

Lithophyllum spp. form unusual maerl beds in the North East Atlantic: the case study of *L. fasciculatum* (Lamarck) Foslie, 1898, in Brittany

Viviana Peña^{1,2,3,*}, Rodolfo Barreiro¹,
Jason M. Hall-Spencer⁴ & Jacques Grall⁵

¹ BIOCOST Research Group, University of A Coruña, Spain.

² Phycology Research Group, Ghent University, Belgium.

³ UMR 7138 Systématique, Adaptation et Evolution. Muséum
National d'Histoire Naturelle (MNHN), France.

⁴ Marine Biology and Ecology Research Centre,
Plymouth University, Plymouth PL4 8AA

⁵ Séries Faune-Flore Observatoire Marin, UMS3113, Institut Universitaire
Européen de la Mer, Université de Bretagne Occidentale, Brittany France.

Abstract

The most widely recorded maerl-forming species in the NE Atlantic are *Lithothamnion corallioides*, *L. glaciale*, *L. tophiforme* and *Phymatolithon calcareum* although maerl formed by *Lithophyllum* spp. is occasionally found. Here, we studied two of the forms (*incrassata* and *complanata*) described for *Lithophyllum fasciculatum* that we collected in Brittany. Samples were identified using molecular techniques (DNA barcoding) and examined with scanning electron microscopy (SEM). *Lithophyllum fasciculatum* were globular to sub-globular unattached thalli up to 10 cm in diameter that formed maerl beds at 0 to 2 m depth in the eastern part of the Bay of Brest. All anatomical features matched the literature. Reproductive structures were only observed in one encrusting specimen overgrowing *Mimachlamys varia* in the Bay of Brest. Other than in Brittany, *L. fasciculatum* maerl was recorded in Kingstown Bay, Ireland, at 0-3 m depth. In the Irish beds, *L. fasciculatum* co-occurs with the closely similar maerl species *Lithophyllum dentatum*. The taxonomy of NE Atlantic maerl-forming *Lithophyllum* spp. continues to be messy and their ecology has not been studied yet. However, we can assert that they are rare and warrant urgent conservation focus.

Keywords: *Lithophyllum fasciculatum*; *Lithophyllum dentatum*;
maerl; diversity; conservation; Brittany; Ireland

*email address: vpena@udc.es

Des bancs de maerl extraordinaires formés par *Lithophyllum* spp. : le cas de *L. fasciculatum* (Lamarck) Foslie, 1898, en Bretagne

Résumé

Les espèces de maerl les plus fréquentes en Atlantique nord-est sont *Lithothamnion corallioides*, *L. glaciale*, *L. tophiforme* et *Phymatolithon calcareum*. Cependant, d'autres types de bancs de maerl existent, ceux formés par les espèces du genre *Lithophyllum*. Nous rapportons ici la présence en rade de Brest de maerl issu de deux des formes décrites pour *Lithophyllum fasciculatum* (formes *incrassata* et *complanata*). Les échantillons ont été identifiés à la fois par technique moléculaire (barcoding ADN) et par examen au microscope électronique à balayage. Les thalles libres de *Lithophyllum fasciculatum* sont de forme globulaire ou sub-globulaire, atteignant 10 cm de diamètre. Ils forment des bancs de maerl entre 0 et 2 m de profondeur dans la partie est de la rade de Brest. L'ensemble des caractéristiques anatomiques correspondent aux descriptions données dans la littérature. Les structures reproductives ont été observées uniquement sur un thalle encroûtant se développant sur la coquille d'un pétoncle noir *Mimachlamys varia* de la rade de Brest. En dehors de la Bretagne, le maerl à *L. fasciculatum* n'a jamais été observé qu'en Irlande, dans la Kingston Bay (comté de Galway) à des profondeurs variant de 0 à 3 m. En ce site, *L. fasciculatum* cohabite avec l'espèce très proche *Lithophyllum dentatum*. Il faut noter que la taxonomie des espèces de *Lithophyllum* spp. formant du maerl reste aujourd'hui mal comprise et que leur écologie n'a toujours pas été décrite. La seule chose dont nous soyons certains, c'est que ces bancs sont fragiles et rarissimes et nécessitent rapidement des mesures de conservation spécifiques.

