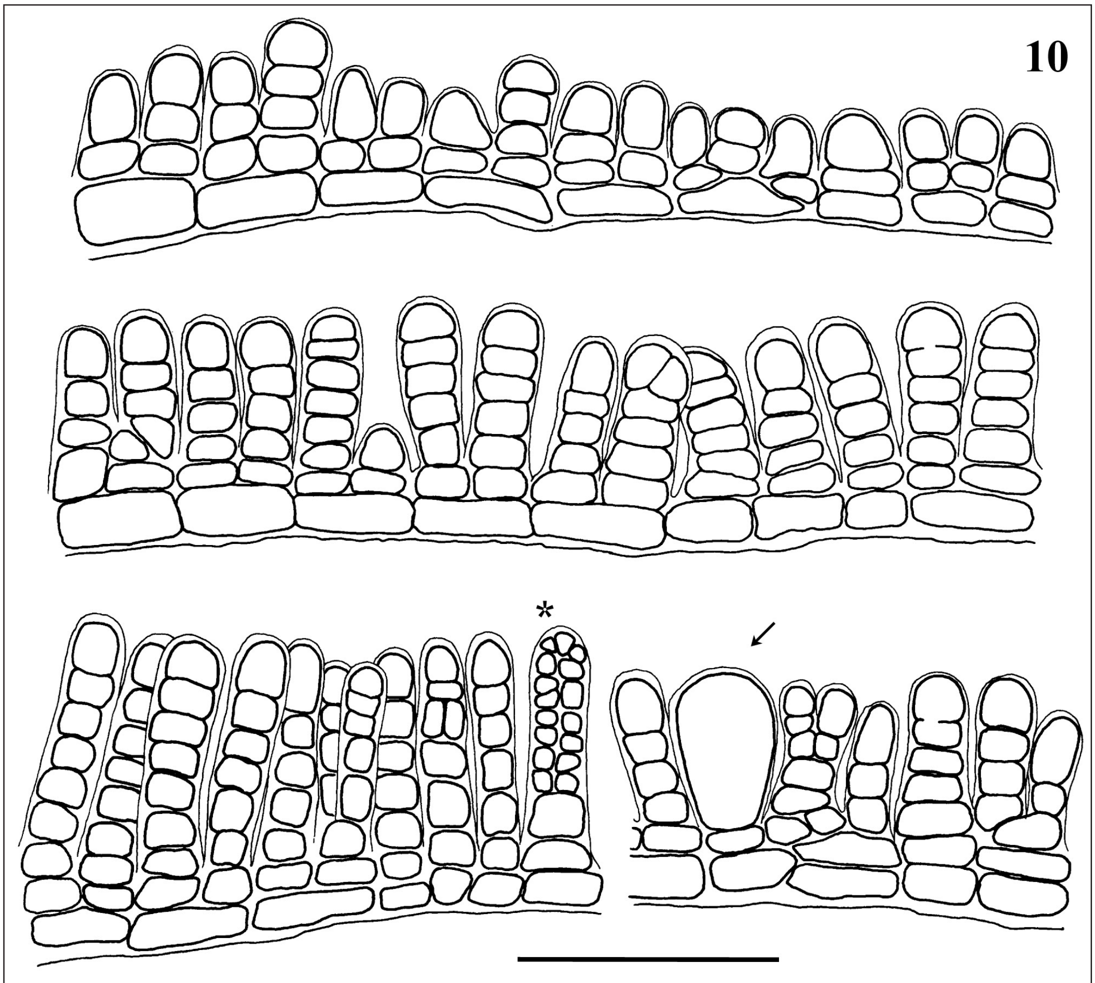


Figure 10.—*Symphyocarpus strangulans*. Transverse sections showing monostromatic basal layer bearing erect filaments, an ascocyst (arrow) and a plurilocular sporangium (asterisk); scale bar = 50 µm.

Henry & South, *Cystoseira usneoides* (Linnaeus) Roberts, *Carpomitra costata* (Stackhouse) Batters, *Sphaerococcus coronopifolius* Stackhouse, *Callophyllis laciniata*, *Kallymenia reniformis*, *Deleseria sanguinea* (Hudson) Lamouroux, *Heterosiphonia plumosa* (Ellis) Batters, *Plocamium cartilagineum*, *Rhodymenia pseudopalmata*, *R. holmesii* Ardissone, *Lomentaria articulata* (Hudson) Lyngbye, *L. clavellosa* (Turner) Gaillon, *Pterosiphonia complanata* (Clemente) Falkenberg, *Corallina officinalis* Linnaeus, *Ptilothamnion pluma* (Dillwyn) Thuret, *Codium vermilara* and *Cladophora pellucida* (Hudson) Kützing.

The unusual features and peculiar habitat of the maërl and gravel bed —depth, low illumination, nature and instability of substratum— determine the characteristic of the biological forms present, which produce a distintive flora arranged in strata. Depending on algal size, the maërl vegetation of the 'Arousa Ría' can be arranged in three strata -meiobiotic, microbiotic and chamaebiotic- following the terminology of L'Hardy-Halos *et al.* (1973). In the meiobiotic stratum, *Desmarestia dudresnayi*, *Kallymenia reniformis*, *Halymenia latifolia*, *Halarachnion ligulatum*, *Polyneura bonnemaisonii*, *Stenogramme interrupta*, *Callophyllis laciniata*, *Drachiella spectabilis*, *Erythroglossum laciniatum*, *Ulva olivascens*, *Dictyota dichotoma*, *Brongniartella byssoides*, *Scinaia interrupta*, and *Cutleria multifida* are present. They are all abundant in spring, summer and autumn, being absent or sparse in winter.

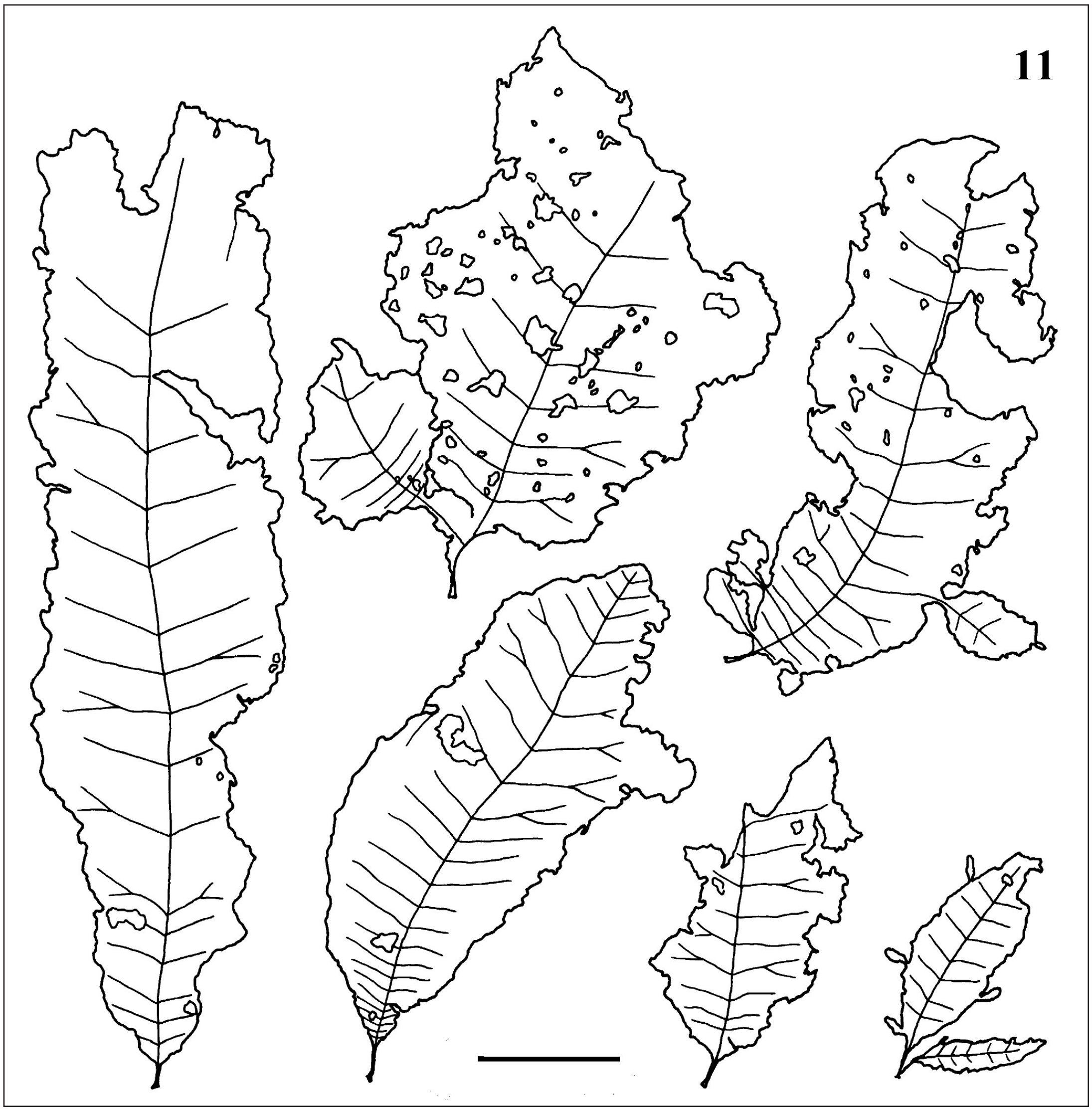


Figure 11.—*Desmarestia dudresnayi*. Blades morphological variations; scale bar = 10 cm.

The microbiotic stratum is constituted by species with spreading filiform systems of axes and branches, in which several apical points of active growth are frequent. The continuous fragmentation of thalli assures the vegetative propagation of individuals. The seaweeds living over maërl, gravel and pebbles have several attachment points to the substratum, helping consolidate the sediment that remains bound by filiform algae, reducing the substratum movements. Moreover, each individual keeps certain independence among parts of its thallus, an important feature if fragmentation of epibionthic algae takes place. A characteristic example is *Gelidiella calcicola*, displaying several fixation points to substratum and with an active apex that regenerates the fragmented thallus. This species forms bushes of maërl and shells fragments joined together by the algae thallus (Fig. 5). As a result, *G. calcicola* grows over this calcareous substratum forming a network of filiform branches. According to Cabioch (1969) and Maggs & Guiry (1987), it is very successful as a creeping species on subtidal loose-lying corallines, and that is why *G. calcicola* plays an important role in stabilizing maërl beds. A similar strategy of living can be found in *Gelidium maggsiae* Rico

& Guiry, a species collected in the Piedra Seca lighthouse at 20 metres depth (Bárbara *et al*., 2002).