Mots-clés : *Lithophyllum fasciculatum* ; *Lithophyllum dentatum* ; maerl ; diversity ; conservation ; Brittany ; Irlande

Introduction

Maerl beds are formed by the accumulation of unattached non-geniculate coralline algae; these beds are widespread but patchily distributed along the Atlantic coasts of Europe where they occur from the low intertidal down to 40 m or more (Hall-Spencer *et al.*, 2010; Teichert *et al.*, 2012). Maerl beds provide a wide range of ecological niches for abundant associated flora and fauna (Barberá *et al.*, 2003; Peña *et al.*, 2014a). However, anthropogenic impacts such as dredging/extraction (for fertiliser production, water treatment, or shipping traffic), eutrophication, destructive fishing (e.g. with dredges or trawls), aquaculture, and the spread of invasive species such as the gastropod *Crepidula fornicata* (Linnaeus, 1758)

seriously damage their structure and biodiversity (Grall & Glémarec, 1997; Hall-Spencer & Moore, 2000; Grall & Hall-Spencer, 2003; Wilson *et al.*, 2004; Hall-Spencer *et al.*, 2006; Peña & Bárbara, 2008a).

Two maerl species commonly recorded on the European coasts (*Phymatolithon calcareum* (Pallas) Adey & McKibbin and *Lithothamnion corallioides* (P. L. & H. M. Crouan) P. L. & H. M. Crouan) are listed in Annex V of the European Community Habitats Directive 1992 as species whose exploitation requires management, and maerl beds are included in Special Areas of Conservation under Annex I habitats 'sandbank covered by seawater all the time' and 'large shallow inlets and bays'. Another two widespread species of maerl in NE Atlantic are *Lithothamnion glaciale* Kjellman and *L. tophiforme* (Esper) Unger. Besides, circa twenty other species are reported to form maerl in the region but they are scarce and their taxonomic status is often uncertain (Irvine & Chamberlain, 1994; Hall-Spencer *et al.*, 2010; Peña *et al.*, 2011; Pardo *et al.*, submitted). Recently, molecular tools such as DNA barcoding has improved our ability to accurately identify and assess species diversity in groups with high morphological plasticity such as the coralline algae (Walker *et al.*, 2009; Kato *et al.*, 2013). In this regard, on-going DNA barcoding projects "MAERL" and "NGCOR" focus on assessing the diversity of maerl and crustose non-geniculate coralline algae along the OSPAR area (Peña *et al.*, 2014; Pardo *et al.*, submitted).

Lithophyllum fasciculatum (Lamarck) Foslie is a minor maerl-forming species with reports from western Ireland, Britain and Brittany (Harvey, 1847; Foslie, 1899; Lemoine, 1913; Cabioc'h, 1968; Irvine & Chamberlain, 1994). The high morphological variability of the Irish *L. fasciculatum* maerl thalli led Foslie (1900) to describe four forms: f. *incrassata*, f. *divergens*, f. *compressa* and f. *eunana*. Later, a fifth form (f. *complanata*) was cited in Foslie & Printz (1929). According to Cabioc'h (1968), most of the specimens encountered in Brittany corresponded to form *incrassata* which is considered as the type for this species.

The present study aims to draw attention to *Lithophyllum fasciculatum* maerl by presenting our observations on collections from Brittany (Anse du Roz, Bay of Brest, 2005, 2011). Much of the Bay of Brest (30 % of its surface) is covered by maerl beds (Grall, 2002). Mixed with *Lithothamnion corallioides*, *Lithophyllum fasciculatum* forms shallow maerl beds (0-2 m depth) in the south-eastern part of the bay (figures 1A-B). The identity of the thalli studied as *L. fasciculatum* was corroborated with molecular techniques (DNA barcodes, Pardo *et al.*, submitted). Representative samples from several morphologies were examined under scanning electron microscope (SEM, model JEOL JSM 6400, Universidade da Coruña, Spain) and deposited in the herbarium SANT Algae (Universidade de Santiago de Compostela, Spain).