In the microbiotic stratum *Rhodophyllis divaricata* is frequent, as well as several members of the Ceramiales (40% total flora) especially *Antithamnion densum*, *Ceramium flaccidum*, *Spermothamnion repens*, *Tiffaniella capitata*, *Drachiella minuta* and *Pterosiphonia parasitica*. The chamebiotic stratum is composed by maërl (*Lithothamnion corallioides* and *Phymatholithon calcareum*) and species living over these coralline algae and broken shells. Thus, *Cruoria cruoriaeformis*, *C. rosea*-stage, *Peyssonnelia dubyi*, *Symphyocarpus strangulans* and *Aglaozonia parvula*-stage are abundant in all over the year because they are adapted to the movement between the maërl thalli.

The vegetation living over maërl, gravel and pebbles presents marked seasonal changes. Table I reveals a higher species richness in summer than in winter, when light and temperature reach their minima. Furthermore, substratum movements in winter (wave-exposure and sand-cover) limit the settlement and growth of large algae. Crustose and creeping algae are permanent over the substratum forming a constant microbiotic and chamebiotic algal strat, more evident in winter. In contrast, the meiobiotic stratum is variable throughout the year. Several foliose macrophytes like *Halarachnion ligulatum*, *Halymenia latifolia*, *Stenogramme interrupta*, *Desmarestia dudresnayi*, *Dictyota dichotoma* and *Undaria pinnatifida* are absent in winter, but they grow in abundance in summer. *Callophyllis laciniata*, *Kallymenia reniformis*, *Drachiella spectabilis* and *Brongniartella byssoides* are present throughout the year, although they are more abundant and have a larger size in summer than in winter.

The seasonal alternation of life-history stages is important. Crustose forms remain on maërl and gravel beds, even in the unfavourable season, and develop erects fronds in the favourable one, as the 'seed bank' described by Edwards (2000). Crustose stage of heteromorphic life-histories support the population during the unfavorable season whereas upright phases are not yet developed. This process can be observed in the *Cruoria rosea*-stage that produces *Halarachnion ligulatum* in summer. *Cutleria multifida* is only present in summer, whereas its *Aglaozonia*-stage lives on gravel all over the year, being abundant in winter. The sporophytic blades of *Desmarestia dudresnayi* are present in spring and summer, but are absent in autumn and winter. Other species showing similar life strategies are *Bonnemaisonia asparagoides* and its stage *Hymenoclonium serpens*. Likewise, crusts of *Haematocelis fissurata* (P. Crouan & H. Crouan) Denizot -the sporophytic stage of *Sphaerococcus coronopifolius*- was collected in the Piedra Seca lighthouse at 30 metres depth (Bárbara *et al*., 2002).