Results

The maerl thalli of *L. fasciculatum* conformed to forms *complanata* and *incrassata* (figures 2A-B). Macroscopically, all samples were globular to sub-globular unattached thalli up to 10 cm in diameter, sparsely to densely branched. Colour was violet to lilac-grey when dry. Branch morphology was variable, ranging from compressed to cylindrical,

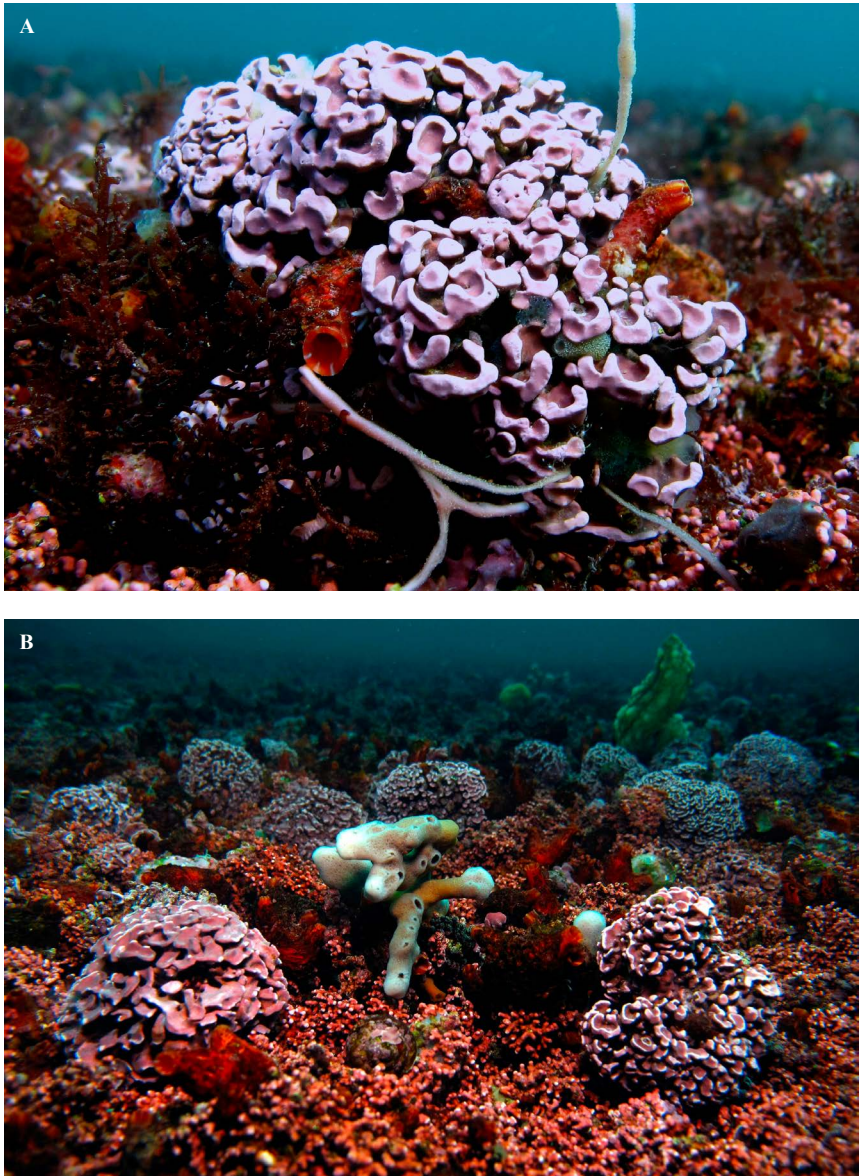


Figure 1: Maerl bed of *L. fasciculatum* in Brittany, Bay of Brest in 2011. Pictures with the courtesy of Alain Pibot. **A.** A single *Lithophyllum fasciculatum* thallus in its environment; **B.** General view of a maerl bed composed of *Lithophyllum fasciculatum* together with *Lithothamnion corallioides* thalli.

sometimes expanded at the apices which may be concave, dimpled with thickenings or even flat and tabular.

The microscopic examination revealed that the thallus was radially organized. In longitudinal section, the medulla occupied a large area of the branches and consisted of arching tiers of rectangular cells 21-38 μm in length by 7-14 μm in diameter (figure 3A). Cortical filaments were laterally aligned, cells mostly elongate in branches of the f. *complanata* (17-23 μm in length by 10-11 μm in diameter, figure 3B). Secondary pit connections between cells were evident (figure 3C). The subepithallial initials were as long as or longer than cells subtending them. Flattened epithallial cells were disposed in 1-2 layers (figure 3D). Trichocytes were absent. In surface view, epithallial cells were thick walled and polygonal (figure 3E). No reproductive structures were recorded in the maerl samples. However, thanks to our molecular data, we detected a fertile encrusting specimen of *L.*



Figure 2: *Lithophyllum fasciculatum* in Brittany. **A.** Maerl of *L. fasciculatum* under form *incrassata*; **B.** Maerl of *L. fasciculatum* under form *complanata*; **C.** Encrusting fertile specimen of *L. fasciculatum* overgrowing *Mimachlamys varia*. Scale bars: A = 2 cm; B = 1 cm; C = 1.5 cm.

fasciculatum overgrowing *Mimachlamys varia* (Linnaeus, 1758) at 2 m depth in the Bay of Brest (figure 2C). DNA barcodes from maerl and encrusting coralline algae collections also confirmed the occurrence of *L. fasciculatum* in Brittany and Ireland (Pardo *et al.*, submitted). In Ireland (Kingstown Bay, 0-3 m depth), *L. fasciculatum* was recorded under forms *complanata* and *divergens* living in sympatry with the very similar maerl species *L. dentatum* (Kützing) Foslie (figures 4A-C).