ACKNOWLEDGEMENTS

We thank Dr. H. Stegenga, Dr. Y.S.D.M. de Jong and Dra. C.A. Maggs for the information on Dasyaceae algae and thank Dra. C.A. Maggs for the identification of some ceramiacean algae. We thank Dr. Farnham for his comments and corrections of the text. We also thank to IGAFA for support with some field-work and we are grateful to Ricardo Figueiro and Dr. J. Cristobo for their help with dredging and SCUBA diving, respectively. We appreciate Dr. J. Cristobo's help for taking the photograph in Fig. 2. Finally, thanks to Dra. S. Calvo and Dr. R. Barreiro for improving the English manuscript. Contribution to the PGIDIT03PXIB10301PR project (Xunta de Galicia).

BIBLIOGRAFÍA

ADEY, W. H. & MCKIBBIN, D. L. 1970. Studies on the maërl species *Phymatolithon calcareum* (Pallas) nov. comb. and *Lithothamnium corallioides* Crouan in the Ría de Vigo. *Bot. Mar.* 13: 100-106.

AFONSO-CARRILLO, J. & GIL-RODRÍGUEZ, M.ª. C. 1982. Sobre la presencia de un fondo de maërl en las islas Canarias. *Collect. Bot.* (Barcelona) 13: 703-708.

BALLESTEROS, E. 1989. Composición y estructura de los fondos de maërl de Tossa de Mar (Gerona, España). *Collect. Bot*. (Barcelona) 17: 161-182.

BALLESTEROS, E. 1993. Algunas observaciones sobre comunidades de algas profundas en Lanzarote y Fuerteventura (Islas Canarias). *Vieraea* 22: 17-27.

BALLESTEROS, E. 1994. The deep-water *Peyssonnelia* beds from Balearic Islands (Western Mediterranean), P.S.Z.N.I. *Mar. Ecol.* 15: 233-253.

BÁRBARA, I. & CREMADES, J. 1996. Seaweeds of the Ría de A Coruña (NW Iberian Peninsula, Spain). *Bot. Mar.* 39: 371-388.

BÁRBARA, I.; CREMADES, J.; VEIGA, A. J.; LÓPEZ VARELA, C.; DOSIL, J.; CALVO, S.; PEÑA, V. & LÓPEZ RODRÍGUEZ, M.ª C. 2002. Fragmenta chorologica occidentalia, Algae, 7814-7892. *Anales Jard. Bot. Madrid* 59: 292-297.

BÁRBARA, I.; CREMADES J.; VEIGA, A. J. & LÓPEZ RODRÍGUEZ, M.ª C. 2003. *Dasysiphonia* sp. (Ceramiales, Dasyaceae) nuevo rodófito alóctono para la Península Ibérica. *Anales Jard. Bot. Madrid* 60: 440-443.

BARBERÁ, C.; BORDEHORE, C; BORG, J. A.; GLÉMAREC, M.; GRAS, J.; HALL-SPENCER, J. M.; DE LA HUZ, CH.; LANFRANCO, E.; LASTRA, M.; MOORE, P. G.; MORA, J.; PITA, M. E.; RAMOS-ESPLÁ, A. A.; RIZZO, M.; SÁNCHEZ-MATA, A.; SEVA, A.; SCHEMBRI, P. J. & VALLE, C. 2003. Conservation and management of northeast Atlantic and Mediterranean maërl beds. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13: 65-76.

BASSO, D. 1995. Living calcareous algae by a paleontological approach: the genus *Lithothamnion* Heydrich nom. cons. from the soft bottoms of the Tyrrhenian Sea (Mediterranean). *Riv. It. Paleont. Stratig.* 101: 349-366.

BIRKETT, D. A.; MAGGS, C. A. & DRING, M. J. 1998. *Maërl (volume V). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs.* Scottish Assoc. Marine Science/UK Marine SACs Project.

BLUNDEN, G.; FARNHAM, W. F.; JEPHSON N.; FENN, R. H. & PLUNKETT, B. A. 1977. The composition of maërl from the Glenan Islands of southern Brittany. *Bot. Mar.* 20: 121-125.

BLUNDEN, G.; FARNHAM, W. F.; JEPHSON, N.; BARWELL, C. J.; FENN, R. H. & PLUNKETT, B. A. 1981. The composition of maërl beds of economic interest in Northern Britain, Cornwall and Ireland. *X[th] Int. Seaweed Symp.* 10: 651-656.

BOILLOT, G. 1961. La répartition des sédiments en baie de Morlaix et le baie de Siec. *Cahiers de Biol. Mar.* 2: 53-66.

BOUDOURESQUE, C. F. 1985. *Groupes écologiques d'algues marines et phytocenoses benthiques en Méditerranée Nordoccidentale: une revue*. Lab. Arago, Univ. P. et M. Courie & Univ. Luminy.

BOUXIN, H. & DIZERBO, A.H. 1971. Les algues de l'Archipel des Glenan (Finistère). *Bot. Rhedonica, Sér. A* 10: 199-226.

CABIOCH, J. 1964. *Étude des fonds de maërl de la baie de Morlaix*. Thèse Doctoral, Paris.

CABIOCH, J. 1966. Contribution à l'étude morphologique, anatomique et sytématique de deux Mélobésiées: *Lithothamnium calcareum* (Pallas) Areschoug et *Lithothamnium corallioides* Crouan. *Bot. Mar.* 9: 33-53.

CABIOCH, J. 1968. Contribution à la connaissance des peuplements de la Manche occidentale. *Cahiers de Biol. Mar.* 9 (suppl.): 493-720.

CABIOCH, J. 1969. Les fonds de maërl de la baie de Morlaix et leur peuplement végétal. *Cahiers de Biol. Mar.* 10: 139-161.

CABIOCH, J. 1974. Un fond de maërl de l'Archipel de Madère et son peuplement végétal. *Bull. Soc. Phycol. France*: 74-82.

CONNOR, D. W.; BRAZIER, D. P.; HULL, T. O.; HOLT, R. H. F.; NORTHEN K. O. & SANDERSON W. G. 1997. *Marine Nature Conservation Review: marine biotope classification for Britain and Ireland. Volume 2. Sublittoral biotopes.* Version 97.06. JNCC Report No. 230. JNCC, Peterborough.

DIXON, P. S. & IRVINE, L. M. 1977. *Seaweeds of the British Isles, vol. 1 Rhodophyta, part. 1 Introduction, Nemaliales, Gigartinales*. B. M. (N. H.) London.

DONZE, M. 1968. The algal vegetation of the «Ría de Arousa» (NW. Spain). *Blumea* 16: 159-192.

DREW, E. A. & ROBERTSON, W. A. 1974. Direct observation of *Desmarestia dudresnayi* Lamour. *ex* Leman in the British Isles and in the Mediterranean. *British Phycol. J.* 9: 195-200.

EDWARDS, M. S. 2000. The role of alternate life-history stages of a marine macroalga: a seed bank analogue. *Ecology* 81: 2402-2415.

FARNHAM, W. F. & JEPHSON, N. A. 1977. A survey of the maërl beds of Falmouth (Cornwall). *British Phycol. J.* 12: 119.

FELDMANN, J. 1943. Contribution à l'étude de la flore marine de profondeur sur les côtes d 'Algérie. *Bull. Soc. Hist. Nat. Afrique du Nord* 34: 150-157.

FLETCHER, R. L. 1987. *Seaweeds of the British Isles. Volume 3 Fucophyceae (Phaeophyceae). Part. 1*. B. M. (N. H.) London.

FLORES-MOYA, A.; SOTO, J.; SÁNCHEZ, A.; ALTAMIRANO, M.ª; REYES, G. & CONDE, F. 1995. Check-list of Andalisia (S. Spain) Seaweeds. I. Phaeophyceae. *Acta Bot. Malacitana* 20: 5-18.

FOSTER-SMITH, R. & DAVIES, J. 1993. Studies on Orkney maërl deposits. *Report to Scottish Natural Heritage*.

GIACCONE, G. 1965. Le fitocenosi marine nel settore di Capo Zafferano (Palermo). *Lavori dell'Istit Bot. e Giard. Col. di Palermo* 22: 3-69.