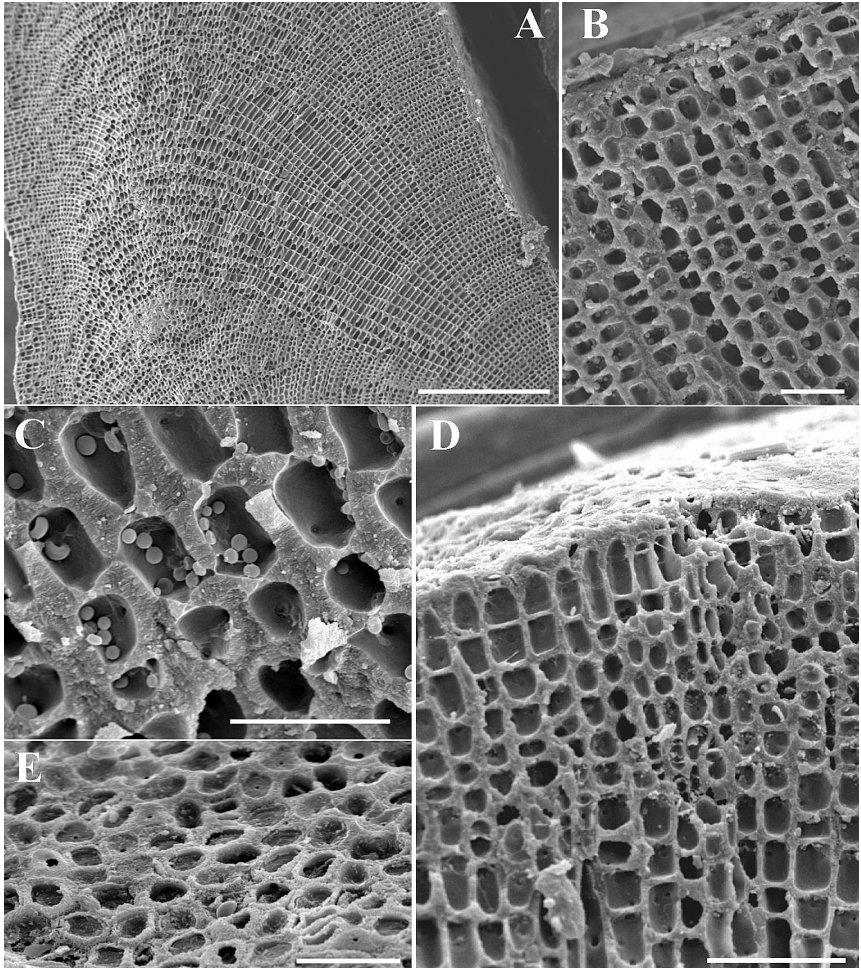


Figure 3: Morphological examination of *Lithophyllum fasciculatum* in Brittany (SEM). **A.** Thallus radially organized; **B.** Cortical filaments laterally aligned; **C.** Secondary pit connections between cells; **D.** Flattened epithallial cells disposed in 1-2 layers; **E.** Thick-walled and polygonal epithallial cells in surface view. Scale bars: A = 250 μ m; B, C, E = 20 μ m; D = 40 μ m.

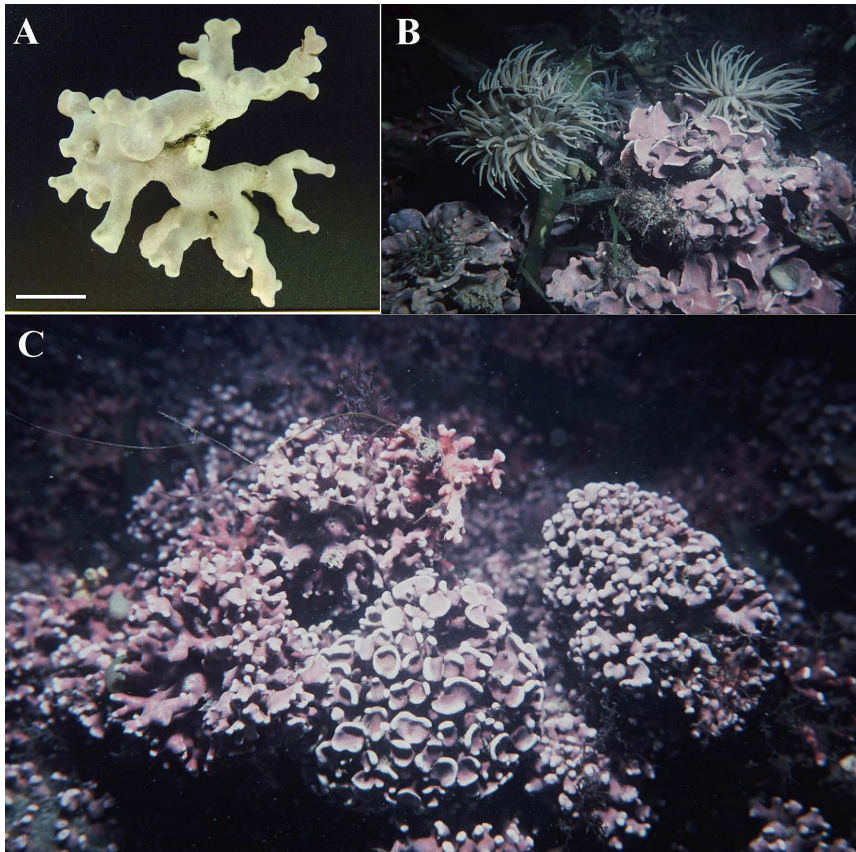


Figure 4: *Lithophyllum fasciculatum* and *L. dentatum* in Kingstown Bay, Ireland; **A.** Maerl of *L. fasciculatum* under form *divergens*; **B.** Maerl of *L. dentatum* that co-occurs with *L. fasciculatum*; **C.** Maerl of *L. fasciculatum* under form *complanata*.