GRALL, J. & GLÉMAREC, M. 1997. Biodiversité des fonds de maërl en Bretagne: approche fonctionnelle et impacts anthropiques. *Vie et Mileu* 47: 339-349.

HALL-SPENCER, J. M. 1995. *Lithothamnion corallioides* (P. & H. Crouan) P. & H. Crouan may not extend into Scottish waters. *Coralline News,* 20: 1-3.

HAMEL, G. 1931-39. *Phéophycées de France*. Paris.

HARDY, G. & GUIRY, M. D. 2003. *A check-list and Atlas of the Seaweeds of Britain and Ireland*. British Phycol. Soc., Calway.

HOEK, C. VAN DEN & BREEMAN, A. M. 1990. Seaweed biogeography of th North Atlantic: where are we now?. En D. J. Garbary & R. R. South (Eds.), *Evolutionary Biogeography of the Marine Algae of the North Atlantic*: 55-86. Springer-Verlag, Berlin.

HOEK, C. VAN DEN & DONZE, M. 1966. The algal vegetation of the rocky cote basque (SW France). *Bull. Centr. Etudes Rech. Sci*., 6: 289-319.

HUVE, H. 1956. Contribution à l'étude des fonds à *Lithothamnin soltum* (?) Foslie de la région de Marseille. *Rec. Trav. Sta. Mar. d'Endoume* 20: 105-134.

JACQUOTTE, R. 1962. Etude des fonds de maërl de Méditeranée. *Rec. Trav. Sta. Mar. d'Endoume* 26: 141-235.

LEMOINE, MM P. 1910. Répartition et mode de vie du maërl (*Lithotamnium calcareum*) aux environs de Concarneau (Finistère). *Ann. Inst. Océan.* 3: 1-30.

L'HARDY-HALOS, M. T.; CASTRIC-FEY, A.; GIRARD-DESCATOIRE, A. & LAFARGUE, F. 1973. Recherches en scaphandre autonome sur le peuplement végétal du substrat rocheux: L'Archipel de Glénan. *Bull. Soc. Sci. Bretagne* 48: 103-128.

MAGGS, C. A. 1983. A seasonal study of seaweed communities on subtidal maerl (unattached coralline algae). *Progr. Underwater Sci.* 9: 27-40.

MAGGS, C. A & HOMMERSAND, M. H. 1993. *Seaweeds of the British Isles. 1 Rhodophyta. Part 3A Ceramiales*. B. M. (N. H.) London.

MAGGS, C. A. & GUIRY, M. D. 1987. *Gelidiella calcicola* sp. nov. (Rhodophyta) from the British Isles and Northern France. *British. Phycol. J.* 22: 417-434.

MIRANDA, F. 1934. Materiales para una flora marina de las rías bajas gallegas. *Bol. Soc. Esp. Hist. Nat.* 34:165-180.

OTERO-SCHMITT, J. & PÉREZ-CIRERA, J. L. 2002. Infralittoral benthic biocenoses from Northern Ría de Muros, Atlantic coast of Northwest Spain. *Bot. Mar.* 45: 93-102.

POTIN, P.; FLOCH, J. Y.; AUGRIS, C. & CABIOCH, J. 1990. Annual growth rate of the calcareous red alga *Lithothamnion corallioides* (Corallinales, Rhodophyta) in the Bay of Brest, France. *Hydrobiologia,* 204/205: 263-267.

RINDI, F. & CINELLI, F. 1995. Contribution to the knowledge of the benthic algal flora of the Isle of Alboran, with notes on some little-known species in the Mediterranean. *Cryptogamie, Algol.* 16:103-114.

SAUVAGEAU, C. 1925. A propos de la rencontre du *Desmarestia dudresnayi* Lamx. dans le golfe de Gascogne. *Rev. Algol.* 2: 1-13.

SOTO, J. 1990. Vegetación algal sobre sustrato móvil de la zona circalitoral del sureste de la Península Ibérica: una aproximación. *Fol. Bot. Misc*. 7: 43-49.

SOTO, J. & CONDE, F. 1989. Catálogo florístico de las algas bentónicas marinas del litoral de Almería (Sureste de España). *Bot. Complut.* 15: 61-83.

UNEP/IUCN/GIS *Posidonie.* 1990. Livre rouge "Gérerd Vuignier" des végétaux, peuplements et paysages marins menacés de Méditerranée. *MAP Technical Report Series N.° 43, UNEP*, Athens.