Discussion

All the anatomical features observed in Breton samples of maerl matched previous descriptions of *L. fasciculatum* in the literature (Cabioc'h, 1968; Irvine & Chamberlain, 1994), as well as the diagnostic features of the genus *Lithophyllum* (Woelkerling, 1988). However, a recent assessment of the type material for *L. fasciculatum* collected in the Mediterranean (*Millepora fasciculata* Lamarck) revealed the misapplication of the epithet *fasciculatum* to *Lithophyllum* plants (Woelkerling *et al.*, 1998). Further studies of the McCalla samples of *Lithophyllum agariciformis* illustrated by Harvey (1847) might be necessary for a better taxonomic circumscription of this entity.

We did not find reproductive structures in our maerl specimen. However the species was recorded fertile as an encrusting specimen overgrowing living *Mimachlamys varia* in the Bay of Brest. Previously in Brittany, only Cabioç'h (1968) recorded fertile maerl and encrusting *L. fasciculatum* on dead shells in the same maerl bed studied (Anse du Roz). In maerl beds, thallus fragmentation is often proposed as the main mechanisms for propagation because reproductive structures are only occasionally recorded, or very rarely in the case of sexual structures (Lemoine, 1910; Suneson, 1958; Cabioç'h, 1969; Adey & McKibbin, 1970; Bosence, 1976; Woelkerling & Irvine, 1986; Irvine & Chamberlain, 1994; Peña & Bárbara, 2008b; Peña *et al.*, 2014b).

In our study, Breton maerl *L. fasciculatum* corresponded to forms *complanata* and *incrassata*. The less densely and open branched form *divergens* described in Ireland went unrecorded in Brittany (Cabioç'h, 1968). The two forms of *L. fasciculatum* examined in this study belong to the same species. This suggests that the degree and form of excrescence development in *L. fasciculatum* are highly variable and influenced by environmental factors, as previously proposed for other coralline species (i.e. underlying sediment grain size, weight and size of specimen, light and wave action- Adey, 1966) following the pattern of maerl forms described for *Lithothamnion corallioides* and *Phymatolithon calcareum* (Irvine & Chamberlain, 1994).

In Britain and Ireland, the closely resembling species *Lithophyllum dentatum* was also reported (Harvey, 1847; Foslie, 1899; Irvine & Chamberlain, 1994). In Kingstown Bay (Galway County, Ireland), *L. fasciculatum* co-occurs with *L. dentatum* in shallow beds. There, the morphology of *L. fasciculatum* maerl seemed to gradually change into a *L. dentatum* appearance with decreasing wave action. The high morphological variation of these two species greatly complicates their identification. At microscopic scale, Irvine & Chamberlain (1994) noted that *L. fasciculatum* may show up to 3 layers of epithallial cells while *L. dentatum* had only a single layer. Cabioç'h (1968) also observed rectangular medullary cells of *L. fasciculatum* compared to the ovoid cells in the Mediterranean plants of *L. dentatum*. DNA barcodes obtained from these Atlantic maerl species also revealed that they must be closely related. Further studies combining molecular and anatomical data, particularly from reproductive structures, are required to disentangle the taxonomy of Atlantic *Lithophyllum* maerl.

Our DNA barcodes for maerl and encrusting coralline collections in the OSPAR region indicate that *L. fasciculatum* was only found in Brittany and Ireland, whereas *L. dentatum* was only observed in Ireland (Pardo *et al.*, submitted). Within both regions, these original maerl beds are composed by different forms of *L. fasciculatum* which can co-occur with *L. dentatum* in Ireland. The restricted distribution of shallow maerl beds built by *Lithophyllum* spp. makes it necessary to design conservation measures in both countries to preserve these distinctive and splendid maerl species.

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